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Examining Hybrid Striped Bass Stocking Rates in Texas Reservoirs: A Trade-off between Abundance and Stocking Efficiency

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Abstract: Hybrid striped bass (HSB), which includes palmetto bass (female striped bass *Morone saxatilis* × male white bass *M. chrysops*) or its reciprocal sunshine bass (female white bass × male striped bass) support popular fisheries in many Texas reservoirs. Data from 41 reservoirs sampled using gill nets from 1996–2021 (total of 255 reservoir-yr) were used to develop stock-recruit models where fingerling stocking rates were used to predict CPUE of adults in gill nets. Adult relative abundance was described using two size classes based on the statewide 458-mm minimum length limit, catch of fish below (CPUE_{SUB}) and above (CPUE_{458}) the limit. A linear mixed-effect model showed stocking rate explained 41–46% of variation in CPUE estimates. Mean stocking rate from 3–4 yr prior to each gill-net sample were best for predicting recruits for the CPUE_{458} size class, while stocking rate calculations from years 3–5 and 3–6 explained less variation. The cost-effectiveness of the three primary stocking rates (12, 25, and 37 fingerlings ha^{-1}) was evaluated by comparing the stocking costs to the predicted HSB CPUE for each stocking rate. Stockings were less cost-effective at progressively greater stocking rates. Biologists should consider the trade-offs between stocking for increased relative abundance and using hatchery resources efficiently. We recommend stocking HSB fingerlings at 25 fingerlings ha^{-1} as a general guideline for establishing robust fisheries while maintaining an intermediate level of cost-effectiveness. Stocking at rates higher than 25 fingerlings ha^{-1} should be reserved for reservoirs where survival of stocked HSB is adequate and documented angler effort is high enough to justify the additional costs.

Key words: fingerlings, palmetto bass, stock-recruit, sunshine bass

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Hybrid striped bass (HSB), which includes the palmetto bass (female striped bass *Morone saxatilis* × male white bass *M. chrysops*) and the sunshine bass (female white bass × male striped bass) have been widely stocked into reservoirs throughout the United States to create recreational and trophy fisheries (Bettinger and Wilde 2013). The 2016 USFWS national survey estimated 4,696,000 anglers spent 72,173,000 days of fishing for moronids in United States which places them as the 6th most popular species group (USFWS and USCB 2018). The Texas Parks and Wildlife Department (TPWD) has stocked on average 1.8 million fingerlings annually from 2002–2022 (TPWD, unpublished data) making them an important component of the overall statewide fisheries management program. As of 2022, there were 23 reservoirs that were part of the HSB stocking program in Texas, which is one of only three states, along with Illinois and Nebraska, that have twenty or more HSB fisheries (Collier et al. 2013). Creel data showed that mean directed effort for HSB was approximately 6.6% of the total fishing effort from 2004–2022 among 23 reservoirs (TPWD, unpublished data). However, directed angler effort can exceed 30% of total angler effort in the most popular *Morone* fisheries, such as Lake Tawakoni and Richland-Chambers Reservoir. Due to long-term changes in climate, declining water quality, and reservoir aging, HSB are expected to become increasingly important components of moronid fisheries in the 21st century (Bettoli 2013).

Evaluations of HSB stocking rates are rare in scientific literature. Year-class strength of stocked HSB declined when the stocking rate exceeded 23 fingerlings ha^{-1} in Monroe Reservoir, Indiana (Hoffman et al. 2013), suggesting that density-dependent processes can reduce HSB survival. Similarly, relative mortality rates of HSB increased when stocking rate exceeded 22 fingerlings ha^{-1} in Clarks Hill Reservoir, Georgia (Germann and Bunch 1983). Lower recruitment at higher stocking rates have been observed for other species. Mortality of stocked striped bass increased with stocking rate in Smith Mountain Lake, Virginia (Moore et al. 1991). Research on walleye (*Sander vitreus*) stockings have shown density-dependent processes resulted in reduced abundance after stocking rates were increased (Fayram et al. 2005, Jacobson and Anderson 2007). Conversely, Fielder (1992) reported a positive linear relationship between walleye stocking rates and abundance, suggesting stocking rate was not a limiting factor.

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Reservoirs in Texas are typically stocked with HSB fingerlings (average 38 mm TL) at rates of 12, 25, or 37 fish ha^{-1} based on the abundance of available prey resources. Additionally, TPWD limits the HSB stocking rate to 25 fish ha^{-1} for reservoirs over 4047 ha to equitably allocate statewide fingerling resources. Reservoir stocking rates can be further altered during years of below average hatchery production, increasing annual variability in stocking rates. Thus, identifying and addressing inefficiencies in the HSB stocking program could allow managers to better allocate fingerlings and create more consistent stocking rates across years.

Cost effectiveness is an important component of successful stocking programs. Significant investments in fish stocking requires stocking practices to be evaluated to ensure they provide acceptable return on investment of fisheries management funding (Hunt et al. 2017). Comparing the known cost per fish produced and the total number that are subsequently caught in a fishery provides a direct approach to examine production cost relative to yield (Leber et al. 2005). Similarly, predicted relative abundance of adult HSB derived from stock-recruit models can be used to calculate a cost-per-recruit. Understanding the cost-effectiveness of the different HSB stocking rates commonly used in Texas will aid fisheries managers in decision making and improve the overall efficiency and consistency of the stocking program. The specific objectives of our study were to 1) derive a stock-recruitment relation between HSB fingerling stocking rates and CPUE estimates from standardized gill net population surveys, and 2) evaluate cost-effectiveness of the three primary HSB stocking rates used in Texas.

Methods

Study Area

Data from 41 Texas reservoirs were included in the dataset used to develop stock-recruit models. Reservoirs covered a wide geographical area (Figure 1) and ranged in size from 363–46,337 ha with 6 reservoirs over 10,000 ha, 16 from 2000–10,000 ha, and 19 under 2000 ha. Among reservoirs, mean secchi disk depth was 0.9 m (range 0.3–3.1 m) and mean specific conductance was 659 µS cm^{-1} (range 106–8831 µS cm^{-1}). Trophic classification data was only available for 26 of the 41 reservoirs, however most reservoirs were classified as either mesotrophic or eutrophic (Texas Commission on Environmental Quality 2020). Fish communities were representative of most Texas reservoirs and consisted of sunfish (*Lepomis* spp.), largemouth bass (*Micropterus salmoides*), crappies (*Pomoxis* spp.), white bass, and various catfish (Ictaluridae) species. Gizzard shad (*Dorosoma cepedianum*) and threadfin shad (*D. petenense*) were the primary forage species for HSB. Gizzard shad occurred in all reservoirs and threadfin shad occurred in all but two reservoirs.

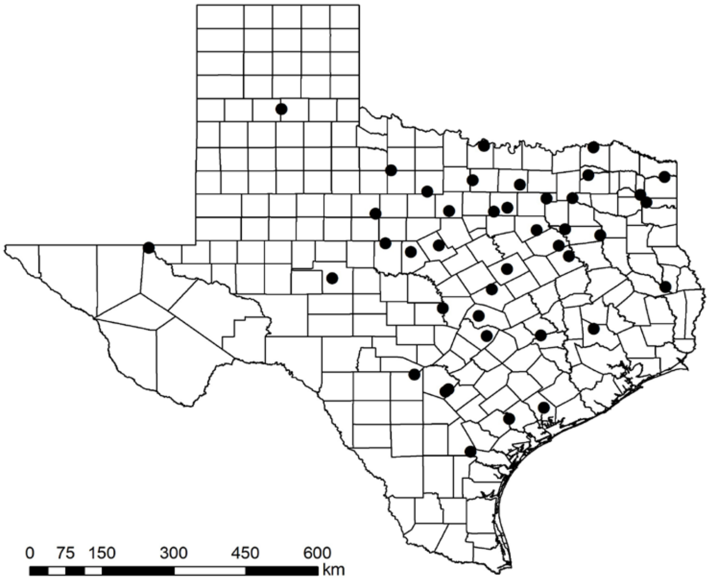

Figure 1. Geographical distribution of 41 Texas reservoirs stocked with hybrid striped bass from which data was compiled for this study. A total of 255 gill net surveys from 1996–2021 were included in the dataset.

Data Sources

Relative abundance data for HSB were collected from 1996–2021 by fisheries management personnel during standardized spring gill-net surveys following established sampling procedures (TPWD, Inland Fisheries Division, unpublished manual revised 2022). Gill nets were 38.1 m long and 2.4 m deep, and consisted of five 7.6-m monofilament panels, each with a mesh size of 25, 38, 51, 64, or 76 mm (bar measure) arranged in ascending order. Gill nets were set in the afternoon, fished overnight, and retrieved the following morning. One net fished overnight was defined as 1 net-night. Gill nets were set on the bottom perpendicular to the nearest shore, with the smallest mesh directed toward shore. We sought only to evaluate fingerling stockings, thus reservoirs that received a mix of fingerling and fry stockings within 6 yr prior to each gill-net survey were excluded from the dataset. We chose 6 yr as the cut-off as age data from Texas HSB populations shows few live beyond age 7 and thus any stockings conducted 7 yr or more before each gill-net survey would likely have negligible impacts in CPUE estimates.

Gill-net CPUE was calculated for two size classes of HSB using the statewide 458-mm minimum-length limit as the point of demarcation: the observed relative abundance of HSB below the minimum-length limit ($\mathrm{CPUE}_{\mathrm{SUB}}$) and the HSB relative abundance above the minimum-length limit (CPUE_{458}). Because age data were not available for most gill-net surveys, we were unable to pair individual yearly stocking rates with specific year-classes of HSB.

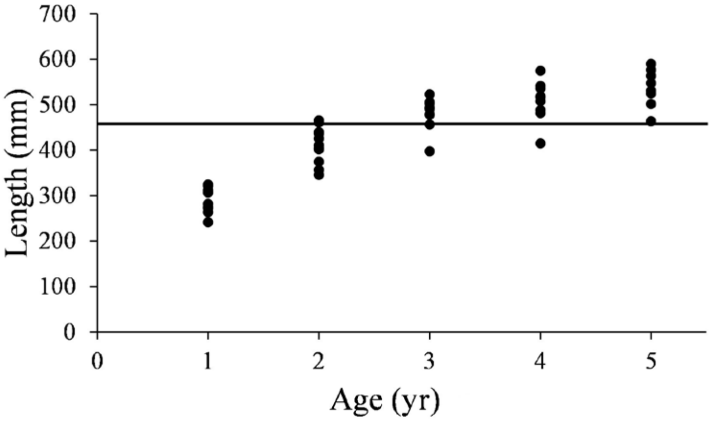

Figure 2. Mean length at age of hybrid striped bass from 12 Texas reservoirs depicting the range of observed growth rates. Eleven of the twelve reservoirs had mean length at age estimates at or above the minimum length limit by age 3. Horizontal black line indicates the minimum length limit of 458 mm.

Thus, we evaluated several mean stocking rate year combinations that should correlate with the two size classes of HSB defined in this study based on unpublished TPWD growth data. The majority of HSB in Texas reservoirs reach the minimum length limit by age 3 (Figure 2), thus we assumed stockings conducted 1–2 yr before the gill net survey would contribute to the relative abundance of sub-legal size HSB while stockings conducted 3 yr or more before the gill net survey would contribute to the relative abundance of legal-size HSB. We calculated the mean stocking rates from 3–4, 3–5, and 3–6 yr prior to each gill-net survey to determine which year-combination was best for predicting CPUE_{458}. Mean stocking rates (fingerlings ha^{-1}) were calculated by taking the mean number of fingerlings stocked for each year combination and dividing by the reservoir surface area (ha) at the time of the netting survey. Reservoir water level and elevation-area-capacity curves were obtained from Texas Water Development Board (2022) and USGS (2022). Data on HSB fingerling production costs were obtained from TPWD hatchery staff and used to calculate stocking costs ha^{-1}.

Data Analysis

We used a linear mixed-effect model to describe the stock-recruit relationship between stocking rates (stock) and relative abundance of HSB (recruits) collected from gill-net surveys. We included reservoir as a random effect to account for inherent differences among reservoirs. Models were run for each HSB size class and stocking-year combination.. Due to expected left skew and heterogeneous variance (Maceina and Pereira 2007), we $\log_e$-transformed our stock-recruit data prior to analysis. Because some relative abundance estimates were zero, a value of 1 was added to each CPUE estimate prior to log transformation. Fingerling production costs were calculated from data from 2010–2019. Mean fingerling production costs were calculated by taking the total HSB program costs divided by the total number of fingerlings produced each year and averaged for the entire 10-yr period. The relative cost-effectiveness for each stocking rate (12, 25, 37 fingerlings ha^{-1}) was calculated by taking the stocking costs ha^{-1} divided by the predicted HSB CPUE from the linear mixed-effect model. All statistical analysis was completed using Program R (R Core Team 2021). The nlme package (Pinheiro et al. 2021) was used to calculate the mixed-effect models, and the MuMIn package (Barton 2022) was used to approximate conditional r^2 values for the mixed-effect models. All tests were considered significant at $P \leq 0.05$.

Results

Mean CPUE_{SUB} among all gill net surveys was 2.9 HSB net-night^{-1} (SD = 4.0; range 0.0–28.8). Mean CPUE_{458} among all gill net surveys was 2.2 net-night^{-1} (SD = 2.9; range 0.0–20.6). Mean stocking rate was 22.6 fingerlings ha^{-1} with an interquartile range of 10.1–32.7 fingerlings ha^{-1}. Mean stocking rate from 1–2 yr prior to each gill net survey explained 41% of the variation in CPUE_{SUB} ($n = 244$; $P < 0.0001$; Figure 3) with an estimated equation of $\log_e \mathit{Recruit} = (0.5365 \times \log_e \mathit{Stock}) - 0.5029$. Mean stocking rate from 3–4 yr prior to each gill net survey explained 46% of the variation in CPUE_{458} ($n = 255$; $P < 0.0001$; Figure 3) with an estimated equation of $\log_e \mathit{Recruit} = (0.3231 \cdot \log_e \mathit{Stock}) - 0.0863$. The inclusion of older stocking year combinations (3–4, 3–5, 3–6) did not explain additional variation in HSB relative abundance. Stock-recruit models that included mean stocking rates calculated from 3–5 and 3–6 yr prior to each gill net survey explained slightly less variation (44–45%) compared to stocking rate from 3–4 yr prior.

From 2010 to 2019, the average cost per HSB fingerling produced was US$0.36 and ranged from $0.05 to $0.71 among years. Mean number of fingerlings produced annually during this period was just over 1.2 million. When costs for each stocking rate were compared to predicted HSB CPUE from the stock-recruit models, stockings were shown to be less cost-efficient as stocking rates increased for both size classes (Table 1). Increasing the stocking rate from 12 to 25 fish ha^{-1} resulted in a concomitant increase of 8% (CPUE_{SUB}) and 34% (CPUE_{458}) per recruit, whereas increasing the stocking rate from 25 to 37 fish ha^{-1} resulted in an increased cost-per-recruit of 10% (CPUE_{SUB}) and 23% (CPUE_{458}). Overall, increasing the stocking rate from 12 to 37 fish ha^{-1} resulted in increased cost-per-recruit of 20% (CPUE_{SUB}) and 64% (CPUE_{458}).

Table 1. Comparison of stocking costs (US$) per hectare, predicted relative abundance ($CPUE_{SUB}$ and $CPUE_{458}$; fish net-night^{-1}), and relative cost-per-recruit (stocking cost ha^{-1} divided by predicted CPUE) for three different annual stocking rates (fingerlings ha^{-1}) used by the Texas Parks and Wildlife Department for hybrid striped bass. Stocking costs were calculated from an average production cost of $0.36 per fingerling. Values in parentheses are ± 1 SE.

Annual stocking rate	Cost	Predicted CPUE	Relative cost-per-recruit
$CPUE_{SUB}$			
12	$4.46	1.33 (0.67–2.24)	$3.35 (1.99–6.66)
25	$8.89	2.45 (1.33–3.92)	$3.63 (2.27–6.68)
37	$13.36	3.33 (1.82–5.24)	$4.01 (2.55–7.34)
$CPUE_{458}$			
12	$4.46	1.07 (0.54–1.79)	$4.17 (2.49–8.26)
25	$8.89	1.59 (0.85–2.61)	$5.59 (3.41–10.46)
37	$13.36	1.95 (1.07–3.20)	$6.85 (4.18–12.49)

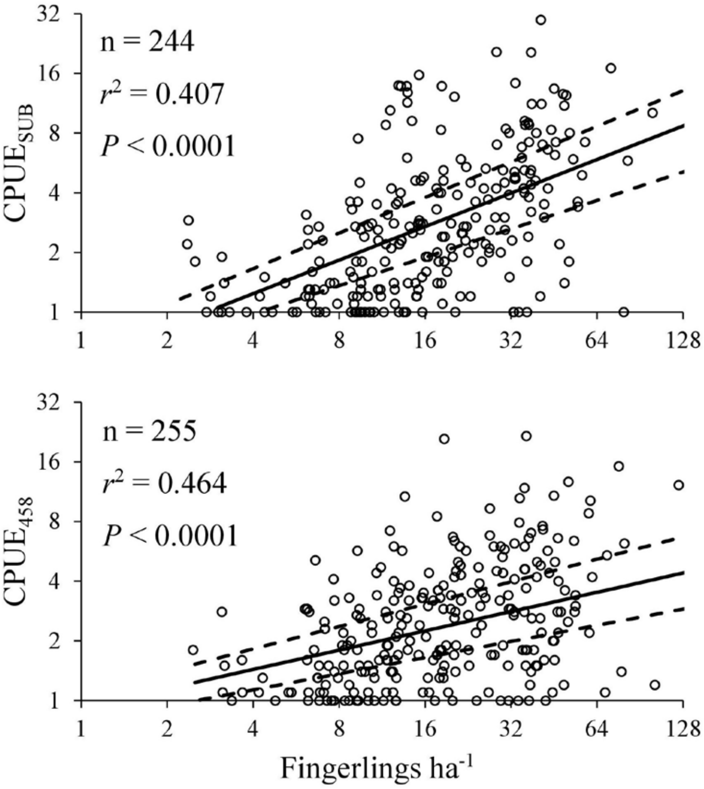

Figure 3. Gill-net catch rate (CPUE, fish net-night^{-1}) of two size classes of hybrid striped bass (SUB and 458) as a function of the mean stocking rate of fingerlings stocked prior to each gill net survey for 41 Texas reservoirs. Dashed lines indicate 1 SE from the trend line. Data is presented in log-log scale with untransformed values on the x-y axes. Note that a value of 1 was added to each CPUE value to allow for log-linear model computation.

Discussion

The amount of variation in HSB relative abundance explained by our stock-recruit models was moderate (41–46%) and similar to or in some cases slightly higher than other studies that used pooled datasets for examining stock-recruit relationships (Beard et al. 2003, Fayram et al. 2005, Bunnell et al. 2006, Siepker and Michaletz 2013). The inclusion of each reservoir as a random effect in our linear mixed-effect model allowed us to model HSB relative abundance while accounting for inherent differences among reservoirs. Reservoirs in this study varied in morphology, productivity, hydrology, and water chemistry and stocking success was likely affected by these differences. Myers et al. (1999) suggested that combining data across many stocks may reduce the uncertainty of the biological processes underlying their population dynamics. However, using spatially extensive data sets can introduce large amounts of system-specific variation (Pritt et al. 2019), thus accounting for this variation within a mixed-effect model with reservoir system as a random effect was essential in describing the overall average effect of stocking rates on HSB relative abundance.

The model for predicting relative abundance of legal-size HSB ($CPUE_{458}$) explained slightly more variation than the $CPUE_{SUB}$ model, possibly due to issues related to gill-net selectivity. Although selectivity has not been evaluated for the TPWD gill-net configuration, Shoup and Ryswyk (2016) evaluated the North American standard gill net for HSB and found relative retention probabilities exceeded 80% for HSB from 320–569 mm. The TPWD gill net configuration differs from the North American standard gill net in that it lacks the smallest mesh (19 mm) and has larger incremental increases in mesh size. It also includes a larger mesh (76 mm) that is not present on the North American standard gill net. Therefore, it is likely that the TPWD gill net configuration would be slightly more selective for larger HSB, but less selective for smaller HSB, when compared to the North American standard gill net. Because HSB >458 mm may have had higher retention probabilities in the TPWD gill net compared to smaller HSB, relative abundance estimates for $CPUE_{458}$ may have been more accurate than $CPUE_{SUB}$ and resulted in higher r^2 values. Future work regarding the selectivity of HSB in the TPWD gill-net configuration would be valuable in understanding HSB retention probabilities and obtaining more accurate CPUE and size structure estimates.

The relation between CPUE and mean fingerlings stocking rates was well represented by a linear model, suggesting that density dependence was not a limiting factor mediating stocking success in Texas reservoirs. These results differed from those of Hoffman et al. (2013) who found density-dependent impacts on HSB year-class strength as stocking rates increased. Stocking rates used in our study likely did not exceed carrying capacity in most reservoirs, as HSB fingerlings are typically stocked in Texas reservoirs known to contain abundant shad populations. For example, the stocking rate of HSB was increased from 20 fish ha^{-1} biennially to 50 fish ha^{-1} annually in two Texas reservoirs with no significant decrease in the gill net catch rate of gizzard shad (Moczygemba et al. 1991). Hoffman et al. (2013) noted that their conclusion of density-dependence was based off a single data point, which may have been spurious. Hanson et al. (1998) and Beard et al. (2003) suggested using Ricker models for walleye stock-recruit models due to walleye being cannibalistic, but this has not been reported for HSB and shad are usually their principal prey in southeastern U.S. reservoirs (Williams 1970, Ware 1974, Germann and Bunch 1985, DeMauro and Miranda 1990, Michaletz 2014). Our results suggest that fisheries managers of Texas reservoirs could choose to stock HSB at higher rates with the expectation that density-dependent factors will not significantly impact relative abundance.

Although most stock-recruit studies examine natural recruitment as a product of the abundance of sexually mature adults, our study predicted the number of fish that recruit to the fishery based off stocking rates, similar to the approach used by Fielder (1992) and Fayram et al. (2005) for walleye. However, lack of age-specific data required us to use a mean stocking rate over multiple years that generally aligned with two size classes of HSB. In general, the stock-recruit model agreed with the unpublished TPWD age data that determined the majority of HSB over 458 mm are composed primarily of 3- and 4-yr-old fish. Models that included stocking data from 5 yr or more prior to gill-net surveys generally did not improve the model fit. Thus, future studies aimed at assessing stocking efficacy of HSB in Texas reservoirs should focus on quantifying abundance of age-3 and age-4 HSB.

Stockings became less cost effective at progressively higher stocking rates. As stocking rates increased, the added costs of additional fingerlings outpaced the predicted increased in HSB relative abundance. For example, increasing the annual HSB stocking rate from 25 to 37 fingerlings ha^{-1} would increase the predicted CPUE$_{458}$ by only 23% while increasing stocking costs by 50%. Our results were similar to those of Jacobson and Anderson (2007), who found that increasing walleye stocking rates 30% would increase walleye abundance by only 3% and increase the stocking cost by 28%. Thus, lower stocking densities provide greater cost-effectiveness but might result in lower population abundances that may be undesirable to anglers.

Management Implications

Survival of stocked HSB is a complicated process with numerous variables influencing success, many of which are out of the control of fisheries managers. Despite high variability, we found stocking rate was an important factor in determining HSB relative abundance, which is directly controlled by fisheries managers. Trade-offs between stocking at higher rates to increase relative abundance and the need to use hatchery resources efficiently must be carefully considered. Based on our results, we recommend stocking HSB fingerlings at 25 fingerlings ha^{-1} as a general guideline for establishing robust fisheries while maintaining an intermediate level of cost-effectiveness. Stocking at rates higher than 25 fingerlings ha^{-1} should be reserved for reservoirs where survival of stocked HSB and angler effort are high enough to justify the additional costs.

The two primary indicators of a successful HSB fishery are the presence of an abundant population and adequate angler effort. Both HSB relative abundance and angler effort must be commensurate with the stocking rate to provide a positive return on investment. Results from this study can be used to develop minimum benchmarks for future evaluations of a HSB fisheries in Texas. Furthermore, HSB fisheries must be evaluated on a regular basis to determine if HSB relative abundance and angler effort is sufficient to support stocking at a given rate. If HSB relative abundance measures consistently fall below a minimum threshold at a given stocking rate, stocking rates should be altered, or reservoirs should be removed from the HSB stocking program.

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High Mortality of Largemouth Bass Implanted with Transmitters at Colder Water Temperatures

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Abstract: Biotelemetry via surgical implantation of an electronic tag is a common way to examine fish behavior and movement. Previous studies suggest higher post-operative survival should be expected when implanting tags at colder water temperatures. However, during the initial part of our study, all 26 adult largemouth bass (*Micropterus salmoides*) we implanted with transmitters at water temperatures from 14 to 17 C at Toledo Bend Reservoir, Texas, died within 4 wk post-surgery. To further investigate this phenomenon, we conducted two tagging trials at 13 C, observing post-operative mortality of 100% ($n = 5$) and 58% ($n = 12$); all fish that died developed external fungal infections (i.e., saprolegniasis). Post-operative survival was 100% in a third trial at 24 C ($n = 6$) and no fungal infections were observed. Subsequently, tagging mortality was ≤20% when 81 largemouth bass were tagged at water temperatures from 22 to 30 C at Toledo Bend and Lake Fork reservoirs. Our results suggest that immunosuppression of largemouth bass coupled with greater fungal virulence in colder water likely caused the complete mortality of 31 largemouth bass initially implanted with transmitters at Toledo Bend Reservoir and in our first trial. Investigators conducting surgeries during similar conditions should be aware that high post-surgical mortality could result if fungal virulence is high during tagging.

Key words: surgery, immunosuppression, fungus, *Saprolegnia*, acclimation

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Biotelemetry is commonly used to monitor fish movement and habitat use (Baras 1991, Cooke et al. 2012, Hockersmith and Beeman 2012), and many biotelemetry studies have focused on largemouth bass (*Micropterus salmoides*) (e.g., Warden and Lorio 1975, Mesing and Wicker 1986, Colle et al. 1989, Sammons et al. 2003, Hunter and Maceina 2008, Goclowski et al. 2013) due to their importance as sport fish (Heidinger 1976, Pullis and Laughland 1999, USFWS and USCB 2018). Surgical implantation of an electronic tag into the coelom is common in long-term biotelemetry studies (Bridger and Booth 2003, Cooke et al. 2011). As such, the invasive nature of the approach requires consideration of post-operative effects because reduced health can affect fish behavior and habitat use, and mortality can reduce sample size.

Water temperature is considered the controlling variable of fish biology and can influence the surgical process in numerous ways, including magnitude of capture and handling stress, effectiveness of anesthesia, rate of incision healing and recovery, and suture performance (Cooke et al. 2011). However, of the 108 surgical or tagging-effects studies reviewed by Cooke et al. (2011), only three examined water temperature. Bunnell and Isely (1999) found that water temperature (either 10 or 20 C) during surgery had no effect on mortality of rainbow trout (*Oncorhynchus mykiss*), but transmitter expulsion rates were higher at warmer water temperatures. Knights and Lasee (1996) and Walsh et al. (2000) found post-operative mortality was only observed at warmer water temperatures for bluegill (*Lepomis macrochirus*) (20 C) and hybrid striped bass (*Morone saxatilis x M. chrysops*) (22–29 C). No mortalities were observed in either study at lower temperatures (6 C and 12–18 C, respectively). Although warmer water temperatures typically increase wound-healing rates (Anderson and Roberts 1975), Knights and Lasee (1996) and Walsh et al. (2000) recommended implantation of transmitters at colder temperatures due to slower fish metabolism, decreased tissue inflammation and infection rate, and reduced mortality.

Consistent with these procedural recommendations, we implanted radio transmitters into adult largemouth bass at Toledo Bend and Lake Fork reservoirs, Texas, to investigate temporal movement and habitat use. We conducted our initial surgeries during fall when water temperatures were cooler and declining to minimize infection rate, handling stress, and mortality. The objectives of this paper were to 1) document the high surgery-related mortality we experienced under these conditions, which was unexpected and not described in previous research, and 2) examine causes of mortality via surgical trials and additional tag implantations at both reservoirs.

Methods

Toledo Bend Reservoir Radio Tag Study

During November 2019, 26 largemouth bass (358–545 mm TL) were collected for radio-tag implantation from Toledo Bend Reservoir, Texas-Louisiana, with boat-mounted, pulsed-60 DC electro-

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fishing gear (Model GPP 5.0, Smith-Root Inc., Vancouver, Washington) operated at 500 V and 4 amps. Surface water temperatures ranged 14–17 C and had consistently declined from 21 C during the 14 days prior to fish collection. Prior to surgery, instruments and radio transmitters (model F1835B, Advanced Telemetry Systems [ATS], Isanti, Minnesota; 16 g) were sterilized overnight in a 10% bleach/distilled water solution (Stoskopf 1993, Noga 2000) and Betadine® (10% povidone-iodine solution) (Bowker and Trushenski 2019), respectively. Fish were held for 10 to 30 min in a 379-L holding tank with reservoir water at ambient temperatures and dissolved oxygen at saturation levels, before being placed on the surgical table mounted inside the electrofishing boat and immobilized using electroanesthesia as described by Jennings and Looney (1998). Gills were irrigated with a continuous flow of oxygen-saturated water throughout the surgical process. The transmitter was washed with distilled water to remove Betadine®, inserted into the body cavity through a 2-cm incision posterior to the pelvic girdle and above the ventral midline, then pushed over the pelvic girdle to minimize risk of expulsion. The external antenna was passed through the body cavity wall approximately 2-cm posterior to the incision using the shielded needle technique described by Ross and Kleiner (1982). Incisions were closed using size one nylon monofilament non-absorbable suture material, with three simple interrupted knots, and three total sutures. Two sets of surgical equipment were alternated for a minimum of 10 min between surgeries (one used, one sterilized with 10% bleach/distilled water solution). Fish were externally tagged (Floy T-Bar model FD-68BC, Floy Tag and Mfg., Inc., Seattle, Washington) as described by Guy et al. (1996) for identification if caught by anglers. The duration of each procedure took 3.5 to 5.0 min. Prior to release, fish were immersed in a 3% non-iodized salt solution for 30 sec (Carmichael et al. 1984, Noga 2000), then held approximately 15 min for observation in the holding tank described above. All fish appeared healthy following surgery and were released within 100 m of their capture site to prevent displacement effects.

Fish were initially tracked 2 wk following surgery by boat using an ATS R2000 receiver and a directional yagi antenna. Each transmitter was equipped with a mortality sensor, such that signal rate doubled if there was no movement for 24 h. Due to high mortality observed during the initial tracking event, fish were tracked three times during the following 2 wk. During each of these tracking events, signals were obtained from all transmitters to confirm existing mortality signals and monitor surviving fish. The implantation of transmitters at Lake Fork Reservoir initially scheduled for December 2019 was delayed due to mortality observed at Toledo Bend Reservoir.

Experimental Trials of Tagging Mortality

Three surgical trials were conducted to examine post-operative mortality using identical collection, electroanesthesia, and surgical equipment and methods described above. The first two trials were conducted at ambient water temperatures. In the first trial, five implanted fish and five controls (i.e., untagged) 381–445 mm TL were collected from Lake Athens, Texas, in December 2019 at 13 C. In the second trial, 12 implanted fish and 2 controls (375–544 mm TL) were collected from Sam Rayburn Reservoir, Texas, in January 2020 at 13 C. Reservoir water temperatures were relatively stable for 3 and 6 wk prior to fish collection at Lake Athens and Sam Rayburn Reservoir, respectively. During the second trial, we investigated incision sealing by increasing suture number to either four or five sutures for three fish each. A tissue adhesive (3M Vetbond®, St. Paul, Minnesota) was also applied to the incision of six fish (two fish each with three, four, and five sutures). For both of these trials, surgeries were conducted during the day of collection, but fish were held 1–4 h prior to surgeries.

The third trial was conducted using six implanted fish and two controls (390–505 mm TL); fish were collected from Sam Rayburn Reservoir in February 2020 at an ambient water temperature of 13 C. Fish were transferred to hatchery raceways at 13 C, then water temperature was gradually heated to 24 C over a period of 7 days. Surgeries were conducted after an additional 7 days of acclimation with water temperature maintained at 24 C. After surgeries in all three trials, fish were held at 24 C for 5 wk in hatchery raceways for observation. All raceways were aerated (>7.5 ppm dissolved oxygen) via continuous water flow from the reservoirs in which fish were collected and juvenile koi (*Cyprinus carpio*) abundance was maintained to provide on-demand forage.

Subsequent Field Studies

During May to July of 2020 and May to June of 2021, a total of 43 (356–606 mm TL) and 38 largemouth bass (362–615 mm TL) were implanted with transmitters at Toledo Bend and Lake Fork reservoirs, respectively. Ambient water temperatures during surgeries ranged from 22–31 C. Fish collection and surgical procedures were identical to methods previously described, except that 13 fish from Toledo Bend Reservoir and 6 fish from Lake Fork Reservoir were collected via angling. Based on the findings from the 2019 Toledo Bend Reservoir study and our surgical trials described below (i.e., 37 of 38 fish died within 21 days post-surgery and the remaining fish died within 28 days), we conservatively defined surgery-related mortality as deaths occurring less than 28 days after surgeries.

Results

During the initial tracking event at Toledo Bend Reservoir 2 wk after surgeries, signals were obtained from all 26 transmitters and 23 were indicating mortality. During the following 2 wk, mortality signals were received from all 26 transmitters and no movement was observed, resulting in 100% mortality of our surgically implanted fish (Table 1; Figure 1).

Post-operative mortality from our two surgical trials at 13 C were also high. In our first trial in December 2019 at Lake Athens, all five of our implanted fish died, three within 2 wk post-surgery and two during the third week (Table 2; Figure 1). Conversely, all five control fish were alive and released at the conclusion of the trial. In our second trial in January 2020 at Sam Rayburn Reservoir, 7 of 12 implanted fish died, four within 1 wk post-surgery, and three during the second week (Table 2; Figure 1). Our additional measures to ensure incision sealing (i.e., added sutures and adhesive) did not reduce mortality. At the conclusion of the trial, five surgery fish and both control fish were alive and visibly healthy (i.e., no infections and healed incisions), and were released. All 12 fish that died from both trials became lethargic a few days prior to death, suspended high in the water column, and developed external infections that initially emanated from the incision site and then expanded over the body (Figure 2). These infections were likely *Saprolegnia* spp. or other fungi/water molds, although no necropsies were conducted.

During the third Sam Rayburn trial at 24 C, we observed no fungal infections or mortality of six implanted fish or two control fish over the 5-wk observational period (Table 2; Figure 1). Similarly, post-operative mortality from our subsequent field studies in

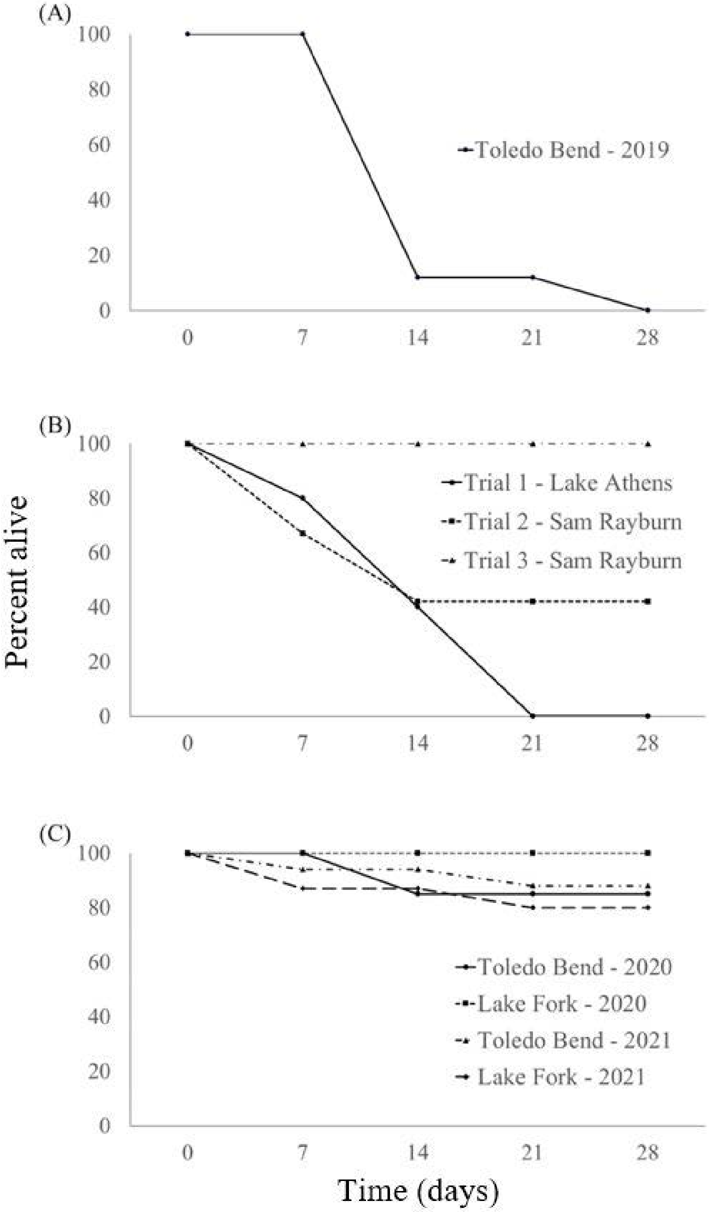

Figure 1. Percent of tagged fish found alive (1-wk intervals) during the initial study on Toledo Bend Reservoir, Texas (A), in three trials using fish from two Texas reservoirs (B), and during subsequent field studies on Toledo Bend and Lake Fork reservoirs, Texas (C).

Table 1. Post-operative mortality (defined as deaths occurring < 28 days after surgeries) of adult largemouth bass surgically implanted with radio transmitters and released at Toledo Bend and Lake Fork reservoirs, Texas. For implanted fish, mortalities are in parentheses.

Reservoir	Water temperature (C)	Date	Implanted fish	Mortality rate (%)
Toledo Bend	17	20 Nov 2019	15 (15)	
	14	21 Nov 2019	11 (11)	
		Total	26 (26)	100
Toledo Bend	23	5 May 2020	4 (0)	
	25	22 May 2020	7 (1)	
	27	2 June 2020	4 (0)	
	29	1 July 2020	7 (1)	
	30	29 July 2020	4 (2)	
		Total	26 (4)	15
Lake Fork	25	22 May 2020	11 (0)	
	25	28 May 2020	12 (0)	
		Total	23 (0)	0
Toledo Bend	22	24 May 2021	7 (1)	
	25	9 June 2021	8 (0)	
	29	24 June 2021	2 (1)	
		Total	17 (2)	12
Lake Fork	26	10 June 2021	2 (0)	
	31	15 June 2021	7 (1)	
	28	29 June 2021	6 (2)	
		Total	15 (3)	20

2020 and 2021 (22 to 30 C) was relatively low for both years (15% and 12% at Toledo Bend and 0% and 20% at Lake Fork; Table 1; Figure 1). Angled fish experienced 23% post-operative mortality at Toledo Bend (3 of 13 fish) and 17% at Lake Fork (1 of 6 fish). Mortality of fish collected from electrofishing was only 8% at Toledo Bend in 2020 (1 of 13 fish) but was 22% at Lake Fork in 2021 (2 of 9 fish).

Table 2. Results from three surgical trials examining post-operative mortality (defined as deaths occurring < 28 days after surgeries) of adult largemouth bass collected from two Texas reservoirs and implanted with radio transmitters, then held 5 wk in hatchery raceways for observation. For trials 1 and 2, surgeries were conducted at ambient water temperatures. For trial 3, fish were collected at an ambient water temperature of 13 C, then raceway water was heated to 24 C over a 7-day period. Surgeries were conducted after an additional 7 days of acclimation at 24 C. For implanted and control fish, mortalities are in parentheses.

Surgery trial	Water temperature (C)	Date	Implanted fish	Mortality rate (%)	Control fish
Trial 1 – Lake Athens	13	11 Dec 2019			
Three sutures			5 (5)	100	5 (0)
Trial 2 – Sam Rayburn	13	6–7 Jan 2020			
Three sutures			4 (0)		
Three sutures, adhesive			2 (2)		
Four sutures			1 (1)		
Four sutures, adhesive			2 (1)		
Five sutures			1 (1)		
Five sutures, adhesive			2 (2)		
		Total	12 (7)	58	2 (0)
Trial 3 – Sam Rayburn	24	4 Feb 2020			
Three sutures			6 (0)	0	2 (0)

Figure 2. Fungal infection emanating from the incision site on a largemouth bass that died from surgical implantation of a radio transmitter at a water temperature of 13 C.

Discussion

During preparation for largemouth bass telemetry research at Toledo Bend and Lake Fork reservoirs, our literature review found only three studies that examined transmitter implantation effects on largemouth bass; two on juvenile fish (Cooke et al. 2003, Thompson et al. 2014) and one on adult fish (Crumpton 1982). Crumpton (1982) found that surgically implanted dummy transmitters had no effects on swimming, feeding, spawning, or catchability of adult largemouth bass and no surgery-related mortality was reported. We found no previous research that had examined effects of water temperature on post-operative health and mortality of largemouth bass, but investigations with bluegill (Knights and Lasee 1996) and hybrid striped bass (Walsh et al. 2000) suggest that surgeries at colder temperatures (6 C and 12–18 C, respectively) minimize tagging mortality. Although prior studies examining impacts of water temperature on adult largemouth bass mortality are tournament-related, the relationship is exponential with approximately 10% mortality at 15 C and 24% at 25 C (Wilde 1998). Therefore, we expected low mortality associated with our first set of surgeries at Toledo Bend Reservoir when water temperatures ranged from 14–17 C. However, within 4 wk post-surgery, all 26 of the surgically implanted fish had died.

All fish that died during our two trials at 13 C acquired fungal infections (i.e., saprolegniasis), which have been previously observed in fish surgically implanted with transmitters. Mellas and Haynes (1985) attributed mortality of white perch (*Morone americana*) to saprolegniasis with surgeries at stable, warmer temperatures (20–23 C). Knights and Lasee (1996) observed post-operative saprolegniasis in bluegill at colder temperatures (6 C) but documented no mortality. However, immunosuppression of channel catfish (*Ictalurus punctatus*) and mortality from *Saprolegnia* spp. has been documented during colder and declining water temperatures. Bly and Clem (1991) found that a rapid water temperature decline (23 to 11 C in 24 h) produced immunosuppression in channel catfish, and fish required up to 6 wk of acclimation for immune responses to recover. Bly et al. (1992) determined that *Saprolegnia* spp. zoospore abundance and potential virulence was 2–5-fold higher at water temperatures of 10 C than 20 C. Further, a temperature shock from 22 to 10 C in 24 h resulted in immunosuppression of channel catfish, an infection rate of 92%, and a mortality rate of 67% within 21 days. The researchers identified *Saprolegnia* spp. as the primary pathogen and causative agent of mortality. However, when fish were acclimated at 10 C for 8 wk or were held at ambient 22 C prior to exposure to *Saprolegnia* spp. (i.e., immunocompetent in both cases), no mortalities were observed. A similar study found that temperature shock and skin abrasions were needed to induce high *Saprolegnia* spp.-related mortality in channel catfish (Howe et al. 1998).

We suggest that decreasing, colder water temperatures in November (range = 13–17 C and declined from 21 C in 14 days) resulted in immunosuppression of largemouth bass at Toledo Bend Reservoir concomitant with high virulence conditions for saprolegniosis (*sensu* Bly and Clem 1991). Coupled with stressors and incisions from surgeries, these factors may have been key contributors of the 100% mortality observed for the 26 largemouth bass tagged in Toledo Bend Reservoir. A similar set of conditions were present during our first Lake Athens trial, which occurred following only 3 wk of relatively stable water temperatures. This immunosuppression/saprolegniosis/acclimation hypothesis during colder and declining temperatures is supported by considerably lower post-operative mortalities observed from our second cold-water trial, and our third trial and field work at Toledo Bend and Lake Fork reservoirs at warmer water temperatures. The reduced mortality we experienced from the second trial at 13 C (58%) may have resulted from 6 wk of relatively stable water temperatures prior to the trial that allowed recovery of immune response by the fish. During the third trial at 24 C, we observed no saprolegniosis or mortality of six implanted fish or two control fish within 5 wk post-surgery. Similarly, post-operative mortality from our field work in 2020 and 2021 at 22–30 C was relatively low for both years. Angling imposes additional stress on largemouth bass (Gustaveson et al. 1991, Brownscombe et al. 2014, Dinken et al. 2022), which may have increased post-operative mortality at Toledo Bend Reservoir in 2020; however, mortality was similar between collection methods at Lake Fork Reservoir in 2021.

We could find no other research that implanted adult largemouth bass with transmitters during fall when water temperatures were below 20 C and declining that resulted in 100% post-operative mortality. However, although many largemouth bass telemetry studies have been conducted, only a few reported post-operative mortalities and details regarding water temperatures were often lacking. Two previous studies surgically implanted largemouth bass during colder winter months (December, Goclowski et al. 2013; February, Sammons et al. 2003). Although no specific water temperatures were reported, no surgery-related mortalities were observed, suggesting that extended acclimation throughout the colder months preceding their surgeries may have contributed to no mortality. Knights and Lasee (1996) reported no surgery-related mortality of bluegill when reducing water temperatures from 20 C to 6 C in 12 days, but surgeries were conducted at water temperatures considerably colder than our study. In addition, fungal virulence could be reduced at 6 C, however *Saprolegnia* spp. can tolerate temperatures as low as 3 C (Willoughby and Roberts 1992, Aly and El-Ashram 2000).

Cooke et al. (2003) found that experienced surgeons can significantly improve survival when compared with inexperienced surgeons when working with juvenile largemouth bass. All surgeries at Toledo Bend Reservoir and the Sam Rayburn Reservoir trials were conducted by the author, and those at Lake Fork Reservoir and the Lake Athens trial by the coauthor. Prior to this study, the two surgeons were unexperienced. Both surgeons conducted extensive research on methods, consulted with fish health experts and experienced surgeons, practiced sutures on foam medical kits, and honed the entire procedure on numerous moribund and live largemouth bass until each was comfortable with the entire surgical process. Total training for each surgeon was approximately 15 h. Overall, our post-operative mortalities did generally decline with the increasing number of surgeries each surgeon conducted. However, we propose the reduction in mortality was likely unrelated to increased experience. Both surgeons were equally confident with each completed surgery, and all were conducted with identical methodology. Further, mortality rates were similar between surgeons (e.g., 100% for 2019 Toledo Bend and Lake Athens surgeries; ≤ 20% for subsequent field studies), suggesting equal surgical abilities. Therefore, surgical methodology or surgeon experience likely had little effect on mortality of tagged fish.

This study is the first to observe high largemouth bass mortality during tagging surgery in colder, declining water temperatures. However, our three surgical trials should be viewed as preliminary, as they were exploratory in nature and conducted prior to awareness of the potential for declining water temperatures to cause immunosuppression in fishes when fungal virulence could be high. Sample sizes were also low and inconsistent which prevented any statistical analyses. Additional trials should be conducted to examine largemouth bass immunosuppression and related post-operative mortality, particularly to determine water temperatures, trends required to instigate immunosuppression, and acclimation time required for immunorecovery. Also, necropies are needed to confirm the identity of the primary fungi/water molds causing mortality, as the *Aphanomyces* water mold is also virulent at colder water temperatures (Hawke et al. 2003) and has caused mortality in numerous freshwater species, including largemouth bass (Sosa et al. 2007).

Our findings should caution future investigators about conducting surgeries during similar conditions that may result in unnecessary loss of fish, additional costs, and sample-size reductions due to high post-surgical mortality. In addition, our results suggest that other studies are needed to determine if the immunosuppression or temperature acclimation dynamic could also influence mortality of largemouth bass during other common but stressful handling events, such as at fish hatcheries or tournaments. Finally, little if any research has been done on susceptibility of other black bass species to immunosuppression or fungal infection. Some of these fishes support popular and economically important fisheries, and some evidence exists that they may have different responses to stressors than largemouth bass (e.g., Hartley and Moring 1995, Ricks 2006).

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Hydrilla Management Impacts on a Largemouth Bass Fishery: A Case for a Balanced Management Approach

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Abstract: Lake Austin, in central Texas, supported a popular trophy largemouth bass (*Micropterus salmoides*) fishery concomitant with conservative hydrilla (*Hydrilla verticillata*) management during the period 2002–2011. However, a change from this conservative approach to an aggressive stocking rate of triploid grass carp (*Ctenopharyngodon idella*) in response to excessive hydrilla growth between 2011–2013 subsequently resulted in the eradication of all submerged aquatic vegetation (SAV). The loss of SAV quickly changed the angling dynamics of the reservoir, resulting in a controversial decline in the quality angling experience. The objectives of this case study were to compare how available population metrics of largemouth bass and important prey fish differed between periods of SAV presence (1997–2013) and absence (2014–2022) to inform which SAV management approach better supports a sustainable trophy fishery goal. These comparisons revealed evidence of declines in largemouth bass relative abundance (CPUE), body condition (W_r), and growth rates when SAV became absent, but no changes in population length structure. There were no apparent changes observed in selected prey species populations between the two periods. While linking changes in fish population metrics with a single environmental attribute in a reservoir is difficult, SAV has been widely associated with quality largemouth bass fisheries. As such, our results suggest a long-term conservative triploid grass carp stocking management approach to best protect SAV habitat that supports adequate largemouth bass population performance alongside other reservoir functions. Management needs to consider multiple priorities among relevant stakeholders in support of a balanced system for all uses. Further, SAV surveys should explore use of volumetric biomass assessments in response to triploid grass carp herbivory for better supplemental stocking estimates while trying to anticipate how climate driven changes in hydrology and temperature might impact SAV extent.

Key words: lake habitat, reservoir, triploid grass carp, trophy bass

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Largemouth bass (*Micropterus salmoides*) support popular recreational fisheries in aquatic systems across the southern U.S. (Chen et al. 2004). In reservoirs, productive high-quality fisheries are dependent on numerous biotic and abiotic factors including habitat, water quality, and hydrology (e.g., floods and droughts). Fisheries management in reservoirs is especially challenging due to the varied ecosystem services desired such as flood control and hydropower generation, municipal and agricultural needs, and non-angling recreational uses. Further, commercial and residential shoreline development often results in associated pressures for the removal of submerged aquatic vegetation (SAV), coarse woody habitat (CWH), and shoreline vegetation. These common practices can decrease the amount of physical habitat, prey, and plant litter that support productive fisheries (Schindler et al. 2000, Roth et al. 2007). Although there are many interdependent drivers of fishery condition, a diverse SAV assemblage is recognized as a critical component for fish recruitment, growth, foraging, and refugia (Smith and Orth 1990, Nohner et al. 2018). Furthermore, changes in SAV extent have commonly been linked to largemouth bass population characteristics (e.g., Carpenter and Lodge 1986, Bettoli et al. 1993, Maceina 1996, Brown and Maceina 2002, Sammons et al. 2005).

Management of SAV becomes controversial especially when non-native species such as hydrilla (*Hydrilla verticillata*) develop dense stands that impede recreational use, access, or flood control operations. Excessive SAV growth can negatively affect largemouth bass prey visualization and ambush abilities, while also impeding angler efficiency (Savino and Stein 1982, Colle et al. 1987, Bettoli et al. 1992). Conversely, anglers often associate species such as hydrilla with quality recreational fisheries, leading them to oppose SAV control efforts (Slipke et al. 1998). Especially contentious is the use of triploid grass carp (*Ctenopharyngodon idella*) when other options (e.g., herbicides) are not viable (Bettoli et al. 1993, Webb et al. 1994). Although the potential for grass carp reduction of hydrilla is well documented (Colle and Shireman 1980), precise control is difficult to achieve due to carp consumption of SAV

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decreasing over time, requiring restocking, as well as escapement during floods, difficulty of removal, and potential for SAV overgrazing (Pípalová 2006). Use of grass carp has resulted in complete loss of SAV and corresponding reduction in overall fishery quality (Bettoli et al. 1993, Brown and Maceina 2002, Chilton et al. 2008).

Lake Austin in central Texas, USA, is well known for producing trophy-sized (>3.6 kg) largemouth bass (De Jesús and Farooqi 2017). During the timeframe encompassed by our study, Lake Austin's status as a trophy bass fishery was demonstrated by recorded fishing tournament results and entries into Texas Parks and Wildlife Department (TPWD) angler programs (e.g., Angler Recognition Program and Toyota ShareLunker Program). Eventually, Lake Austin became nationally renowned for its exceptional bass fishery and made headlines amongst the top bass conservation societies in their national top rankings during this period.

Prior to 2009, the SAV at Lake Austin was managed by targeting hydrilla coverage through a conservative incremental grass carp stocking strategy, while relying on other beneficial aquatic macrophytes to supplement habitat for the bass fishery (Chilton and Magnelia 2008). However, beginning in 2009, there was a regional drought-of-record that reduced cooler flows from hypolimnetic releases into Lake Austin, stimulating rapid spread of hydrilla (Shivers et al. 2018), and resulting in increased pressure from dam operators and public stakeholders to deviate from the conservative stocking approach of triploid grass carp. After complying with these demands there was a near complete elimination of SAV after 2013 that has persisted through the present, despite management efforts to restore SAV (Bellinger and Schad 2019). Following the loss of SAV, anglers believed that the largemouth bass fishery in Lake Austin declined and blamed the management authorities for this change. To this end, our goal was to learn from this case experience by analyzing available fisheries data and to develop an improved balanced SAV management approach that would restore a quality trophy fishery at Lake Austin, while considering other user interests.

Study Area

Lake Austin is a 33 km long, 648-ha mainstem impoundment on the Colorado River in Austin, Texas that was constructed in 1939 (see Chilton and Magnelia 2008). Water levels in Lake Austin are maintained at approximately 150 m above mean sea level but have been periodically drawn down (~3 m) for a few weeks during the winter for SAV control and to allow for maintenance of bulkheads and docks (De Jesús and Farooqi 2017). The reservoir has an average depth of 3.5 m and a maximum depth of 20 m near the Tom Miller Dam. The reservoir shoreline and riparian habitat are steadily being converted from earthen banks with abundant terrestrial and emergent aquatic vegetation (e.g., *Typha* spp., *Schoenoplectus* spp., and *Justicia americana*), and SAV (e.g., *Potamogeton* spp., *Chara* spp., *Vallisneria americana*, *Ceratophyllum demersum*) to hardened revetment, residential lawns, and vegetation-free littoral zones; at the time of this study over 50% of the lakeshore had been developed and hardened (De Jesús and Farooqi 2017). Prior to and during establishment by hydrilla, another non-native aquatic plant, Eurasian watermilfoil (*Myriophyllum spicatum*), had been a predominant species and was managed with winter drawdowns. Eurasian watermilfoil competed strongly alongside hydrilla, notably in the upper sections of the reservoir, where inflows from hypolimnetic releases from Lake Travis maintain cooler water temperature (Smith and Barko 1990).

Hydrilla was first reported in Lake Austin in 1999. At that time, coverage was low enough to qualify for a Tier I response which entailed an immediate response toward eradicating the problem within a small area (Chilton 2018). An official task force created in 1999 to discuss, evaluate, and develop SAV control measures comprised numerous governmental entities including City of Austin (COA) Watershed Protection, Parks and Recreation, and Water and Wastewater Departments; the Lower Colorado River Authority (LCRA); Travis County; and TPWD Inland Fisheries. The LCRA also formed a Lake Austin Advisory Panel representing local civilian stakeholders that drafted a resolution to support the task force management plan.

In 2000, the task force completed an integrated management plan. However, hydrilla expanded in coverage during the development of this plan. Thus, the response level was reclassified from Tier I to Tier II, which meant the plant could only be managed as a maintenance function (i.e., no eradication) due to the perceived difficulty in full eradication at a larger scale. A review of hydrilla treatment options found that biological control was the most viable option, but initial treatment proposals using triploid grass carp were twice denied by TPWD due to concerns about SAV overgrazing. Hydrilla control in Texas has generally been very conservative since aggressive grass carp stocking to control hydrilla at Lake Conroe in the 1980s led to complete SAV eradication and angler uproar (Bettoli et al. 1993). Instead, TPWD designed a conservative stocking regime to prevent total eradication of SAV in Lake Austin and funded a radio-tag study during simulated flood conditions to assess potential escapement, which was found to be negligible (Bonner et al. 2002, Chilton and Magnelia 2008).

In 2003, two non-government organizations won a temporary restraining order against TPWD that prevented sterile (triploid) grass carp stocking state-wide. These groups agreed to withdraw their motion in exchange for a science-based resolution evaluating statewide stockings approaches. Lake Austin was accepted as a test case to explore conservative incremental triploid grass carp stocking approaches (Chilton and Magnelia 2008). The goal for Lake Austin was for hydrilla coverage not to exceed 40 ha (COA 2000). This goal was considered a balanced approach by TPWD biologists that would meet the interests of the various stakeholders.

The stocking rate of grass carp was generally less than 11 fish ha^{-1} (or 25 fish ac^{-1}) of hydrilla. However, with the onset of a drought-of-record in 2009, reduced flows through the reservoir and subsequent warmer water temperatures are believed to have favored the rapid and substantial expansion of hydrilla to a peak in 2012 (Figure 1). Increased hydrilla biomass in the reservoir led to concerns among controlling authorities that a sudden large flow event could dislodge a significant amount of hydrilla biomass that would damage property and infrastructure as had occurred previously on Lake Austin (Gilroy 2005). Further, vociferous anecdotes of hydrilla-related drowning and hazardous boating conditions expressed by citizens in the late 2000s increased pressure for more frequent stockings. Therefore, public safety and protection of infrastructure, which are primary reservoir functions, took precedence when altering the SAV control strategy. Over 39,000 grass carp were stocked from 2011–2013 at a rate of 15–60 fish ha^{-1} (Figure 1), which rapidly increased abundances, resulting in more than 56,700 triploid grass carp stocked between 2003 and 2013. The subsequent loss of SAV in the reservoir after 2013 suggests grazing rates exceeded SAV reproductive potential (van der Lee et al. 2017).

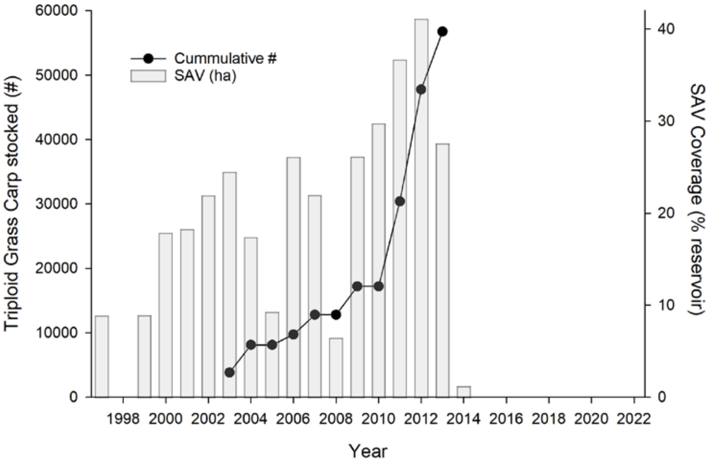

Figure 1. Lake Austin submerged aquatic vegetation (SAV) coverage (% of total reservoir surface area, vertical gray bars, right y-axis) and cumulative triploid grass carp stocked (# stocked, solid circles, left y-axis) between 1997 and 2022.

Methods

Aquatic Vegetation Surveys

Routine aquatic vegetation surveys of Lake Austin were conducted by TPWD (De Jesús and Farooqi 2017). To estimate areal coverage of SAV (ha) from these boat surveys, vegetation boundaries were identified with GPS, sight, and sonar and the total area was determined with geographic information system (GIS) mapping. Plant species composition was determined from random rake samples periodically pulled during each survey (De Jesús and Farooqui 2017). In response to hydrilla establishment, survey frequency was increased from once per year in the 1990s to two to three times per year in 2001. Increased monitoring in spring and sometimes summer was designed to closely track the changes in areal hydrilla coverage in response to triploid grass carp estimated abundance after stocking events. For this study, if multiple surveys were conducted in a year, we averaged the coverage observations to derive mean annual SAV coverage.

Fish Sampling and Population Metrics

Lake Austin fishery surveys were conducted by TPWD between 1997–2022 and included two types: a comprehensive survey, conducted in in 1997, 2000–2001, 2004, 2008, 2012, 2016–2017, and 2020, in which largemouth bass, sunfish (*Lepomis* spp.), and gizzard shad (*Dorosoma cepedianum*) were collected, and a largemouth-bass-only survey, which was conducted in all other years from 2000–2022. Both survey types were completed in October or November at 12–18 sites per survey year, with sites randomly distributed throughout the lake. Boat electrofishing was done at each sample site for 5 min, with catch per unit effort (CPUE) expressed as number of fish caught per hour (fish h^{-1}). Fish were processed alive in the field and released except for largemouth bass kept for aging purposes. A total of 390 discreet sample sites evenly distributed throughout the reservoir were surveyed between 1997–2022.

Prey fish were identified, counted, and measured (TL; mm). Sunfishes were composed primarily of redbreast sunfish (*L. auratus*), bluegill (*L. macrochirus*), and redear sunfish (*L. microlophus*), and were subsequently grouped at the genus level for all analyses. Largemouth bass were measured (TL, mm) and weighed (g). Sagittal otoliths were collected during comprehensive survey years and in 2017. Prior to 2008 largemouth bass of varying sizes were aged; however, after 2008, only 13 largemouth bass 330–405 mm were randomly selected per year for aging. The change was made to determine the approximate time needed to reach the statewide harvestable minimum length of 356 mm.

Data Analyses

Largemouth bass proportional stock density (PSD) was calculated using the standard-length categories found in Neumann et al. (2012). Body condition was assessed using relative weight (W_r; Neumann et al. 2012). Largemouth bass CPUE and W_r were calculated for all fish stock size and larger (CPUE-203 and *Wr*-203), and for those larger than the statewide minimum-length limit (CPUE-356 and *Wr*-356). A W_r of 100 has been suggested to reflect condition of good habitat and abundant prey (Murphy et al. 1991), but W_r values as low as 85 have been deemed acceptable in Texas reservoirs (M. De Jesús, TPWD, personal observation). If the lake-wide mean W_r of largemouth bass is below 85, there may be deficiencies in the prey population (e.g., small sizes, low biomass), and/or strong density dependent interactions negatively impacting largemouth bass condition (Schindler et al. 1997, Fox and Neal 2011). The proportion of gizzard shad small enough to be susceptible to largemouth bass predation (<200 mm) was expressed as an index of vulnerability (IOV; DiCenzo et al. 1996), although the net mesh size (~1.27 cm [~0.5”] bar mesh) potentially selected for larger gizzard shad.

Sample years were divided into two periods to examine changes in fish metrics due to SAV. Periods were defined as SAV presence (1997–2013) and absence (2014–2022). To test for the negative impacts of reservoir aging on fishery quality (Miranda et al. 2010), we first applied the Mann-Kendall test (M-K S; $\alpha = 0.05$) to determine whether there was a monotonic decline in fishery metrics through time. Differences in mean CPUE, PSD, *Wr*, and age at 330–405 mm length between SAV periods were examined using a Student’s *t*-test ($\alpha = 0.05$). A Mann-Whitney (M-W) *U* test statistic was used to test for a significant change in largemouth bass age reaching harvest size between periods of SAV presence and absence. Gizzard shad IOV and largemouth bass age data were $\log_{10}$-transformed prior to analysis to normalize the data. Analyses were conducted using the Real Statistics Resource Pack (Zaiontz 2023) and SigmaPlot (Systat Software, Inc. 2018).

Results

Submerged Aquatic Vegetation

Average SAV coverage from 1997–2013 was 150.1 ± 24.7 ha (mean ± 95% CI). This translated to approximately 22% of the reservoir area, varying from 3% (2008) to 40% (2012; Figure 1). Declines in SAV appeared coincident with triploid grass carp stocking (Figure 1). Since 2013, annual SAV total coverage has been less than 0.5 ha system-wide; however, in 2022 SAV patches of southern naiad (*Najas guadalupensis*), Eurasian watermilfoil, water celery (*Vallisneria americana*), and pondweeds (*Potomogeton* spp.) were observed re-establishing throughout the reservoir.

Largemouth Bass

A total of 2581 largemouth bass were collected across all survey years, with 1885 (73%) >203 mm TL, of which 640 were greater than 356 mm TL. System-wide average TL during the SAV period was 325 ± 9 mm, and after 2013 was 331 ± 12 mm. Largemouth bass PSD after 2013 increased 8% (Table 1; Figure 2A). However, largemouth bass population size structure did not significantly differ either through time (M-K $S = -17$, $P = 0.65$) or between SAV periods ($t_{22} = -1.2$, $P = 0.25$; Fig. 2A).

Largemouth bass stock catch rates (CPUE-203) across years varied from 36 fish h^{-1} to 114 fish h^{-1} whereas harvest size catch rates (CPUE-356) ranged from 7 fish h^{-1} to 38 fish h^{-1} (Table 1; Figure 2B). Only the CPUE-356 significantly declined through time (M-K $S = -43$, $P < 0.05$). Average CPUE-203 and CPUE-356 during the period of SAV presence was 69.4 ± 11.5 and 23.2 ± 5.6 fish h^{-1}, respectively. After 2013, rates declined to 44.0 ± 11.6 and 16.3 ± 4.5 fish h^{-1} for CPUE-203 mm and CPUE-356 mm largemouth bass, respectively. Only CPUE-203 significantly declined after 2013 ($t_{22} = 2.66$, $P = 0.01$), although CPUE-356 trended downward after 2013 ($t_{22} = 1.55$, $P = 0.14$; Table 1; Figure 2B).

Condition of largemouth bass declined over time for both stock and harvest-sized fish (M-K $S < -107$, $P < 0.05$; Figure 2C). Mean *Wr*-203 peaked at 99 in 2001 and declined to 78 in 2018. Mean *Wr*-356 peaked at 104 in 2001 and declined to 79 in 2022 (Figure 2C).

Table 1. Ranges of metrics for Lake Austin, Texas, largemouth bass and prey fish for 1997–2022 and mean ± 95% CI for the periods of submerged aquatic vegetation (SAV) presence (1997–2013) and absence (2014–2022). Metrics include catch per unit effort (CPUE; fish h^{-1}), proportional stock distribution (PSD), relative weight (W_r), and total length (TL; mm). Asterisks denote significant *t*-test comparisons of fish metrics between periods of SAV and No SAV: *$P < 0.05$, **$P < 0.001$.

	Largemouth Bass					Gizzard Shad		Sunfish	
Period	**CPUE-203**	**CPUE-356**	**PSD**	**W_r-203**	**W_r-356**	**CPUE**	**TL**	**CPUE**	**TL**
All years	36.7–114.0	7.8–37.5	39.1–78.4	78.5–98.7	79.3–104.6	21.5–109.3	221.3–337.4	132.7–480.0	91.7–128.1
SAV	65.8 ± 10.3*	21.9 ± 4.8	53.3 ± 4.5	92.0 ± 1.8**	97.9 ± 2.2**	56.9 ± 26.1	267.7 ± 34.1	275.2 ± 95.5	107.8 ± 10.0
No SAV	44.0 ± 11.6	16.3 ± 4.5	58.4 ± 8.2	83.1 ± 1.7	85.6 ± 2.0	63.8 ± 45.8	268.8 ± 8.2	247.6 ± 58.0	99.9 ± 11.8

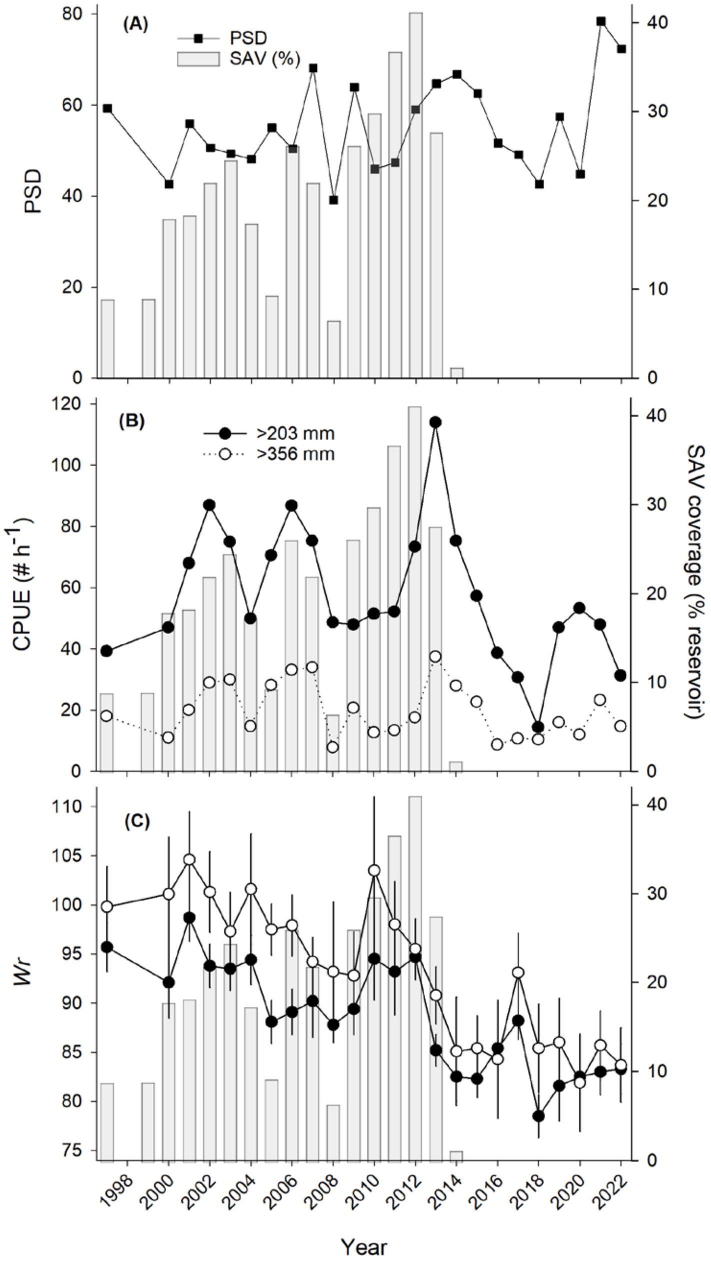

Figure 2. Temporal patterns of A) largemouth bass proportional stock density (PSD; mean ± 95% CI); B) catch per unit effort (CPUE; fish h^{-1}) for total length (TL) >203 mm (closed circles) and TL >356 mm (open circles); and, C) relative weight (W_r) for TL >203 mm (closed circles) and TL >356 mm (open circles) (mean and 95% CI) collected during electrofishing surveys. Annual average submerged aquatic vegetation (SAV) coverage (gray bars; % total reservoir area; right y-axis) also shown.

Between periods, mean *Wr*-203 and *Wr*-356 were lower after SAV loss ($t_{22} = 6.48$ to 7.79, $P < 0.001$; Table 1). System-wide, over 70% of largemouth bass had $W_r > 85$, but that proportion declined by almost half after 2013. The average age of a largemouth bass between 330–405 mm prior to 2013 was 2.6 ± 0.2 years ($n = 67$), but following the loss of SAV, the average age for this group increased to 3.5 ± 0.6 years ($n = 26$; M-W $U = 542$, $P = 0.002$).

Prey Species

Comprehensive surveys collected more than 750 gizzard shad, with CPUE ranging from 21 fish h^{-1} to 109 fish h^{-1} (Figure 3A; Table 1). Most gizzard shad (~80%) were greater than 200 mm TL (i.e., IOV <20%; Figure 3B). Gizzard shad CPUE was similar through time (M-K $S = 4$, $P = 0.74$) but TL increased over time (M-K $S = 36$, $P < 0.01$; Figure 3). Gizzard shad mean CPUE and mean TL were similar between SAV Periods ($t_7 = -0.28$ to -0.04, $P > 0.79$; Table 1). Over 3200 sunfishes were collected, with CPUE ranging 130–480 fish h^{-1} (Figure 3C). Most (67%) sunfishes collected were less than 125 mm TL (Figure 3D). Mean CPUE and mean TL were similar between SAV periods ($t_7 = 0.38$ to 0.97, $P > 0.36$; Table 1), but both increased over time (M-K S 26–36, $P < 0.01$; Figure 3).

Discussion

With the loss of SAV from Lake Austin in 2013, stock-sized largemouth bass electrofishing catch rates and body condition significantly declined, corroborating anecdotal claims from anglers. Prior to 2013, CPUE-203 was comparable to or greater than other U.S. lakes and reservoirs (Hansen et al. 2015, Schoenebeck et al. 2015). Fluctuations in fishery metrics observed prior to 2013 likely reflected inter-annual differences in SAV extent (5–35%). For example, the decline in CPUE-203 between 2008 and 2010 may have reflected changes in fish catchability or natural population variations following SAV coverage declines from 2007 to 2009 (Bayley and Austen 2002, Brown and Maceina 2002). However, as SAV coverage increased after 2010, there was a corresponding increase in largemouth bass CPUE. Changes and general improvements in fishery quality with deliberate management, but not wide-spread elimination, of hydrilla coverage have been documented in numerous reservoirs across the southeastern U.S. (Wrenn et al. 1996, Brown and Maceina 2002, Sammons et al. 2005).

The largemouth bass PSD across all years (50–80) is suggestive of a fishery managed for trophy fish (Willis et al. 1993). Additionally, prior to 2013 more fish showed W_r >85, especially for fish >356 mm TL, suggesting favorable habitat conditions for foraging and growth (Maceina and Murphy 1988, Blackwell et al. 2000). Productive habitat is one of several supporting factors needed to sustain a trophy fishery at Lake Austin, along with Florida bass genetics, selection for growth, reduced mortality from high angler release rates, and prolonged growing seasons. These factors likely combined to create trophy fish production that was manifested by a large increase in legacy-class (>5.9 kg) ShareLunker fish caught by anglers during this period of desired SAV coverage. Of the 21 legacy-sized largemouth bass caught in Lake Austin and donated to the program since 1994, 18 were caught while hydrilla was present. Lake Austin was nationally ranked in the top 10 bass lakes

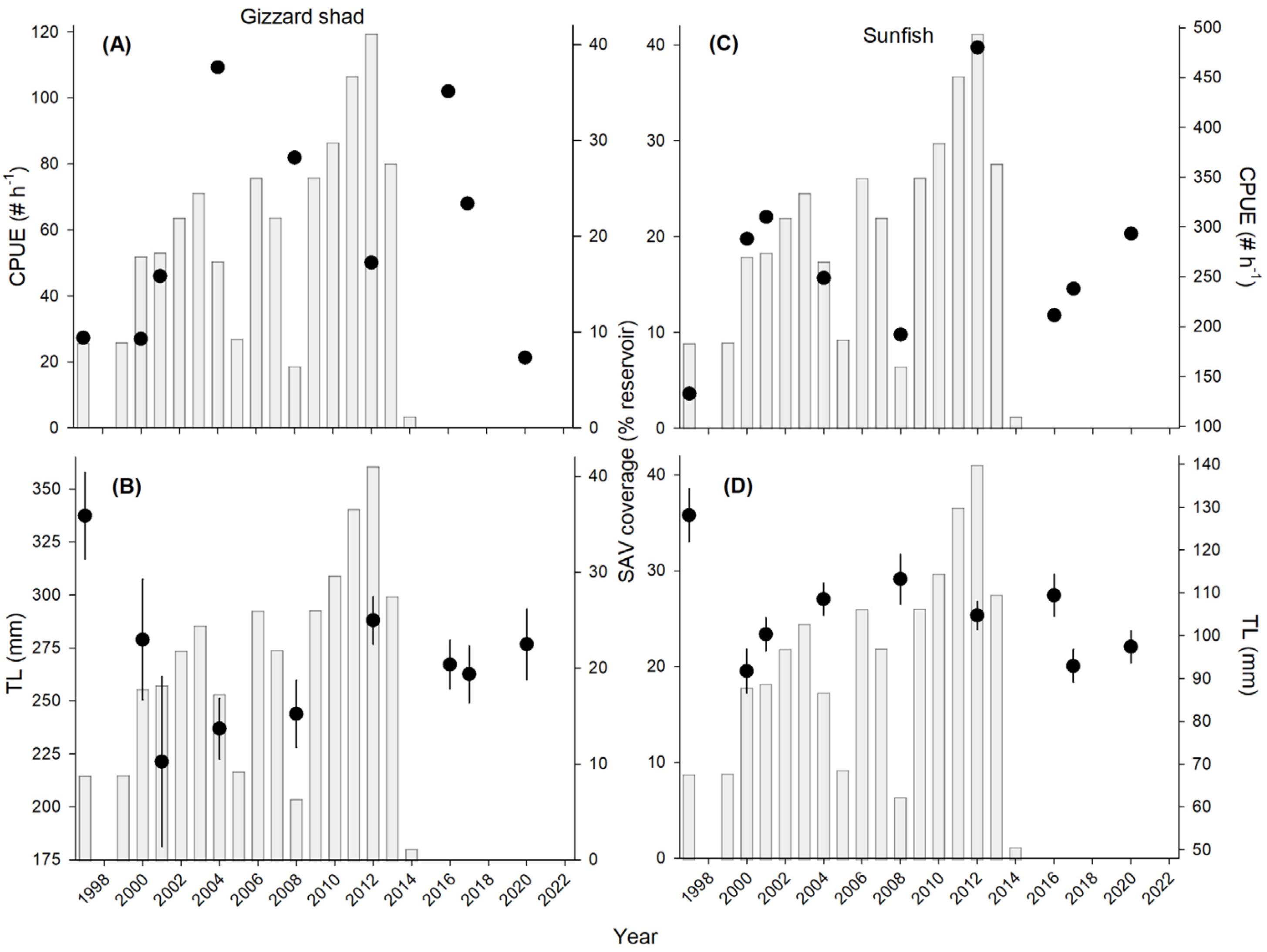

Figure 3. Temporal patterns of catch per unit effort (CPUE; fish h^{-1}) and mean ± 95% confidence error total length (TL; mm) for gizzard shad (A & B; left y-axis) and sunfish (C & D; right y-axis), respectively. Annual average submerged aquatic vegetation (SAV) coverage (gray bars; % total reservoir area; middle y-axes) also shown.

in the nation for two consecutive years by Bassmaster Magazine. Although anglers still report trophy-size catches (i.e., 3.6–5.5 kg) from Lake Austin, no legacy-size fish were reported caught again in the reservoir until 2022. In the short-term, losing areas to target concentrated populations of largemouth bass as habitat becomes scarcer makes catching quality fish more difficult (Sammons et al. 2003). However, long-term habitat depletion, caused by extended herbivory pressure, would be expected to hinder trophy fish production potential.

Although negative impacts to largemouth bass condition were evident after 2014, our results suggest that W_r also declined between 2011 and 2013, when hydrilla coverage was greatest (30–40%; De Jesus and Farooqi 2017). Similarly, excessive growth of hydrilla in the Spring Creek arm of Lake Seminole negatively affected largemouth bass W_r relative to other sections where hydrilla extent was lower (Brown and Maceina 2002). The temporary W_r decline in Lake Austin could have been due to the dense topped-out hydrilla stands impeding largemouth bass foraging success (Colle and Shireman 1980, Savino and Stein 1982). Thus, there is likely an upper limit of SAV extent that maximizes benefits to largemouth bass. Above these limits, SAV coverage should be controlled for best largemouth bass performance.

The largemouth bass condition declines throughout the study likely reflecting the well-documented negative effects of reservoir aging and residential development on largemouth bass populations (Miranda et al. 2010, Gaeta et al. 2011, Miranda and Krogman 2015). The sudden loss of SAV (and especially hydrilla) after 2013 appears to have amplified the natural aging effects. The PSD of nearly 60 coupled with the apparent declines in CPUE of smaller largemouth bass after 2013 could indicate recruitment issues to adult bass due to the loss of hydrilla (Bettoli et al. 1993, Webb et al. 1994). Growth of young largemouth bass to harvest sized adults also appeared to decline as noted by the increase in age of bass >356 mm TL.

The influence of SAV loss did not appear to negatively affect the forage fish captured in Lake Austin, as gizzard shad and sunfish population CPUE and lengths did not significantly decline after the loss of SAV. In fact, TL of both groups and sunfish CPUE appeared to increase through time. In contrast, the sunfish population in Lake Conroe, Texas, collapsed after the loss of hydrilla due to grass carp stocking (Bettoli et al. 1993). However, the infrequency of sampling may be obfuscating actual population changes and patterns. Survey results did suggest the Lake Austin sunfish population overall is dominated by small fish (<150 mm TL), which may indicate resource limitations (Garvey et al. 2002, Aday et al. 2005). Small sunfish can be less optimal prey items for adult largemouth bass (Blackwell et al. 2000). Additionally, few gizzard shad that were caught would be susceptible to largemouth bass predation based on the observed IOV (DiCenzo et al. 1996). Threadfin shad (*D. petenense*) also are common in Lake Austin and an important prey option for largemouth bass. However, few threadfin shad and small gizzard shad were netted during surveys, contributing a possible bias in reported IOV values, as well as inhibiting our ability to quantify any changes in these potentially significant prey resources.

Management Implications

This study has documented that concomitant with the loss of SAV, largemouth bass densities and body condition can be negatively impacted. Prior to 2013, a robust trophy fishery was maintained alongside the active SAV management strategy sustaining a plant assemblage within a desired range of 10–30% SAV coverage, similar to recommendations for other southern U.S. reservoirs (Brown and Maceina 2002, Gilroy 2005, Bonvechio and Bonvechio 2006, Chilton and Magnelia 2008). A trophy largemouth bass fishery is a desired final management goal for many southern U.S. reservoirs, and SAV plays a critical supporting role in meeting this outcome. While primary reservoir operations will often constrain management efforts, controlling authorities should always consider the multiuse aspect of reservoir systems, including economically important fisheries (Miranda 1996).

This study also highlights though the long-term difficulties managing an aggressive non-native aquatic plant in the face of stochastic, uncontrollable environmental conditions and competing municipal and recreational reservoir uses. Interannual density and coverage of hydrilla are sensitive to reservoir flow rates (Sammons et al. 2005, Shivers et al. 2018) which dramatically declined through Lake Austin during the drought. Conditions favorable for rapid hydrilla expansion could become more frequent, as climate projections suggest increased frequency and duration of drought conditions (Nielsen-Gammon et al. 2020). Large-scale harvesting or herbicide treatments are not feasible in Lake Austin because of its use for municipal drinking water, thus future hydrilla control will likely involve triploid grass carp stockings. Future management of habitat and fisheries in Lake Austin should learn and adapt from past strategy implementation and system responses. For example, future SAV extent determinations and control efforts should incorporate volumetric assessments to supplement areal coverage when determining the effects of stocked triploid grass carp densities to better inform decisions about supplemental stockings of these fish. Diminishing vertical densities (biomass) of hydrilla observed during surveys in 2012 suggested grass carp had started to widely reduce SAV biomass which should have discouraged additional stocking. Unfortunately, only the areal coverage of hydrilla was used during the planning of continued stocking, leading to overstocking.

Until recently, the abundance of grass carp combined with a return to normal hydrologic management in 2015 continued to suppress SAV growth outside of herbivore exclusion pens meant to serve as founder colonies for plant re-establishment (Bellinger and Schad 2019). However, abundant patches of SAV, comprised primarily of Eurasian watermilfoil and southern naiad (*Najas guadalupensis*), were finally observed in 2022. This is presumably due to triploid grass carp densities declining low enough to allow plants to begin regrowing. Beyond responsible SAV management to prevent another decade of SAV absence, riparian trees, shoreline vegetation, and CWH should be preserved and enhanced to the greatest extent possible to improve ecological conditions that will also bolster the largemouth bass fishery. Structure and habitat could be preserved or enhanced with incentives, development regulations, active habitat restoration, and installation of littoral habitat and living shorelines to help slow the natural reservoir aging process. Finally, history dictates that a collaborative management approach amongst stakeholders is crucial toward understanding and balancing the needs and desires of all interest groups (Chilton et al. 2008).

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Dynamics and Economic Contribution of Large Bass Tournaments at Lake Fork Reservoir, Texas

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Abstract: An economic valuation of the recreational sport fishery of Lake Fork in northeast Texas was completed in 2014 and 2015, finding that angler direct expenditures totaled US$18.8 million annually on fishing trips to the reservoir. Although some largemouth bass (*Micropterus salmoides*) tournament anglers were included in that study, it did not assess economic impacts of six large (>200 participants) tournaments during the study period. Since 2006, largemouth bass tournament effort at Lake Fork has generally increased to comprise half of all fishing activity in the reservoir and is currently believed to account for most of the Lake Fork sport fishery's economic value. This is despite supporting a renowned trophy fishery for largemouth bass managed by a highly restrictive slot-length limit that makes it difficult to conduct tournaments using traditional formats. To estimate economic contribution of large tournaments, we surveyed anglers from six of the largest events at Lake Fork between July 2015 and June 2016. A total of 7923 anglers participated in these tournaments, resulting in $4.7 million in direct expenditures and an overall economic value of $5.7 million. Understanding the economics of tournaments is important to fisheries managers, businesses, and local economic development groups engaging in decisions that may impact tournament angling. This study found that substantial tournament activity and associated economic benefit still occurs at Lake Fork despite the restrictive slot-length limit.

Key words: tournament angling, survey, expenditures, largemouth bass

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Anglers contribute millions of dollars in annual expenditures to use a freshwater fishery (Anderson et al. 1986, Martin 1987, Schorr et al. 1995). These fishing expenditures support local and regional businesses, creating a source of personal income and jobs (Schorr et al. 1995, Hunt et al. 1996). Because fishery management decisions often include consideration of the economic impact of a fishery, economic valuation of a fishery is important to protect or enhance these resources (Schorr et al. 1995).

An economic valuation of the recreational sport fishery of Lake Fork, Texas, was completed in 2014 and 2015 and found that anglers spent US$18.8 million annually on fishing trips to the reservoir (Hunt and Parker 2016). Tournament effort accounted for 42% of all angler effort during the 36-day creel survey when contact information was collected, so some largemouth bass (*Micropterus salmoides*) tournament anglers were encountered and included in the study. However, the random study design resulted in the omission of six large tournaments held annually at Lake Fork. Despite their omission from the 2014 and 2015 economic study, these large events were believed to contribute significantly to the overall local and regional economic value of the Lake Fork fishery. A similar economic study at Sam Rayburn Reservoir, Texas, found that black bass tournament angling accounted for two-thirds of the total economic value of the Sam Rayburn fishery in 2008 (Driscoll and Myers 2013). Lake Fork likely hosts a fraction of the 400+ tournaments held annually at Sam Rayburn Reservoir, due to its smaller relative size and restrictive regulation for largemouth bass; however, we identified 63 advertised events held at Lake Fork during the 2014–2015 economic study. Taking into consideration unadvertised small club tournaments (≤20 participants), it is likely that well over 100 competitive angling events for largemouth bass occur annually at Lake Fork. In addition to thousands of tournament participants, these participants also bring additional non-participants (family/friends) to the area who contribute to the local economy by shopping and other leisure activities.

Restrictive regulations, like the 406–610-mm slot-length limit at Lake Fork, are generally believed to limit competitive angling activity because they prohibit anglers from temporarily retaining bass in size ranges desirable for potential prizes (Dotson et al. 2013, Driscoll and Myers 2013, Maahs et al. 2022). However, tournament fishing effort has followed an increasing trend at Lake Fork since it was first estimated during annual surveys in 2005 (Figure 1), except for 2020 when the Covid-19 pandemic forced

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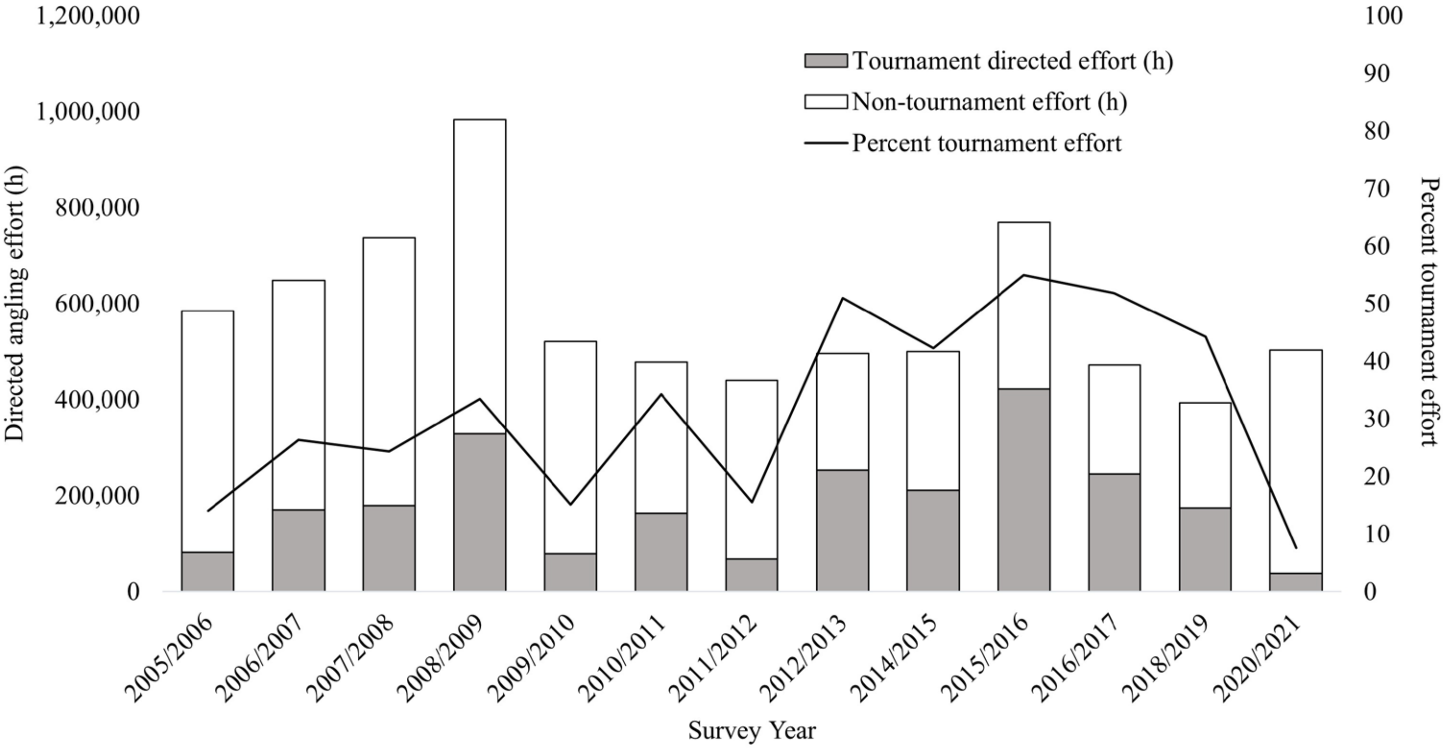

Figure 1. Creel estimates of tournament and non-tournament fishing effort (h) and percentage of total effort for largemouth bass at Lake Fork Reservoir, Texas, 2005–2021 (Norman et al. 2022). Survey period was 1 June through 31 May each year.

the cancellation of most organized events (Norman et al. 2022). Tournament frequency also generally increased throughout Texas by greater than 40% between 2005 and 2013 (Driscoll et al. 2012). At Lake Fork, tournament effort exceeded non-tournament effort for the first time in 2012 and 2013, accounting for just over half (51%) of all largemouth bass angling effort (Storey 2016). Because many tournament participants were randomly encountered and included in the 2014 and 2015 economic study, the majority of the $18.8 million in direct angler expenditures estimated by that study can likely be attributed to tournament anglers. However, creel surveys were routinely avoided during the largest annual tournaments (>200 participants) and were excluded from this valuation, limiting understanding of the impacts of these large events. Therefore, the objective of this study was to evaluate the relative economic contribution of six large bass tournaments at Lake Fork in 2015 and 2016.

Methods

Study Area

Lake Fork is a 10,862-ha reservoir on Lake Fork Creek and Caney Creek, tributaries of the Sabine River, near Quitman, Texas. The reservoir's primary uses include municipal water supply and recreation, with largemouth bass as a major sport fish. Slot-length limits were initiated for largemouth bass starting in 1985, and the 406–610-mm slot-length limit has been in place since 2000 (Norman et al. 2022).

Tournaments

Of the six large tournaments at Lake Fork in 2015 and 2016 evaluated in this study, four exhibited an hourly prize format, offering prizes for the heaviest fish weighed in each hour (Sealy Big Bass Splash [BBS], Berkley Big Bass [BBB], Legend of Lake Fork [LLF], and Skeeter Owners [SKO]; Table 1). These tournaments were individual events held over a two to three-day period. The other two events, the Mad Dog Moore (MDM) and Bass Champs North (BCN) tournaments, offered prizes for the heaviest daily bag limit of five largemouth bass and additional prizes for heaviest bass caught in a single day (Table 1). These tournaments were two-person team events, and each lasted only one day. Participants per tournament ranged 336–2367 across the six tournaments.

Survey Administration

Prior to each tournament, tournament organizers were solicited to obtain participant contact information. Organizers of the

Table 1. Tournament details for six large tournaments held on Lake Fork Reservoir, Texas, in 2015–2016. Prize amounts in US$.

Tournament	Dates	Format	Duration (Days)	# of participants	Top prize distributed
Mad Dog Moore (MDM)	12 September 2015	5 fish, big fish pot	1	336	$5100
Sealy Big Bass Splash (BBS)	18–20 September 2015	hourly big bass	3	2367	$7000 + truck & boat
Berkley Big Bass (BBB)	17–18 October 2015	hourly big bass	2	1136	$1000 + boat
Bass Champs North (BCN)	27 February 2016	5 fish, big fish pot	1	667	$28,000
Legend of Lake Fork (LLF)	13 May 2016	hourly big bass	3	1227	$500 +boat
Skeeter Owners (SKO)	9 June 2016	hourly big bass	2	2190	$700 + boat

MDM tournament provided names and addresses for all participants following the event. The organizer for the LLF tournament required us to collect contact information directly from participants at boat access sites during the event. When we obtained contact information for MDM and LLF events, participants were randomly selected to receive a survey using a random number generator in Microsoft Excel (Microsoft Corp, Redmond, Washington). Organizers of the other four tournaments sought to maintain participant confidentiality, so hard copies of our survey instrument and materials were provided directly to tournament organizers to conduct in-house mailings and we requested that recipients be randomly selected. We were unable to quantify undeliverable surveys returned to tournament organizers. For all six events, surveys were distributed to at least 10% of the participants in each event or a minimum of 100 for events with less than 1000 participants. Because participant numbers were not available prior to each tournament, the number of surveys provided to organizers was based on the number of participants of each tournament the prior year.

Surveys were distributed by mail or email as close to the event date (within one month) as possible to reduce recall bias (Connelly et al. 2000). Anglers were instructed to complete the questionnaire regarding the tournament event specified on the survey. Mailed surveys included a postage-paid return envelope along with a weblink to an online version of our survey hosted on SelectSurvey.net to increase response rate. A unique code including the tournament date was assigned to each survey to track each participant's response method. Due to logistics of distribution by tournament organizers, we did not attempt to track individual participation and survey response from more than one event. If a respondent received and submitted a survey response from more than one event it was considered a separate trip and analyzed as a unique response.

In addition to mailed surveys, participants in two of the six tournaments received emailed surveys. Participants of the BBS tournament who did not provide an email address during event registration ($n = 127$) received a mailed survey, and an additional 1607 participants received an email invitation with a link to our online survey. Participants of the LLF tournament, contacted in person at boater access sites, were given the opportunity to provide a mailing address ($n = 68$) or an email address ($n = 33$) and surveys were distributed according to participants' preferences.

Thank you/reminder postcards were mailed to participants of the MDM Bass Tournament and the LLF tournament using contact information obtained for these participants. We received only one undeliverable mail survey each for the MDM and LLF tournament and our response rate was adjusted. To reduce difficulty and workload for organizers conducting direct mailings, thank you/reminder postcards were not mailed to participants of those four events.

Survey Questions and Analyses

Our survey instrument consisted of questions concerning general characteristics and party expenditures for 13 expense categories of participant's primary tournament trip and separate practice trips (Appendix 1). Tournament practice or "pre-fishing" is common among tournament anglers and was defined as a separate angling trip to the reservoir, completed before an upcoming event. Mean party size (people per vehicle) and trip length (days) were derived from questionnaire return data. In addition to questions about expenditures, we also asked anglers to report information about the number and sizes of fish caught and retained for tournament weigh-ins to better understand management implications and angler motivations.

Expenditures per angler were computed for each tournament separately using data from returned questionnaires. Expenses in each category (lodging, fuel, meals, etc.) were summed for primary tournament trips and divided by the number of tournament participants in each party to estimate mean trip expenditures per angler. Total direct expenditures were estimated by multiplying mean total expenditures per tournament angler by the total number of tournament anglers registered for each event. We assumed the proportion of respondents who reported taking a separate practice trip was equal to the proportion of total tournament participants taking a practice trip. Therefore, practice trip expenditures were estimated by multiplying mean practice trip expenditures per angler by the estimated number of tournament participants taking a practice trip. Total expenditures by category were estimated by calculating the proportion of expenditures reported in each category multiplied by the total estimated tournament expenditures for primary and practice trips. Expenditures were estimated by trip type (event and practice trip), and residency location. Residency locations were local (within 56.3 km [35 miles] of Lake Fork), non-local (elsewhere in Texas), and out-of-state.

We also determined anglers' willingness to pay (WTP) above current trip costs (consumer surplus, CS) which was used to estimate the economic value of each tournament. The online survey option prevented us disseminating and randomly determined bid values to each respondent and using these responses to estimate WTP (Loomis 2006). Therefore, we estimated consumer surplus by using median values determined from an open-ended contingency valuation for each event (Kealy and Turner 1993). Typically, economic value of recreational angling is defined as the total value above direct expenditures that anglers are willing to pay (Steinback 1999). Therefore, total direct expenditures and total consumer surplus were summed to estimate total economic value of each event.

A Shapiro-Wilk test for normality was performed on mean daily and total expenditures and estimates and associated relative standard errors (RSEs) were estimated from $\log_{10}$-transformed data (Toivonen et al. 2004, Oh and Ditton 2008, Wilson 2018). A one-way ANOVA and Tukey's multiple comparison were performed on transformed data to evaluate differences in expenditures among tournaments and angler type (local, non-local, and out-of-state). All statistical tests and analysis were performed using JMP (SAS Institute Inc. 2014), with $a = 0.05$ to assess significance. Relative standard errors were calculated for base-level estimates on raw questionnaire data (e.g., mean party size, mean trip length, catch rates).

Results

Response

A total of 2470 mailed and emailed surveys were distributed to tournament participants, and we received 555 returned surveys for an overall adjusted response rate of 22%. Fourteen email surveys and two mail surveys were returned as undeliverable from addresses provided to us by tournament participants or organizers. Response rates for individual tournaments ranged from 20% to 37% (Table 2). Forty-two percent of LLF Tournament participants who provided an email address completed our online survey, which was the highest response rate in the study.

Tournament participants from 16 U.S. states responded to our survey (Figure 2). For the hourly big-bass tournaments, the proportion of out-of-state respondents ranged 8–57%. No surveys were returned by out-of-state participants in the two tournaments without hourly prize formats (MDM and BCN), and we only initially received two out-of-state addresses for MDM participants from the tournament director. Overall, 21% of respondents were from out-of-state, but most respondents (66%) were non-local Texans. Tournament participants from 54 of 254 Texas counties (21%) were represented in our survey. Local anglers accounted for just 13% of tournament participants.

Tournament Participation and Characteristics

Collectively, 7923 anglers participated in these six tournaments. Each of the hourly big bass tournaments registered more than 1000 participants (Table 1). Anglers fishing in these tournaments were often accompanied by family or friends who did not participate in the tournaments, comprising 7–24% (mean 22%) of total party size. The primary tournament trip lasted an average of 5.7 days (RSE = 7) for out-of-state participants, whereas those of non-local Texans averaged 3.5 days (RSE = 3), and those of local participants lasted 3.1 days (RSE = 8).

Table 2. Number of distributed surveys and response rates by mode for six large tournaments held on Lake Fork Reservoir, Texas, in 2015–2016.

	Mail					Email				
Tournament[a]	**Distributed**	**Returned by mail**	**Completed online survey**	**Undeliverable**	**Response rate (%)**	**Distributed**	**Completed online survey**	**Undeliverable**	**Response rate (%)**	**Overall response rate (%)**
MDM	172	51	8	1	34	0				34
BBS	127	28	2	–[b]	24	1607	312	7	20	20
BBB	114	25	2	–[b]	24	0				24
BCN	150	28	2	–[b]	20	0				20
LLF	68	22	1	1	34	33	11	7	42	37
SKO	199	59	4	–[b]	32	0				32

a. MDM = Mad Dog Moore; BBS = Big Bass Splash; BBB = Berkley Big Bass; BCN = Bass Champs North; LLF = Legend of Lake Fork; SKO = Skeeter Owners.

b. Mailings returned to tournament organizers as undeliverable were non-reported or were unconfirmed.

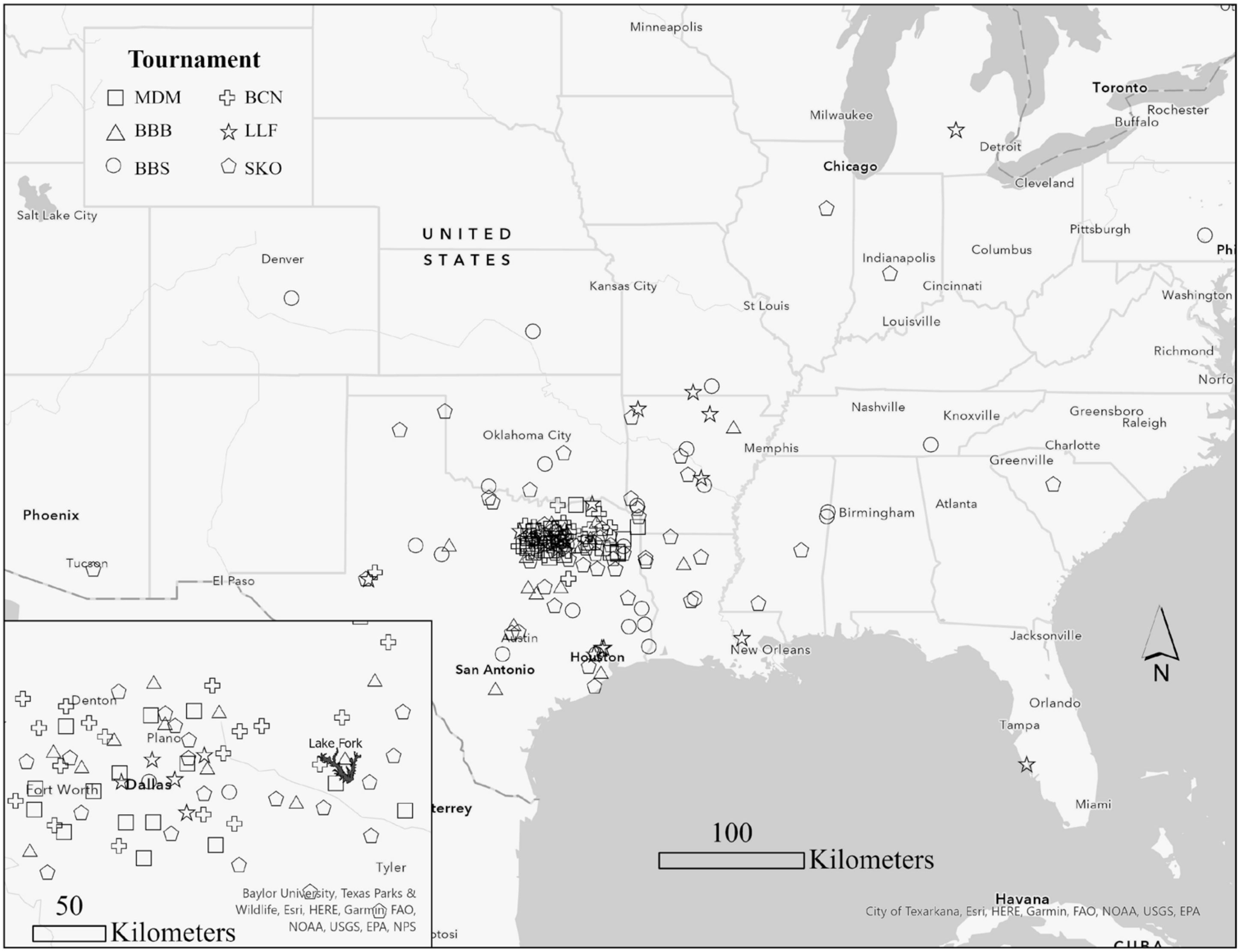

Figure 2. Map of home residence for mail survey respondents from six large tournaments held on Lake Fork Reservoir, Texas, in 2015–2016 ($n = 212$). Tournaments included Mad Dog Moore (MDM), Big Bass Splash (BBS), Berkley Big Bass (BBB), Bass Champs North (BCN), Legend of Lake Fork (LLF), and Skeeter Owners (SKO).

Anglers fishing the two 5-fish format tournaments reported catching an average of 15.5 (RSE = 17) and 8.1 (RSE = 30) bass per team, but only brought an average of 1.7 (RSE = 15) and 1.1 (RSE = 32) bass to the weigh-in. Just 13% of MDM survey respondents reported bringing a bag limit of five fish to the weigh-in, and no respondents of the BCN tournament retained five fish. However, official tournament results indicated that 37% of MDM teams (Mad Dog Moore 2015) and 16% of BCN teams weighed in five bass during the tournament (Bass Champs 2016). No largemouth bass over the slot limit were reported caught by survey respondents for either tournament, and just 12% and 22% of bass reported caught were within the slot. One largemouth bass (3.95 kg) above the slot limit was included in the winning team's bag at the MDM tournament, and two largemouth bass (4.89 and 4.21 kg) above the slot limit were weighed during the BCN tournament. Participants of hourly big-bass format tournaments reported catching an average of 5.3 (RSE = 8) largemouth bass per angler per day during the four events, and 2% of those participants reported catching a bass over the slot limit. Only seven respondents (1%) from all events reported harvesting a fish after a tournament.

Expenditures

Overall, the six events resulted in $4.7 million in direct expenditures, of which $3.3 million (70%) were spent in the local area (Table 3). The BBS tournament accounted for more than a third (35%) of this value ($1.7 million). A small proportion of overall

Table 3. Estimated total direct expenditures (US$ spent) of tournament anglers at six large tournaments held on Lake Fork Reservoir, Texas, in 2015–2016. Relative standard errors are in parentheses. Dashes indicate associated expenditures were not reported.

	Primary trip				Practice trip			
Tournament[a]	**Local**[b]	**Non-local, Texas**	**Outside Texas**	**Total**	**Local**	**Non-local, Texas**	**Outside Texas**	**Total**
MDM	$85,750 (12)	$17,018 (31)	–	$102,768 (10)	$20,442 (20)	$3121 (40)	–	$23,563 (21)
BBS	$1,049,984 (5)	$321,214 (10)	$81,767 (11)	$1,452,965 (4)	$163,020(12)	$49,322 (24)	$2407 (22)	$214,749 (4)
BBB	$328,929 (17)	$125,448 (35)	$4799 (50)	$459,177 (12)	$27,055 (41)	$26,237 (37)	–	$53,292 (42)
BCN	$118,415 (21)	$63,671 (23)	$17,043 (25)	$199,129 (11)	$42,038 (29)	$35,191 (43)	–	$77,229 (23)
LLF	$576,253 (16)	$337,163 (30)	$32,162 (30)	$945,578 (15)	$28,759 (75)	$9077 (100)	–	$37,836 (54)
SKO	$786,895 (9)	$218,715 (23)	$65,228 (24)	$1,070,838 (9)	$43,989 (30)	$16,046 (35)	$1519 (100)	$61,554 (25)
Total	$2,946,226 (10)	$1,083,230 (23)	$200,998 (20)	$4,230,455 (9)	$325,303 (25)	$138,994 (38)	$3927 (52)	$468,223 (19)

a. MDM = Mad Dog Moore; BBS = Big Bass Splash; BBB = Berkley Big Bass; BCN = Bass Champs North; LLF = Legend of Lake Fork; SKO = Skeeter Owners.
b. Local: spent within 56.3 km (35 miles) of Lake Fork.

expenditures (4%) were encumbered outside of Texas. Median consumer surplus (CS) ranged from $50 to $200 per tournament angler across tournaments. Estimated CS for the six events totaled $955,000, resulting in an overall economic value of $5.7 million.

Overall, approximately a third (34%) of respondents reported taking a separate practice trip prior to the primary tournament event, which accounted for approximately 10% of total direct expenditures (Table 3). Practice trips were more common and thus accounted for a greater percentage of overall expenditures at events with a 5-fish format such as the MDM tournament (19%) and the BCN tournament (28%); roughly half (48% and 51%, respectively) of the participants of these two events reported taking a separate practice trip prior to the event.

Mean daily expenditures ($154, RSE = 3) for angler's primary trip ranged from $134 (RSE = 7) for the SKO tournament to $205 (RSE = 10) for the LLF tournament. Mean daily expenditures were significantly different among tournaments ($F_{5,\,549} = 2.6$, $P = 0.02$); however, pairwise comparisons indicated only LLF daily expenditures were significantly greater than the SKO event ($P = 0.02$; Figure 3) which attracted a greater number of local participants. Local participants spent less ($102, RSE = 9) than non-local Texans ($152, RSE = 3) and out-of-state participants ($158, RSE = 6; $F_{2,\,552} = 5.9$, $P < 0.01$). Daily expenditures by non-local and out-of-state participants were similar ($P = 0.9$).

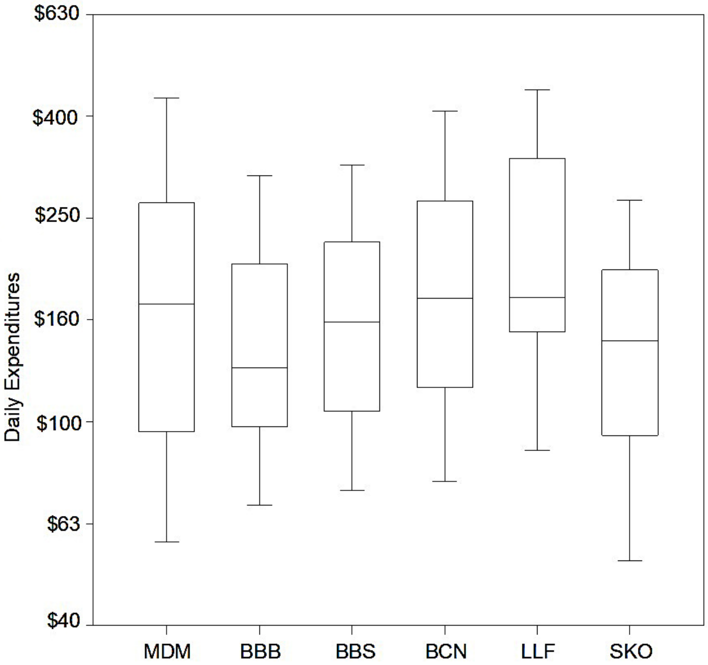

Figure 3. Box plot for daily expenditures (US$) by tournament at Lake Fork Reservoir, Texas, in 2015–2016, including Mad Dog Moore (MDM), Big Bass Splash (BBS), Berkley Big Bass (BBB), Bass Champs North (BCN), Legend of Lake Fork (LLF), and Skeeter Owners (SKO).

Tournament entry fees was the largest individual expense category for all six tournaments, accounting for 28–50% of mean daily expenditures (Table 4). Vehicle and boat fuels (21%), lodging (17.4%), and meals and groceries (17%) accounted for an additional 55% of each party's total direct expenditures associated with primary tournament trips. Bait and tackle accounted for just under 7% of angler expenditures on average. Entry fees and fuel costs each accounted for just over $1 million in direct expenditures associated with the six events, followed closely by lodging ($0.8 million). When combined, $0.8 million was spent on restaurant meals and groceries, and approximately $0.4 million was spent for bait and tackle purchased in association with tournament trips. Participants also spent nearly $0.1 million for fishing licenses and $0.2 million was spent outside of Texas (Table 4).

Table 4. Total direct angling expenditures (US$) by expense category for each tournament primary and practice trip for six large tournaments held on Lake Fork Reservoir, Texas, in 2015–2016. Relative standard errors are in parentheses, and dashes indicate associated expenditures were not reported by survey respondents.

Expense type	MDM[a]	BBB	BBS	BCN	LLF	SKO	Total
Tournament fees	$36,322 (9)	$162,416 (10)	$377,073 (3)	$84,037 (5)	$218,437 (8)	$219,409 (6)	$1,097,694 (6)
Fuel (Auto/Boat)	$36,100 (11)	$144,153 (15)	$351,249 (6)	$71,025 (11)	$239,637 (25)	$234,589 (8)	$1,076,753 (12)
Lodging	$11,727 (23)	$59,773 (27)	$325,127 (6)	$35,114 (23)	$185,115 (15)	$211,737 (15)	$828,592 (13)
Restaurant meals	$12,274 (17)	$53,747 (14)	$170,600 (67)	$30,335 (20)	$97,442 (26)	$125,522 (14)	$489,921 (14)
Groceries	$10,339 (16)	$34,030 (28)	$109,600 (6)	$10,811 (19)	$73,873 (28)	$120,930 (14)	$359,583 (16)
Bait and tackle	$12,391 (21)	$33,303 (21)	$111,328 (9)	$23,249 (39)	$91,615 (35)	$75,937 (19)	$347,823 (22)
Fishing license	$4603 (25)	$7624 (41)	$37,736 (14)	$1054 (56)	$21,633 (23)	$21,212 (23)	$93,862 (21)
Launch fees	$853 (22)	$2935 (37)	$7489 (13)	$785 (47)	$3631 (41)	$3171 (25)	$18,865 (26)
Other transportation	–	–	$6046 (47)	–	–	–	$6046 (47)
Fishing guide	$162 (100)	–	$35,560 (24)	–	$6917 (100)	$25,804 (55)	$68,442 (44)
Boat rental	$23 (100)	–	$5585 (41)	$1874 (72)	$1729 (100)	–	$9211 (58)
Other	$1539 (41)	$9688 (78)	$45,876 (21)	$1031 (91)	$11,223 (80)	$27,335 (37)	$96,691 (39)
Out of state	–	$4799 (80)	$84,174 (13)	$17,043 (60)	$32,162 (51)	$66,747 (38)	$204,925 (33)

a. MDM = Mad Dog Moore; BBS = Big Bass Splash; BBB = Berkley Big Bass; BCN = Bass Champs North; LLF = Legend of Lake Fork; SKO = Skeeter Owners.

Discussion

Our study demonstrates that despite a highly restrictive slot limit, bass tournaments, some with unique formats, continued to be valuable additions to the state and local economies around Lake Fork. This was especially true for large tournaments with high participation, as anglers spent an estimated $4.7 million in just these six tournaments, which was 25% of the total direct annual expenditures ($18.8 million) by all anglers fishing Lake Fork the year before (Hunt and Parker 2016). The estimated economic value of these six tournaments was approximately equal to the annual estimated value of all tournaments in 2013 ($4.6 million in 2016 dollars) at Lake Guntersville, Alabama (Maceina et al. 2018). The total number of anglers fishing a total of 259 Lake Guntersville tournaments in 2013 (9035) was only slightly greater than the total number fishing just our six studied tournaments at Lake Fork. The greater number of participants attending each event and two to three-day duration of our studied events likely contributed to the greater estimated expenditures at Lake Fork.

Administration and Response

We believe our overall response rate was sufficient to precisely estimate the economic contribution of these six large annual tournaments at Lake Fork. While our levels of response resulted in acceptable levels of precision (RSE < 15) for total primary trip expenditure estimates, the precision of expenditures associated with practice trips and some expense categories could have been improved with increased survey distribution and response. Our attempt to improve response rates by offering mail recipients the option to complete the survey online resulted in limited online response and may have reduced response rates overall (Medway and Fulton 2012, Flüß et al. 2014).

Our results suggest a trade-off may exist between increasing response rate and increasing sample size depending on the method used to collect contact information. Our highest response rate (37%) from an individual tournament occurred when contact information was obtained in person at the LLF event. However, this required substantial effort yet obtained the smallest number of contacts (101) for any event. Obtaining contact information in person provided us the ability to distribute thank you/reminder cards or emails to participants, but few additional surveys were completed after follow-up correspondence, suggesting the direct contact with participants alone may have improved response rate over other events. Face-to-face survey modes are known to improve response rates over telephone or email surveys (Schonlau et al. 2002), and initial face-to-face contact has demonstrated an increased response rate for internet-based surveys as well (Cook et al. 2000, Porter and Whitcomb 2003). However, using this methodology for future surveys of tournament anglers may not be warranted if email addresses for all participants can be obtained from tournament organizers. During the BBS tournament, we received email addresses for more than 1600 participants. Although the overall response rate was only 20%, the number of usable responses was ten-fold greater than the other five tournaments without incurring any additional costs associated with mailings, staff, or travel time. Future surveys using email invitations and an online-only platform could also be conducted anonymously through tournament organizers but would require cooperation and successful distribution.

Our study also highlights that a census of tournament activity should be conducted along with future economic studies where tournament activity is suspected to account for a substantial proportion of angler effort. A similar economic study by Anderson et al. (2002) concluded that their study design did not adequately include tournament angling at Sam Rayburn Reservoir, and likely underestimated overall angler expenditures. While large tournaments can now be identified online and through public forums, robust creel surveys can also adequately encounter most of the smaller tournaments held throughout the year at a reservoir. Contact information for each tournament director and additional tournament participants can then be obtained to disseminate additional surveys to participants and obtain more accurate data on angler expenditures throughout the year (Maceina et al. 2018).

Economics

Economic dynamics of angling at Lake Fork appear to have shifted through time. Hunt and Parker (2016) reported a decline of $24 million in angling expenditures between the 1995 and 2015 economic studies, when adjusted for inflation, and attributed that to decreased visitation to Lake Fork by non-local Texans. However, angler effort estimates have varied by as much as 100% from year to year over the last two decades (Storey 2016, Norman et al. 2022). Further, respondents of our tournament study were primarily (66%) non-local Texans or from out-of-state (21%). Because creel surveys during the six tournaments we studied were not included in the 2014 and 2015 economic study (Hunt and Parker 2016), and many smaller tournaments (e.g., club, trail/series, small open) may be missed during usual roving creel surveys, we suspect many non-local visitors were missed. The estimated annual expenditures by Lake Fork anglers would likely be much greater if a census and separate analysis of tournaments was conducted like the 2008 study on Sam Rayburn Reservoir (Driscoll and Myers 2013). Although overall angling effort for largemouth bass increased by 54% between the 2014–2015 and 2015–2016 creel surveys, estimated tournament effort doubled during this period (Storey 2016). While tournament effort was not routinely documented during creel surveys at Lake Fork until 2005, the proportion of tournament anglers increased from 14% to 55% between 2005 and the time of our study (Storey 2016). Because tournament anglers spend more money per day to fish than non-tournament anglers (Driscoll and Myers 2013, McKean et al. 2014, Maceina et al. 2018), and often comprise more than 40% of total angler effort at Lake Fork, it is likely that tournament anglers and competitive events now account for most fishing associated expenditures and new monies entering the Lake Fork area.

Except for the slightly greater daily expenditures observed during the LLF tournament, daily expenditures were similar among tournaments. The proportion of out-of-state anglers participating in each event varied by tournament, and out-of-state anglers spent nearly twice as long and twice as much money on their trips to Lake Fork than did either local or non-local anglers. While we only received returned surveys from six states for the LLF, out-of-state participants represented almost half (48%) of our total response for this tournament. Anglers from 19 states registered for the 2016 LLF tournament (Hampton 2016), and overall, 20% of respondents traveled from out-of-state to fish the big-bass tournaments included in our study. Almost all (95%) monies spent outside of the state were associated with each angler's primary trip, suggesting that few anglers traveling from other states conducted a separate practice trip prior to a tournament event.

Fuels (vehicle and boat) and lodging composed a slightly higher proportion of overall expenses (49%) at Lake Guntersville (Maceina et al. 2018) and Sam Rayburn Reservoir (46%) tournaments (Driscoll and Myers 2013) than the tournaments in our study (41%). However, the relative short travel time to the Dallas-Fort Worth metroplex, where most participants lived, may have reduced lodging and travel costs compared to other studies. Tournament entry fees also comprised a considerable portion of angler expenditures and although the fate of entry fees varies across events, typically most fees collected are redistributed among tournament anglers as prizes or cover hosting expenses, with the remaining monies being profit for tournament organizers. Even when entry fees were not included, surveyed tournament anglers still spent more than twice as much per day than that reported by local, non-tournament anglers in the prior year (Hunt and Parker 2016). Similarly, in 2001–2002 estimated tournament fishing at the Hudson River, New York, was valued at $423 (2016 dollars) per angler trip, compared to $104 (2016 dollars) per angler trip for other sport fishing (McKean et al. 2014). A similar study at Lake Guntersville, Alabama, found that tournament anglers spent an average of $514 (2016 dollars) per tournament in 2013 (Maceina et al. 2018), more than twice the average ($207; 2016 dollars) expenditures per visit of all bass anglers in 2012 (McKee 2013). Driscoll and Myers (2013) also found that tournament anglers still spent more than non-tournament anglers and contributed most of the annual direct expenditures (69%) at Sam Rayburn Reservoir even when entry fees were excluded from economic estimates.

Non-contestants made up a significant portion of each party traveling to the Lake Fork area for tournaments and pre-event practice. It is unknown how many of these individuals also participated in fishing, or if they simply accompanied tournament participants to Lake Fork to pursue other leisure or recreational activities. While our study accounted for the total expenditures encumbered by each party, we did not attempt to estimate the specific amount attributable to non-contestants; however, that amount may be considerable. O'Keefe and Miller (2011) found that 16%

of those traveling to a single Lake Michigan tournament were non-contestants whose non-tournament activities contributed almost $600,000 of expenditures. When assessing the total economic impact of organized events, it may be important for local businesses and economic development agencies to recognize that these events typically result in considerably more people traveling to the area than the total number of contestants registered for each event. These individuals may be pursuing other activities or shopping in the local area.

Consumer surplus for tournament participants was much lower than Hunt and Parker (2016) reported in the 2014 to 2015 economic survey that included non-tournament anglers. At Sam Rayburn Reservoir, Driscoll and Myers (2013) found that non-tournament anglers suggested they would spend considerably more (91%) for their fishing than did tournament anglers (25% to 35%). This is likely because tournament anglers already spend more money than non-tournament anglers for their fishing, often traveling further distances and paying tournament fees. It is not known how our WTP estimates may have been impacted using an open-ended contingent valuation as opposed to the use of bid-value/regression analysis often used to estimate consumer surplus in similar studies; however, we found CS was in the range of that reported by Sam Rayburn tournament anglers observed by Driscoll and Myers (2013). While the use of open-ended or dichotomous-choice formats is controversial, we favored the ability to provide an online option at the time of our survey. Further, studies evaluating differences in open-ended and closed-ended contingent valuations have found either no difference between methods or that close-ended contingent valuations can result in overestimating WTP (Kealy and Turner 1993, Lunander 1998, Grutters et al. 2009).

Management Considerations

The high-value prizes offered (e.g., cash, boats, and trucks) by the largest events (>1000 participants) incentivize participation, substantially increasing the number of anglers traveling to Lake Fork for these events. Our results suggest that the proportion of survey respondents (2%) who reported catching a bass above the slot limit, and likely qualifying for a high value prize (e.g., boat or vehicle) during one of the big bass events, may be relatively high in comparison to similar public contests. The likelihood of catching a fish ≥610 mm and winning a big bass tournament might be reduced without such a restrictive regulation. Additionally, the format of big bass events has also allowed anglers to occasionally win these prizes by submitting individual sub-slot (<406 mm) bass (Sealy Outdoors 2023), which would be unlikely at reservoirs managed with minimum length limits.

Although the regulations allow the option to accommodate newer tournament formats, such as catch-weigh-release (e.g., Champions Tour, Major League Fishing, Student Angler Tournament Trail, etc.), the long-standing restrictive harvest regulation (Storey and Jubar 2008) at Lake Fork creates a unique dynamic for those anglers that participate in live weigh-in tournaments at the reservoir. Additional live weigh-in tournaments effort could increase the overall associated fishing mortality (Meals and Miranda 1994, Hysmith et al. 2013, Sylvia and Weber 2022) and ultimately reduce the incidence of catches of fish above the slot limit in successive years if anglers were allowed to retain bass currently protected by the slot limit. Further, it is unknown if the apparent increase in tournament activity at Lake Fork has been additive or has come at a cost of displacing traditional non-tournament anglers. However, Hunt and Parker (2016) noted that 52% of anglers responding to the 2014–2015 survey indicated that they try to avoid fishing during tournaments at Lake Fork. If harvest regulations were less restrictive and subsequently encouraged additional tournament activity, it is likely that the increase would result in a further reduction in non-tournament fishing effort at the reservoir. Surprisingly, many open-ended comments by survey respondents (i.e., tournament anglers) suggested that the frequency of tournaments is already too high at Lake Fork.

Local marinas and government sponsored access sites in predominately rural areas surrounding most reservoirs are rarely designed to support parking and facilities for large events such as our studied tournaments. As a result, these tournaments often result in congestion of parking areas and roadways surrounding the reservoir (Yow et al. 2008). While encouraging additional tournament activity through infrastructure improvements at Lake Fork may be controversial, such actions may be important to better accommodate large events considering the substantial economic impact to the local area. Additionally, infrastructure improvements that encourage adequate fish care during the tournament weigh-in process may help to conserve bass and preserve Lake Fork's status as a world-class trophy bass fishery.

Acknowledgments

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Appendix 1. Survey Instrument Used in this Study.

Lake Fork Reservoir
Tournament Angler Survey

Texas Parks and Wildlife Department

Funded By the Wood County Economic
Development Commission

You participated in the bass tournament indicated below at Lake Fork Reservoir. To ensure that we get the most accurate economic estimates, please answer questions 1–4 with this specific tournament in mind. For your convenience you may complete this survey online at https://www.selectsurvey.net.

Tournament Name: ____

1. How many total days did you spend on this trip to Lake Fork for this tournament? _________ Day(s)

2. Did the following people travel with you in the same vehicle to the Lake Fork tournament?

	(Circle one)	If "YES" how many people?
Spouse	Yes No	________
Children	Yes No	________
Friends/other family	Yes No	________
Other tournament anglers	Yes No	________

3. How much did your group (those traveling in your vehicle) spend on the following items on this specific Lake Fork tournament trip? Please include total expenses for your entire group, as reflected in your response to Question 2.

	Within 35 miles of Lake Fork	Elsewhere in Texas
Automobile transportation (fuel, car rental, repairs, etc.)	US$	US$
Other transportation (airplane, etc.)	US$	US$
Boat rental	US$	US$
Boat operation (fuel, oil, service, etc.)	US$	US$
Boat launch fees	US$	US$
Entrance or parking fees	US$	US$
Lodging (hotel, camp site, resort rental, etc.)	US$	US$
Restaurant meals	US$	US$
Groceries (food, drink, ice, etc.)	US$	US$
Bait and tackle (**purchased during this trip**)	US$	US$
Fishing guide fees	US$	US$
Fishing license	US$	US$
Tournament entry fee	US$	US$
Other expenses (please list: e.g. golf, shopping, etc.)	US$	US$
Total:	**US$**	**US$**
If you traveled from another state, how much did you spend **outside** Texas for this trip?		US$

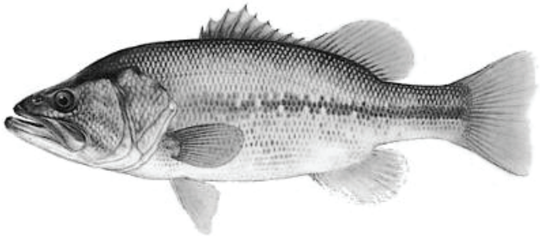
4. If the cost of goods and services were to increase so this trip cost more than it did (refer to **Total** in Question 3), how much more would you have been willing to pay rather than **NOT** have gone fishing on this trip? $_____

5. Is most of your fishing at Lake Fork **tournament angling** or **non-tournament angling**? (Circle one)

Tournament angling **Non-tournament angling**

6. How many **years** have you fished tournaments at Lake Fork;

(Number of years) of the last **5 years**? ____; of the last **10 years**? ____.



Many anglers also spend considerable time practice fishing for tournaments. For study purposes, we are defining practice fishing as days spent specifically preparing for this tournament <u>on separate trip(s) prior to your actual tournament trip</u>. To ensure that we get the most accurate economic estimates, please answer questions 7–9 with days primarily attributed to practice fishing for this specific tournament in mind. If no separate trips were taken, please skip to Question #10.

7. How many total days, **NOT** including the days you reported in Question 1, did you spend **practice** fishing at Lake Fork prior to the trip for this tournament? ____________Day(s)

8. Did the following people travel with you in the same vehicle on the **practice** days you reported in Question 7?

	(Circle one)	If "YES" how many people?
Spouse	Yes No	________
Children	Yes No	________
Friends/other family	Yes No	________
Other tournament anglers	Yes No	________

9. How much did your group (those traveling in your vehicle) spend on the following items on the **practice** days you reported in Question 7? Please include total expenses for your entire group, as reflected in your response to Question 8.

	Within 35 miles of Lake Fork	Elsewhere in Texas
Automobile transportation (fuel, car rental, repairs, etc.)	US$	US$
Other transportation (airplane, etc.)	US$	US$
Boat rental	US$	US$
Boat operation (fuel, oil, service, etc.)	US$	US$
Boat launch fees	US$	US$
Entrance or parking fees	US$	US$
Lodging (hotel, camp site, resort rental, etc.)	US$	US$
Restaurant meals	US$	US$
Groceries (food, drink, ice, etc.)	US$	US$
Bait and tackle (**purchased during this trip**)	US$	US$
Fishing guide fees	US$	US$
Fishing license	US$	US$
Other expenses (please list)	US$	US$
Total:	**US$**	**US$**
If you traveled from another state, how much did you spend outside Texas?		US$

10. If you caught any largemouth bass longer than 24 inches or greater than 7 pounds (lbs.) during this tournament, please list the approximate length and weight of those fish in inches and pounds (lbs.)

(E.g. 24.25", 8.3 lbs; or 24.25", 8 lbs. 5 oz.)

____

____

11. Not including this tournament, how many tournaments did you participate in since this time last year in:

Lake Fork Reservoir	________Number of tournaments
Freshwater elsewhere in Texas	________Number of tournaments
Freshwater outside of Texas	________Number of tournaments
Saltwater	________Number of tournaments

12. If you caught **largemouth bass** during this tournament, please list the number of fish you caught in each length category (**lengths in inches**) during this tournament:

Total number of largemouth bass **caught** in each size group:

____ <12″ ____ 12 to 16″ ____ 16 to 24″ ____ >24″

Number of largemouth bass brought to the tournament **weigh-in**:

____ < 12″ ____ 12 to 16″ ____ >24″

Number of largemouth bass **harvested** (i.e. **not released** after the tournament):

____ <12″ ____ 12 to 16″ ____ >24″

13. What steps did you use to care for fish retained in your livewell during this tournament? (Check all that apply.)

	Yes	No
Livewell chemical additives (please list):		
Aeration/recirculation		
Oxygen injection (compressed gas from a tank)		
Temperature control (ice)		
Fizzing fish (released air in swim bladder)		
Other (please list):		

14. If you have access to the internet, would you be willing to provide us with your e-mail address to receive a copy of the economic study results? Email: ______________________________________

15. Did the person to whom this survey was addressed complete the survey? (Circle one)

1) YES 2) NO

16. What is the zip code of your permanent residence? ___________

17. Please use this space to provide us with additional comments you may have: ____
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We sincerely appreciate you taking the time to complete this questionnaire. Please return the completed questionnaire in the enclosed postage-paid reply envelope to: **Texas Parks and Wildlife, Attn: Dan Bennett, 2122 Old Henderson Hwy., Tyler, TX 75707, dan.bennett@tpwd.texas.gov, 903-593-5077.**

Comparison of Two Otolith Processing Methods for Estimating Age of Silver Carp

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Abstract: Accurate age estimates are critical in the development, implementation, and assessment of silver carp (*Hypophthalmichthys molitrix*) management plans. Lapilli otoliths are the most commonly used calcified structures for silver carp age estimation, but studies on the precision of two established preparation methods [i.e., grind-and-burn (GB), thin-section (TS)] are lacking. Therefore, we assessed within-reader, between-reader, and between-method precision for 125 silver carp collected from six rivers throughout the Lower Mississippi River Basin (Arkansas, Cache, Mississippi, St. Francis, White, and Yazoo). Additionally, we compared the effort and material costs associated with each method. Overall, younger ages were estimated with the GB method (median estimated age = 6 yr, range = 3–12) than the TS method (median estimated age = 7 yr, range = 3–13). Between-method comparisons revealed low agreement (average CV = 16.40) and significant bias (Evans-Hoenig $\chi^2 = 31.81$, $P < 0.01$) between the two methods, particularly in older individuals. The TS method (average CV = 12.50) displayed similar between-reader precision to the GB method (average CV = 11.75). Younger age estimates for the GB method may be a result of misidentification of annuli near the otolith margin as both readers reported that TS otoliths offered clearer views than GB otoliths. Processing effort (TS method = 6.7 min otolith^{-1}; GB method = 4.6 min otolith^{-1}) and material costs (TS method = US\$0.37 otolith^{-1}; GB method = \$0.34 otolith^{-1}) were similar for the two methods and are likely not a factor when choosing an age estimation protocol. Our results indicate that use of the TS method for silver carp age estimation may lead to less biased age estimates, especially in established populations with greater abundances of older individuals, assuming putative additional annuli observed in thin-sections are true annuli.

Keywords: precision, lapilli, reader agreement, *Hypophthalmichthys molitrix*

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Age estimation is an essential aspect of fish population assessment with direct implications for management (Kerns and Lombardi-Carlson 2017). Fish ages estimated from calcified structures are often used to estimate population parameters such as growth and mortality, and play important roles in understanding processes such as maturation schedules (Olsen et al. 2004, Gobin et al. 2021), recruitment dynamics (Maceina 1997, Yule et al. 2008), and movement patterns (Poole and Reynolds 1996, Crozier and Hutchings 2014). Conversely, the inability to accurately estimate fish age can result in mismanagement of a fishery. For example, if ages for a population are systematically overestimated, mortality will be underestimated and may lead to incorrect management actions (Yule et al. 2008, Hamel et al. 2016). Therefore, emphasis should always be placed on obtaining accurate, precise, and unbiased age estimates before implementing management actions. This is especially challenging when age estimation procedures have not been developed for the species of interest.

Silver carp (*Hypophthalmichthys molitrix*) escaped aquaculture ponds in Arkansas during the 1970s and have invaded much of the Mississippi River Basin (Kolar et al. 2007). Resource managers are particularly concerned about silver carp due to their ability to alter aquatic communities (Sampson et al. 2009, Solomon et al. 2016, Harris et al. 2022), negatively impact native fishes (Irons et al. 2007, Pendleton et al. 2017, Chick et al. 2020), and even injure boaters (Vetter et al. 2015, Spacapan et al. 2016). Therefore, managing silver carp populations has become a high priority, primarily through targeted removal programs (Seibert et al. 2015). However, effective assessment of program outcomes relies heavily on

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population parameters calculated from age estimates. For example, if inaccurate ages lead to incorrect assumptions of life history (i.e., faster growth, higher natural mortality, lower age at maturity, higher fecundity than actually occurring), agency personnel might conclude that targeted removal would be an ineffective control strategy (Klein et al. 2023, Sammons et al. 2023) and focus their efforts elsewhere (Vander Zanden and Olden 2008).

The accuracy of silver carp age estimates remains unknown given that no structure or processing method has been validated (Spurgeon et al. 2015). Additionally, since precise age estimates can still be inaccurate (i.e., precisely wrong, or biased, sensu Campana 2001), measures of precision cannot substitute for measures of accuracy. If the accuracy of estimated ages is unknown or questionable, however, high-precision protocols are preferred over low-precision protocols (Campana et al. 1995). Seibert and Phelps (2013) found that for silver carp, lapilli otoliths provided more precise age estimates compared to postcleithra, pectoral fin rays, and vertebrae. These findings were consistent with studies of related species, such as common carp (*Cyprinus carpio*; Phelps et al. 2007) and numerous other cyprinids (Hawkins et al. 2004, Quist et al. 2007, Phelps et al. 2017). The literature, however, highlights two different otolith processing techniques commonly used for silver carp age estimation – the “thin-section” method (TS method; Hayer et al. 2014, Sullivan et al. 2020, Werner et al. 2022) and the “grind-and-burn” method (GB method; Seibert et al. 2015, Ridgeway and Bettoli 2017, Tripp and Phelps 2018). Comparisons of these two processing methods have shown differences in precision for other species (e.g., Stransky et al. 2005, Edwards et al. 2011, Sakaris and Bonvechio 2020, McKeefry et al. 2023), but this has not been evaluated for silver carp.

Because precise, unbiased age estimates are needed to accurately calculate many population parameters, our first objective was to compare the precision of two processing methods for silver carp otoliths and test for bias within the age estimates. For this objective, precision was defined as the repeatability of an age estimate. Because true bias (i.e., systematic difference in age estimate and true age) could not be determined, bias was defined as a systematic difference between age estimates from the two methods. Given that precision depends not only on the quality of the procedure (i.e., the readability of annual zonation patterns) but also the consistency of the readers, between- and within-reader precision also were compared. Because resource managers often must consider cost and effort associated with age estimation, our second objective was to compare the effort taken to process a set of 10 otoliths and the costs of consumable materials for each processing method.

Methods

Fish Collection

During July–September 2019, silver carp were collected throughout the Lower Mississippi River Basin using daytime, boat-mounted electrofishing (Smith-Root, Vancouver, Washington; pulsed DC, 500V, 60 pulses per second). Rivers sampled included the Arkansas, Cache, Mississippi, St. Francis, White, and Yazoo rivers. Site selection was based on macrohabitat availability (e.g., river side-channels, sandbars, and backwater areas; DeGrandchamp et al. 2008) that were situated near river access sites. Upon capture, total length (TL, mm), weight (g), and sex were recorded for each specimen. Lapilli otoliths were extracted by incision between the preopercle and opercle bones using a reciprocating saw and forceps (Seibert and Phelps 2013). Upon extraction, otoliths were thoroughly cleaned using water and paper towels to remove any residual tissue (Secor et al. 1992) and placed into coin envelopes. Otoliths were allowed to air dry for a minimum of 1 wk before processing (Long and Grabowski 2017). Fish collection was performed under University of Arkansas at Pine Bluff Institutional Animal Care and Use Committee guidelines (id# UAPB2018-05).

Otolith Processing

One otolith from each pair was arbitrarily selected and processed via the GB method as described in Seibert and Phelps (2013). Each reader processed approximately half of the GB otoliths. The anterior side of each otolith was ground using a sequential series of wetted 600-grit and 2,000-grit sandpaper to reveal the nucleus. Otoliths were polished using diamond lapping film to increase clarity. After grinding and polishing, otoliths were heated ground side (i.e., anterior side) down on a hotplate to increase zonation of annuli (Seibert and Phelps 2013, Long and Grabowski 2017). A hotplate was used instead of an open flame to reduce the likelihood of “over-burnt” otoliths (McKeefry et al. 2023). After heating, each otolith was placed posterior side down in putty and submerged in immersion oil (Resolve™ low viscosity immersion oil, Richard Allan Scientific, Kalamazoo, Michigan). A dissecting microscope (Leica MZ95, Leica Microsystems GmbH, Wetzlar, Germany) was used to view GB otoliths using reflected light via a fiber-optic light cable. The orientation of the otolith and the fiber-optic light cable were adjusted for each otolith to optimize readability. Each otolith was imaged using a camera affixed to the microscope and interfaced to a desktop computer (resolution: 1280 × 1080 pixels; SPOT Idea CMOS Microscope Camera, Diagnostic Instruments, Sterling Heights, Michigan). Digital images were obtained using SPOT Advanced imaging software (Diagnostic Instruments). All steps of the GB method were timed for a subset of 10 otoliths to estimate effort associated with the processing technique.

The second otolith from each pair was processed via the TS method as described in Sullivan et al. (2020). Each reader processed approximately half of the TS otoliths. A clear, cold-setting embedding resin was mixed with slow hardener at a 25:3 ratio by weight (Epofix™, Electron Microscopy Sciences, Hatfield, Pennsylvania). The resin-hardener mix was applied to form a base layer in the wells of plastic embedding molds (multi-well embedding mold, 0.63-cm × 1.27-cm wells, Electron Microscopy Sciences). The base layer was allowed to cure until the epoxy became tacky (approximately 30 min). Each otolith was placed concave side down on the base layer of resin and covered with a top layer of resin, following the same mixing protocol (25:3 resin:hardener ratio by weight). Resin was allowed to cure for a minimum of 24 h before sectioning. After curing, an approximately 0.8-mm thick section was removed from each otolith by cutting along the transverse plane through the otolith core using a low-speed saw (Isomet® 1,000 Precision Saw, Buehler, Lake Bluff, Illinois). Sections were first polished with wetted 2,000-grit sandpaper and then diamond lapping film to increase clarity. After polishing, each otolith was placed on a clear, glass microscope slide with a drop of immersion oil (Resolve™ low viscosity immersion oil, Richard Allan Scientific) and viewed under a compound microscope (BX53M, Olympus, Center Valley, Pennsylvania) using transmitted light. Otolith orientation and brightness were adjusted for each otolith to optimize readability. Each otolith was imaged using a camera (resolution: 1600 × 1200 pixels; DP21, Olympus) affixed to the microscope and interfaced to a desktop computer. Digital images were obtained using cellSens imaging software (cellSens Standard, Olympus). All steps of the TS method were timed for a subset of 10 otoliths to estimate effort associated with this technique.

Age Determination and Precision

Two readers estimated age twice independently for each imaged otolith (i.e., two estimates per reader per image) by recording the number of opaque bands (i.e., white bands under reflected light [GB method], dark bands under transmitted light [TS method]). Readers estimated age without knowledge of fish length or ages previously assigned by themselves or the other reader. Furthermore, to ensure independence, samples were randomized and neither reader estimated both ages for an image on the same day. Because fish were collected in middle to late summer, the outer edge of the otolith was not considered as an annulus (Vilizzi and Walker 1999, Scarnecchia et al. 2006). To obtain a consensus age for each image, a concert read was performed and an agreeable age estimate was determined without knowledge of the paired estimate from the other technique or fish length.

Precision was analyzed across three dimensions: within reader, between readers, and between methods. Within-reader precision represented how often the two age estimates from a single reader agreed for each method. To examine within-reader precision, the two age estimates from each reader for each method were compared. Between-method precision represented similarity between consensus age estimates from the two methods. Between-reader precision (agreement in age estimates between readers) for each method was examined by comparing the four sets of age estimates (two sets of age estimates from each reader).

Each dimension of precision was examined using three different approaches: qualitative evaluation of raw data plots, precision indices, and symmetry testing (McBride 2015, Ogle 2016). Qualitative evaluation of raw data plots was conducted using age-bias graphs, allowing the visual identification of systematic differences (i.e., bias) between two sets of age estimates (Campana et al. 1995). Average coefficient of variation (ACV; Chang 1982, Campana et al. 1995) was used to quantify the similarity (i.e., precision) of different sets of age estimates (Beamish and Fournier 1981). Two other measures of precision, exact agreement rate and rate of agreement within 1 yr, are also reported for each comparison (Campana 2001). Symmetry testing examines systematic bias as deviations in symmetry from the diagonal agreement line in age-agreement tables (McBride 2015) and was conducted using Evans-Hoenig symmetry tests (Evans and Hoenig 1998). Symmetry testing was restricted to the within-reader and between-method comparisons as Evans-Hoenig symmetry tests require two sets of ages and the between-reader comparison was conducted on four sets of ages. A two-sample Kolmogorov-Smirnov test was used to compare age distributions between the two processing methods (Higgins 2004, Ogle 2016). All analyses were performed using the Fisheries Stock Assessment (FSA) package (Ogle et al. 2021) in Program R (R Core Team 2022) with $\alpha = 0.05$ as the threshold for statistical significance.

Total effort for each method was compared by calculating processing effort per 10-otolith sample, with effort partitioned by the steps of each method. Explicitly, the final cure time (minimum of 24 h) was not included in effort estimation for the TS method because it is not an active effort. In other words, the time associated with this step does not require the presence of agency personnel or researchers and may be used to process or estimate age from other trays of otoliths, or focus on other, unrelated tasks. The costs of consumable materials per otolith for each method also were compared, but not non-consumable materials, such as microscopes, low-speed saws, and hotplates. Item costs were obtained from vendor websites. Cost per otolith was calculated by estimating the number of otoliths that could be processed by each item. Where possible, estimates for items were calculated volumetrically (i.e., cutting fluid, epoxy, immersion oil), while others were approximated from the amount of material used during the processing of the otoliths reported in precision comparisons (i.e., sandpaper, lapping film).

Results

A total of 125 silver carp (median TL = 805 mm, range = 427–1025 mm) were collected for age analyses. Approximately equal numbers of silver carp were collected from each river (median = 20 individuals, range 18–24). Within-reader bias was not observed for Reader 2 in either method but was present in both methods for Reader 1 (Table 1; Figure 1). Reader 2 was more precise than Reader 1 for both the TS method and GB method (Table 1; Figure 1). However, within-reader bias showed no trends with fish age (Table 1; Figure 1).

Between-reader comparisons yielded similar levels of precision for each method (Table 1; Figures 2 and 3). However, between-method comparisons revealed significant bias and little agreement between the two processing methods (Table 1; Figure 4). Age estimate distributions significantly differed between the two methods

Table 1. Measures of precision and bias of silver carp age for within-reader, between-reader, and between-method comparisons using otoliths from 125 silver carp processed via the thin-section (TS) and grind-and-burn (GB) methods. Note: between-reader comparisons were based on more than two sets of age estimates and measures of bias (i.e., Evans-Hoenig symmetry testing) could not be calculated for those comparisons.

	Within Reader 1		Within Reader 2		Between Readers		
Statistic	**TS**	**GB**	**TS**	**GB**	**TS**	**GB**	**Between Methods**
Average CV (ACV)	14.06	9.64	5.71	7.58	12.50	11.75	16.40
Evans-Hoenig χ^2	17.60	15.69	2.29	4.09			31.81
Evans-Hoenig *P*	< 0.01	< 0.01	0.52	0.25			< 0.01
Exact agreement (%)	20.8	40.8	53.6	48.0	7.0	12.0	22.4
Agreement within 1 yr (%)	73.6	85.6	93.6	93.6	55.0	66.0	62.4

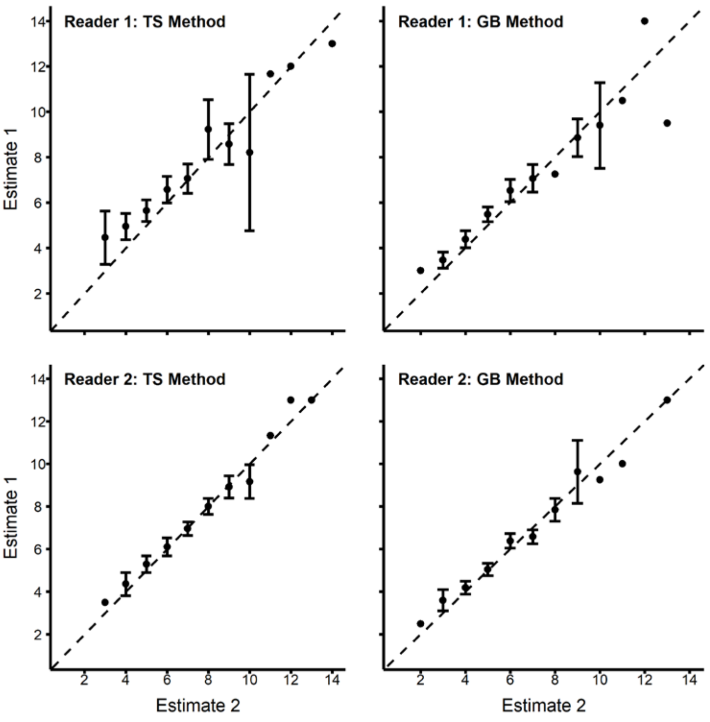

Figure 1. Age-bias graphs for each of the four pairwise, within-reader comparisons where readers used otoliths to estimate the age (yr) of silver carp. Error bars represent the 95% confidence interval about the mean age estimate assigned during the first read for all fish assigned an estimated age during the second read. Dashed line represents a 1:1 relationship. Note: error bars are not shown if fewer than five individuals were estimated of a given age.

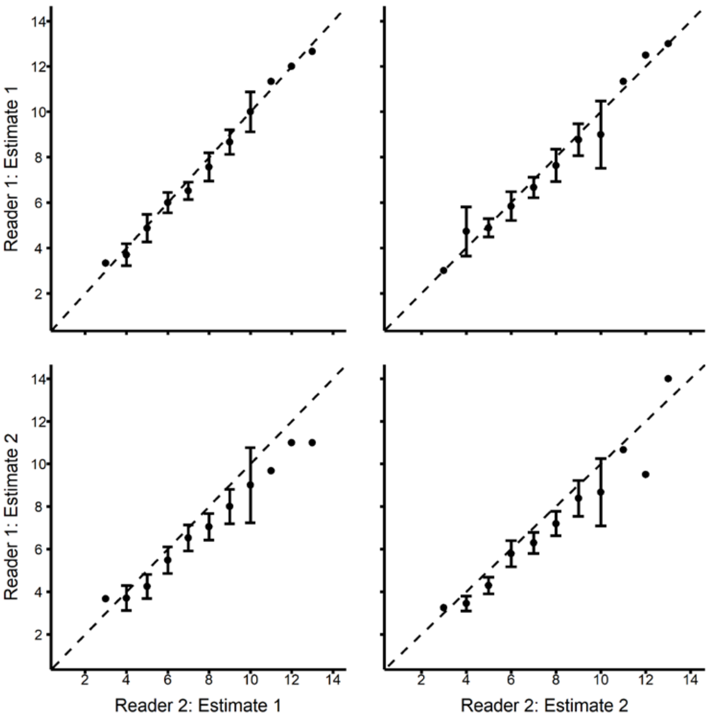

Figure 2. Age-bias graphs for each of the four pairwise comparisons to assess between-reader precision using otoliths processed with the thin-section method. Error bars represent the 95% CI about the mean age (yr) estimate assigned during the first read for all silver carp assigned an estimated age during the second read. Dashed line represents a 1:1 relationship. Note: error bars are not shown if fewer than five individuals were estimated of a given age.

(two-sample K-S test, $D = 0.24$, $P \leq 0.01$) with the TS method ranging from 3–13 yr (median = 7) and the GB method ranging from 3–12 yr (median = 6; Figure 5). Processing effort was 46% greater for the TS method (6.7 min otolith^{-1}) than the GB method (4.6 min otolith^{-1}; Table 2), but consumable costs were relatively similar on a per otolith basis for both methods (Table 3).

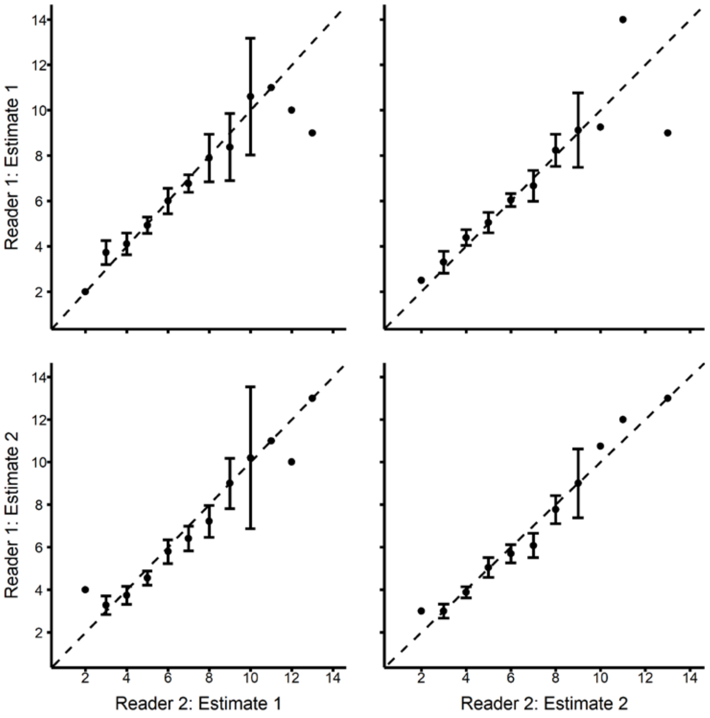

Figure 3. Age-bias graphs for each of the four pairwise comparisons to assess between-reader precision using otoliths processed with the grind-and-burn method. Error bars represent the 95% CI about the mean age (yr) estimate assigned during the first read for all silver carp assigned an estimated age during the second read. Dashed line represents a 1:1 relationship. Note: error bars are not shown if fewer than five individuals were estimated of a given age.

Table 2. A comparison of effort to perform the thin-section and grind-and-burn otolith processing techniques (per 10 otoliths).

Thin-Section Method		Grind-and-Burn Method	
Step	Effort (min per 10 otoliths)	Step	Effort (min per 10 otoliths)
Mixing epoxy (bottom layer)	2	Otolith grinding	18
Applying epoxy (bottom layer)	3	Otolith polishing	8
Placing otoliths in mold	4	Otolith burning	20
Bottom layer of epoxy to begin curing	30		
Mixing epoxy (top layer)	2		
Applying epoxy (top layer)	3		
Sectioning otoliths	23		
Total	67 min	**Total**	46 min
Per otolith	6.7 min	**Per otolith**	4.6 min

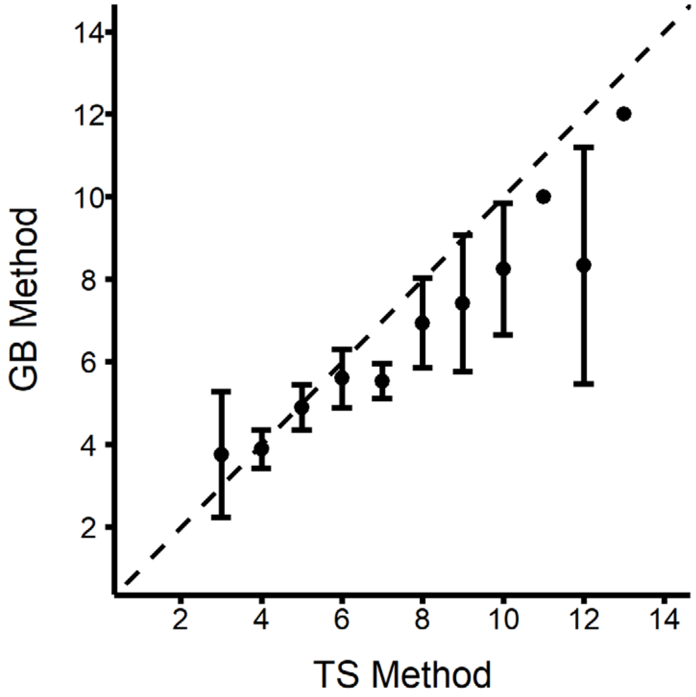

Figure 4. Age-bias graph comparing estimates from two otolith processing methods. Error bars represent the 95% CI about the mean age (yr) estimate assigned during the first read for all silver carp assigned an estimated age during the second read. Dashed line represents a 1:1 relationship. Note: error bars are not shown if fewer than five individuals were estimated of a given age.

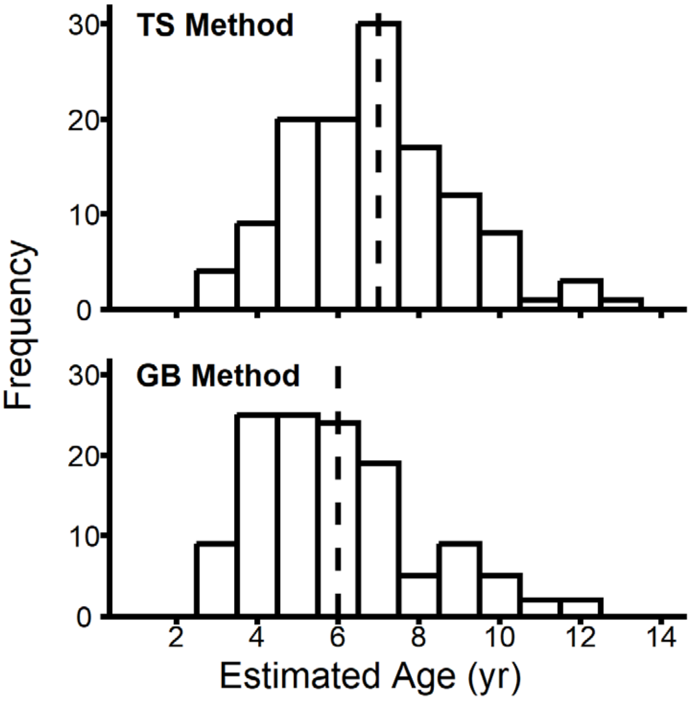

Figure 5. Age estimate distributions for otoliths from 125 silver carp processed via the thin-section method and grind-and-burn method. Median estimated age is represented by a dashed line.

Table 3. Estimated costs (US$) of consumable materials required for the grind-and-burn and thin-section otolith processing methods. These materials can be obtained from various vendors; thus, less-expensive options may be available.

Thin-Section Method				Grind-and-Burn Method			
Item	Item cost	Estimated otoliths	Cost per otolith	Item	Item cost	Estimated otoliths	Cost per otolith
Epredia Resolve Immersion Oil (M3000)	$28.00	1770	$0.02	Epredia Resolve Immersion Oil (M3000)	$28.00	885	$0.03
2000-grit wet/dry sandpaper (10-pack)	$7.98	500	$0.02	600-grit wet/dry sandpaper (10-pack)	$7.98	250	$0.03
Buehler Isocut fluid (0.95 L)	$63.00	4023	$0.02	2000-grit wet/dry sandpaper (10-pack)	$7.98	500	$0.02
EMS diamond lapping film (8″ × N/H PSA)	$32.00	125	$0.26	EMS diamond lapping film (8″ × N/H PSA)	$32.00	125	$0.26
EMS Epofix kit, includes 1 L resin and 130 ml hardener	$190.00	4432	$0.04				
EMS multi-well embedding mold	$12.00	1200	$0.01				
Total	$332.98		$0.37	**Total**	$75.96		$0.34

Discussion

Our between-method comparisons indicated that, on average, age estimates differed between the two methods used to prepare and interpret otoliths. On average, the GB method produced age estimates approximately 1 yr younger than the TS method for silver carp. Furthermore, age estimate differences between methods appeared to become more severe with older age classes of silver carp, which has been reported for other species (Stransky et al. 2005, Edwards et al. 2011, McKeefry et al. 2023). For example, Edwards et al. (2011) reported that cracked-and-burned otoliths consistently underestimated age in burbot (*Lota lota*) compared to thin sections. Thin sections also offered better clarity at the otolith margins, which resulted in fewer age discrepancies with older individuals. McKeefry et al. (2023) found that cracked-and-burned otoliths produced significantly younger age estimates than thin-section otoliths for lake whitefish (*Coregonus clupeaformis*) due to clarity at the otolith margin. Interestingly, McKeefry et al. (2023) documented "over-burnt" otoliths, which resulted in the loss of outer annuli. In our study study, different microscopes were used for each processing technique (i.e., compound microscope for the TS method; dissecting microscope for the GB method), following typical protocols for each method (Quist and Isermann 2017). Thus, increased clarity at the otolith margin in TS otoliths may have been influenced by microscope type, in addition to processing technique. Furthermore, ages were estimated from photos in an effort to minimize the variability introduced by differential placement of side illumination in the GB method (Stransky et al. 2005). Restricting the light angle to a fixed point could have artificially lowered the age estimates in the GB method, as changing the angle of illumination can increase discernability in outer annuli (Sakaris and Bonvechio 2020). Nonetheless, the TS method allowed readers to better discern annuli at the otolith margin and distinguish the otolith edge with the outermost annuli, thus, eliminating the "edge effect" (Frommel et al. 2021).

Within- and between-reader comparisons revealed generally low precision in both processing methods, suggesting silver carp age estimation may be relatively difficult. This general finding has been supported by previous work (e.g., Kolar et al. 2007, Hayer et al. 2014). However, currently no single structure and preparation method has been validated for this species. Therefore, multiple structures and procedures have been used to estimate silver carp age with varying levels of success. Broaddus and Lamer (2022) reported 70.3% exact between-structure agreement among pectoral ray, postcleithra, and vertebrae from silver carp collected in the Upper Mississippi River. Lebeda (2020) found that silver carp ages estimated from pectoral fin-ray sections in Kentucky Lake had an exact between-reader agreement of 87% but were considerably less precise for fish older than 6 yr. Fernholz (2018) noted that sectioned lapilli otoliths resulted in an exact agreement of only 31% for silver carp in the Tennessee and Cumberland rivers. For silver carp collected from the Illinois River, Morgeson (2015) noted difficulty estimating age and low between-reader precision from sagittal otoliths and postcleithrum. In a review of 117 studies referencing age estimation precision, Campana (2001) found a median CV value of 7.6% for between-reader comparisons, which is much lower than most reported values from silver carp age estimation studies, including ours. One possible explanation of lower precision in silver carp age estimation is their fast growth rate, which can result in faint annuli that are easily overlooked (Kowalewski et al. 2012). When combined with the high longevity of many populations (i.e., up to 15 age classes) that results in crowding at the otolith margin in older individuals, overall difficulty increases. Additionally, false annuli (i.e., checks; Buckmeier et al. 2012) are commonly observed during silver carp age estimation. In this study, lower within- and between-reader precision relative to other species (i.e., Campana 2001), could have been a result of these issues.

The relative difficulty of silver carp age estimation may necessitate more intensive training programs than required for other species. In this study, both readers were moderately experienced (3–5 yr) in estimating age from otoliths in other species (e.g., bluegill [*Lepomis macrochirus*], smallmouth bass [*Micropterus dolomieu*], and walleye [*Sander vitreus*]) but were relatively new to silver carp age estimation (1–2 yr). As such, before age estimation began, both readers defined criteria for identifying annuli by using the available published and gray literature. Still, the relatively low precision in this study could be a result of reader experience and inadequate training. Reader experience has been shown to be positively associated with the precision of age estimations (Campana and Moksness 1991, Campana 2001, Rude et al. 2013, McKeefry et al. 2023). This trend can be attributed to increased pattern recognition in more experienced readers (Morison et al. 2005). Therefore, to alleviate this issue, management agencies and researchers conducting silver carp age estimation should develop thorough training programs and consider increasing the minimum number of training otoliths required for new readers (e.g., Morison et al. 2005).

The TS method required approximately 50% more time effort per otolith than the GB method for silver carp age estimation. Edwards et al. (2011) reported that the section method required considerably greater effort to process otoliths than the crack-and-burn method. Sakaris and Bonvechio (2020) found that total expended effort, including time taken to estimate age, also was greater with the cut method than the ground method for blue catfish (*Ictalurus furcatus*) and channel catfish (*I. punctatus*), but less than the ground method for flathead catfish (*Pylodictis olivaris*). Sakaris and Bonvechio (2020) noted the cut method was likely quicker than the ground method for flathead catfish because the population sampled contained a larger proportion of older individuals with larger, thicker otoliths. Studies reporting processing times, including Edwards et al. (2011) and Sakaris and Bonvechio (2020), often include the time required to allow the top layer of epoxy to fully cure for the TS method. Since this step does not require active effort (i.e., this step does not require the presence of agency personnel or researchers), removing this down time from the calculation might be more insightful. For example, as the authors of this study waited for the epoxy to begin curing, we would section another batch of otoliths, practically eliminating the down time. In this study, removing this time resulted in minimal differences between the processing times of the two methods.

Total costs of consumable materials were approximately 450% greater for the TS method than the GB method with silver carp. When the number of otoliths that could be processed with the purchased materials was considered, however, the differences between methods were minimal. Similar analyses (e.g., Edwards et al. 2011, Sakaris and Bonvechio 2020) have also reported large differences in the total cost of consumable materials but did not calculate the cost per otolith. Since the true difference in cost between the two methods are relatively small when considered per otolith, cost is probably not an important consideration once the commitment to age fish has been made.

Overall, this study documents relatively small changes in age estimation protocol can result in different age estimates in silver carp. Furthermore, structure processing protocol might be equally important as structure selection for silver carp age estimation given that differences in precision were similar between the two processing methods compared in this study and the four structures compared in Seibert and Phelps (2013). Still, this study did not use known-age fish, so further work is needed to confirm that the additional annuli observed in thin-sections represent true annual increments. Additionally, relatively low precision in within- and between-reader comparisons highlights the need for known-age structures to aid in training and quality control programs specific to silver carp age estimation. Given that silver carp age estimation studies are relatively new, there are few resources currently available to researchers and biologists to create these programs. Cost and effort are similar for both methods and likely not an important factor when selecting a silver carp otolith processing protocol. Our results indicate that use of the TS method for silver carp age estimation may lead to less biased age estimates, especially in established populations with greater abundances of older individuals, assuming putative additional annuli observed in thin-sections are true annuli.

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Comparing Naïve Occupancy Versus Modeled Occupancy to Monitor Declines in Rare Species

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Abstract: Monitoring changes in occupancy (i.e., probability a site has at least one individual of a species) across time is considered an inexpensive alternative to monitoring changes in abundance and can be used to monitor multiple species simultaneously across a watershed. Occupancy can be measured as the proportion of sites where a species is detected during surveys (i.e., naïve occupancy), but is more commonly modeled by surveying sites multiple times to estimate detection probability and address false-positive survey errors (sites that are occupied but with no survey detections of the species). This results in an unbiased estimate of occupancy, but at the expense of more effort. The purpose of this study was to determine management implications of using naïve occupancy versus using modeled occupancy. We generated simulated data to represent monitoring a population, then compared performance of using naïve occupancy vs. modeled occupancy for detecting changes. Different sampling scenarios were compared using different values of catchability (0.05 to 0.70) and various levels of known occupancy decline (35%, 55%, and 85%). Power to detect declines in both naïve occupancy and modeled occupancy increased with higher catchability and greater declines. Naïve occupancy and modeled occupancy performed similarly when catchability was high. Modeled occupancy performed slightly better than naïve occupancy at lower catchability; however, at a catchability of 0.05, neither occupancy approach was successful at correctly estimating the correct decline. Although modeled occupancy provides more accurate estimates of species occupancy, results of our study indicate that regulatory agencies concerned with personnel constraints could likely use a naïve occupancy approach to maximize geographical coverage without sacrificing their ability to correctly assign conservation status to imperiled species.

Keywords: catchability, detection, monitoring, presence-absence

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Monitoring of population trends is an important component of conserving imperiled species. Estimates of population trends provide vital information for determining population viability and conservation status (O'Grady et al. 2004) and are important components of most conservation status rubrics, including the ones used by the International Union for the Conservation of Nature (IUCN 2022) and NatureServe (Master et al. 2012). Species monitoring often involves comparing changes in abundance over time. However, determining abundance for numerous species is usually considered cost prohibitive (Noon et al. 2012), and a more cost-effective alternative is to monitor changes in species occupancy.

Determining occupancy (the number or proportion of sites where a species is found or predicted to occur) is typically less labor intensive than measuring abundance, thus more sites can be sampled for a given level of effort (Strayer 1999, Joseph et al. 2006, Pollock 2006, Noon et al. 2012). Monitoring changes in occupancy can be an effective means to detect changes in population status (Noon et al. 2012). A change in occupancy suggests that the proportion of occupied sites has changed but does not necessarily indicate that abundance differs (Strayer and Smith 2003, MacKenzie 2005), but occupancy and abundance are usually strongly correlated (Gaston et al. 2000, Joseph et al. 2006, Hui et al. 2012). Occupancy is also a state variable appropriate for large-scale monitoring by itself (MacKenzie et al. 2017).

Monitoring changes in occupancy is typically done in one of two ways. The first is monitoring changes where a species is detected or not detected after surveying a location with only one sampling event per season (e.g., Strayer and Fetterman 1999, Ewing and Gangloff 2015). The observed proportion of sites with detections is termed naïve occupancy (Wintle et al. 2004, MacKenzie 2005), which does not account for imperfect detection (i.e., detection probabilities < 1). The second method accounts for imperfect detection and potential false absences (sites that are occupied but in which the species was not detected during surveys) but requires repeated surveys of sites during each sampling period, usually by vising each site multiple times (e.g., Sewell et al. 2012, Barata et al. 2017).

Catchability (q), is the probability of capturing any individual of a particular species, given that it is present at a site (Bayley and Peterson 2001, Peterson and Bayley 2004, Smith 2006). It is considered a random variable conditional on factors such as observer

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experience, search time, sampling conditions, gear, and biological factors such as age and sex, and can be estimated using techniques such as mark/recapture or multiple pass depletion (Bayley and Peterson 2001, Peterson and Bayley 2004, Smith 2006). In the occupancy context, detectability, p, is the per-survey probability of detecting a species at a site where it is present (Bayley and Peterson 2001, MacKenzie et al. 2002, Peterson and Bayley 2004).

Effective monitoring requires sound sampling design with sufficient power and ability to accurately detect changes of interest to avoid drawing incorrect conclusions about a population (Field et al. 2007). Accounting for imperfect detection is considered more statistically and biologically sound than basing inference on naïve occupancy when monitoring changes in occupancy (MacKenzie 2005, Kéry and Schmidt 2008). Trends derived from two or more naïve occupancy estimates will produce biased estimates unless the detectability is virtually equal across samples, as is often assumed (MacKenzie 2005, Kéry and Schmidt 2008). However, the assumption of equal detectability across samples is often incorrect (Kéry and Schmidt 2008). Nevertheless, several studies have shown that monitoring naïve occupancy could be effective at detecting declines in occupancy. Strayer (1999) and Pollock (2006) found that monitoring naïve occupancy has adequate power to detect a statistically significant decline in occupancy, especially if decline was high (Strayer 1999). Joseph et al. (2006) found that monitoring naïve occupancy can even be more effective than measuring declines in abundance for assigning the correct IUCN conservation status.

The IUCN assigns a threat category, Critically Endangered, Endangered, Vulnerable, or Least Concern, to taxa based on multiple quantitative criteria. Criterion A is a reduction in population size. A reduction in population can be measured by declines in abundance, area of occupancy, extent of occurrence, or some other index appropriate index. The thresholds for Critically Endangered are a reduction of ≥80%, ≥50% for Endangered, and ≥30% reduction for Vulnerable over a 10-yr or three-generation period (IUCN 2022). The IUCN protocol is used by many countries, states, and other entities to determine conservation status of a species. An advantage of the IUCN protocol and similar protocols is that they do not require highly accurate estimates of population decline, as they assign ranks based on specific ranges of population decline.

Changes in occupancy are often used to measure population declines (e.g., Strayer and Fetterman 1999, Joseph et al. 2006, Sewell et al 2012, Ewing and Gangloff 2016, Barata et al. 2017). Measuring changes in modeled occupancy is resource intensive in the sense that sites must be surveyed multiple times per time point (i.e. "season"; see below), generally at least three times and often more (MacKenzie and Royle 2005). Consequently, this limits the number of sites that can be surveyed on a given budget (Field et al. 2005). One appeal of using naïve occupancy over modeled occupancy is that typically many more sites could be sampled for a given amount of effort. Agency biologists are often tasked with managing hundreds of species across multiple watersheds. Because of this, biologists are often interested in sampling more sites because it gives them information about a greater portion of the landscape and a greater number of species. Therefore, biologists must balance the tradeoff of sampling more sites less intensively (i.e., fewer site visits) or fewer sites more intensively (i.e., more site visits). However, there have been few if any studies comparing the relative performance of modeled occupancy vs. naïve occupancy. The purpose of this study was to compare changes in modeled occupancy versus naïve occupancy in a monitoring scheme to determine what the practical ramifications are when accounting for detection when monitoring for changes in occupancy. Our objective was to determine the relative performance of using modeled occupancy vs naïve occupancy of determining the correct IUCN conservation classification.

Methods

We use a simulation approach to compare modeled occupancy and naïve occupancy in a monitoring context. First, we generated populations of known occupancy consisting of various numbers of individuals arranged among 500 sites. The populations followed a zero-inflated Poisson distribution (Wenger and Freeman 2008) with a mean abundance of 10 individuals per site and an initial occupancy of 20% (i.e., 20% of sites contain at least one individual). We then simulated sampling these sites with observation error, by first calculating detectability at each site. Detectability (p) was estimated as a function of catchability (q) and the number of individuals of a species present at a site (n) using the formula $p = 1 - (1 - q)^n$ (Bayley and Peterson 2001). This generated a per-survey probability of detecting the species if present at a given site (Bayley and Peterson 2001, Peterson and Bayley 2004). We then generated a uniformly distributed random number between 0 and 1. If the random number was less than or equal to the detection probability, then the species was considered detected at that site during the survey. If the random number was greater than the detection probability (Strayer 1999), then the species was recorded as not detected at that site. We used mean catchability (q) values ranging from 0.05 to 0.70, based on catchability ranges reported in the literature for nongame fishes (Bayley and Peterson 2001) and freshwater mussels (Meador et al. 2011). Catchability is usually dependent on sampling conditions and should be considered as a random variable (Peterson and Bayley 2004), so we modeled q as a beta distributed random variable with a standard deviation of one-tenth of the mean (Wintle et al. 2004).

Our model assumed we had the resources to conduct 210 surveys in each season. Here a season is defined as a time period where the occupancy state of a site is unlikely to change, that is the site is always occupied or unoccupied during the surveying period (MacKenzie et al. 2017). We simulated surveying 210 sites one time per season to estimate naïve occupancy and 70 sites three times per season as three sampling occasions is typically the minimum number recommended for estimating occupancy (Field et al. 2005, MacKenzie and Royle 2005). This allowed for comparing tradeoffs of sampling more sites once or a lesser number of sites more intensively. Naïve occupancy was calculated as the number of sites where the species was detected divided by the total number of sites sampled. Modeled occupancy was calculated using a single-species, single-season occupancy model with no covariates (MacKenzie et al. 2017).

We then simulated declines in occupancy in our population of 35%, 55%, and 85%. We chose these percentage declines because they are just slightly larger than the thresholds established by the IUCN (2022) for different conservation status levels. Population reductions were achieved by reducing abundances at randomly selected sites to zero until the desired percent reduction in occupancy was attained (Strayer 1999). Since natural populations tend to fluctuate in abundances and occupancy over time, abundances at each site were multiplied by a random uniform number between 0.5 and 1.5 which simulated anywhere from a 50% decline to a 50% increase in abundance. These populations were then sampled as before, with the same sites being sampled. Naïve occupancy and modeled occupancy were again calculated, and percent reduction in occupancy was calculated based on the differences between the occupancy prior to the reduction and afterwards.

This process was repeated 1000 times for each catchability value. To evaluate relative performance of the two different methods, we calculated proportions of the 1000 simulations that the model correctly predicted the correct IUCN classification based on the decline in occupancy. We then assessed whether simulations were able to assign population decline to the correct IUCN category at least 80% of the time, comparable to the frequently used threshold for power analyses in ecological studies (Field et al. 2007). All analyses were done in R version 4.2.3 (R Core Team 2023). We used the R package unmarked version 1.2.5 (Fiske and Chandler 2011) for occupancy modeling. Artificial populations of known occupancy were generated using the R package VGAM version 1.1-8 (Yee 2010).

Results

Naïve occupancy and modeled occupancy performed similarly when catchability was high but modeled occupancy performed slightly better than naïve occupancy at lower catchability. Under a 35% decline scenario, modeled occupancy reached the 80% correct categorization threshold at a catchability of approximately 0.15, whereas, naïve occupancy did not reach this threshold until catchability reached 0.3 (Figure 1). At a 55% decline the two

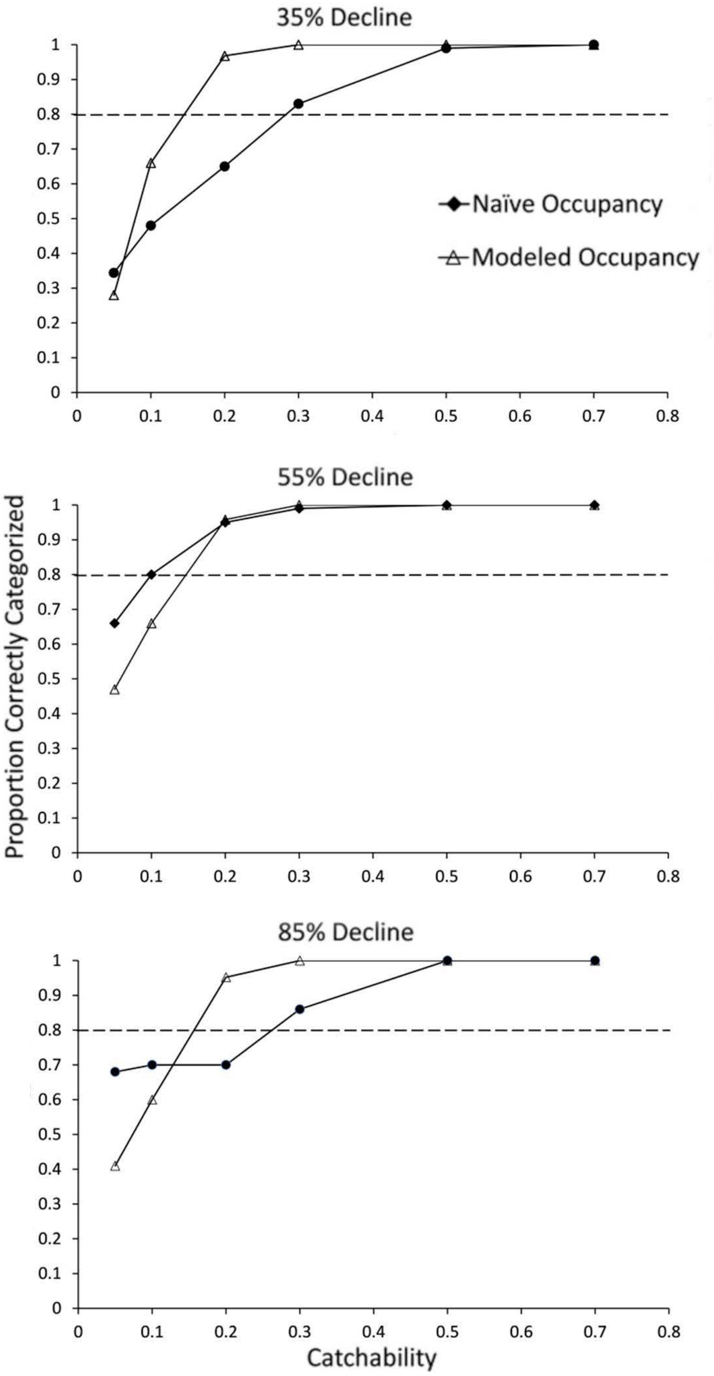

Figure 1. Proportion of 1000 model runs using modeled occupancy or naïve occupancy that correctly placed the estimated population decline in the correct IUCN category as a function of catchability (q). The dashed line represents where the proportion of correct model runs exceeds 0.8. Models were run over a range of catchabilities at three levels of population declines.

modeling approaches performed more closely; however, the naïve approach reached the 80% threshold when catchability was only 0.10 while the modeled approach did not reach this threshold until catchability exceeded 0.15 (Figure 1). At higher catchabilities, the two approaches performed virtually identically. At an 85% decline, the naïve approach outperformed the modeled approach at catchabilities <0.10 but thereafter the modeled approach performed better, reaching the 80% threshold at a catchability of approximately 0.15 (Figure 1). The naïve approach did not exceed the 80% threshold until catchability reached approximately 0.28. Changes in modeled occupancy were typically more precise and accurate than naïve occupancy. Modeled occupancy had narrower ranges and interquartile ranges and the medians of the model runs for modeled occupancy were usually closer to the true value of the decline than those for naïve occupancy (Figure 2).

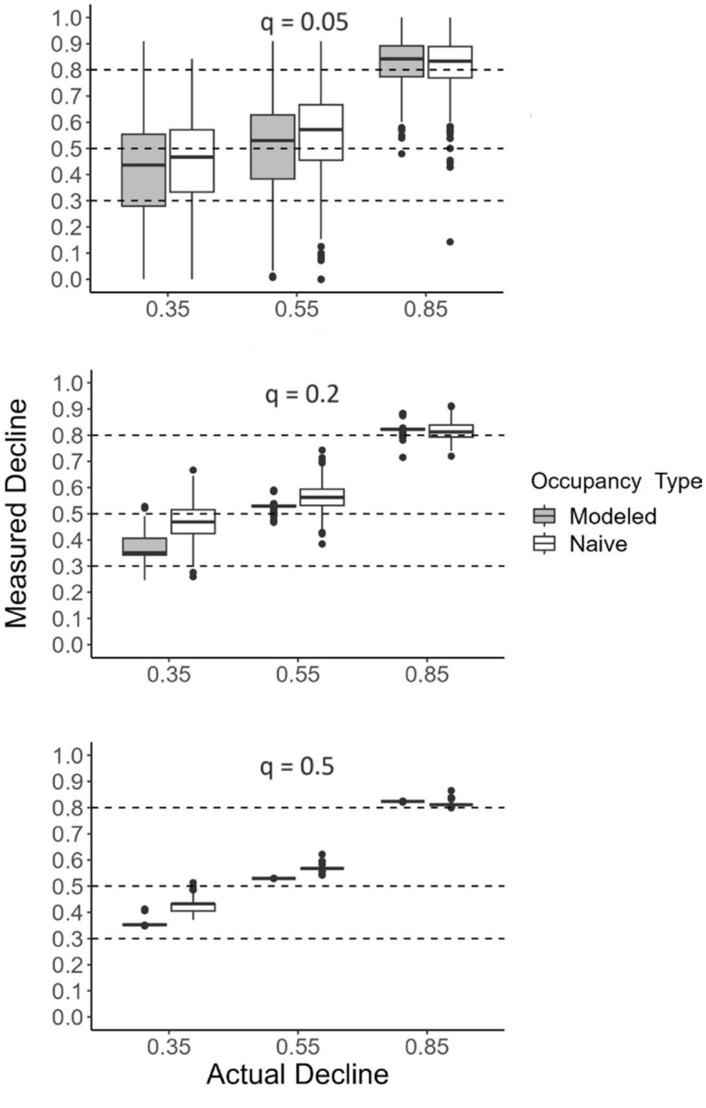

Figure 2. Box plots showing the distribution of estimated population decline based on 1000 model runs using modeled occupancy or naïve occupancy for three different catchability (q) values. Horizontal dashed lines represent the different threat categories based on the IUCN (2022) protocol (Vulnerable = 30–50% decline, Endangered = 50–80% decline, and Critically Endangered = >80% decline).

Discussion

Modeled occupancy performed better than naïve occupancy for monitoring population declines. Modeled occupancy typically had a higher proportion of correctly allocating declines to the correct IUCN conservation status category, greater accuracy, and better precision than naïve occupancy. Our results are in line with those of previous authors that noted modeled occupancy is superior to using naïve occupancy (i.e. MacKenzie 2005, Kéry and Schmidt 2008). Neither method was effective at the lower end of catchability values used during this study (≤0.1). However, this changed for modeled occupancy as catchability approached 0.2 and for naïve occupancy as catchability approached 0.3 where both methods exceeded 80% correct allocation.

Despite not performing as well as modeled occupancy, naïve occupancy still appeared to be a useful method for monitoring populations under some circumstances. Even at the lowest level of decline (35%), naïve occupancy attained appropriate power once catchability reached 0.3 and approached 100% correct allocation at higher levels of catchability. These results are consistent with those of previous studies that found that using naïve occupancy can be effective for monitoring populations (Strayer 1999, Joseph et al. 2006, Pollock 2006). Perhaps the most useful role for naïve occupancy will be for monitoring large numbers of species across large landscapes such as entire watersheds. This method is especially useful when highly accurate or precise measures of population decline are not required, such as when using a protocol such as those of the IUCN (2022) or NatureServe (Master et al. 2012) where status is assigned based on measured declines falling within a specified range.

This study underscores the need to increase catchability as much as possible when conducting surveys. One way to increase catchability is to use experienced personnel when monitoring, especially for very rare, cryptic, or hard to sample species. For example, Rondel (2019) noted that catchability of a rare, federally listed mussel species increased as surveyor experience increased. Conducting sampling during appropriate conditions also increases catchability. For example, sampling during low flow and sunny conditions has been shown to increase catchability for many species of freshwater mussels (Smith 2006, Meador et al. 2011). Increasing search effort at a given location also increases catchability (Metcalfe-Smith et al. 2000, Smith 2006, Reid 2016). Lastly, using the correct gear is extremely important, as Bayley and Peterson (2001) noted extreme differences in catchability of stream fishes depending on the gear type used.

The results of this study are not intended to set guidelines when trying to establish a given level of power to detect a decline. There are more factors than catchability that determine the power to detect population declines using occupancy. Factors such as population abundance, initial occupancy of the population, magnitude of decline, and sample size are also extremely important in determining power to detect a population decline (Strayer 1999, Rhodes et al. 2006, Guillera-Arroita and Lahoz-Monfort 2012, Ewing and Gangloff 2015).

Monitoring changes in abundance is often expensive and requires extensive field surveys. This can make it infeasible to monitor abundance for numerous species across large landscapes such as entire watersheds as resource agencies are often tasked to do, often with limited budgets and personnel constraints. Estimating a species' occupancy typically requires much fewer resources than abundance thus lending itself to large-scale monitoring (Noon et al. 2012). It also can be effective at monitoring numerous species at once, especially those species that lend themselves to omnibus surveys where numerous species are monitored simultaneously (Manley et al. 2004, Noon et al. 2012). Monitoring changes in modeled occupancy is typically more statistically and biologically sound when monitoring occupancy than monitoring changes in naïve occupancy (MacKenzie 2005, Kéry and Schmidt 2008). However, this study has shown that using naïve occupancy can be effective, especially when catchability is high, plus it has the advantage over modeled occupancy of being able to survey more sites across thus providing better coverage across a landscape.

There are circumstances where using naïve occupancy is not adequate and should not be used. Strayer (1999) and Manley et al. (2004) found that naïve occupancy was not effective at monitoring very rare species or highly endemic species. In these cases, dedicated studies utilizing modeled occupancy should be used. Modeled occupancy also has the advantage of utilizing environmental covariates to make to make occupancy predictions stronger (MacKenzie et al. 2017) and so in practice, modeled occupancy might perform even better against the naïve model than this study suggests. Also, research studies designed to examine the effects of environmental factors or land uses on changes in occupancy, as well as those examining temporal changes where detectability may have changed significantly over time, should use modeled occupancy rather than naïve occupancy (MacKenzie et al. 2017). However, this study does show that agencies facing manpower shortages and concerned about monitoring changes in geographic extent could use naïve in lieu of modeling occupancy.

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Impacts of Introduced Blueback Herring on Piscivorous Sportfish in a Southeastern U.S. Reservoir

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Abstract: Non-native species have sometimes been introduced to increase forage availability and sportfish production, but such introductions have potential for negative as well as positive effects. In 2010, non-native blueback herring (*Alosa aestivalis)* were found in Lewis Smith Lake, Alabama, due to illegal stocking. Our objective was to quantify food habits and determine potential impacts of blueback herring introduction on body condition and growth of important sportfishes in Lewis Smith Lake. Largemouth bass (*Micropterus salmoides*), Alabama bass (*Micropterus henshalli*), and striped bass (*Morone saxatilis*) were sampled in 2013 and 2014, and diets of these post-blueback herring introduction piscivores were quantified. Relative weight and length-at-age data from these fish were combined with data from Alabama Department of Conservation and Natural Resources and Auburn University collected prior to blueback herring introduction to quantify any changes in relative weights or length at age. Overall, piscivore diets included blueback herring at lower percentages (4.5, 19.5, and 6.6% for largemouth bass, Alabama bass, and striped bass, respectively) than other fish prey (52.2%, 58.7%, and 92.2% for largemouth bass, Alabama bass, and striped bass, respectively). Only summer striped bass diets contained high proportions of blueback herring. Relative weights of all sizes of largemouth bass and Alabama bass and intermediate sized striped bass were significantly higher after blueback herring introduction. This increased condition did not result in increased mean-length-at-age for piscivores age-4 and younger (except age-1 and age-2 striped bass). Blueback herring contributed to piscivore diets and increased body condition of some piscivores, with little change observed in growth. However, long-term effects should be assessed as blueback herring densities increase in the reservoir.

Key words: diet composition, growth, introduced species, relative weight, sportfish

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Native and nonnative prey species have been introduced both legally as part of management efforts and illegally by the public to increase sportfish growth, condition, and abundance (Moyle 1976, Kircheis and Stanley 1981, Ney 1981, Noble 1981, Wydoski and Bennett 1981, DeVries and Stein 1990, Rahel and Smith 2018). Stocking prey species has been used as a management tool to provide additional forage that may allow sportfish to transition to piscivory at earlier life stages, which can provide improved growth and survival of recreationally and economically important species (e.g., Ludsin and DeVries 1997). Introductions can lead to positive, negative, or negligible effects on aquatic communities (Adams 1996, Gozlan et al. 2010). Piscivores that transition to novel prey sources may benefit from these introductions, whereas other species that do not transition to them or are ecologically displaced may decline (Ellis et al. 2011). Although stocking non-native and potentially invasive species has been increasingly scrutinized over time (Jackson et al. 2004, Kolar et al. 2010), illegal introductions by anglers continue to occur (Rahel 2004, Johnson et al. 2009), either to intentionally establish populations or through careless "bait bucket" releases. Introduced prey species can affect established fishes differently across multiple life stages, leading to complex interactions that are difficult to anticipate and predict (Devlin et al. 2017, DeBoer et al. 2018). For these reasons, it is important to fully understand the range of potential impacts an introduced prey may have on fish communities before deciding whether to stock a new species.

Blueback herring (*Alosa aestivalis)* is an anadromous and planktivorous species with a native range from St. Johns River, Florida, to Prince Edward Island, Canada (Loesch 1987, Bozeman and Van Den Avyle 1989) that has been stocked into many inland lakes and reservoirs, to increase forage for piscivorous gamefish. Blueback herring can thrive in landlocked environments; in southeastern U.S. reservoirs where they have been introduced they can establish self-sustaining populations if sufficient cool water thermal refuge

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is provided (Bulak and Walker 1979, Prince and Barwick 1981, Coutant 1997, Nestler et al. 2002, Winkelman and Van Den Avyle 2002, Grove et al. 2022). However, little is known about the overall impacts of introduced blueback herring in these reservoirs on resident fishes.

The primary positive effect of blueback herring on the growth and abundance of piscivores is attributed to their direct contribution as a high-calorie prey type to predator diets (Bart et al. 2021). Due to both spatial overlap and shared thermal preference between striped bass (*Morone saxatilis)* and blueback herring, striped bass are likely to feed on introduced blueback herring (Rice et al. 2013). Other piscivorous species such as spotted bass (*Micropterus punctulatus*), and Alabama bass (*Micropterus henshalli*) that tend to use deeper water habitats (Hunter and Maceina 2008) might also feed on blueback herring and potentially exhibit increased growth.

Negative impacts of blueback herring introductions are largely attributed to competition with or predation on juvenile piscivores or the resident prey species. However, the evidence for potential negative effects resulting from blueback herring introduction is mixed. Blueback herring may negatively affect resident fish populations by impacting zooplankton communities (e.g., Brooks and Dodson 1965), although some evidence suggests that blueback herring and native prey fishes consume different sizes of zooplankton (Davis and Foltz 1991, Grove et al. 2022). Blueback herring can also have direct negative impacts on other fish populations by consuming eggs and larval fishes (Bulak and Walker 1979, Guest and Drenner 1991, Goodrich 2002, Winkelman and Van Den Avyle 2002, Wheeler et al. 2004). These combined negative effects have been shown to cause declines in sportfish populations. For example, in North Carolina, walleye (*Sander vitreus*) populations in Lake Glenville and Hiwassee Reservoir, and largemouth bass (*Micropterus salmoides*) populations in Lake Norman were reported to decline after the stocking of blueback herring (Wheeler et al. 2004). Although the exact mechanism for the decline was not identified, egg predation was suspected as one mechanism. Lake Burton, Georgia, experienced complete year-class failures of largemouth bass as well as decreased abundances of both black crappie (*Pomoxis nigromaculatus*) and white bass (*Morone chrysops*) following introduction of blueback herring (Wheeler et al. 2004). However, declines in largemouth bass may have been caused more by non-native Alabama bass introductions than blueback herring (Sammons et al. 2023). Regardless, predicting the effects of introducing new species into established systems is complex and full of uncertainty.

Here we examine the influence of introduced blueback herring on piscivorous sportfish diets, growth, and condition in Lewis Smith Lake, Alabama, following their illegal introduction sometime prior to 2010, when they were first identified in the reservoir by Alabama Department of Conservation and Natural Resources (ADCNR) biologists (Jay Haffner, ADCNR, personal communication); they have since spread throughout the reservoir. This project began in 2013 and was the first to study the blueback herring population in the reservoir, focusing on potential impacts of blueback herring introductions on popular sportfishes in these systems that may prey on blueback herring including largemouth bass, Alabama bass, and striped bass. Objectives for this work were to: (1) determine diet composition of three primary piscivores in the system (largemouth bass, Alabama bass, striped bass), including the contribution of introduced blueback herring, and (2) compare relative weights and growth of these piscivores before and after blueback herring introduction.

Study Area

Lewis Smith Lake is a large (8538 ha), mesotrophic reservoir located in north central Alabama (Cullman, Walker, and Winston counties), with three major branches (Ryan, Rock, and Sipsey creeks) characterized by steep banks, rocky substrate, and deep waters (maximum depth > 100 m). The three branches differ in water clarity and primary production, and a thermocline develops in May that usually persists until November (Bayne et al. 1998, Allen et al. 1999, Moss et al. 2003, Grove et al. 2022). The recreational fishery includes several species, with largemouth bass, Alabama bass, and striped bass the most sought-after fishes. A study conducted from 2010–2011 estimated the striped bass fishery was worth US$0.9–1.2 million in yearly revenue (Lothrop et al. 2014).

Methods

Sampling was conducted from January 2013 through November 2014 within the Ryan Creek, Rock Creek and Sipsey Creek branches. Each branch included an upstream and downstream sampling site to account for longitudinal within-reservoir variation in productivity (Bayne et al. 1998, Allen et al. 1999; Grove et al. 2022). Juveniles and adults of largemouth bass, Alabama bass, and striped bass were collected at night by boat electrofishing or gill nets. From January through September 2013, both collection methods were used once per month during the same sampling trip. From October 2013 through November 2014, collection methods alternated monthly. While this meant that striped bass and black basses were primarily collected in alternating months, this did not introduce any bias given that we considered relative weights across fish and diets on a seasonal basis. Electrofishing samples consisted of two 10-min transects at each sampling site using pulsed DC (7.5 GPP, Smith-Root Inc., Vancouver, Washington). Multiple sized gill nets were used to ensure the full size range of striped bass was captured. Gill-net sampling at each site consisted of two gill nets with different mesh sizes (one 38 m × 2.5 m multiple mesh size net with 5–7.6-m panels with mesh sizes ranging from 5 to 15.2 cm, and one 38 m × 2.5 m experimental net with 5–7.6-m panels with mesh sizes ranging from 7.6 to 17.8 cm) that soaked for 6 h. Gill nets were set at the thermocline during summer and nearer the surface after the reservoir was no longer stratified during winter to maximize seasonal catch rates by accounting for fish movement due to temperature tolerances of striped bass (Schaffler et al. 2002, Nestler et al. 2002, Brandt et al. 2009). The thermocline was determined using a YSI 85 multimeter (YSI Incorporated, Yellow Springs, Ohio). Dissolved oxygen and temperature were recorded every 2 m and the thermocline was determined when dissolved oxygen declined rapidly from normoxic to hypoxic.

All fish collected were placed on ice and returned to the lab for further processing the following day. In the lab, fish were measured (TL, mm), weighed (g, nearest 10 g for fish over 5443 g), and stomach contents were removed and frozen (from all largemouth bass and striped bass, and a subsample of 10 randomly selected Alabama bass from each date); sagittal otoliths were removed for aging. Standardized spring electrofishing data for largemouth bass and Alabama bass were provided by ADCNR to supplement post-introduction piscivore length, weight, and age data. Samples were collected during 15 March–30 April in 2016 and 2019, and consisted of 10 sampling sites each year that were selected in a stratified random approach (stratified across morphology of the reservoir) and sampled for 30 min each. All fish were weighed, measured, and had otoliths removed for aging. Pre-blueback herring introduction data were collected from 2005 to 2007 by Shepherd and Maceina (2009) who sampled black bass and striped bass from Ryan and Sipsey creeks and the dam forebay using similar gears as this study. Only fish collected in the spring (approximately at the time of annulus formation) were used in length-at-age analysis. Additional length, weight, and age data collected by ADCNR as described above from 2002 to 2007 were used for pre-introduction largemouth bass and Alabama bass data.

All prey items were identified to the lowest possible taxonomic level and measured (length) under a dissecting microscope, with severely decomposed prey fish identified by otolith morphology. Species-specific length-weight regressions were applied to individual diet items and the total mass estimated by summation was used to estimate consumed prey biomass. Prey species length-weight regressions were taken from published information (Benke et al. 1999). A length-weight regression was generated for blueback herring using intact collected samples of the species from the field. Prey biomass estimates were used to calculate proportional composition by weight for each individual predator, with prey grouped for diet analyses as blueback herring, black bass, threadfin shad (*Dorosoma petenense*), gizzard shad (*Dorosoma cepedianum*), minnows, sunfish (*Lepomis* spp.), crayfish, insects, or other.

Relative weights of largemouth bass, Alabama bass, and striped bass were calculated using equations in Neumann et al. (2012), with the relative weight equation for spotted bass used for Alabama bass. Otoliths were aged independently by two readers, with otoliths from largemouth bass and Alabama bass <5 yr old read whole under a dissecting scope. Otoliths of older black bass and all striped bass were sectioned transversely through the nucleus using a low-speed diamond-bladed saw (South Bay Technologies Model 65, San Clemente, California), then affixed to a microscope slide and read under a compound microscope. If readers did not agree on whole-read otoliths, the otolith was sectioned transversely and reexamined. Otoliths were discarded if readers failed to agree following sectioning. All otoliths were measured from the focus to the posterior-most end of each annulus (nearest 0.001 mm) using an image analysis system. Total length at the *i*th age ($TL_{i;}$) was estimated using the direct proportion method (Le Cren 1947):

$$TL_i = \frac{S_i}{S_c} \times L_c$$

where TL_i is the back-calculated length of the fish at the formation of the *i*th increment, L_c is the length of the fish at capture, S_c is the radius of a sagittal otolith at capture, and S_i is the radius of a sagittal otolith at the *i*th increment (Quist et al. 2012). Growth past the final annulus across seasons was controlled by using back-calculated ages. Shepard and Maceina (2009) data used TL at capture given that all data were derived from spring collections.

Statistical Analysis

Average catch per electrofishing hour (CPE) for largemouth bass and Alabama bass before and after blueback herring introduction were compared using two sample *t*-tests with unequal variance. Diet and relative weight data were categorized into four seasons, defined as Spring (March–May), Summer (June–August), Fall (September–November), and Winter (December–February). Chi-square goodness of fit tests were used to analyze the proportional contributions by weight of diet types in largemouth bass, Alabama bass, and striped bass to determine if the relative contribution of the observed diet categories differed. Relative weights of these piscivorous fishes were compared before (2002–2007) versus after (2013–2019) blueback herring introduction across three size groups (length range within a species divided into thirds) using two-way analysis of variance. Average lengths at age were compared at age-1 through age-4 for piscivore populations pre- versus post-blueback herring introduction using *t*-tests with the fishmethods package (Nelson 2023, R Core Team 2023). All fish used in this analysis from the post-introduction period were from year classes spawned after blueback herring introduction. Statistical tests used $\alpha = 0.05$ to assess significance.

Results

Black Bass CPE and Diets

Mean catch rate of Alabama bass increased from 33.6 fish h^{-1} before blueback herring introduction to 50.7 fish h^{-1} afterwards: ($t_{11} = 2.16$, $P = 0.054$). Conversely, mean catch rate of largemouth bass was similar before (23.3 fish h^{-1}) and after (19.1 fish h^{-1}) blueback herring introduction ($t_{11} = 1.01$, $P = 0.33$).

We collected 495 largemouth bass, 253 striped bass, and 1734 Alabama bass for food-habit analysis. Blueback herring composed a significantly lower proportion of diets than other prey fish (threadfin shad and sunfishes) or crayfish in all piscivore diets that contained fish and crayfish ($\chi^2 = 182.8$, df = 12, $P < 0.0001$; Table 1). For striped bass, threadfin shad (79% of prey biomass) and gizzard shad (12%) accounted for most of the prey consumed when pooled across seasons ($\chi^2 = 353.6$, df = 6, $P < 0.0001$; Table 1). Alabama bass consumed nearly equal proportions of blueback herring (19%), crayfish (21%), and threadfin shad (20%) across seasons. However, diet proportions contributed by blueback herring were much lower for largemouth bass (5%) and striped bass (7%) across seasons. Blueback herring were seasonally important, as they were consumed at disproportionally high rates during the summer for both Alabama bass ($\chi^2 = 115.6$, df = 7, $P < 0.0001$) and striped bass ($\chi^2 = 68.6$, df = 3, $P < 0.0001$).

Relative Weight

We used length categories (TL, mm) of <329 (small), 329–458 (medium), and >458 (large) for largemouth bass. For Alabama bass the small, medium, and large categories were <322, 322–443, and >443, respectively, and for striped bass they were <543, 543–886, and >886, respectively. Relative weights of fish collected post-blueback herring introduction were greater than those collected prior to the introduction for largemouth bass ($F_{1, 2005} = 453.9$, $P < 0.0001$), Alabama bass ($F_{1, 3324} = 532.8$, $P < 0.0001$), and striped bass ($F_{1, 962} = 27.5$, $P < 0.0001$). The size group × time period interaction term was not significant for either largemouth bass ($F_{2, 2005} = 1.8$, $P = 0.16$) or Alabama bass ($F_{2, 3324} = 0.5$, $P = 0.62$), with relative weights greater after introduction for all three size groups for both species ($P < 0.006$; Figure 1). For striped bass, the size group × time period interaction term was significant ($F_{2, 962} = 5.0$, $P = 0.007$), with relative weights of small and large fish similar between time periods but those of medium fish being greater post-blueback herring introduction ($P < 0.0001$; Figure 1).

Table 1. Seasonal and total annual diet percentages (% by biomass, averaged across individuals) for largemouth bass, Alabama bass, and striped bass during 2013–2014 in Lewis Smith Lake, Alabama. Seasons are defined as Spring = March–May, Summer = June–August, Fall = September–November, Winter = December–February. Prey types: BASS = *Micropterus* spp., BBHR = blueback herring, CRAY = crayfish, GIZS = gizzard shad, INST = insects, MINN = minnows, SUNF = sunfish, and THSH = threadfin shad.

			Prey Type								
Species	**Season**	***n***	**BASS**	**BBHR**	**CRAY**	**GIZS**	**INST**	**MINN**	**SUNF**	**THSH**	**Other**
Largemouth Bass	Fall	28	–	–	66.63	–	–	–	22.89	10.48	–
	Winter	91	0.12	1.05	70.04	–	0.00	1.99	20.62	6.19	–
	Spring	42	4.02	19.43	9.67	–	0.78	4.38	35.42	26.31	–
	Summer	71	4.27	0.51	24.63	–	0.44	0.58	59.86	9.69	–
	Total	365	2.20	4.52	43.12	–	0.30	1.82	36.20	11.84	–
Alabama bass	Fall	36	–	16.85	31.48	–	0.01	2.48	20.99	26.32	1.88
	Winter	99	–	9.86	46.18	0.92	0.09	0.74	26.66	15.55	0.00
	Spring	78	4.39	11.04	6.77	6.35	1.73	4.81	51.59	13.30	0.01
	Summer	152	3.62	30.82	2.86	–	3.62	1.51	33.88	23.69	0.01
	Total	232	2.09	19.12	21.39	1.27	1.72	1.87	32.58	19.72	0.23
Striped bass	Fall	50	–	11.99	0.58	12.71	–	–	–	74.73	–
	Winter	35	–	0.26	0.27	0.18	–	–	–	99.30	–
	Spring	26	–	8.85	4.89	75.29	0.02	–	1.15	9.80	–
	Summer	17	15.98	60.57	9.01	0.00	–	–	–	14.44	–
	Total	128	0.68	6.56	1.27	12.05	0.00	–	0.14	79.31	–

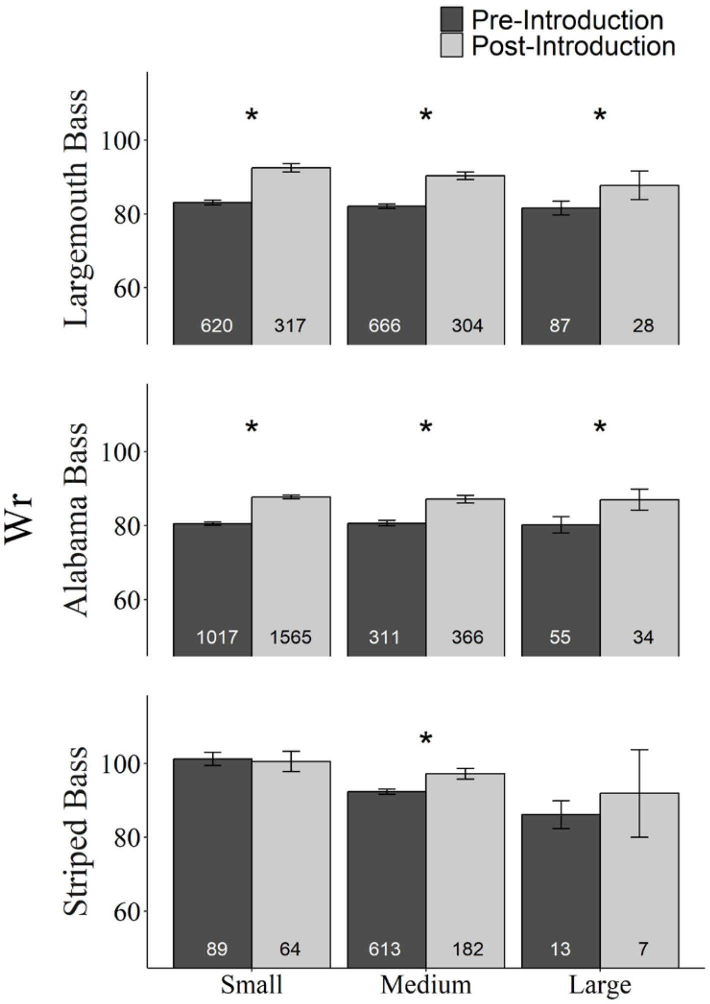

Figure 1. Pre- and post-blueback herring introduction relative weights (Wr; mean ± 95% CI) of largemouth bass, Alabama bass, and striped bass combined across three study areas within Lewis Smith Lake, Alabama. Asterisks indicate significant differences between collections before versus after blueback herring introduction within a species, and sample sizes are listed at the bottom of each bar.

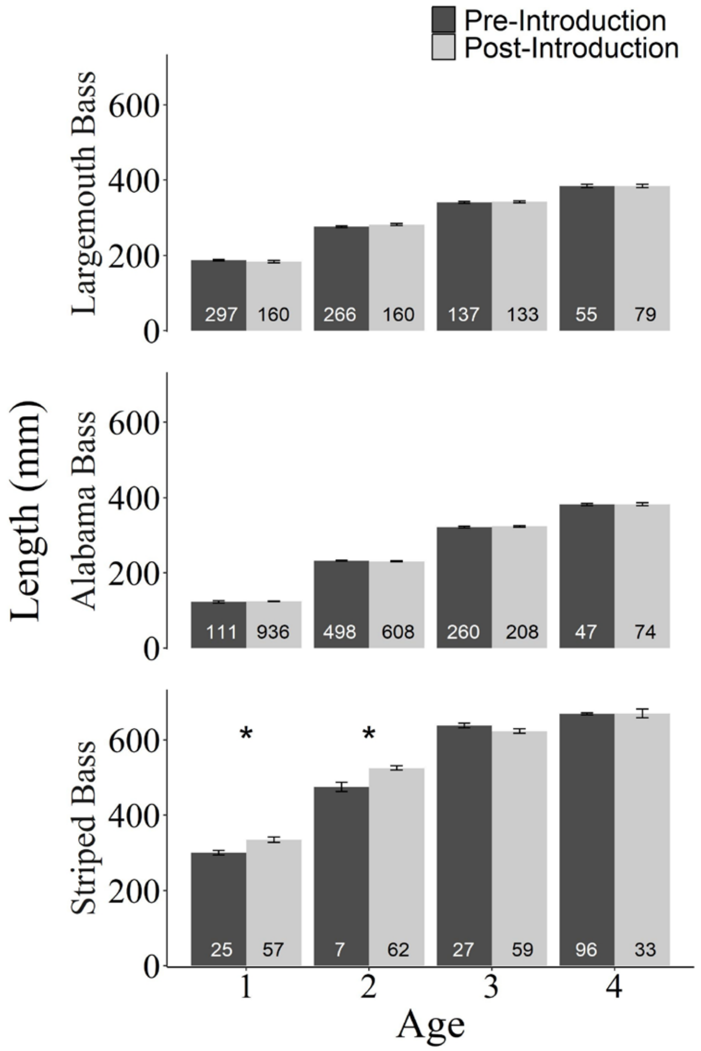

Figure 2. Mean length (mm) at age of largemouth bass, Alabama bass, and striped bass in Lewis Smith Lake, Alabama before and after blueback herring introduction (± SE). Asterisk denotes significant differences in length at age before versus after blueback herring introduction, and sample sizes are listed at the bottom of each bar.

Growth

Mean lengths of age-1 and age-2 striped bass were larger following the introduction of blueback herring (age-1: $t_{73} = -3.61$, $P < 0.0005$; age-2: $t_8 = -3.64$, $P = 0.005$; Figure 2). However, mean lengths by age were similar between time periods for largemouth bass (age-1: $t_{295.0} = 0.94$; age-2: $t_{365.0} = -1.62$; age-3: $t_{268.0} = -0.40$; age-4: $t_{268.0} = -0.049$; $P \geq 0.11$ for all comparisons), Alabama bass (age-1: $t_{122.8} = -0.32$; age-2: $t_{1100.6} = 0.89$; age-3: $t_{432.6} = -0.62$; age-4: $t_{118.7} = -0.12$; $P \geq 0.38$ for all comparisons), and age-3 and age-4 striped bass (age-3: $t_{67.41} = 1.82$, $P = 0.07$; age-4: $t_{35.22} = 0.13$, $P = 0.90$).

Discussion

In this study, we compared condition and growth of three piscivore species in Lewis Smith Lake, Alabama before versus after the introduction of blueback herring and quantified diet composition after blueback herring were established in the reservoir. Existing forage species, including threadfin shad, sunfish, and crayfish contributed the majority of prey biomass for all three of the piscivores in this study despite the introduction of blueback herring. These prey groups provided ~70–90% of biomass of piscivore diets across seasons. However, blueback herring were a seasonally important diet item for some piscivores in the spring and summer. This was apparent for striped bass as their diets were composed of 61% blueback herring in summer compared to 0.3% in winter. Some deep-water reservoirs in the southeastern U.S. provide cool water refuges during the summer for blueback herring and striped bass, which have a cooler thermal maximum limit compared to most native southeastern U.S. fish species found in reservoirs (Nestler et al. 2002, Rice et al. 2013, Sammons and Glover 2013, Bart 2018). Alabama bass differ from largemouth bass in that they prefer deeper, cooler water and are likely using similar thermocline areas during the summer as striped bass and blueback herring (Hunter and Maceina 2008), whereas largemouth bass are commonly found in shallow shoreline areas or coves. This temporary habitat overlap likely explains the greater contribution of blueback herring to the diet of striped bass and Alabama bass during stratification. Given the relatively greater contribution to the diet, previous bioenergetics simulations predicted that Alabama bass and striped bass are most likely to benefit from the introduction of blueback herring (Bart et al. 2021). This increased benefit may be limited to months with the warmest epilimnetic water temperatures and may be leading to the increased relative weight of black basses and medium size striped bass. Further supporting this theory is the increased length-at-age of age-1 and age-2 striped bass.

Any positive effects of blueback herring may be negated if blueback herring were to reduce threadfin shad and gizzard shad populations, which collectively constituted the majority of striped bass diets. If blueback herring outcompete threadfin shad and become the dominant zooplanktivore in the system, the impacts could be potentially negative for striped bass, given the importance of threadfin shad as prey (Shepard and Maceina 2008, Bart et al. 2021), unless striped bass were to increase their consumption of blueback herring to compensate. Already, relative abundance of threadfin and gizzard shad have apparently declined following the introduction of blueback herring (C. McKee, personal observation). Largemouth bass are less likely to be impacted by the introduction of blueback herring because of greater reliance on sunfish and crayfish as prey items but could still suffer direct competition at larval stages or larval and egg predation. Positive impacts on Alabama bass due to the blueback herring introduction might be expected to result in both increased relative weight and individual growth given the level of contribution to their diets compared to largemouth bass and striped bass diets. However, significant increases were only observed for relative weight. Potential reductions in *Dorosoma* spp. abundance may limit impacts to Alabama bass growth as blueback herring replace shad in their diets. Alternatively, the increase in Alabama bass CPE after the blueback herring introduction could indicate that increased energy from blueback herring in Alabama bass diets may be allocated to reproduction rather than growth. However, these changes in CPE may be due to other factors that are changing in the reservoir that confound responses to the blueback herring introduction. As with most introductions, not all impacts are negative. Even though blueback herring are not contributing greatly to piscivore diets, known differences in caloric density compared to native prey may be responsible for the observed increased relative weights in this study (Bart et al. 2021).

Caution should be exercised when considering management activities that could potentially lead to the spread of blueback herring given the potential negative consequences for fish populations, aquatic communities, and ecosystem function (Johnson and Goetll 1999, Ellis et al. 2011, Vivian and Frazer 2021). Unintended consequences could also impact angler success and potentially cause a negative economic impact. For example, the striped bass fishery is an important economic activity for the area surrounding Lewis Smith Lake and negative impacts to the fishery could also result in fewer trips and reduced angler spending (Lothrop et al. 2014). Unfortunately, introductions are sometimes facilitated by individuals who are only interested in the potential positive effect the introduction might have on the species in which they are interested. Clearly a full understanding of the complexity of interactions that can occur when novel and potentially invasive species are introduced is needed (Johnson et al. 2009). In this instance, desired benefits to native predators are not yet manifesting, and the risks associated with blueback herring introductions do not appear to be worth the perceived benefits.

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Urban Deer Management Status within the United States: A Synthesis of State Wildlife Agencies' Urban Deer Management Resources

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Abstract: Across the U.S., the presence of white-tailed deer (deer; *Odocoileus virginianus*) in urban areas can create conflicts with residents (e.g., ornamental plant damage). State wildlife agencies approach urban deer management differently from traditional deer management due to diverse community groups, urban stakeholder viewpoints about deer, and other aspects of wildlife management in urban environments. With this variation in mind, we reviewed deer management resources across the U.S. to understand the current state of urban deer management. Of the 46 states with deer populations, 21 had publicly available deer management plans (DMPs; 46%), 22 had only online urban deer management resources available (48%), and three had no urban deer-related information available even though deer were present (7%). Our synthesis revealed that public input was incorporated in all DMPs including input from traditionally under-represented stakeholders. Of 21 DMPs, 16 (76%) incorporated urban deer management-related programs. Eighteen DMPs (86%) expressed deer impacts on people as a major issue. Subsequently, 13 DMPs (62%) contained focused goals addressing damage and conflict management. Lethal control remained the most common urban deer management tool. States' online urban deer management resources varied in content, quality, and ease of navigability. Overall, states lacked strategies, protocols, and supplemental resources to effectively address site-specific urban deer management. Our research identified urban deer management gaps in deer management resources, and we provide state wildlife agencies with eight recommendations for integrating urban deer management information. Managers can use our recommendations to help stakeholders address urban deer-related concerns, improve urban deer management materials, and facilitate state wildlife agency-stakeholder collaboration.

Keywords: community-based, conflict, damage, stakeholder, urban

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White-tailed deer (*Odocoileus virginianus*; hereafter, deer) overabundance in urban, suburban, and semirural areas (hereafter, urban) has been an ongoing problem in the U.S. After extirpation in many regions during the late 1800s through the early 1900s (Warren 2011), deer populations recovered in much of the U.S. (Decker and Connelly 1989). In the southeastern U.S., deer population densities have recovered to levels comparable to pre-Euro-American settlement of 54.3–59.7 deer km^{-2} (21–23 deer mi^{-2}; Hanberry and Hanberry 2020), but instances of greater deer densities (≥77.7 deer km^{-2} [≥30 deer mi^{-2}]) are also common in urban areas across the U.S. (DeNicola and Williams 2008, Urbanek and Nielsen 2013). Human populations in metropolitan areas across the U.S. increased 9% from 2010–2020 (U.S. Census Bureau 2021) while urban and agriculture development simultaneously increased (Kim 2000, Hanberry and Hanberry 2020, Lichter et al. 2020). These alterations to the human-deer interaction interface have supported increased negative interactions between deer and humans, often resulting in deer populations exceeding social carrying capacity in urban areas (Decker and Chase 1997, Parsons 1998, Warren 2011, Hanberry and Hanberry 2020). Additionally,

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deer often experience high survival and fecundity (Etter et al. 2002, Storm et al. 2007) in developed areas because of nutritious food resources and lack of predation and hunting pressure (Butfiloski et al. 1997, Stout et al. 1997, Lauber and Knuth 2000, Curtis 2020). Larger deer populations come with associated drawbacks such as vehicle collisions (Huijser et al. 2009, IIHS 2019), damage to landscape plantings (Connelly et al. 1987, Kilpatrick and LaBonte 2003, Urbanek et al. 2013), agricultural depredation (Conover 1995, West and Parkhurst 2002), and concerns about deer impacts to human health (Kilpatrick and Walter 1997, Stout et al. 1997, Rudolph et al. 2011). Therefore, the negative impacts of overabundant deer populations in urban landscapes justify urban deer management actions that effectively reduce deer-human conflicts.

Managing urban deer is complicated. Under the public trust doctrine, state wildlife agencies (hereafter, SWAs) are entrusted to sustainably manage deer for all potential beneficiaries (Rudolph et al. 2011, Westerfield et al. 2019, Stinchcomb et al. 2022). While SWAs have traditionally managed deer populations with regulated hunting (Doig 1995, Geist et al. 2001), hunting is restricted in urban areas due to limited access, legal constraints, human safety concerns, and non-consumptive social values (Butfiloski et al. 1997, Messmer et al. 1997b, Stout et al. 1997, Rudolph et al. 2011, Curtis 2020). Social factors add complexity to urban deer management because stakeholder groups hold diverse views on wildlife making it difficult to reach a consensus on proposed management solutions (Decker and Enck 1996, Messmer et al. 1997a, Baker and Fritsch 1997, Parsons 1998, West and Parkhurst 2002). Regardless of social complexities, previous research has recommended that SWAs incorporate urban stakeholders into deer management decisions (Decker and Chase 1997, Messmer et al. 1997a, Koval and Mertig 2004, Urbanek et al. 2012, Curtis 2020). As a result, several SWAs have begun to integrate urban stakeholder input into deer management planning processes (Anderson 1997, Raik et al. 2003, Raik et al. 2006, Rudolph et al. 2011, Baumer and Pomeranz 2017).

How SWAs incorporate urban deer management into their publicly available white-tailed deer management plans (hereafter, DMPs) has been unclear (Messmer et al. 1997a, Urbanek et al. 2011). Messmer et al. (1997a) and Urbanek et al. (2011) reported that most SWAs acknowledge that urban deer issues exist; however, few SWAs have developed urban deer management resources, and even fewer have incorporated stakeholder input. In the mid-1990s, some SWAs began engaging with communities and other stakeholder groups, in a process commonly known as community-based deer management, to collaboratively formulate site-specific deer management (i.e., municipality level) rather than statewide urban deer management planning (Raik et al. 2003, Decker et al. 2004, Lauber 2010, Curtis 2020). The effectiveness of community-based deer management can depend on several factors. A community's capacity to learn, lead, and gather for a collective purpose are important dimensions to achieve successful community-based deer management (Raik et al. 2005, Raik et al. 2006). The level of SWA involvement in decision making has also been suggested to play a role in the effectiveness of community-based deer management (Decker and Chase 1997, Raik et al. 2003). Rudolph et al. (2011) and Baumer and Pomeranz (2017) proposed that if deer management plans in general have defined clear, practical, and relevant topic categories (e.g., goals, objectives, management actions, budget, timetable, etc.), then community-based deer management has a higher likelihood of progressing effectively.

Community-based deer management is an important first step in SWAs' involvement in urban deer management. However, a research gap exists in identifying the status of state-specific urban deer management planning and ascertaining the type, content, and quality of available resources related to urban deer management. Our research aims to 1) characterize the status of SWA urban deer management across the U.S.; 2) describe best-management practices available for urban deer management; 3) increase the understanding of stakeholder involvement in decision-making for urban deer management; and 4) provide recommendations on how SWAs can incorporate stakeholder input and urban deer management practices into urban deer management planning. Understanding the current state of urban deer management will enable SWAs to evaluate their resources, identify where resources are underperforming, and identify best management practices available to ensure urban deer management efforts are effective.

Methods

From January 2022 through January of 2023, we searched for digitized DMPs using internet search engines, a list of general keywords (e.g., "management plan," "deer") and specific phrases (e.g., "Minnesota white-tailed deer management plan," "Deer management in Ohio"), SWA employee contacts, and by directly accessing SWA websites. In each DMP, we noted specific details to characterize the current state of urban deer management (Table 1). We categorized SWA issues related to urban deer including: 1) deer impacts on people (e.g., property damage, deer vehicle collisions, human health); 2) impacts on deer (e.g., diseases, non-hunting mortality events, supplemental feeding); 3) deer impacts on ecosystems (e.g., damage to ecosystem structure and function, impacts to biodiversity, invasive species spread); 4) hunters and hunting (e.g., opportunities to hunt, decreased access to private lands, retaining hunters); 5) changing views and land uses (e.g., conflicting stakeholder views, urbanization, support for hunting); 6) rules and regulations (e.g., local firearm ordinances, changing

Table 1. Ten standardized factors noted from publicly available state white-tailed deer management plans to better understand the status of urban deer management in the U.S.

Plan detail	Definition	Example(s)
State issues	Specifically mentioned problems that states are facing when managing deer.	Deer impacts on people
Stakeholder input	Public input utilized for decision-making and plan creation.	Stakeholder comments taken after a public meeting
Urban deer management section	A major section heading focusing on urban deer management topics in a respective state.	Georgia's 17-page urban deer management section
Goals	Broad statements about an agency's aim to manage specific resources related to urban deer management.	Be responsive to public concerns and maintain open communication with the public regarding deer-related issues[a]
Objectives	Statements about what an agency plans to achieve in relation to an urban deer management-related goal.	Provide assistance to the public regarding deer-human conflicts[a]
Strategies	Statements about what actions will be taken to achieve an urban deer management-related objective.	Use various media outlets to distribute information which addresses deer-human conflicts[a]
Notable details	Unique urban deer-related information not contained in goal, objective, or strategy sections.	Programs available to resolve urban deer-human conflict
Supplemental materials	Additional resources listed to educate the public about, or help resolve, urban deer-related issues.	Damage prevention technical guides
Available staff	State wildlife agency employee(s) designated to help resolve deer-human conflicts.	An urban deer biologist
Management techniques	Methods used by state agencies, or residents, to manage urban deer.	Lethal control, repellents, and exclusion

a. AGFC 2019.

hunting seasons and limits); and 7) education (e.g., educating the public about deer and deer management).

We searched for additional urban deer management resources by examining SWA websites. We only considered additional resources that were linked on respective SWA websites and that were directly related to resolving deer-human conflicts in urban settings. For example, technical guides and SWA deer management websites were considered official additional resources. Technical guides provided steps for urban communities to understand and resolve urban deer issues, and SWA deer management websites provided methods to minimize deer-human conflicts. Additionally, we contacted two SWA employees from Alabama and West Virginia for help locating respective online urban deer management-related resources. Using information from DMPs and additional SWA resources, we characterized the current state of SWA urban deer management.

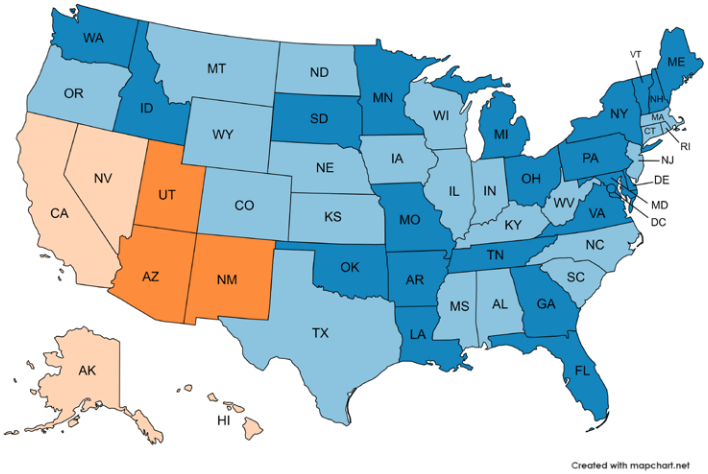

Figure 1. State designations of publicly available urban deer management-related resources across the U.S. as of 9 January 2023. Dark blue: urban white-tailed deer management considered in state white-tailed deer management plan; Light blue: only online urban white-tailed deer management resources available; Dark orange: no white-tailed deer plan or urban white-tailed deer management resources available; Light orange: no white-tailed deer populations in the state.

Results

Of the 46 states with deer populations, 21 (46%) SWAs had DMPs (Figure 1). All urban deer management-related information was included within DMPs, and no SWA had a stand-alone urban deer management plan. Nineteen DMPs (90%) discussed issues that managers face in their respective states (e.g., deer impacts on people; Table 2), as well as common goals (e.g., hunting and deer-related recreation; Table 3). Deer population management was the most frequently mentioned goal in all 21 DMPs, and 13 DMPs (62%) noted damage management and conflict management as important goals.

Among DMPs, several themes for urban deer management approaches emerged. First, all DMPs noted that technical assistance is a standard practice for urban deer management (e.g., in-person assistance to a homeowner's association, technical guidance over the phone to a property owner experiencing damage). Second, all DMPs incorporated public input from both non-traditional (e.g., non-hunters, animal activists) and traditional (i.e., hunters and farmers) stakeholder groups in some capacity. For instance, Maryland hosted public meetings to solicit feedback from stakeholders and formally surveyed 2200 of its residents (i.e., 800 from the public, 800 deer hunters, and 600 landowners) in 2018

Table 2. Publicly available state white-tailed deer management plans in the U.S. ($n = 21$) that note having management issues that fall into seven issue categories as of 9 January 2023. "X" marks a state that acknowledged a particular issue in their plan.

State plan	Changing views and land uses	Impacts on deer	Deer impacts on people	Hunters and hunting	Deer impacts on ecosystems	Rules and regulations	Education
Arkansas	X	X					X
Delaware	X	X	X	X	X		X
Florida	X	X	X		X		X
Georgia	X	X	X	X	X	X	X
Idaho	X	X	X	X			
Louisiana	X	X					
Maine	X	X	X	X	X	X	
Maryland	X		X	X	X		
Michigan	X	X	X	X	X		X
Minnesota	X	X	X	X	X		
Missouri	X	X	X	X			
New Hampshire	X	X	X	X	X		
New York	X	X	X	X	X	X	X
Ohio	X	X	X	X			
Oklahoma							
Pennsylvania		X	X		X	X	
South Dakota	X	X	X	X			
Tennessee	X	X	X		X		
Vermont	X	X	X	X	X		
Virginia	X	X	X	X	X	X	
Washington	X	X	X	X		X	
Number (%) of plans	19 (90)	19 (90)	18 (86)	15 (71)	13 (62)	6 (29)	6 (29)

Table 3. Publicly available state white-tailed deer management plans in the U.S. ($n = 21$) that have goals in seven frequently mentioned goal categories as of 9 January 2023. "X" marks a state that acknowledged a particular goal in their plan.

State plan	Deer population management	Hunting and deer-related recreation	Communication and education	Damage and conflict management	Habitat	Achieving stakeholder satisfaction	Operational resources
Arkansas	X		X		X	X	
Delaware	X	X	X	X	X		X
Florida	X				X	X	
Georgia	X	X	X	X			
Idaho	X	X		X	X		
Louisiana	X	X	X	X	X	X	
Maine	X	X	X			X	
Maryland	X	X	X	X			X
Michigan	X	X	X	X	X		
Minnesota	X		X	X	X	X	X
Missouri	X	X	X				
New Hampshire	X			X			
New York	X	X	X	X	X		X
Ohio	X	X	X				
Oklahoma	X	X	X		X	X	
Pennsylvania	X	X	X	X			
South Dakota	X				X	X	
Tennessee	X		X	X		X	X
Vermont	X	X		X	X	X	
Virginia	X	X		X	X		
Washington	X	X			X		
Number (%) of plans	21 (100)	15 (71)	14 (67)	13 (62)	13 (62)	9 (43)	5 (24)

Table 4. Publicly available state white-tailed deer management plans in the U.S. ($n = 21$ plans) that noted deer management techniques in the context of urban deer management as of 9 January 2023.

Technique	State Plan	Number (%) of plans
Lethal control	Arkansas, Delaware, Florida, Georgia, Idaho, Louisiana, Maine, Maryland, Michigan, New York, Ohio, Oklahoma, Pennsylvania, South Dakota, Tennessee, Vermont, Virginia, Washington	18 (86)
Modifying human behavior	Arkansas, Delaware, Florida, Georgia, Louisiana, Maryland, Michigan, New York, Oklahoma, Pennsylvania, South Dakota, Tennessee, Vermont, Virginia	14 (67)
Exclusion	Delaware, Georgia, Idaho, Maryland, Michigan, Minnesota, South Dakota, Vermont, Virginia	9 (43)
Repellents	Delaware, Georgia, Maryland, Michigan, Minnesota, South Dakota, Virginia	7 (33)
Fertility control	Delaware, Georgia, Maryland, Pennsylvania, South Dakota, Vermont, Virginia	7 (33)
Harassment or scare devices	Delaware, Idaho, Michigan, Minnesota, South Dakota, Virginia	6 (29)
Relocation	Delaware, Georgia, Maryland, Pennsylvania, South Dakota, Vermont	6 (29)
Changing regulations	Georgia, Idaho, Maryland, Oklahoma, South Dakota	5 (24)
Habitat modification	Georgia, Michigan, South Dakota	3 (14)
Predator reintroduction	Delaware, Georgia, Maryland	3 (14)
Changing infrastructure	Delaware, South Dakota	2 (10)

to ascertain their views on deer management issues. Other states scientifically surveyed public viewpoints on deer and deer management by creating surveys through their SWA (e.g., Minnesota) or through a third-party (e.g., Georgia contracting with Responsive Management Inc.). Additionally, states such as South Dakota created citizen task forces to provide public input-based deer management recommendations. The last theme shared across all DMPs was that their respective SWAs were actively developing plans, policies, and/or programs, as well as training their staff, to effectively manage urban deer-related issues. Sixteen DMPs (76%) specifically listed developing or currently available urban deer management programs. Vermont, for instance, used the Landowner-Hunter Connection program to match landowners experiencing deer damage with hunters to reduce locally overabundant populations. Additionally, Louisiana was developing urban archery hunt programs to reduce urban deer populations. Minnesota and New York were, in some areas, monitoring the outcomes of deer population reductions using a program called Assessing Vegetation Impacts from Deer (Curtis et al. 2021), which monitors deer browsing pressure on woodland vegetation to determine if deer population reductions have improved vegetation growth over time.

Georgia, Idaho, Pennsylvania, and South Dakota (19%; 4 DMPs) were the only SWAs to incorporate a specific urban deer management section in their DMPs. The other 17 SWAs only included aspects about how they planned to address urban deer management through other sections of their plans. Delaware, Idaho, New Hampshire, New York, Pennsylvania, and Virginia (29%) were the only SWAs to provide urban deer management supplemental materials (e.g., hyperlinks to deer-human conflict resolution resources) in their DMPs. However, few hyperlinks to supplemental materials were functional and some supplemental materials did not have associated hyperlinks. Delaware, Maryland, and New York (14%) were the only SWAs to note staff designated to help resolve deer-human conflicts in their DMPs. For example, New York's Big Game Team offered educational resources, recommendations, and strategies for communities to manage deer. Deer management plans often mentioned management techniques proposed for urban deer management (Table 4). Lethal control was the most common urban deer management technique encouraged by 18 of the 21 DMPs (86%). Some DMPs mentioned management techniques such as fertility control (33%; 7 DMPs), relocation (29%; 6 DMPs), and predator reintroduction (14%; 3 DMPs) but discouraged SWA personnel and stakeholders from using these techniques because of practicality, safety concerns, cost restraints, time considerations, disease transmission potential, legal constraints, and other factors.

Of the 46 states with deer populations, 25 (54%) SWAs did not have a DMP. Of these states, 22 (88%) had online urban deer management resources available (e.g., technical guides and SWA deer management websites). However, the amount of information available, ease of locating the information, and type of information available were highly variable. Five of the 22 states (23%) had technical guides available (e.g., Connecticut, Indiana, New Jersey, Rhode Island, Texas), and all 22 states had SWA deer management websites (e.g., Alabama, Colorado, Connecticut, Illinois, Indiana, Iowa, Kansas, Kentucky, Massachusetts, Mississippi, Montana, Nebraska, New Jersey, North Carolina, North Dakota, Oregon, Rhode Island, South Carolina, Texas, West Virginia, Wisconsin, and Wyoming), which included nuisance deer websites, living with deer websites, deer damage websites, and conflict control websites.

Discussion

Based on our results, SWAs have improved how they approach urban deer management compared to previous studies. In 2011, only 33 SWAs considered urban deer an issue in their state (Urbanek et al. 2011). At the time of this study, 43 SWAs had resources available to address urban white-tailed deer issues. In 1997, only 6 of 21 state urban deer management programs were developed with public input (Messmer et al. 1997a), while all 21 DMPs during the time of our synthesis integrated public input formally (e.g., human dimensions surveys), informally (e.g., holding a public meeting), or a combination thereof. Throughout DMPs, lethal control remains the most encouraged urban deer management technique, but DMPs highlighted that SWAs are frequently encouraging their staff and stakeholders to also utilize non-lethal management techniques (e.g., exclusion, repellents, scare devices, changing laws and ordinances, and modifying infrastructure and habitat resources) to mitigate deer-human conflicts. Researchers have encouraged SWAs to use social science methods (e.g., surveys, focus groups, citizen task forces, workshops) to improve the effectiveness of urban deer management techniques, better understand stakeholder perceptions of deer-human conflicts, and enhance the quality of public input (Decker and Enck 1996, Decker et al. 2002, Urbanek et al. 2012, Curtis 2020). Our research demonstrates that SWAs are incorporating more social science methods into their public input and planning processes.

Even though SWAs are making improvements in urban deer management resources, many still fall short in specific areas. For instance, 22 of the 46 states with deer populations were missing DMPs, and only 4 DMPs included urban deer management sections. Other DMPs were missing hyperlinks, or provided non-functional hyperlinks, to urban deer management-related supplemental materials which could provide stakeholders additional opportunities to learn more about minimizing deer-human conflicts. Lastly, 18 DMPs did not list specific staff designated to help resolve deer-human conflicts. Furthermore, the DMPs that did have staff listed did not include sufficient contact information (i.e., phone numbers, email addresses) for those individuals. Shortfalls with SWA urban deer management resources leave stakeholders struggling to locate resources and make it difficult to interpret available information. Improving urban deer management resources would assist SWAs in meeting expectations set by the public trust doctrine to sustainably manage deer for all potential beneficiaries.

Most SWAs have opportunities to improve the structure and content of urban deer management information in DMPs. State wildlife agencies should aim to proactively address urban deer management issues but recognize if their agency can, or has enough justification to, allocate sufficient resources to urban deer management (McMullin et al. 1993, Doig 1995, Hewitt and Messmer 1997). One option that SWAs can use to begin improving their urban deer management resources is to designate a specific urban deer management section in their DMP. We recommend that urban deer management sections should include the eight characteristics detailed in Table 5. Regarding recommendation seven, community-based deer management strategies should include four elements. First, strategies should address how SWAs can collaborate with communities to build partnerships, local leadership, credibility, common purpose, and knowledge (Raik et al. 2003, Raik et al. 2005, Curtis 2020). Second, strategies should address how communities can establish clear, practical, and relevant objectives (Rudolph et al. 2011). Third, strategies should articulate what should be included in a community-based deer management plan (e.g., budgets, timetables, how to measure and evaluate outcomes, establish who is responsible, identify permitting requirements; Baumer and Pomeranz 2017, Westerfield et al. 2019, Curtis 2020). Finally, strategies should address how a SWA plans to follow-up with collaborating communities once plans have been implemented.

Table 5. Eight recommended characteristics that state wildlife agencies can include in urban deer management resources to help improve state urban deer management.

Recommendations
Provide background information on urban deer management in their state (e.g., how deer-human conflicts have changed in urban areas over time, economic costs and benefits, review of urban deer management literature, stakeholder views).
Articulate goals, objectives, and strategies directly related to how a state plans to address urban deer management.
Describe urban deer management techniques that are available, encouraged, discouraged, and commonly used by stakeholders and state wildlife agency staff.
List specific contact information for staff, or external contractors, specifically trained to resolve deer-human conflicts.
Include links to other urban deer management supplemental materials (e.g., deer-human conflict resolution websites).
Describe programs available in the state used to assist in urban deer management (e.g., urban deer hunter certification programs).
Articulate strategies for community-based deer management that can be implemented across the state.
Provide anonymous community-based deer management plan examples detailing what prompted each community to act, challenges they faced, outcomes they experienced, how they built community support, and how they managed negative publicity.

State wildlife agencies can scale and adapt our eight recommendations based on their staffing resources, financial capacity, time allocation ability, general SWA culture, potential for litigation, stakeholder needs, and other factors. For instance, if a SWA has sufficient resources and few urban areas with deer-human conflicts, it may choose to focus on creating an urban deer management section within its DMP, conducting community-based deer management, and providing on-site technical assistance. Conversely, if a SWA has limited resources and numerous urban areas with deer-human conflicts, that SWA may choose to create online, self-help type resources focusing on certain recommendations that stakeholders may deem important (e.g., recommendation 3, 5, and 6; Table 5). Furthermore, if a SWA does not have the capacity to create online, self-help type resources, that SWA can point stakeholders to preexisting urban deer management resources such as Cornell University's Community Deer Advisor website (https://deeradvisor.dnr.cornell.edu/). If stakeholder groups or individuals challenge a SWA on lethal deer management techniques, that SWA may choose to focus on collecting additional public input to explore management techniques (e.g., fencing, education) that could be used to reduce deer-human conflicts instead of focusing on reducing deer populations through lethal control. If SWAs scale and adapt our eight recommendations to fit their capabilities and the needs of their stakeholders, then they should have sufficient urban deer management resources to address deer-human conflicts in their region.

Management Implications

Traditional resource management has often been seen as reactive (Decker et al. 1983, Lal et al. 2001). However, we found several DMPs that indicated SWAs are transitioning to proactive deer management (e.g., FFWCC 2008, VDGIF 2015, SDDGFP 2017, IDFG 2019, TWRA 2019). Our recommendations (Table 5) will allow SWAs to take the necessary steps to proactively manage deer. When SWAs provide stakeholders with the proper tools, contacts, background information, strategies, and resources, stakeholders are empowered to manage localized deer conflicts themselves. If stakeholders need additional assistance, our recommendations provide SWAs with the foundation to create protocols to assist. Establishing clear guidelines for urban deer management will enable SWAs and stakeholders to navigate their way through community-based deer management together.

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What are Hunters Willing to Pay for Chronic Wasting Disease (CWD) Management? A Comparison of Different Contingent Valuation Approaches

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Abstract: Wildlife management agencies in regions where chronic wasting disease (CWD) is prevalent have adopted costly management practices to mitigate the spread of this fatal and highly transmissible disease. Non-market valuation represents a critical tool for managers attempting to address these costs, but the mode and methods of contingent valuation (CV) questions can impact valuations due to biases inherent to self-reporting economic decisions. We administered online ($n = 1430$) and phone ($n = 602$) surveys in North Carolina and South Carolina to assess what hunters with licenses to hunt white-tailed deer (*Odocoileus virginianus*) were willing to pay for CWD testing and carcass disposal across survey modes and CV methods. Among the online survey respondents, 34.1% ($n = 488$) were willing to pay for testing and 43.4% ($n = 620$) were willing to pay for disposal. From our phone sample, 48.6% ($n = 293$) were willing to pay for testing and 50.7% ($n = 306$) for disposal. Survey mode affected mean willingness to pay (WTP) in open-ended questions, with lower estimates from the online survey ($M =$ US\$15.96 for testing; \$14.74 for disposal) than for the phone survey ($M =$ \$22.90 for testing; \$22.80 for disposal). Different CV methods, however, yielded minor differences in WTP estimates reported on our phone survey (dichotomous choice: $M =$ \$24.80 for testing; \$24.50 for disposal). Greater WTP estimates in phone surveys, relative to online, may be explained by interviewer effects. The fact that cost-efficient, open-ended WTP methods produced average WTP values nearly identical to those generated by the more complex and costly dichotomous choice methods is encouraging, but greater variance for open-ended methods remains an important limitation. Our research provides some justification for using relatively easy open-ended CV methods of assessing WTP for wildlife disease management and underscores the need to account for survey mode when collecting and interpreting data about WTP.

Key words: economics, human dimensions, non-market, social science, wildlife disease

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Recent outbreaks of wildlife diseases have made disease management a policy priority for state wildlife agencies. The World Health Organization recognizes wildlife diseases, especially those with zoonotic potential, as a global concern, with potential for significant economic impacts (Thulin et al. 2015). With limited public funding available for management, policy makers and management officials need to be able to justify and encourage public investment in wildlife disease mitigation. Non-market valuation methods can serve as a critical tool in disease management and decision making by informing efforts to estimate costs of effectively managing wildlife diseases (Bennett and Balcombe 2012), as well as efforts to assess potential economic support for management among key stakeholder groups (Smith et al. 2019, Ufer et al. 2022). Non-market valuation allows for the estimation of values people place on ecosystem goods and services for which there are no market prices (Manero et al. 2022). One of the challenges in managing wildlife disease is the lack of measurable transactions; however, application of non-market valuation methods can assist with placing an economic value on mitigating impacts of wildlife diseases.

Contingent valuation (CV) may be the most frequently used

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non-market valuation tool for estimating the costs and benefits of wildlife disease management (Elkstrand and Loomis 1997, Ufer et al. 2022). With the contingent valuation method, respondents are asked to state their preferences in hypothetical or contingent markets that allows analysts to estimate demands for goods or services that are not traded in markets (Bishop and Heberlein 1979). This tool is widely used in cost-benefit analysis and environmental impact assessment (Kapper 2004). Contingent valuation approaches, usually asked via a survey, form the core of economic valuation studies investigating wildlife disease management because they reveal patterns in the public's willingness to pay (WTP) for solutions (Mitchell and Carson 1988). Willingness to pay provides a monetary measure of how much the good or service is worth to individuals. Contingent valuation studies are used to measure the public's WTP for a myriad of conservation goods including preventing species loss by introducing a hypothetical plan to protect habitat of endangered species (Elkstrand and Loomis 1997) and maintaining non-consumptive wildlife tourism by proposing a wildlife conservation trust fund (Barnes et al. 1999).

The CV approaches used in many wildlife disease economics studies may, however, be vulnerable to at least two forms of bias. First, the mode of administration can introduce limitations. For example, online surveys tend to overrepresent high income and younger demographics (Ball 2019) and both groups tend to report higher WTP than their counterparts, yielding higher overall CV estimates. As another example, social desirability bias may also contribute to lower WTP values in mail surveys relative to telephone surveys, where respondents attempt to show support for interviewers by reporting higher WTP values (Lindberg et al. 1997). Second, frequent usage of open-ended rather than dichotomous choice questions in wildlife disease related CV research may also create biased valuation estimates. Surveys using open-ended questions may yield low response rates, high item nonresponse, and possibly inaccurate valuations because they lack cues to realistic values (Frew et al. 2003). Further, open-ended formats are vulnerable to strategic bias because the respondent has more autonomy to answer the WTP question in a way that is favorable to them (Doyon and Bergeron 2016). Scholars also suggest dichotomous choice methods yield more valid results because people are conditioned to choose whether to purchase a good at a set price in everyday activities (Kealy and Turner 1993). Despite multiple limitations, open-ended CV approaches offer important benefits including reduced starting point biases (Lusk and Hudson 2004) and avoiding 'yeah-saying' (i.e., a respondent's tendency to say "yes" to any payment amount for provision of a public good without really meaning it) from the respondent (Alvarez-Farizo et al. 1999). Evidence suggests mean WTP values found from the dichotomous choice methods consistently exceeded the mean WTP values derived from the open-ended methods (Brown et al. 1996).

We build on this research by comparing estimates of WTP for chronic wasting disease (CWD) management derived from two types of survey modes (online and phone) and valuation methodologies (open-ended and dichotomous choice questions) for North and South Carolina hunters. CWD is a fatal disease that is associated with a prion found in the central nervous system of family Cervidae. The threat posed by CWD has become an obstacle to maintaining hunting participation around the U.S. (Lyon and Vaske 2010), with the potential to reduce the economic stability of the communities that depend on white-tailed deer (*Odocoileus virginianus*) hunting (Needham et al. 2004). CWD is a costly disease because wildlife agencies have to provide financial support to increase surveillance and security of highly impacted areas (Rivera et al. 2019), compensate for sample testing (Carlson 2018), and pay for the depopulation of captive cervid facilities (WLAB 2006).

We focused on hunters' WTP for CWD testing and carcass disposal, two services critical to control the disease. Both services could also be considered public goods in the eyes of hunters. Recent studies have assessed hunters' WTP for other CWD management practices, such as acquiring a voucher for free processing of a deer (Adhikari et al. 2022) or purchasing a voluntary CWD stamp to fund disease prevention (Ufer et al. 2022). However, to our knowledge, no other study has reported the amounts that hunters, or any other stakeholder group, would be willing to pay for both CWD testing and safe disposal. We addressed three research questions: (1) What is the predicted amount that the "average" hunter would be willing to pay for testing and disposal across both online and phone surveys derived from the open-ended and dichotomous choice questions?; (2) How different are the average WTP amounts for testing and disposal derived from the open-ended questions across both survey modes and derived from the phone survey across both CV methods?; and (3) How do the demographic attributes of hunters predict their WTP for testing and disposal? The CWD management context represents an important one for understanding biases in non-market valuation given both the growing cost of managing this disease and the rapid expansion of economic research employing diverse modes and methods.

Methods

Survey Methods

Our study of hunters' WTP for CWD management focused on two southeastern states: North Carolina, where the disease was detected in 2022, and South Carolina, where the disease had not yet been detected at the time of the study. In North Carolina, we administered our survey to a simple random sample of 8490 adult (age 18 yr or older) North Carolina-licensed hunters who were licensed to hunt white-tailed deer between 2018 and 2020. Most (*n* = 5178) had email addresses and received invitations to take an online Qualtrics (Qualtrics, Provo, Utah) survey in March of 2022. Participants contacted via email were sent one invitation and three reminders, each sent a week apart (Dillman et al. 2014). We deleted records for those who requested to be removed from the contact list (*n* = 9). The hunters who did not share email addresses were mailed postcards (*n* = 3312) with a link and a QR code to the online survey. We mailed three postcard reminders at two-week intervals.

In South Carolina, we administered a survey to a simple random sample of 10,000 adult (age 18 yr or older) South Carolina-licensed hunters who were licensed to hunt white-tailed deer in 2022. We sent them email invitations to take an online Qualtrics survey in October 2022. As with the North Carolina survey, we sent one invitation email and three reminder emails, each sent a week apart. We deleted records of those who asked to be removed from the contact list for this study (*n* = 7).

We also conducted phone interviews with hunters who had not responded to the requests to complete the online survey, starting in June 2022. The phone-based questionnaire used a subset of the questions from the online instrument that included willingness to pay (WTP) items. In North Carolina, the phone survey sample was randomly selected from the nonrespondents to the online survey (*n* = 9000). In South Carolina, the phone survey sample was randomly selected from a list of hunters who did not respond to the online survey (*n* = 8000) and hunters who did not have an email address on file (*n* = 230). This study was approved by the Human Subjects Institutional Review Board of North Carolina State University (protocol #24355).

We consulted with North Carolina Wildlife Resources Commission (NCWRC) biologists to ensure our questionnaire language and content were factually correct and appropriate. We pretested the questionnaire with 200 randomly selected hunters from the same population as the main survey, 121 of whom received an email link and 79 of whom received a postcard to complete our survey. Then, following previous examples of scale validation (Peterson et al. 2017, Valdez et al. 2018, Casola et al. 2020), we conducted cognitive interviews with 10 additional hunters whom we knew through personal acquaintances (graduate students, faculty, etc.).

We administered our online survey to North Carolina hunters from March to May of 2022, so it did not coincide with the state's white-tailed deer hunting season (September to February). We independently measured WTP for CWD testing and WTP for safe disposal of a CWD-infected carcass with two separate open-ended questions. Before we asked participants the WTP for CWD testing and disposal questions, we primed them with the following context: "Testing harvested deer for CWD and disposing of CWD infected carcasses in a safe way can be an expensive part of effective CWD management. Safe disposal of deer carcasses that are infected with CWD requires burial, incineration, or using a sanitary landfill. In the following questions, please think about how important testing and carcass disposal is to you and how much you would be willing to pay for these management activities." We then asked participants if they were willing to pay a fee to get a deer that they harvested tested for CWD. If the participant said "yes," we asked, "How much would you be willing to pay to get a deer you harvested tested for CWD?" as an open-ended question. After the questions on CWD testing, we applied the same approach towards determining hunter willingness to pay for CWD disposal. We asked the participants if they were willing to pay a fee to safely dispose of the carcass if they harvested a deer in a county in which CWD was prevalent. If the participant said "yes," we asked, "How much would you be willing to pay to safely dispose of the carcass?" as an open-ended question. Participants were not required to answer any of these four WTP questions.

All participants were asked to indicate their gender identity (male, female, or other), age (phrased as what year they were born), education (less than a high school diploma, high school or GED, college degree, or advanced degree beyond 4-yr degree), political identity (assessed using a five-point scale, adapted from Casola et al. (2020) and Beall et al. (2021), ranging from very conservative to very liberal), and current approximate annual household income before taxes, ranging from less than US$10,000 to $150,000 or more.

For South Carolina's online survey instrument, we used the same questions as North Carolina's online survey instrument (other than changing North Carolina to South Carolina in the question stems). This enabled us to make direct comparisons between states during analyses. An unexpected new detection of CWD in North Carolina forced us to make several small changes to the online survey instrument during data collection after 343 responses were already recorded. We changed the wording of some questions to reflect the most up-to-date status of CWD in North Carolina (e.g., we changed "If Chronic Wasting Disease is detected in North Carolina, how much would you be willing to pay to get a deer you harvested tested for CWD?" to be "How much would you be willing to pay to get a deer you harvested tested for CWD?"), but the instruments in both states were completely identical outside of these changes. The online survey to South Carolina hunters was administered from October to November of 2022, which overlaps with the white-tailed deer hunting season for this state (August to January).

Phone survey for both states consisted of a subset of questions from the online survey, including the open-ended WTP questions, and a set of dichotomous choice contingent valuation questions to estimate the non-market value of CWD testing and disposal (Hanemann et al. 1991). For the dichotomous choice questions, we presented randomized initial bid amounts from a pre-selected set of values of \$5, \$10, \$15, \$20, and \$25. These amounts were suggested by the NCWRC team responsible for the CWD Response Plan, and they are based on both the cost of testing during the study period and what they considered realistic fee amounts. The range of potential bid amounts reflected what the NCWRC considered management-relevant ranges high enough to defray costs, but low enough to be feasible. If the respondent said "yes" to the initial bid amount (either \$10, \$15, or \$20), we presented a follow-up question with a second bid that was randomly selected from the selection of larger values. If the respondent said "no" to the initial bid amount, the randomly selected follow-up bid we provided was a lower amount (Hanemann et al. 1991). This dichotomous choice methodology produced intervals within which the respondent's true WTP amount was nested. For example, if the respondent said yes to the initial bid of \$10 and no to a follow-up bid of \$20, then we would know their true WTP is between \$10 and \$20. After the questions on CWD testing, we applied the same approach towards determining their willingness to pay for CWD disposal. We asked participants if they were willing to pay a fee for safe disposal if they harvested a deer in a county in which CWD was prevalent. If the participant said "yes," we would ask them the WTP bid questions. We used the same values of \$5, \$10, \$15, \$20, and \$25 for the disposal questions. The phone surveys were conducted from June 2022 to January 2023 in North Carolina and December 2022 in South Carolina.

Data Analysis

First, we calculated the number of respondents who were willing to pay for both CWD testing and disposal using descriptive statistics (e.g., counts and percentages). For phone surveys, we defined compliance rate as the proportion of people from the sample frame who answered questions after answering the phone. We then calculated mean WTP based on open-ended responses. We fit linear regression models in R (R Core Team 2021) to estimate the effect of all variables on WTP for the subset of the sample who indicated they would be willing to pay for each form of CWD management. Then, we used the linear regression models to predict specific values for mean WTP and their associated 95% CIs for testing and disposal for the average respondent from the open-ended questions on our online survey and phone survey (Research Question 1).

Using the dichotomous choice responses for WTP for CWD testing and disposal, we fit a parametric accelerated failure time model using the "survival" package (Therneau and Grambsch 2000) in R (R Core Team 2021). This allowed us to create an interval censored regression model that estimated parameters by maximum likelihood (Batte et al. 2007, Yang et al. 2014, Dahal et al. 2018). A gaussian distribution was used in the final analysis because it has a strong theoretical foundation within WTP studies (Ghosh et al. 2013, Daziano and Achtnicht 2014). The natural log of the WTP interval was modeled as a function of gender (indicator: female = 0, male = 1), age (a continuous variable), and education level (indicator: no college = 0, college = 1). We used the interval censored regression model to predict mean WTP for testing and disposal from the dichotomous choice questions on our phone survey (Research Question 1).

For both survey modes and CV methodologies, we generated a mean WTP estimate and associated 95% confidence intervals using the 'predict' function in R. We report modified confidence intervals since we limited the lower confidence limit to \$0.00 to demonstrate the fact that WTP would not be negative (Haab and McConnell 1998, Hanley et al. 2009). To compare WTP value estimates for testing and disposal across survey mode and CV method, we used 95% confidence intervals to assess differences (Research Question 2). We only compared dichotomous choice and open-ended estimates using the phone survey data to reduce the burden for participants in the online survey (specifically, the time required to complete the dichotomous choice questions) and leverage the ability of interviewers to assist participants over the phone as they answer the relatively complex dichotomous choice questions (Arrow et al. 1993, Chung and Chiou 2017).

We used linear regression models to examine associations between demographic variables and our two dependent variables: (1) WTP amounts for testing reported from the open-ended questions on the online and phone surveys and (2) WTP amounts for disposal reported from the open-ended questions on the online and phone surveys (Research Question 3). For the online survey, the demographic attributes included gender (0 = female, 1 = male), age (continuous variable), education level (coded as a categorical variable from 1 being less than high school diploma to 4 being advanced degree beyond 4-yr degree), political identity (0 = Moderate/Liberal, 1= Conservative), income level (coded as a categorical variable from 1 being <\$10,000 to 9 being ≥\$150,000), and state (0 = South Carolina, 1 = North Carolina). For the phone survey, the demographic attributes only included gender, age, education level, and state. Prior to interpreting models, we tested for assumptions of multicollinearity in our regression models using variance inflation factors (VIFs) (Craney and Surles 2002). Tests indicated low levels of multicollinearity between all variables (VIF < 2.0 for each variable). We assessed model fit with R^2. Wherever possible, we used pairwise exclusion for missing values to maximum use of available information in analyses.

We tested for nonresponse bias in our sample by comparing the data we obtained from our online survey with the data we obtained from our phone survey, as well as for differences between hunters in North Carolina who completed the questionnaire before CWD was detected in the state and afterwards, using independent samples *t*-tests for numeric data (Lawson et al. 2019) and chi-square tests for categorical data (Etter and Perneger 1997). For all statistical tests we used α = 0.05.

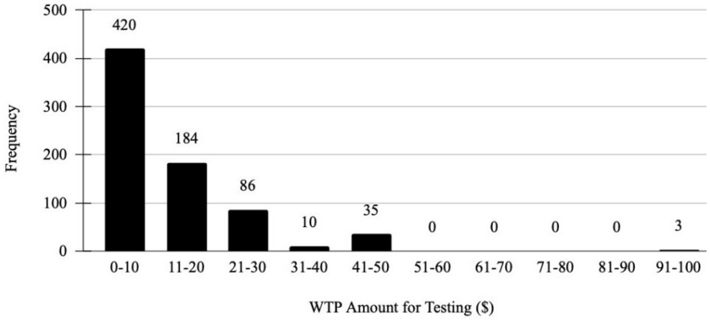
Results

For our online survey in North Carolina, we received 727 responses (for a response rate of 8.6% after removing 126 incorrect addresses), with 526 responses (72.4%) coming from email recruitment and 201 responses (27.6%) coming from postcard recruitment. For our online survey in South Carolina, we received 703 responses from email recruitment, for an online survey response rate of 7.03%. We surveyed 302 participants via phone from North Carolina, with a compliance rate of 50.8%. Our research partner Southwick Associates surveyed 300 participants via phone from South Carolina but did not report compliance rates.

Hunters who responded to each survey were predominantly male (85% and 91.2%, respectively). Most respondents to both the online survey (67%) and phone survey (52.3%) reported having a college degree (2-yr Associate's degree, 4-yr college degree, or higher). The average age among respondents was 54.1 yr old (SD = 14.7, range 18–88) for our online sample and 45.9 yr old (SD = 15.3, range 18–89) for our phone sample. Respondents from our phone sample were younger than those from our online survey sample, were slightly less likely to be female, and less likely to have obtained a college degree. Despite significant differences, all the effect sizes for these relationships were small (i.e., below the 0.6 threshold for medium effect size for Cohen's *D* for *t*-tests (Lovakov and Agadullina 2021) and below the 0.1 threshold for Phi for chi-square tests (Kotrlik et al. 2011), thus we decided that weighting was not necessary. Also, there were no demographic differences between North Carolina hunters pre- and post-detection of CWD in the state. The number of respondents who completed our WTP questions was 1320 from our online survey (110 item nonresponses) and 577 from our phone survey (26 item nonresponses).

On average, less than half of the hunters were willing to pay for testing (34.1% for online survey; 48.6% for phone survey) and disposal (43.3% for online survey; 50.7% for phone survey). The mean WTP from our online survey for testing was \$17.65 (SD = 17.54) and for safe disposal was \$16.32 (SD = 12.26; Figure 1). The mean WTP from our phone survey for testing was \$22.69 (SD = 15.52) and for safe disposal was \$22.60 (SD = 14.65; Figure 2).

(a) Distribution of WTP Estimates for Testing from Online Survey



(b) Distribution of WTP Estimates for Disposal from Online Survey

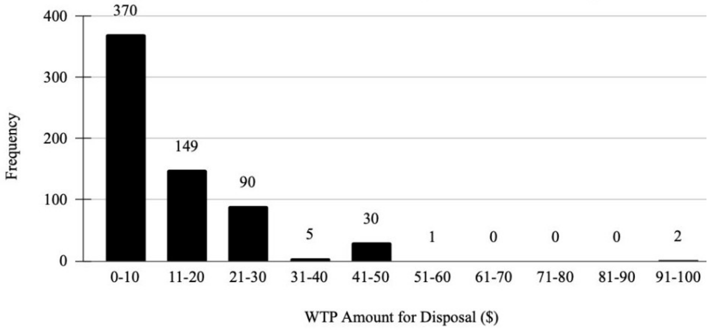
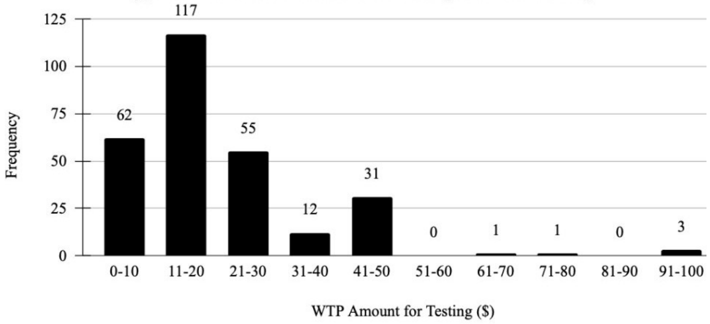


Figure 1. Distributions of the willingness to pay (WTP) amounts that people reported for (a) testing and (b) carcass disposal on the open-ended questions for the online survey.

(a) Distribution of WTP Estimates for Testing from Phone Survey



(b) Distribution of WTP Estimates for Disposal from Phone Survey

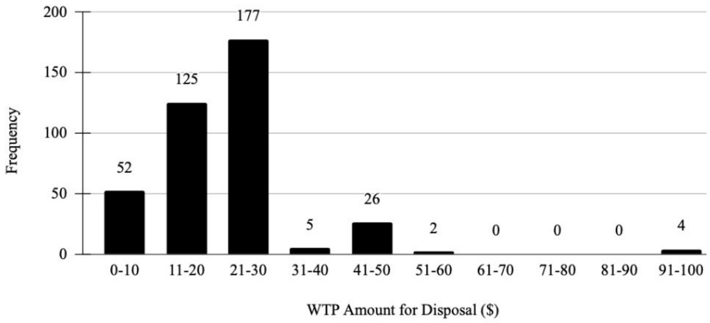


Figure 2. Distributions of the willingness to pay (WTP) amounts that people reported for (a) testing and (b) carcass disposal on the open-ended questions for the phone survey.

Based on predicted means for the average survey participant in

Table 1. Parameter estimates (β and $\beta_{standardized}$ [scaled in standard deviation units]) from a linear regression model examining demographic variables associated with North Carolina and South Carolina hunters' willingness to pay (WTP) for chronic wasting disease testing asked via the open-ended question on our online survey ($n = 488$) and disposal asked via the open-ended question on our online survey ($n = 620$).

	Testing[a]				Disposal[a]			
Variable	β	SE	$\beta_{standardized}$	P	β	SE	$\beta_{standardized}$	P
Intercept	14.71	5.06	–	0.004	12.02	3.73	–	0.001
Gender	0.71	2.82	0.01	0.80	0.11	1.99	0.002	0.96
Age	–0.03	0.05	–0.02	0.59	0.02	0.04	0.02	0.63
Education	0.88	1.03	0.04	0.39	0.25	0.81	0.01	0.76
Political identity	–4.57	1.58	–0.11	0.004	–1.30	1.21	–0.05	0.29
Income	0.43	0.34	0.05	0.21	0.36	0.26	0.06	0.17
State	0.53	1.42	0.01	0.71	–0.57	1.09	–0.02	0.60

a. $R^2 = 0.018$ for testing model; $R^2 = 0.007$ for disposal model.

Table 2. Parameter estimates (β and $\beta_{standardized}$ [scaled in standard deviation units]) from a linear regression model examining demographic variables associated with North Carolina and South Carolina hunters' willingness to pay (WTP) for chronic wasting disease testing asked via the open-ended question on our phone survey ($n = 293$) and disposal asked via the open-ended question on our phone survey ($n = 306$).

	Testing[a]				Disposal[a]			
Variable	β	SE	$\beta_{standardized}$	P	β	SE	$\beta_{standardized}$	P
Constant	21.80	5.98	–	<0.001	21.76	5.54	–	<0.001
Gender	5.85	3.47	0.10	0.09	–3.15	3.42	–0.05	0.36
Age	–0.16	0.06	–0.16	0.01	–0.08	0.06	–0.08	0.18
Education	0.60	1.48	0.02	0.69	2.34	1.38	0.10	0.09
State	1.43	1.89	0.05	0.45	1.01	1.78	0.03	0.57

a. $R^2 = 0.033$ for testing model; $R^2 = 0.020$ for disposal model.

our sample (online: male, college-educated, and 52 yr old; phone: male, college-educated, and 46 yr old), respondents to the open-ended CV questions on the online survey were willing to pay lower amounts for testing ($15.96, 95% CI: [0.00–49.83]) and disposal ($14.74 [0.00–39.02]) compared to respondents who answered our open-ended questions on the phone survey (testing: $22.90 [0.00–53.42]; disposal: $22.80 [0.00–51.69]). Although the mean point estimates of WTP were lower for the online survey than the phone survey, all the estimates had overlapping confidence intervals. Based on predicted means, respondents to the open-ended questions were willing to pay nearly identical amounts for testing ($22.90 [0.00–53.42]) and disposal ($22.80 [0.00–51.69]) compared to the amounts reported from the dichotomous choice CV questions (testing: $24.80 [23.31–26.29]; disposal: $24.50 [23.11–25.89]).

Our models examining the effect of demographic variables on WTP for testing and disposal had low predictive power ($R^2 < 0.04$). However, as hunters became more liberal, they reported higher WTP for CWD testing on the online survey ($B = –0.11$, $P = 0.004$; Table 1). As hunters became older, they reported lower WTP for CWD testing on the phone survey ($B = –0.16$, $P = 0.01$; Table 2). We did not detect statistically significant relationships between demographic variables and WTP for safe disposal of carcasses (Tables 1 and 2).

Discussion

Our findings contribute to the literature on WTP for CWD management studies (Zimmer et al. 2012, Adhikari et al. 2023) by suggesting that, when estimating WTP for CWD management, and possibly other non-market goods, survey mode (online vs. phone) impacts results, but method (open-ended vs. dichotomous choice), surprisingly, may not. Social desirability bias and anchoring may explain why phone survey estimates of WTP were higher than online survey estimates (Holbrook and Krosnick 2010).

Other studies have demonstrated similar patterns, with people indicating that they are willing to pay more money when asked in a way that requires direct interactions with researchers (Lindberg et al. 1997, Leggett et al. 2003). Priming respondents by asking questions about WTP and even suggesting potential price ranges is considered a best practice for CV (Johnston et al. 2017). In this study, phone respondents received priming with specific dollar amounts in the dichotomous choice questions they received prior to the open-ended questions. That priming may have encouraged higher open-ended WTP responses. Ultimately, however, observed differences between methods were minimal, suggesting that open-ended CV models may be relatively resistant to these common biases when employed in wildlife management contexts.

Several factors may explain why the WTP estimates for testing and disposal were nearly identical in dichotomous choice and open-ended approaches. First, bias that occurs due to the absence of cues indicating plausible values (Frew et al. 2003) may have less impact because the respondents from our phone survey were primed from the values provided in our dichotomous choice questions that they answered before the open-ended questions. Second, strategic bias (Doyon and Bergeron 2016, Flyvbjerg 2021) may have less impact because the respondents believed that the amounts asked about in our dichotomous choice questions were already vetted by the state agency that sponsored the survey. Therefore, respondents might not have been inclined to report lower amounts when responding to the open-ended questions even though lower costs would be more favorable to them. Although the cognitive burden of coming up with a WTP estimate has been linked to respondents reporting small amounts in open-ended questions (Brown et al. 1996, Mitchell and Carson 2013), that burden and associated biases can be reduced by providing contextual information in the survey prior to asking CV questions (e.g., this study, Mitchell and Carson 2013). Lastly, the open-ended questions created WTP estimates with more variance than the dichotomous choice questions, likely because respondents could answer with very high values if they chose to do so (Burchell and Marsh 1992).

Collectively, a growing number of studies on WTP for CWD management suggest hunters exhibit similar WTP for diverse types of management and safety protocols across most regions where CWD has been detected. To facilitate comparisons between our results and previous work, we present estimates in 2020 USD (USBLS 2010). Hunters in North Carolina and South Carolina, on average, were willing to pay approximately $15–$25 for both CWD testing and safe disposal. This is similar to other estimates: $23.81 for culling to manage CWD in Canada (Zimmer et al. 2012), $22.99 for turning in carcasses of infected deer in Tennessee (Adhikari et al. 2022), and between $13.40 and $25.66 for a fundraising stamp among U.S. and Canadian hunters (Ufer et al. 2022). Potential explanations for the similarity of CWD WTP estimates that have been reported include $15–25 representing the value of doing 'something' to alleviate the incremental loss to the hunting experience (the perceived opportunity cost) caused by unchecked CWD. Second, hunters might suggest values in the range of $15–$25 because they are similar to resident hunting license costs or other related fees (e.g., eRegulations 2023). These relatively low WTP estimates present a challenge to state wildlife agencies when the average amount 33 state agencies paid for all field operations necessary to obtain and test one deer sample in 2021 was $144 (Thompson and Mason 2022).

Few demographic attributes considered in this study were associated with a hunter's WTP for CWD management, and these associations were relatively weak. Hunters' political identity influenced their willingness to pay for CWD testing, with those who identified as moderate or liberal reporting a higher willingness to pay. This finding aligns with previous research in which respondents who self-identified as possessing a liberal political ideology were more willing to pay for a program designed to benefit drinking water quality (Nielsen-Pincus et al. 2017) and more willing to pay for environmental taxes (Fairbrother 2019). We also found that hunters' age can predict their WTP for testing. Younger hunters were willing to pay more for CWD testing, which is consistent with findings that evaluated visitors of national parks and protected areas' WTP to provide economic support for nature conservation (Witt 2019, Aseres and Sira 2020).

Future research could address limitations of our study. As noted above, the order of questions on our phone survey (i.e., dichotomous choice first, open-ended second) could have had an anchoring effect on the respondents. Investigators in a future study could use a randomized question design or a split sample to eliminate this bias. Although we chose not to describe the payment as mandatory since we believed it could lead to strategic bias, future research could explore the role of different payment vehicles in WTP. Payment vehicles can have large impacts on WTP, but are rarely considered in related studies (e.g., this study, Bazghandi et al. 2020, Adhikari et al. 2023). Also, we recognize that the cost for testing might differ from the cost of safe disposal. Therefore, we encourage other researchers to inquire about realistic bid estimates for each CWD management activity under consideration. Any biases related to dates of survey administration compared to hunting season dates are likely absent given the fact that WTP estimates did not vary based on detection status of CWD in North Carolina (pre-detection in March 2022 vs. post-detection) or between North Carolina and South Carolina hunters (March–May 2022 vs. October–November 2022).

Management Implications

In conclusion, our findings show that survey mode can influence how people respond to questions about their WTP, with online formats permitting more privacy that enables participants to state lower—and perhaps more honest—estimates for their WTP compared to phone surveys that introduce an element of social desirability bias. Our findings also suggest that researchers could use the relatively easy open-ended approach, in place of the dichotomous choice approach, and still obtain valid estimates for non-market goods and services that could assist in controlling the spread of wildlife diseases. However, greater variation in CV estimates is likely despite similar mean estimates. Ultimately, our study provided more evidence that hunters are typically willing to pay between $15 and $25 for CWD testing and disposal, mirroring results in states where CWD has been around longer and is more prevalent. Since this range is well below the actual cost of implementing these disease management practices, wildlife managers may need to consider more cost-friendly approaches for them or other funding resources to supplement the amount that hunters are willing to pay for CWD testing and disposal.

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Influence of Mowing and Herbicide Application on White-tailed Deer Use of Perennial Forage Plantings

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Abstract: Plantings of perennial and biennial forage, such as white clover (*Trifolium repens*), red clover (*Trifolium pratense*), and alfalfa (*Medicago sativa*), commonly are used by managers to increase nutritional resource availability for white-tailed deer (*Odocoileus virginianus*). Regular mowing and selective herbicide applications are two common practices used to maintain perennial plantings and reduce weed competition. However, there is little information available on how these management activities influence perennial forages or wildlife response. We evaluated the effects of regular mowing on forage production, forage quality, weed coverage, and deer detections as a case study in a perennial forage planting in Tennessee, May–August 2020. We also evaluated deer detections following application of selective herbicides among four fields in Tennessee and North Carolina, October–November 2021. Regular mowing reduced forage availability by 37% and did not increase forage quality or deer use of the food plots. Additionally, regular mowing decreased coverage of clover and alfalfa, which led to increased weed competition by late summer. Deer use did not change the month following selective herbicide application, but we observed a 67% decrease in deer detections the week following herbicide application. Regular mowing was not an efficient strategy to manage perennial forage plantings. We suggest managers maintain perennial forage food plots with selective herbicide applications in spring and fall and by mowing once during the latter portion of the growing season. Selective herbicides may reduce deer use of forage plantings for a few days after application, but use likely returns to normal soon thereafter.

Keywords: deer forage, food plot, clover, mowing, herbicide

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Management to increase white-tailed deer (*Odocoileus virginianus*; hereinafter, deer) body size, antler size, and productivity often focuses on enhancing forage quality and availability (Mixon et al. 2009, Iglay et al. 2010, Nanney et al. 2018). Antler and body size are strongly influenced by diet quality (French et al. 1956, Harmel et al. 1988, Jones et al. 2010, Michel et al. 2016). Population growth is also influenced by diet, as females produce more offspring when forage availability is improved (Verme 1969, DeYoung et al. 2019). Habitat management practices such as canopy reduction, nonnative plant species control, and prescribed fire often are used to increase forage availability in forests and early successional communities for deer (Turner et al. 2020, Harper et al. 2021, Powell et al. 2022).

Agronomic forages are commonly planted by managers to supplement naturally occurring forage, thereby increasing overall forage quality and availability. Forage plantings (hereinafter, food plots) are particularly important during periods of limited natural forage availability. They also may be used to provide high-quality forage in landscapes where forage availability is limited (Johnson et al. 1987, Edwards et al. 2004). For example, annual warm-season plantings can increase high-quality forage in addition to forage available in managed forests during the growing season (Edwards et al. 2004, Lashley et al. 2011). Both warm- and cool-season forages commonly are used to raise deer diet quality, which will increase antler and body size if sufficient forage is provided (Johnson et al. 1987, Keegan et al. 1989). Food plots also may be used to attract deer for hunting and viewing, which may influence stakeholder satisfaction (Johnson and Dancak 1993). Perennial and biennial plantings of species such as white clover (*Trifolium repens*), red clover (*Trifolium pratense*), alfalfa (*Medicago sativa*), and chicory (*Cichorium intybus*), are intended to supplement forage availability during the gap of productivity between annual warm- and cool-season plantings (Harper 2019). Although perennial forages do not require planting each year, annual management is required to maintain forage production (Ball et al. 2015, Harper 2019).

Mowing and selective herbicide applications are commonly used to maintain perennial food plots and reduce weed competition (Schreiber 1967, Cudney et al. 1992, Green and Legleiter

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2018). Regular mowing stimulates regrowth of perennial plants, which may increase nutritional quality at the whole-plant level (Cassida et al. 2000). However, as concentrate selectors, deer do not eat the less digestible stems, but rather concentrate their foraging on the more digestible leaves of the plant (Lashley et al. 2014). Therefore, the reduction of forage biomass by mowing may be of more importance than the increase in nutrient availability. Herbicides are also used to control weeds and increase forage availability. For example, several grass-selective, broadleaf-selective, and broad-spectrum-selective herbicides can effectively manage weed competition and lead to greater forage availability in perennial forage plantings (Harper 2019). However, little information exists on how deer respond following herbicide applications. Given the common use of mowing and selective herbicides to manage perennial food plots for deer, managers would benefit from quantifying deer use following their applications and the effect of these practices on forage availability and quality. Additionally, this information should be of interest to hunters who may be concerned about deer attraction to food plots if they are mowed or sprayed just prior to or during the hunting season.

We used data from two field experiments to test how mowing and selective herbicide applications influence forage availability, weed control, deer use, and deer detections in perennial food plots. We hypothesized deer detections would be influenced by both mowing and herbicide applications, and predicted both treatments would result in decreased detections. Additionally, we hypothesized mowing would influence forage biomass, but not quality of young and old plant tissues. Finally, we hypothesized mowing would not reduce weed coverage relative to unmowed plantings.

Study Area

We conducted the mowing experiment in 2020 on an established perennial forage planting in a 1.8-ha field on private property in Union County, Tennessee. We established this planting in fall 2017 in a mixture of red clover, white clover, and alfalfa. Soil was Talbott silty clay loam (NRCS 2022). Mean annual precipitation was 125.5 cm, and mean annual temperature was 13.4 C (NOAA 2022).

We conducted the herbicide experiment in 2021 on four established perennial plantings at two sites in North Carolina and Tennessee. Each planting served as a replicate, and average field size was 0.8 ha. All plantings were established in 2018–2019, maintained with an annual treatment of imazethapyr and clethodim, and mowed once annually during August–September to prepare for fall herbicide treatments. The North Carolina site was located on private property in Alamance County and had one, 0.8-ha replicate. The field was planted with a mixture of white and red clover, and soil on the site was Enon sandy loam (NRCS 2022). Mean annual precipitation was 114.6 cm, and mean annual temperature was 14.3 C (NOAA 2022). The Tennessee site was on private property in Union County and had three replicates of various sizes (i.e., 0.1 ha, 1.1 ha, and 1.8 ha). Each field was at least 400 m apart. The 0.1-ha and 1.1-ha fields were planted to a mixture of white and red clover, and the 1.8-ha field was planted to a mixture of white clover, red clover, and alfalfa. Soil at the Tennessee sites was Talbott silty clay loam (NRCS 2022), mean annual precipitation was 125.5 cm, and mean annual temperature was 13.4 C (NOAA 2022).

Methods

Mowing Case Study

We divided the 1.8-ha field into six equal-sized treatment units and randomly assigned three units as mowed and three units as unmowed controls. Prior to study initiation in early May 2020, we sprayed all units with a mixture of 876 ml ha^{-1} of Cleanse™ 2 EC (26.4% clethodim; WinField Solutions, St. Paul, Minnesota) and 292 ml ha^{-1} of Pursuit® (22.9% imazethapyr; BASF Corporation, Research Triangle Park, North Carolina). Rates were based on product label recommendations for control of common weeds in forage plantings and we sprayed based on recommendations for perennial food plot management leading into the growing season (Harper 2019). We also included 0.5% nonionic surfactant (Preference®; WinField Solutions) based on label recommendations. We cut the mowed treatment units the first week of June, July, and August 2020 using a rotary mower at a height of 15–20 cm based on common frequency and height recommendations for perennial food plot management (Tesar and Ahlgren 1950, Kammermeyer et al. 2006).

We measured pretreatment plant coverage and forage biomass to quantify existing plant species composition and biomass from all units during late May 2020 as well as 2 and 4 wk after each mowing event, for a total of six sampling periods. During each sampling period, we collected all forage present within one randomly placed 0.5-m^2 frame in each unit to quantify biomass and quality of forage plants. All random placement for sampling in the study was conducted using ArcGIS Pro 2.5 (ESRI 2020). We also collected forage from one randomly placed 0.5-m exclusion cage in each unit to quantify deer use of perennial forages. Cages were initially placed 2 wk before the first data collection period, and frames and exclusion cages were moved following collection to avoid sampling the same location multiple times. We sorted forages by species and separated young and old tissue to determine whether quality differed based on plant age as has been documented elsewhere (Lashley et al. 2014, Turner et al. 2021). We separated forages based on Lashley et al. (2014) by considering smaller leaves near the tips of stems as young tissue and larger leaves farther down the stems as older tissue. We did not include lignified stems in biomass or nutrient analysis because they do not represent what deer typically select. We weighed forages after drying at 50˚C for 72 h and calculated kg ha^{-1} of biomass of the total young and old tissue within each treatment unit for each collection. To quantify deer consumption of forages within mowed and unmowed plots, we calculated kg ha^{-1} of forage consumed by subtracting the forage production inside exclusion cages versus biomass available outside the exclusion cages. Samples of each species (both young and old tissue) from each treatment and control plot were sent to Clemson University for wet chemistry nutrient analysis of crude protein, phosphorus, calcium, acid detergent fiber, and neutral detergent fiber (Mills and Jones 1996). These nutrients were selected based on their importance to deer nutrition and diet selection (National Research Council 2007, Dykes et al. 2020).

We also used point-intercept transects (Floyd and Anderson 1987) to quantify whether mowing reduced weed coverage During each data collection period, we documented all species present directly under each 1-m mark along a randomly placed 30-m transect in each unit. We then calculated the percent coverage of planted forages (alfalfa/clover), grass, and broadleaf weeds in each unit.

We quantified deer use of each treatment unit with camera traps from June–August. We randomly placed one Reconyx® HyperFire 2 (Reconyx, Holmen, Wisconsin) in each treatment unit on a t-post following the first mowing event. We removed cameras prior to each mowing event and placed them back in same location after mowing. We set the camera to a 1-min delay, with one picture being taken each time the camera was motion activated. To standardize the detection area for each camera, we placed another t-post 1.8 m from the camera and visually judged whether deer were behind or in front of the post. We counted all deer within the picture frame that were between the camera and the t-post and calculated the total deer detections per day in each treatment unit to compare use between treatment and control. We did not identify individual deer, and some individuals likely were counted multiple times within a day. However, given our objective of quantifying relative use, this was not an issue because deer detections were counted the same way in both treatment and control units.

Herbicide Application Trial

We divided each of the four herbicide study replicates into two equal-sized treatment units. We mowed each entire replicate in early September 2022 as annual maintenance of perennial forage plots (Harper 2019). Following mowing, we randomly assigned half of each replicate as the control with no herbicide application, and the other half of the unit was assigned as the treatment to receive herbicide applications. During mid-October 2021, we applied a mixture of clethodim and imazethapyr with a tractor boom sprayer using approximately 140 L ha^{-1} water in each treatment replicate to control grass and broadleaf weeds. We applied 876 ml ha^{-1} of Cleanse™ 2 EC (26.4% clethodim), and 292 ml ha^{-1} of Pursuit® (22.9% imazethapyr). These rates were based on product label recommendations to control various weeds in perennial forage plantings, and we also included 0.5% nonionic surfactant as Preference® based on label recommendations.

We randomly placed three camera traps in each control and treatment unit 1 mo prior to herbicide application to quantify deer use before and after treatment. We used Reconyx® HyperFire 2 or Browning Strike Force® (Prometheus Group, Birmingham, Alabama) cameras, and each replicate received the same model to control for potential differences in detection between camera models. We placed cameras on t-posts 1 m above ground facing north and set to take one motion-activated picture with a 1-min delay. We placed a t-post 1.8 m from each camera to establish our detection area. Cameras were deployed for 4 wk before and 5 wk after herbicide application in treatment and control units, and we counted all deer between the camera and the post in each picture. We then calculated the average deer per day for each camera during each week of the study.

Analysis

All data were tested for normality, equality of error, and independence before we conducted the analysis. For the mowing case study, we used a t-test in Program R to determine whether forage production during each collection period and total forage collection varied by treatment (R Core Team 2023). We used t-tests to determine whether crude protein, phosphorus, calcium, acid detergent fiber, or neutral detergent fiber varied during any collection period based on treatment. We also used t-tests to determine differences in the percent coverage of alfalfa and clover, grass, and broadleaf weeds by treatment period and average deer detections per day on camera traps. We considered each mowed treatment unit within the case study field as a replicate, for a total of three treatment and three control replicates for all analysis.

We used an ANOVA to determine whether herbicide applications influenced deer use of perennial forage plantings. We analyzed the average change in deer detections per day for each camera during the month before and after herbicide was applied. We also tested for differences in deer detections in the week before and after herbicide was applied to determine if the change in detections differed immediately following herbicide application. We included field as a fixed effect in all ANOVA analysis to control differences which might be attributed to the particular field. We set $\alpha = 0.05$ for all analyses.

Results

Biomass of alfalfa and clover prior to treatment implementation was similar between the treatment and control units ($P > 0.05$). Mowing reduced forage biomass during the early June, early August, and late August collection periods, and total forage biomass throughout all sampling periods was reduced by 879.7 (SE = 206.3) kg ha^{-1} ($P = 0.013$; Figure 1). Deer consumed 294.7 (SE = 240.4) kg ha^{-1} less forage in mowed treatments, but this was not statistically different from the control ($P = 0.288$). We did not detect any differences in crude protein, phosphorus, calcium, acid detergent fiber, or neutral detergent fiber following mowing (Table 1). Mowing reduced clover and alfalfa coverage during the early August ($P = 0.019$) and late August ($P = 0.002$) periods, but coverage was similar during the other periods (Table 2). Mowed treatments had 25.6% (SE = 13.9) grass coverage grass coverage during the late August sampling period compared to 1.1% (SE = 1.1) in the unmowed, but means were not statistically different ($P = 0.078$). We detected 1.6 (SE = 0.39) deer per day from our camera traps in mowed units and 2.4 (SE = 0.56) deer per day in control units, which did not vary significantly ($P = 0.211$).

For the herbicide spray trial, we did not detect differences between the change in deer detections in the month before and after treatments ($P = 0.54$; Figure 2). Compared to the week prior to treatment, deer detections decreased 9% in the control and 67% in the treated units the week after herbicide applications occurred, but the pattern of use was not statistically different ($P = 0.07$).

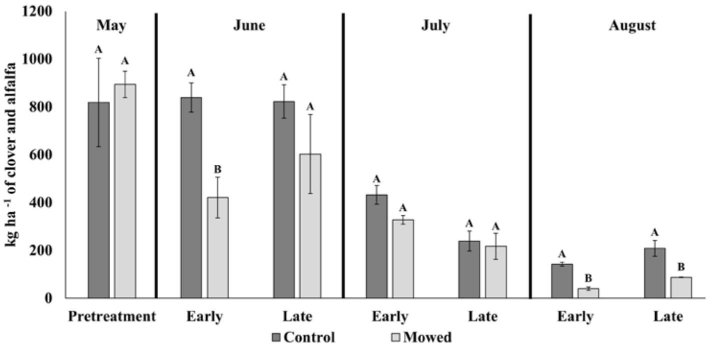

Figure 1. Standing biomass of perennial clover and alfalfa plantings with and without regular mowing during seven collection periods of May–August 2020. Vertical bars represent mowing events in the mowed treatment, and different letters in the same collection period were statistically different. The early sampling period occurred during the middle week of each month, and the late sampling period occurred during the last week of the month. Error bars represent standard error.

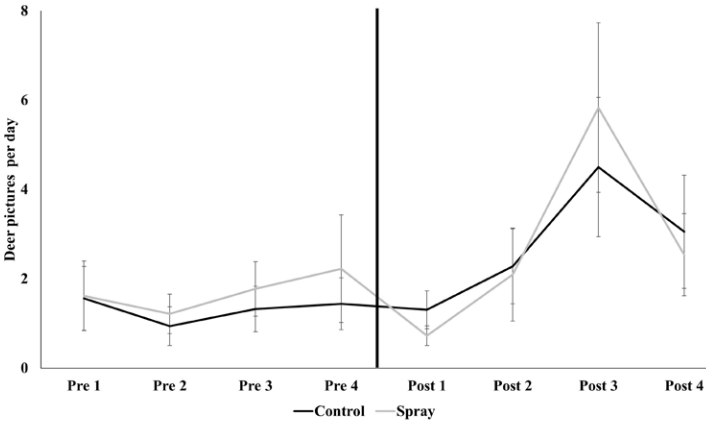

Figure 2. Average deer pictures per camera per day in the four weeks before and after clethodim and imazethapyr were applied to four perennial forage plantings in Tennessee and North Carolina in September, October, and November 2021. Dates represent the start of each sampling week. The black line represents timing of the herbicide treatment, and error bars represent standard error.

Table 1. Number of samples (*n*), percent crude protein (CP), phosphorus (P), calcium (Ca), acid detergent fiber (ADF) and neutral detergent fiber (NDF) of perennial forages collected during June–August 2020 with and without regular mowing. No significant differences between treatments were detected for these measures.

	n	CP	P	Ca	ADF	NDF
Young alfalfa						
Control	17	30.5	0.42	1.47	14.9	20.9
Mow	17	31.4	0.44	1.35	14.6	20.1
Old alfalfa						
Control	18	28.2	0.38	1.69	15.8	21.6
Mow	17	29.8	0.35	1.52	14.4	20.5
Young red clover						
Control	7	26.4	0.35	1.58	16.3	23.9
Mow	9	27.5	0.40	1.27	15.4	22.1
Old red clover						
Control	11	26.7	0.32	1.70	14.2	20.8
Mow	12	28.1	0.29	1.67	13.3	19.6
Young white clover						
Control	13	28.0	0.34	1.38	13.8	17.8
Mow	10	29.7	0.33	1.51	12.6	18.5

Table 2. Percent coverage of clover and alfalfa, grass weeds, and broadleaf weeds during seven collection periods in May–August 2020. Pre-treatment data (PRE) were collected in late May prior to treatment implementation. Mowing events occurred in early June, July, and August, with sampling occurring approximately 2 and 4 wk after mowing. Significant differences between treatments were detected for clover/alfalfa in early and late August (bold).

	PRE	Early June	Late June	Early July	Late July	Early August	Late August
Clover/Alfalfa							
Control	100	100	100	95.6	100	**97.3**	**98.9**
Mow	100	95.6	100	86.7	100	**72**	**77.8**
Grass							
Control	0	0	0	0	0	2.7	1.1
Mow	0	1.1	1.1	2.2	1.1	6.7	25.6
Broadleaf							
Control	0	2.2	2.2	7.7	18.9	12	7.7
Mow	3.3	6.7	8.9	5.5	11.1	1.3	22.2

Discussion

Mowing decreased forage availability for deer and did not improve nutritional quality or weed control in perennial forage plantings. Additionally, regular mowing resulted in decreased coverage of planted forages by August. We failed to detect significant differences in deer use following mowing or herbicide applications given our limited sample size, but our results suggest deer use may decrease for a week following selective herbicide applications.

Food plots are intended to improve diet quality for deer beyond what is naturally occurring, especially during periods of nutritional stress such as lactation and antler growth (Hewitt 2011). Nutritional requirements of deer peak during the growing season, and forage quality may be limited in some regions (Short 1975, Hewitt 2011). Additionally, supplemental forage that exceeds the nutritional requirements of deer may allow deer to benefit from availability of lower-quality natural forages in a mixed diet to meet their nutritional requirements (Hobbs and Swift 1985, Timmons et al. 2010). Thus, the primary goal of food plots should be to provide maximum biomass of forage that is sufficiently high-quality to meet the nutritional demands of deer. Mowing has been promoted as a way to increase forage quality of both native and planted forages (Kirk et al. 1974, Kallenbach et al. 2002, Smith et al. 2018). Forbs and grasses typically produce fresh regrowth following mowing. However, most forbs continue to produce fresh new leaves at the tips of stems through the growing season. Thus, mowing may reduce the overall amount of fresh growth available. The leaves of the planted forages remained palatable and digestible for deer through the growing season, and both the old and young tissue of the planted forages remained similar with regards to the nutritional requirements of deer through the growing season (National Research Council 2007). The lack of change in nutritional quality relative to deer selection is further demonstrated by deer consumption and detections numerically greater in control units, indicating deer were not selecting the mowed units over the control units. Mowing failed to change the quality or use of three perennial agronomic forages in our case study, and we do not recommend regular mowing to change nutrient levels or attractiveness for deer.

The timing of planted forage availability in relation to natural forage availability and physiological requirements is also important to consider. Peak parturition occurs during early June throughout most of the South, which is when we conducted our first mowing treatment with a corresponding decrease in planted forage availability. Declines in natural forage quality in August also occur throughout the South despite ongoing nutritional demands for lactation, but regular mowing decreased planted forage availability during this time. Overall, our mowing treatments resulted in a 37% decrease in biomass during a time when food plots should be managed to provide additional forage to meet nutritional demands.

Frequent mowing may provide an opportunity for weeds to establish in perennial forage plantings, which may lead to decreased production of planted forages and necessitate additional herbicide treatment. Weed coverage was relatively low during June and early July because of the selective herbicides we applied prior to treatment initiation, but grass weed coverage during late August in the mowed units increased to 25.6%. In contrast, grass weed coverage was only 1.1% in the control units. More than 25% coverage of grass weeds is problematic given deer do not select grass during the growing season (Hewitt 2011, Harper et al. 2021). Maintaining a dense stand of forage plants is one of the primary strategies to reduce weed pressure (Légère and Schreiber 1989, Hoy et al. 2002), and coverage of clover and alfalfa was less during August in the mowed treatments. Frequent mowing likely stresses perennial forages and provides an opportunity for weeds to establish (Tesar and Ahlgren 1950), and our results do not indicate it benefits weed control at any period.

Herbicide applications to control weeds are often needed to maintain perennial food plots, but few data exist on deer response to these treatments. Several studies have documented the effects of herbicide treatments on vegetation for wildlife (Lashley et al. 2011, Harper et al. 2021, Turner et al. 2023), but the immediate response of deer following herbicide treatments is scant in the literature. Our limited sample size of four sites prevented detecting significant differences based on treatments, but we believe a 67% reduction in deer detections during the week following herbicide applications is relevant if there is concern about reduced deer activity in food plots soon after herbicide application. Given the selective herbicides we applied, the short-term avoidance was likely related to taste or smell and not changes in forage quality or quantity. Decreased use could not be attributed to disturbance of the field because the treated unit was immediately adjacent to the untreated unit at each site. There appeared to be an increase in use three to four weeks following herbicide applications in both treated and control units, but this likely was a result of decreasing availability of other forages during our sampling period (Pekins and Mautz 1987). Further research should investigate wildlife response to herbicide applications in food plots, as we believe these are among the first results demonstrating a potential behavioral response of a mammal immediately after an herbicide application.

We suggest managers avoid regular mowing of perennial food plots, and instead use selective herbicide applications early in the growing season (i.e., April–May) to reduce weed competition. A single mowing in late summer when perennial forage production is at its lowest (i.e., August or September) is sufficient to maintain perennial plantings, and an additional application of various selective herbicides can be applied to control incoming cool-season weeds if needed following mowing in the fall. This approach increases deer forage availability while maintaining quality of forage plantings. Consideration should be given to the timing of herbicide application to ensure deer do not avoid forage plantings during nutritional stress periods, but our results indicate deer only avoid treated fields for a short period after treatment.

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Changes in Hunter Behavior, Success, and Satisfaction in Relation to Wild Turkey Season Opening Dates and Season Length

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Abstract: Many states throughout the range of wild turkeys (*Meleagris gallopavo*) have delayed their spring wild turkey hunting seasons to allow reproductively active males more time to breed before being harvested and to potentially increase population fecundity rates. Six states in the Southeast recently delayed their spring hunting season by 7 to 14 days. However, there are no published data indicating their previous season frameworks had a deleterious effect on wild turkey reproduction or that delaying the season increased fecundity. In addition to potentially affecting turkey reproduction, changing the season framework may impact hunter behavior (effort and efficiency), success, and satisfaction. Our objective was to see how hunter effort, success, efficiency, and satisfaction changed upon implementing a two-week season delay and a two-week reduction in season length to the spring wild turkey hunting season in south-middle Tennessee. We surveyed 2000 hunters in five focal counties from 2017 to 2022 to document effort, success, efficiency, and satisfaction among hunters. We surveyed the same respondents for all six years and received a total of 2539 surveys with a 22% response rate. We used a two-level structural model with generalized linear models for panel data to assess changes in hunter effort and experience, and then determined how the shift in season framework affected satisfaction. Hunter effort in the delayed counties declined 42% after the delay, and the average number of gobbles heard per trip decreased 39%. Harvest was not affected by the season delay, but hunter efficiency improved 37% following the delay. Hunter success, hunter efficiency, and gobbles heard were strong positive predictors of hunter satisfaction. Our survey highlights how hunter satisfaction should be considered when setting spring hunting season regulations because changes could have a negative impact on satisfaction and therefore, potentially impact agency goals related to hunter participation, retention, and recruitment.

Key words: hunter effort, hunter survey, hunting regulation changes, hunting season start date

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Hunter satisfaction with hunting seasons can strongly influence hunter recruitment and retention (Mehmood et al. 2003, Fulton and Manfredo 2004, Brunke and Hunt 2008, Everett and Nelson 2016) and is not driven only by success (Schroeder et al. 2019, Gruntorad et al. 2020). Hunter satisfaction can be impacted by sociocultural factors, such as tradition or comradery, and experiential factors, such as harvesting game (Hayslette et al. 2010, Watkins et al. 2018). Because conservation dollars are generated through license sales, which can be used to manage wild turkeys (*Meleagris gallopavo*) and many other species, state agencies and other stakeholder groups need to understand the factors that drive hunter satisfaction to generate revenue for conservation and provide high-quality hunting opportunities.

The number of wild turkey hunters has declined in terms of license sales. Chamberlain et al. (2022) reported a 16% decline in spring wild turkey license sales nationwide from 2013 to 2019. In 2016, the national survey of fishing, hunting, and wildlife recreation reported there were 2 million wild turkey hunters that accounted for 13 million hunter days, which is second only to deer hunters (8.1 million hunters and 133 million hunter days, USFWS and USCB 2018). There also was a 25% decline in annual revenue generated from hunting 2011 to 2016 (USFWS and USCB 2018).

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Table 1. Hypothesized effects that a delay of the spring wild turkey hunting season would have on hunters from south-middle Tennessee, 2017–2022.

Metrics	Hypothesized effect on hunters	Justification
Hunter effort	Decrease	There are 14 fewer days in the hunting season for delayed counties and hunters may hunt elsewhere during that time period.
Hunter efficiency	Increase	Males will be more responsive to calls later in April because more hens have begun incubating a nest.
Toms seen per trip	Decrease	Birds might be gobbling less during this time of year and subsequently they may be more difficult to hunt.
Gobbles heard per trip	Decrease	A later hunting season may exclude peak gobbling.
Jakes seen per trip	Increase	The basis behind the hypothesis of a later start date is that there is a reproductive benefit to starting to hunt later in the breeding season, therefore this would increase the number of jakes each year.
Hunter satisfaction	No change	A negative association with gobbles heard and a positive association with hunter efficiency would result in no direct effect on hunter satisfaction as they would cancel each other out.

The decline in hunters and revenue is of concern to state wildlife agencies.

Experiential factors can influence hunter satisfaction, such as harvesting game, opportunities to harvest game, and seeing game (Brunke and Hunt 2008, Ryan and Shaw 2011, Gruntorad et al. 2020). Declining game population sizes also can negatively affect harvest rates (Roberts and Crimmins 2010), potentially reducing hunter satisfaction. Watkins et al. (2018) reported 65% of wild turkey hunters in Tennessee were concerned about a potential decline in the wild turkey population. This perceived decline was supported by Byrne et al. (2015) who reported a general decline in poult-per-hen ratios throughout the Southeast since 1990. In addition to the decline in turkey hunter participation, there is concern that the decline in wild turkey productivity is resulting in declining wild turkey numbers. Johnson et al. (2022) monitored productivity in south-middle Tennessee from 2017 to 2018 and reported relatively low estimates of initial nesting rates (nesting rate = 0.76) and nest success (nest success = 0.31), further suggesting productivity of wild turkeys is low in that area of Tennessee.

A hypothesis about the cause of the decline in productivity is that an early start to the spring turkey hunting season is negatively impacting productivity by harvesting males before they have a chance to breed, disrupting the flock's social hierarchy, and lowering male density too early in the breeding season (Isabelle et al. 2018). Six Southeastern states (Alabama, Arkansas, Georgia, Louisiana, Oklahoma, and Tennessee) have delayed their hunting seasons in response to this hypothesis. However, a later hunting season could negatively impact hunter experiences if the season is misaligned with peak gobbling. Gobbles heard has been identified as a leading factor associated with turkey hunter satisfaction (Wightman et al. 2019, Gruntorad et al. 2020, Wakefield et al. 2020). Therefore, a later hunting season may negatively impact hunter satisfaction if peak gobbling activity no longer occurs during the hunting season.

From 1986 through 2020, the Tennessee spring wild turkey hunting season began on the Saturday closest to 1 April. For the 2021 and 2022 spring wild turkey hunting seasons, the Tennessee Fish and Wildlife Commission voted to delay the spring turkey hunting season start date and reduce the season length by 14 days in Giles, Lawrence, and Wayne counties because of perceived population declines and to determine if delaying the season might increase reproduction and ultimately wild turkey population size. Our objective was to investigate how a 14-day delay in the season start date and a shortening of the spring wild turkey hunting season affected hunter effort (hours spent hunting), hunter success (number of turkeys harvested), hunter efficiency (hours spent to harvest a bird), and hunter satisfaction. We tested three specific hypotheses relative to hunter behavior and the season delay (Table 1):

1. Hunter effort would decrease because the season was delayed and reduced from 44 to 30 days.
2. Hunter success/efficiency would increase because male turkeys would be more responsive to calling in mid-April as more hens begin incubating.
3. Hunter satisfaction would remain the same because although hunter efficiency may increase (hypothesis #2), and thus increase hunter satisfaction, decreased gobbling activity, the shorter, delayed season, and reduced effort (hypothesis #1) would potentially decrease hunter satisfaction simultaneously.

Study Area

Our study area was five counties in south-middle Tennessee: Bedford, Giles, Lawrence, Maury, and Wayne. These five focal counties offered a mix of rural and urban communities with human population sizes ranging from 16,427 to 102,878, with 49.1% of the population male and 50.9% female (TDLWD 2022). The demographic characteristics of our respondents (Table 2) were typical for Tennessee turkey hunters (Watkins et al. 2018; R. Shields, Tennessee Wildlife Resource Agency, unpublished data). We chose to include the five focal counties in our study because spring turkey harvest in Giles, Lawrence, and Wayne counties (hereinafter, "delayed counties") had declined by >50% from 2005–2015, and

Table 2. Demographic information of the wild turkey hunters in Bedford, Giles, Lawrence, Maury and Wayne counties, Tennessee, that responded to our survey at least once from 2017 to 2022.

	2017		2018		2019		2020		2021		2022		Overall	
Group	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	**n**	%
Age (yr)														
≤45	234	43.5	138	38.4	94	33.7	89	32.2	55	33.1	42	30.0	652	37.1
46–60	241	44.8	164	45.7	129	46.2	123	44.6	61	36.7	53	37.9	771	43.9
61–70	57	10.6	55	15.3	50	17.9	57	20.7	45	27.1	38	27.1	302	17.2
71–80	4	0.7	2	0.6	6	2.2	7	2.5	2	1.2	7	5.0	28	1.6
>81	0	0.0	0	0.0	0	0.0	0	0.0	1	0.6	0	0.0	1	0.1
NA[a]	2	0.4	0	0.0	0	0.0	0	0.0	2	1.2	0	0.0	4	0.2
Gender														
Male	505	93.9	341	95.0	262	93.9	255	92.4	156	94.0	128	91.4	1647	93.7
Female	22	4.1	12	3.3	11	3.9	10	3.6	5	3.0	8	5.7	68	3.9
NA[a]	11	2.0	6	1.7	6	2.2	11	4.0	5	3.0	4	2.9	43	2.4
Income (US$)														
<50,000	163	30.3	83	23.1	62	22.2	58	21.0	27	16.3	33	23.6	426	24.2
50,000–99,999	188	34.9	135	37.6	108	38.7	95	34.4	52	31.3	31	22.1	609	34.6
100,000–149,999	92	17.1	60	16.7	50	17.9	41	14.9	37	22.3	33	23.6	313	17.8
150,000–199,999	26	4.8	18	5.0	11	3.9	25	9.1	9	5.4	7	5.0	96	5.5
200,000–249,999	4	0.7	3	0.8	6	2.2	2	0.7	2	1.2	2	1.4	19	1.1
≥250,000	9	1.7	7	2.0	7	2.5	6	2.2	6	3.6	6	4.3	41	2.3
NA[a]	56	10.4	53	14.8	35	12.5	49	17.8	33	19.9	28	20.0	254	14.4
Total	538	30.6	359	20.4	279	15.9	276	15.7	166	9.4	140	8	1758	

a. Declined to answer.

harvest in Bedford and Maury counties ("no-delay counties") were stable or increasing during the same period.

Tennessee has a spring wild turkey hunting season in all counties. In select counties, there is a fall hunting season. During the spring and fall turkey hunting seasons, only bearded turkeys can be harvested which include adult males (toms), juvenile males (jakes), and bearded hens. From 2017 to 2020 the spring bag limit was four bearded turkeys for all counties in Tennessee, but in 2021 and 2022 the bag limit was reduced from four to three for the five focal counties.

In 2022, there were approximately 95,905 wild turkey hunters (resident and non-resident hunters included) in Tennessee (R. Shields, unpublished data). Based on license sales from 2022, there were 23,650 hunters (24.7% of TN hunters) living in the five focal counties with a license enabling them to turkey hunt. During our study period there were 30,000–40,000 turkeys harvested each year in Tennessee, and 2550 birds were killed in the five focal counties in 2022, which represented 8.9% of the 2022 statewide harvest (Tennessee Wildlife Resource Agency, unpublished data).

Methods

We conducted a spring turkey hunter survey every year from 2017 to 2022. We randomly selected 1600 people (320 per county) who lived in one of the five focal counties and had a license to hunt wild turkeys in Tennessee. We also randomly selected 400 additional people (80 per county) who reported harvesting a bird in one of the five focal counties to ensure our sample contained successful hunters, unsuccessful hunters, and non-resident hunters. These same 2000 individuals who were randomly selected in 2016 were surveyed each consecutive year unless they specifically asked to be removed from the survey mailing list.

Our survey included 30–38 questions annually and was arranged in four sections. The first section focused on the hunter's current turkey hunting season in Tennessee. The second section assessed their opinions surrounding spring turkey hunting regulations. The third section documented their perceptions of turkey populations in the five focal counties, and the last section requested demographic information. Our surveys were modeled after Watkins et al. (2018), and questions in each section were modified each year to accommodate new regulatory changes, incorporate new researcher hypotheses, or address respondent confusion about specific questions.

The mailing protocol for our survey followed Dillman (2006). Surveys were mailed to respondents within ten days of the close of the spring turkey hunting season. We included a cover letter with the survey which outlined the purpose of the survey with a pre-paid postage envelope to return the completed survey. We mailed a reminder postcard 1 wk after the initial mailing if we had not received a completed survey. We mailed an additional copy of the survey with a reminder letter if we had not received a completed survey 2 wk after sending the initial survey and cover letter. All mailings and surveys were conducted with an approved University of Tennessee Institutional Review Board human subjects research protocol (#UTK IRB-17-03689-XM).

Statistical Analysis

We calculated hunter effort and birds seen or heard on a per trip basis where a trip was defined as one individual leaving their place of residence to go hunting and returning. A hunter could have more than one trip per day if they returned home and went hunting again later that day. We derived hunter effort by taking the number of trips spent hunting in each county and multiplying it by the average time spent per trip. We calculated hunter efficiency by dividing the hunter's effort by the number of birds harvested which resulted in a metric of hours spent per harvested bird. Hunter success was the number of birds harvested by a hunter in a season. Each respondent reported the number of jakes and number of toms they saw, and how many individual gobbles they heard, on a typical trip. A typical trip was defined by the hunter and their experiences. We removed some surveys because of incomplete answers or individuals who reported implausible responses (e.g., a trip >24 hours, seeing >50 jakes or toms per trip, the number of gobbles heard per trip >200).

Our study was designed as a before-after (2017–2020, 2021–2022), control-impact (no-delay, delay) study (Smokorowski and Randall 2017). We used generalized linear models for panel data to maintain the longitudinal nature of the study which allowed responses to vary by the start date of the spring hunting season (Fulton and Manfredo 2004, Bartolucci et al. 2015). The models were run in a structured modeling framework with two levels of analysis (Fulton and Manfredo 2004, Watkins et al. 2021). The structured model framework allowed the assessment of the direct effects of the season delay (Level 1) and potential indirect effects of the season delay on hunter satisfaction (Level 2).

In Level 1 analyses, we examined a suite of *a priori* models, with one model per response metric (hunter effort, hunter success, hunter efficiency), and one model per experiential factor (toms seen per trip, gobbles heard per trip, jakes seen per trip). For each analysis, the independent variables were treatment group (delayed counties vs. no-delay counties) and timing (before the season delay vs. after the season delay). Our hypotheses were tested by evaluating the significance of the interaction between the two independent variables. For hunter effort and efficiency, if a hunter reported effort in both county groups (hunted in a delayed county and a no-delay county) within the same year / survey (11.1% of sample), we treated them as two separate hunters, one who hunted in no-delay counties and one who hunted in delayed counties. Hunter success was modeled with a single model of the number of birds harvested in a season. For each Level 1 analysis, we used a generalized linear model for panel data with a negative binomial distribution, fit with the pglm package (Croissant 2022) in Program R (R Core Team 2022). Additionally, we also assessed the direct effects of the season delay on hunter satisfaction using a generalized linear model for panel data with an ordinal logit distribution.

In our Level 2 analyses, we fit individual models with hunter satisfaction as the dependent variable and the above metrics as the independent variables. Hunter satisfaction was on a self-reported one to three ordinal scale with one being unsatisfied, two being neutral, and three being satisfied. Therefore, for hunter satisfaction analyses, we used a generalized linear model for panel data with an ordinal logit distribution. We tested the parallel assumption of logistic regression using the brant package (Schlegel and Steenbergen 2022) in Program R for all second-level models. We used $\alpha = 0.05$ for assessing significance in all analyses and referred to relationships as 'weak' for $0.05 < \alpha < 0.10$.

As part of our analyses, we checked for non-response and recall bias in our survey results. We checked for non-response bias by comparing hunter metrics (i.e., hunter effort, gobbles heard, and hunter satisfaction) and demographic information (i.e., age, gender, income) of the first 10% to return a response to the last 10% to return a response (Armstrong and Overton 1977, Watkins et al. 2021). We checked for recall bias by comparing the postmark dates of the completed surveys to the end date of the spring turkey hunting season in delayed and no-delay counties.

Results

We received 2539 surveys from 2017 to 2022, with an average of 423 surveys yr^{-1}, providing an average overall response rate of 22.0%. Of these responses, 1763 respondents hunted in one of the five focal counties, with an average of 294 hunters surveyed in our study area each year. If we adjust the response rates for hunters who hunted in these counties, we had a response rate of 15.2% for surveys from 2017 to 2022. After censoring surveys for inaccurate and unlikely responses, we used 1581 hunter surveys for analyses. In our checks for non-response bias, all statistical tests were insignificant except age where no-delay respondents were 7 yr older, on average, but this bias did not affect assignment to age bracket (i.e., 46–60 yr). We documented similar time-to-response rates in delayed and no-delay counties.

We received 562 surveys from hunters who reported hunting in one of the two no-delay counties with 455 before the season delay (2017–2020) and 107 after the delay (2021–2022). We received 1019 surveys of hunters who reported hunting in a delayed county with 833 before the delay and 186 after the delay. In no-delay counties, we surveyed 342 individual hunters (Before 263 vs. After 79), while in delayed counties we surveyed 604 individual hunters (Before 463 vs. After 141).

Hunter Effort

Hunter effort was not impacted by the season delay in delayed counties, but there was a weak relationship between the two factors ($P = 0.07$), where hunters in delayed counties spent less time hunting throughout the season compared to hunters in no-delay counties (Table 3). Effort declined in all counties from the 2017–2020 hunting season to the 2021–2022 hunting seasons ($\beta = 0.41$ [95% CL: 0.29, 0.53], $P < 0.001$). Delayed-county hunters spent 44.5 (SE = 1.2) h hunting per season and spent 21.9 fewer h, on average, hunting after the season delay (Table 4; Figure 1). Hunters in no-delay counties averaged 38.3 h per season, with a decline of 4.2 h after the delayed season was implemented (Table 4). Hence, delayed counties experienced a 41.5% decline in hunter effort concomitant to an 11.0% decline in no-delay counties.

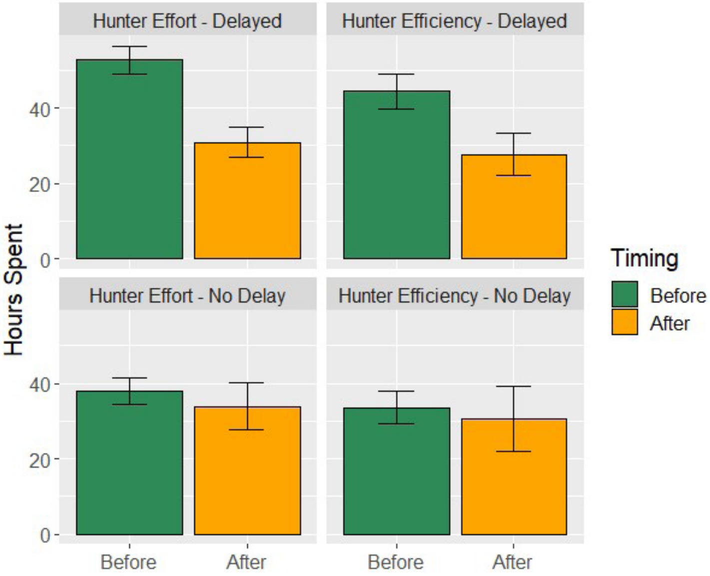

Figure 1. Wild turkey hunter effort (hours spent hunting) and hunter efficiency (hours spent to harvest a bird) during spring hunting season in south-middle Tennessee county groups with and without season delays, before (2017–2020) and after (2021–2022) delays were implemented. Error bars represent 95% confidence intervals.

Table 3. Models (generalized linear models for panel data) of hunter survey data in south-middle Tennessee, with model form, summary statistics, and significance. Timing: dummy variable signifying whether the survey was before (2017–2020) or after (2021–2022) the spring season delay. Treatment: dummy variable denoting whether the survey was from a hunter in a delayed or no-delay county. Bold indicates significant increase ($\beta > 0$) or decrease ($\beta < 0$) associated with season delay (Timing × Treatment models) or significant relationship between hunter satisfaction and predictor variable.

Model	df	β	P
Hunter effort ~ Timing × Treatment	1832	–0.17	0.07
Hunter success ~ Timing × Treatment	1577	–0.19	0.28
Hunter efficiency ~ Timing × Treatment	873	–0.06	0.68
Toms seen per trip ~ Timing × Treatment	1577	–0.25	0.07
Jakes seen per trip ~ Timing × Treatment	1577	0.10	0.54
Gobbles heard per trip ~ Timing × Treatment	1577	**–0.27**	**0.04**
Hunter satisfaction ~ Timing × Treatment	1577	–0.43	0.18
Satisfaction with season delay ~ Timing × Treatment	1630	**–0.84**	**0.004**
Hunter satisfaction ~ Hunter effort	1832	–0.002	0.15
Hunter satisfaction ~ Hunter success	1580	**0.92**	**<0.0001**
Hunter satisfaction ~ Hunter efficiency	873	**–0.01**	**<0.0001**
Hunter satisfaction ~ Toms seen per trip	1580	**0.18**	**<0.0001**
Hunter satisfaction ~ Jakes seen per trip	1580	**0.15**	**<0.0001**
Hunter satisfaction ~ Gobbles heard per trip	1580	**0.03**	**<0.0001**

Table 4. Wild turkey hunter metrics in south-middle Tennessee from 2017 to 2022. Delayed: county group that had a two-week delay in the 2021 and 2022 spring hunting season (Giles, Lawrence, and Wayne counties); No delay: county group without changes to the season start date in 2021 and 2022 (Bedford, and Maury counties). Before: 2017–2020; After: 2021–2022.

	Delayed						No delay					
	Before			After			Before			After		
Metric	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE
Hunter effort	932	52.8	1.9	189	30.9	2.1	587	38.1	1.8	128	33.9	3.2
Hunter efficiency	432	44.4	2.3	85	27.7	2.9	291	33.6	2.2	69	30.6	4.4
Hunter success	833	0.9	0.04	186	0.8	0.07	455	0.9	0.05	107	1.0	0.1
Toms seen	833	2.6	0.1	186	2.4	0.3	455	3.3	0.2	107	4.1	0.4
Gobbles heard	833	9.0	0.5	186	5.5	0.7	455	11.4	0.7	107	13.8	1.9
Jakes seen	833	2.9	0.2	186	3.1	0.5	455	4.1	0.2	107	4.2	0.5
Hunter satisfaction (1–3)	833	1.9	0.03	186	1.8	0.06	455	2.2	0.04	107	2.3	0.08
Season delay satisfaction (1–3)	854	2.2	0.03	201	2.1	0.06	477	2.1	0.04	102	2.4	0.06

Hunter success, efficiency, and experiential metrics

We received 855 surveys from hunters who reported harvesting at least one turkey. Out of the 1581 respondents, 50% reported harvesting zero turkeys per season, 28.3% reported harvesting one bird, 12.1% harvested two birds, and 9.6% harvested ≥ 3 birds per season (representing a season limit of turkeys). Hunter success did not decline because of the later start date in delayed counties (Table 3). Hunters in delayed counties harvested 0.1 fewer birds on average after the season delay, whereas no-delay hunters harvested 0.1 more birds after the delay (Table 4).

Hunter efficiency in delayed counties was not affected by the spring hunting season start date (Table 3) but did increase in the 2021 and 2022 hunting seasons for all counties surveyed ($\beta = 0.32$ [0.14, 0.51], $P < 0.001$). Spring turkey hunters spent 38.1 (SE = 1.4) h on average to harvest one turkey. Hunters in delayed counties reported 16.7 fewer h to harvest a bird after the season delay, a 37.6% decrease (Table 4; Figure 1). Hunter efficiency in no-delay counties also improved after the delay as hunters required 3.0 fewer h (–8.9%; Table 3; Figure 1) to harvest a bird.

The number of birds seen (toms or jakes) per trip by hunters in delayed counties remained similar after the season delay was implemented, but the number of gobbles heard per trip decreased (Table 3). We detected a weak relationship between the number of toms seen per trip and season start date ($P = 0.07$). Delayed-county hunters saw 0.2 fewer toms per trip after the delay (Table 4; Figure 2), whereas hunters in no-delay counties saw 0.8 more toms per trip after the delay (Table 4; Figure 2). Delayed-county hunters heard 3.5 fewer gobbles per trip, and in no-delay counties, hunters heard 2.4 more gobbles per trip (Table 4; Figure 2). In delayed counties, hunters saw 0.2 more jakes per trip after the delay and 0.1 more in no-delay counties (Table 3; Figure 2).

Hunter Satisfaction

Hunter satisfaction was not directly impacted by the season delay (Table 3; Figure 3), but hunters in delayed counties were less satisfied than hunters in no-delay counties ($P < 0.001$). Hunter satisfaction across all hunters from 2017 to 2022 was 2.0, which equates to a neutral reaction to the hunting season (i.e., neither satisfied or dissatisfied). Hunter satisfaction in delayed counties decreased by 0.1 after the delay and stayed below 2.0, indicating dissatisfaction. Hunter satisfaction of no-delay hunters increased by 0.1 in 2021–2022 and remained above 2.0, denoting satisfied hunters (Figure 3).

Hunter satisfaction was not correlated with hunter effort but was positively correlated with hunter success, hunter efficiency, and all experiential metrics (Table 3). We documented negligible support for the relationship between hunter effort and satisfaction ($\beta = -0.002$ [95% CI: –0.005, 0.001]; Table 3). There was a positive relationship between hunter success and satisfaction where hunters who harvested more birds reported greater satisfaction ($\beta = 0.92$ [0.74, 1.10]; Table 3). An increase in hunter efficiency (i.e., less time required to harvest a bird) resulted in greater hunter satisfaction ($\beta = -0.01$ [–0.015, –0.005]; Table 3). We documented positive relationships with hunter satisfaction and toms seen ($\beta = 0.18$ [0.14, 0.23]), gobbles heard ($\beta = 0.03$ [0.02, 0.04]), and jakes seen ($\beta = 0.15$ [0.11, 0.18]).

From 2017 to 2022, 1634 hunters answered a question about their support for a season delay with 1055 delayed-county hunter surveys (Before 854 vs. After 201) and 579 from no-delay counties (Before 477 vs. After 102). Satisfaction with the regulation change was ranked on a scale of one (unacceptable/dissatisfied)

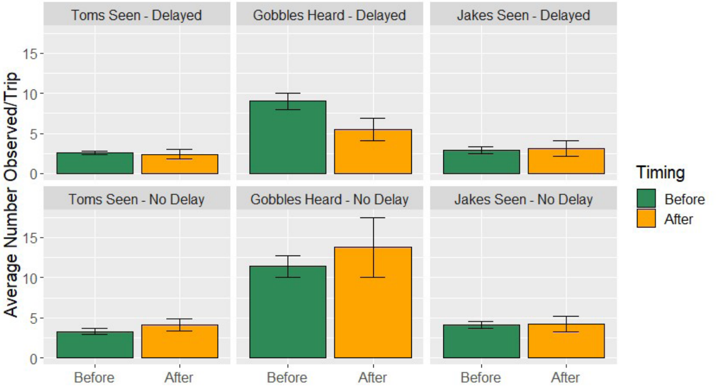

Figure 2. Experiential metrics (number of toms seen per trip, gobbles heard per trip, and jakes seen per trip) by wild turkey hunters during spring hunting season in south-middle Tennessee county groups with and without season delays, before (2017–2020) and after (2021–2022) delays were implemented. Error bars represent 95% confidence intervals.

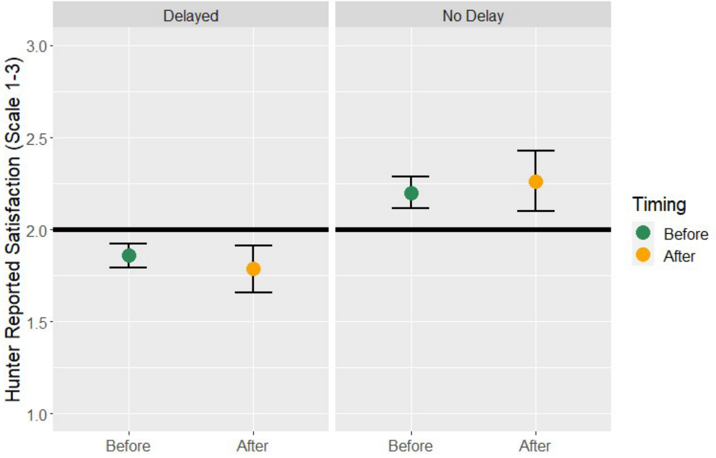

Figure 3. Average wild turkey hunter satisfaction on a 1–3 scale with 1 = "dissatisfied," 2 = "neutral" (thick black line), and 3 = "satisfied" for turkey hunters during the spring hunting season in south-middle Tennessee county groups with and without season delays, before (2017–2020) and after (2021–2022) delays were implemented. Error bars represent 95% confidence intervals.

to three (acceptable/satisfied). Satisfaction with the season delay by delayed-county hunters dropped by 0.1 after the season delay occurred, whereas hunters in no-delay counties increased by 0.3 (Table 4). Satisfaction related to changing the season framework remained in the same category of "neutral" in delayed counties following the delay.

Discussion

Hunter satisfaction was positively correlated with gobbles heard per trip, which was correlated with the timing of the spring hunting season. Hunters were more satisfied with their hunting season if they saw or heard more turkeys or if the birds were easier to hunt successfully (i.e., greater efficiency). Schroeder et al. (2019) and Gruntorad et al. (2020) reported that seeing game had the greatest influence on satisfaction. However, these studies did not measure the impact of hunter effort or efficiency on hunter satisfaction. Hunter effort was not a strong predictor of hunter satisfaction in our study. Most successful turkey hunters in Tennessee harvest only one turkey (50% harvested no birds and 28.3% harvested one bird), so more time spent in the woods often equates to less efficiency (R. Shields, unpublished data). We observed a decline in hunter effort of 42% in delayed counties, but a decline also was observed in control counties (11%). Hours spent hunting was not an important predictor of satisfaction, so the decline in effort likely did not influence hunter satisfaction. The reduction in effort may have been a response to the 14-day season delay, the 14-day reduction in season length, or a combination of both. Hunter success did not change in response to the season delay as hunters in delayed counties harvested the same number of birds (approximately one) before and after the delay. Hunter satisfaction was more strongly related to harvest, which has been documented by others (Fulton and Manfredo 2004, Schroeder 2014, Gruntorad et al. 2020).

Hunter efficiency was a significant predictor of hunter satisfaction but was not explicitly affected by the season delay. We observed changes before and after the season delay in hunter efficiency, but these changes were observed in both county groups. There was a greater increase in efficiency in delayed counties compared to no-delay counties. By opening the season in mid-April, toms are likely more susceptible to calling by hunters because more hens are incubating. The majority of turkey hunters kill only one bird and may quit hunting after harvesting a bird, thus efficiency increased. The increase in hunter efficiency in no-delay counties might have reflected changes in hunting conditions and/or an increase in the number of toms.

Based on our experiential data, fewer gobbles were heard by hunters in delayed counties, whereas hunters in no-delay counties saw and heard more birds. These differences coincided with greater overall satisfaction in no-delay counties. The most substantial change in the experiential metrics was in the number of gobbles heard per typical trip. Hunters reported 39% fewer gobbles per trip in delayed counties, whereas hunters in no-delay counties reported a 21% increase. Previous research has identified factors such as weather (Wightman et al. 2022), changes in population size (Palumbo et al. 2019), and hunter activity (Wakefield et al. 2020, Wightman et al. 2023) as factors influencing gobbling activity. However, we documented no evidence that any of these factors accounted for the differences in gobbles heard between delayed and no-delay counties. Gobbling activity in both county groups was similar prior to the season delay, with hunters reporting 9.0 gobbles per trip in delayed counties and 11.4 in no-delay counties ($P = 0.17$). Therefore, a reduction in gobbling in delayed counties indicates the delayed hunting season began after peak gobbling activity. The decrease in gobbles heard supports our hypothesis that a later hunting season caused hunters to hear fewer gobbles per trip because a later hunting season may not coincide with peak gobbling activity. Gobbling activity (gobbles heard per trip) was correlated with hunter satisfaction similar to results reported elsewhere (Diefenbach et al. 2011, Schroeder 2014, Gruntorad et al. 2020).

We detected a positive relationship between gobbles heard and hunter satisfaction and a negative relationship between gobbles heard and season start date, but we did not see any direct changes to hunter satisfaction. There may be other confounding factors influencing hunter satisfaction that we did not test for such as, perceived population size (Watkins et al. 2018), crowding (Gruntorad et al. 2020) or hunter typology (i.e., appreciative-orientated, affiliation-orientated, and achievement-orientated, Watkins et al. 2018). After the season delay in 2021 and 2022, affected hunters were slightly less satisfied with the regulatory change, whereas hunters in no-delay counties were slightly more satisfied.

Management Implications

Wild turkey management is unique because the wild turkey is the only gamebird species in the U.S. hunted during the breeding season, thereby potentially affecting seasonal productivity negatively. Turkey hunting-season frameworks must be set such that they do not have a deleterious effect on the species' reproductive behavior or population growth. Beyond that, consideration for hunter satisfaction is important to maintain hunter involvement, recruitment, and for some species, management of the population. We documented that a two-week delay in the opening date and a reduction in length of the spring wild turkey season in three counties of south-middle Tennessee did not influence hunter satisfaction directly. However, these regulation changes could indirectly affect satisfaction, as hunters heard fewer gobbles per trip (negative) and increased their hunter efficiency (positive), both of which are strong predictors of hunter satisfaction. There was a strong perception among turkey hunters in the delayed counties that the turkey population had declined considerably compared to several years prior, and hunters wanted some agency action to reverse the decline (R. Shields, unpublished data). However, after two years of the season delay, hunters in delayed counties were less accepting of the delay, likely because they heard fewer gobbles and did not perceive any net benefit from the delay. Based on our wild turkey productivity study, we documented no increase in productivity in delayed counties after the season delay (Quehl 2023), and in an online survey of hunters in the five focal counties in 2023, 69% said they would prefer the spring turkey hunting season reverted back to its historic framework (2020 and earlier) if there was no reproductive benefit for turkeys. We recommend state agencies use hunter satisfaction data when determining the timing of the hunting season, but primarily consider how the timing of the hunting season may affect reproductive success after analyzing vital rate data in relation to season-opening date and length.

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Effects of COVID-19 on Wild Turkey Hunter Satisfaction and Behavior in Tennessee

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Abstract: Understanding hunter satisfaction and behavior under normal and abnormal situations is important for effective management of game species by state wildlife agencies. SARS-CoV-2 (COVID-19) created a global pandemic that coincided with the 2020 spring wild turkey hunting season. Concern was expressed by some wild turkey researchers and biologists that COVID-19 lockdown protocols could result in increased hunting effort and unsustainable harvests because of people having more free time. We assessed how COVID-19 and associated lockdown protocols affected hunter satisfaction and behavior during the spring 2020 wild turkey hunting season by using responses from 2,000 annual surveys of wild turkey hunters (2017–2020) among five focal counties (Bedford, Giles, Lawrence, Maury, and Wayne) in south-central Tennessee. COVID-19 did not result in changes to hunter satisfaction or an increase in hunter effort or harvest of every-year hunters but did result in a 26% increase in new license holders and returning hunters (i.e., hunters that had not hunted in the last 5 yr) compared to the previous 3 yr (2017–2019). Wild turkey harvest peaked at 40,137 birds during COVID-19, 27.8% greater than the previous 3-yr average (31,407 birds, 2017–2019). Wild turkey researchers and biologists were concerned that populations might have been overharvested. However, harvest in Tennessee during 2021–2023 returned to pre-COVID-19 levels. These harvest data indicate the wild turkey population in Tennessee was sufficiently resilient to withstand a significantly greater harvest in 2020. Furthermore, the greater harvest in 2020 was potentially good for the sport of wild turkey hunting considering the increased recruitment of new and returning hunters that were just as successful as every-year hunters.

Key words: COVID-19 impacts, hunter surveys, human dimensions

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The wild turkey (*Meleagris gallopavo*; hereinafter, turkey) is an important upland gamebird across the U.S. (Dickson 2001, Watkins et al. 2018). The number of turkey hunters (hereinafter, hunters) increased 450% from 1973 to 2003 (Wynveen et al. 2005). According to the 2016 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation, over 2 million turkey hunters hunted a total of 13 million days, making turkey the second-most hunted species in the U.S. (USFWS and USCB 2018). However, many southeastern states, including Tennessee, have reported recent declines in turkey harvest (Tapley et al. 2011, Bond et al. 2012, Eriksen et al. 2015). Chamberlain et al. (2022) reported that turkey harvest across the southeastern U.S. decreased 12% from 2014 to 2019. The Tennessee Wildlife Resources Agency's (TWRA) Administrative Region II reported spring turkey harvest declined approximately 30% from 2010 to 2018 (TWRA 2022; Figure 1A). Declines in turkey harvest across the southeastern U.S. likely are a result of declining turkey populations and productivity. Chamberlain et al. (2022) estimated turkey populations across the southeastern U.S. have decreased 9–16% from 2004 to 2019. Byrne et al. (2015) reported declining productivity values in twelve southeastern states (100% of the states reported productivity data). In Tennessee, summer poults-per-hen ratios have declined substantially (69%) over the past 30 yr (Shields 2023). Understanding what is driving these declines in turkey populations and harvest, as well as understanding how these declines are influencing hunter effort and satisfaction, are a priority of turkey researchers and biologists.

Human dimensions research has historically identified that the number of turkeys harvested and hunting licenses sold are a way to measure hunter satisfaction and participation (Hammitt et al. 1989, Heberlein and Kuentzel 2002, Wynveen et al. 2005). However, the idea of "hunter satisfaction" has evolved beyond quantifying harvest and now includes factors such as hunter effort (number of days or hours afield), density of the species hunted, weapon used, past experiences, and hunter perceptions (Potter et al. 1973,

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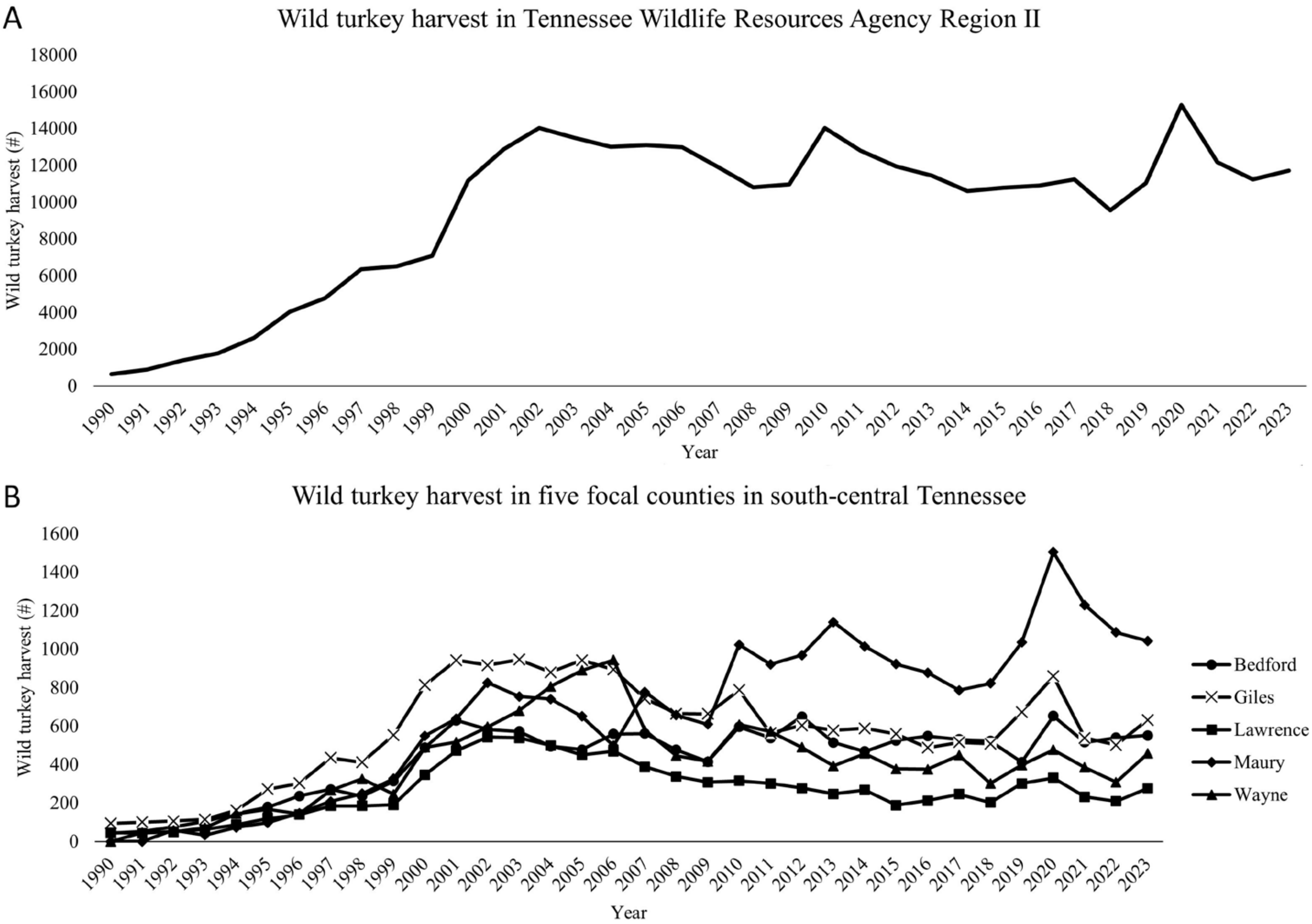

Figure 1. Number of turkeys harvested in A) Tennessee Wildlife Resources Agency's Administrative Region II and B) five focal counties (Bedford, Giles, Lawrence, Maury, and Wayne) in south-central Tennessee, 1990–2023.

Hazel et al. 1990, Wynveen et al. 2005, Harper et al. 2012). Understanding factors that influence hunter satisfaction and behavior helps guide state wildlife agencies managing turkey populations, especially during a period of potential population decline.

Uncontrollable and unpredictable factors (e.g., weather, societal issues) influence hunter behavior and satisfaction (Hammitt et al. 1989, Wynveen et al. 2005). An example was the worldwide spread of SARS-CoV-2 (hereinafter, COVID-19), which caused a global pandemic starting December 2019 (Bergquist et al. 2020, Liu et al. 2020, Velavan and Meyer 2020). The first individual tested positive for COVID-19 in the U.S. on 21 January 2020 (Bergquist et al. 2020, Velavan and Meyer 2020). The number of positive cases in the U.S. increased dramatically by March 2020, which prompted lockdown protocols across the country (Liu et al. 2020, Rutledge 2020). Lockdown protocols forced businesses to reduce hours or lay-off or terminate employees, which resulted in millions of unemployed Americans (Rutledge 2020). In Tennessee, the first confirmed COVID-19 case was announced 5 March 2020, and a state of emergency was declared by the Tennessee governor 12 March 2020 followed soon thereafter by lockdown protocols from 13 March 2020 through 30 April 2020 (TN Office of the Governor 2023). By 1 May 2020, Tennessee businesses and restaurants were allowed to begin opening again with reduced capacity guidelines (TN Office of the Governor 2023).

Lockdown protocols coincided with the start of the spring 2020 turkey hunting season across much of the southeastern U.S. (Danks et al. 2022). In Tennessee, the 2020 spring turkey hunting season began 4 April 2020, two weeks after the governor announced all businesses should use "alternative business models," which included employees working from home, and only five days after the announcement of "Safer at Home" guidelines, which minimized group gatherings (TN Office of the Governor 2023). Some wildlife biologists and researchers across the U.S. hypothesized that various lockdown protocols would increase the number of turkey hunters and the amount of time they hunted. Increased hunting pressure could result in an increased harvest, potentially resulting in an overharvest of already declining turkey populations. Some researchers even called for states to impose emergency changes to the 2020 spring turkey hunting season, including limiting license sales, closing seasons early, and reducing bag limits (Goldman 2020, Chizinski et al. 2021, Danks et al. 2022). Fourteen of 47 state governments (30%) implemented some level of COVID-19 lockdown protocols (i.e., restrictions on public gatherings, state or county stay-at-home orders) that also involved changes to their 2020 spring turkey hunting season (i.e., license sale restrictions, restrictions to public hunting land; Danks et al. 2022). However, these lockdown protocols and changes were not implemented because of concerns related to overharvest of turkey populations, but rather were implemented to address potential human health and safety measures. Despite some lockdown protocols and changes limiting turkey hunting ability or access, some states saw record harvests of turkeys in 2020, including Tennessee. This indicates that Tennessee's increase in turkey harvest was related to COVID-19 given that many turkey populations across the southeastern US are reportedly declining (i.e., a 2020 turkey population boom was unlikely). However, it is unclear if the increased harvest resulted from changes in the hunter population (i.e., new hunters entering the sport, previous hunters returning to the sport), or from changes in hunter behavior in response to the COVID-19 restrictions.

From 2017–2020, we conducted a comprehensive mail-based hunter survey in south-central Tennessee to quantify hunter satisfaction and behavior, and to assess how changes in the hunter population influenced harvest during the COVID-19 pandemic (2020). Our first objective was to measure hunter satisfaction and perceptions about the season framework, quantify hunter effort, determine variables that affected hunter effort, and evaluate how the COVID-19 lockdown protocols affected these metrics. Our second objective was to evaluate whether the increase in overall harvest resulted from increased hunting license sales, increased hunter effort, or both.

Methods

Study Area

This study was conducted in five focal counties (Bedford, Giles, Lawrence, Maury, and Wayne) in south-central Tennessee during the 2017–2020 spring turkey hunting seasons. We selected these five focal counties because they historically have had the greatest harvest in Tennessee, but since the early 2000's, the spring harvest in three of the five focal counties (Giles, Lawrence, and Wayne) had declined (TWRA 2022; Figure 1B).

The season framework was the same for all spring turkey hunting seasons included in our study (2017–2020). Statewide spring turkey hunting season opened on the Saturday closest to 1 April, with a 2-day young sportsman (i.e., youth) hunting season the weekend before the statewide season. Spring turkey hunting season was open for 44 days. All bearded turkeys, regardless of sex or age, were legal to harvest. The daily bag limit for bearded turkey was one turkey per day, with a season bag limit of four turkey (TWRA 2021).

Our target survey population was individuals who hunted turkey in the five focal counties during the 2017 spring hunting season. We used hunting license information from TWRA to generate our list of potential sample individuals (Dillman 2007, Vaske 2008). All individuals who met one of the following criteria for the 2017 spring hunting season were included: 1) individuals residing in one of the five focal counties and purchased a hunting license allowing them to hunt turkeys or 2) individuals who purchased a hunting license that allowed them to hunt turkeys and checked-in a turkey in one of the five focal counties through the TWRA's mandatory harvest reporting system. We then used simple random sampling for each county to select 2000 individuals (400 per focal county) for surveys. We re-sampled the same individuals each year to track changes in attitudes and hunting behavior.

Survey Development, Implementation, and Quality Control

We developed a six-page paper survey for the sampling unit each year (UTK IRB-17-03689-XM). The survey asked questions related to turkey hunting effort, success, and experience. We measured hunter satisfaction on a Likert scale (1 = very dissatisfied, 2 = somewhat dissatisfied, 3 = neither satisfied nor dissatisfied, 4 = somewhat satisfied, 5 = very satisfied). Following Dillman (2007) and Dillman et al. (2014), we mailed the survey packet, which included the survey, a personalized cover letter detailing the purpose of the survey, and a pre-paid return envelope within ten days of the conclusion of the spring hunting season. Two weeks after mailing the initial survey, we mailed a thank you/reminder postcard to each respondent to thank respondents who completed the survey and encourage other respondents to complete the survey. Two weeks after mailing the postcard, we mailed a second survey packet to those who had not returned a survey.

If a hunter returned two surveys, we used the survey returned closest to the end of the spring hunting season to minimize the amount of error introduced through recall bias (Vaske 2008). Any responses that were illegible, reported erroneous values outside the bounds of the hunting season, or left blank, such that calculations could not be performed to obtain hunter effort, were removed from the data set.

Statistical Analysis

We used descriptive statistics to analyze hunter demographics as well as satisfaction relative to the 2017–2020 spring hunting season quality and regulations, and proposed regulation changes (Hammitt et al. 1989, Heberlein and Kuentzel 2002, Shrestha and Burns 2012). We performed Pearson's chi-square tests to compare opinions about turkey population size over multiple years and satisfaction between hunters before COVID-19 (2017–2019) to hunters during COVID-19 (2020).

To determine if hunter effort changed in response to lockdown protocols, we regressed hunter effort for all hunters and only successful hunters as a function of year using a linear mixed effects model analysis of variance with respondent identification number included in the model as a random effect because we monitored the same hunters each year. We calculated hunter effort, hunter effort per harvested bird for successful hunters, total number of birds harvested, take per unit effort, and total number of days hunted for the spring turkey hunting season. We defined hunter effort as the total number of hours hunted by each respondent in any given year and calculated this by multiplying each respondent's answers to the following questions: 1) "How many trips did you go turkey hunting?", and 2) "In a typical hunt, how many hours did you spend hunting (not counting travel time)?" We calculated hunter effort per harvested bird by dividing the total hunter effort (total number of hours hunted) by the number of birds harvested for successful hunters only. We calculated take per unit effort by dividing the number of harvested birds by the total number of days hunted for all hunters. We defined hunter days as the total number of days all respondents reported hunting; a single hunter-day could include multiple hunting trips. We used orthogonal planned contrasts post-hoc to compare hunter effort before COVID-19 to hunter effort during COVID-19. Analyzing 2020 (COVID-19) against a combination of previous years (2017–2019) before COVID-19 allowed comparison between a "normal" spring hunting season and the COVID-19-affected spring hunting season.

We used path analysis to determine factors predicting hunter effort in years before COVID-19 and during COVID-19. Path analysis is a multivariate linear model whereby causal relationships between one dependent (i.e., hunter effort) and two or more independent variables can be determined (Heberlein and Kuentzel 2002, Frey et al. 2003, Lleras 2005, Suhr 2008, Kerr 2017). We developed the original model (Figure 2) tested in the path analysis based on literature review and suspected causal relationships among variables included in the survey. Subsequent models were developed through model modification (Suhr 2008). We used Akaike's Information Criterion (AIC), a comparative fit index (CFI), and a chi-square summary statistic for model selection to identify the best-supported model. We considered models with the least AIC, CFI closest to 1.0, and the smallest chi-square value the top models. However, more confidence was placed on the model

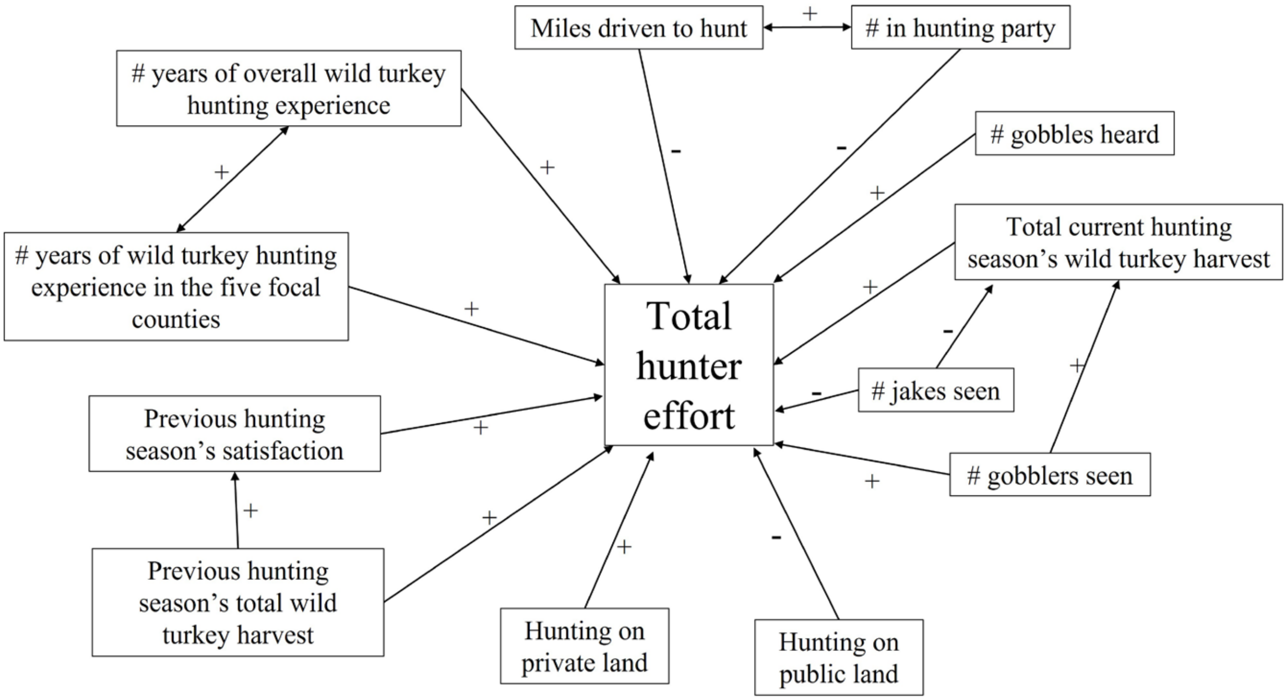

Figure 2. The original path analysis model developed and tested based on literature reviews and suspected causal relationships between the variables included in the turkey hunter effort survey, Tennessee, 2017–2020. The direction and power (+ or -) of the suspected causal relationships are indicated by the direction of the arrows and their associated signs.

AIC and CFI values compared with the chi-square summary statistic because achieving insignificance of the chi-square summary statistic is challenging when sample sizes are large, as in this study (Heberlein and Kuentzel 2002, Frey et al. 2003, Lleras 2005).

Wild Turkey Harvest and License Sales

Hunter-reported big game harvest data in Tennessee were available to the public through the TWRA Hunter's Toolbox, which was linked to TWRA's mandatory harvest reporting system (TWRA 2022). We obtained historical and current statewide spring turkey harvest totals, as well as harvest in the five focal counties through the TWRA Hunter's Toolbox and from TWRA harvest data sets (TWRA, unpublished data).

We obtained hunting license sales information from TWRA, which included the number of hunting licenses sold in each of the following categories that allowed the purchaser to hunt turkeys for each year (2017–2020): 1) new Tennessee resident and non-Tennessee resident hunters; 2) total non-Tennessee resident hunters (non-Tennessee residents who purchased a hunting license, regardless if this was their first Tennessee hunting license or not); and 3) returning Tennessee resident and non-Tennessee resident hunters (Tennessee residents and non-Tennessee residents who had previously purchased a hunting license, but not in the last 5 yr; TWRA unpublished data).

Results

General Survey and Respondent Characteristics

We mailed 8000 surveys (2000 surveys/year) to the same individual hunters selected in 2017 among our five focal counties. We received 2021 completed surveys (25% response rate), of which 1487 were from individuals who responded that they hunted at least one year in one of the five focal counties (19% response rate). Age of respondents ranged from 18–80 yr (median = 50, mean = 48). Most respondents were male (96%). Experience of respondents hunting turkeys in the five focal counties ranged from 1–63 yr (median = 18, mean = 17).

Wild Turkey Harvest

The 2020 statewide spring turkey harvest was the greatest ever recorded in Tennessee (40,137), representing a 29.0% increase above the 5-yr harvest average (31,123 birds, 2015–2019) and a 27.8% increase above the 3-yr harvest average during our survey study (31,407 birds, 2017–2019). Within the five focal counties, the record turkey harvest occurred in 2020 with 3827 birds reported, which was a 43.6% increase above the 5-yr harvest average (2663 birds, 2015–2019) and a 42.0% increase above the 3-yr harvest average during our survey study (2694 birds, 2017–2019; Figure 1B).

Hunter Satisfaction and Behavior in Response to COVID-19

For the following results, "current" refers to the year in which each survey was sent. Satisfaction with the current spring hunting season did not differ between before (median = 3 [neither satisfied nor dissatisfied]) and during COVID-19 (median = 3; $x^2 = 5.53$, df = 4, $P = 0.24$). However, 45% of respondents reported some level of dissatisfaction (responded with "somewhat dissatisfied" or "very dissatisfied") with the current spring hunting season and 63% of respondents reported the quality of their current spring hunting season was worse compared with a spring season 5 yr ago (Table 1). COVID-19 did not affect hunter's opinions on the current spring hunting season regulations. When respondents were asked how they felt about the current spring hunting season regulations, on average, 65% reported some level of satisfaction (responded with "somewhat satisfied" or "very satisfied") with the current season length, 55% reported some level of satisfaction with the season opening and closing dates, 53% reported some level of satisfaction with the current season bag limit, and 64% reported some level of satisfaction with the current daily bag limit. COVID-19 did not affect hunter's opinions on proposed spring hunting season regulations. When respondents were asked how willing they would be to support various proposed regulation changes, on average, 65% reported some level of satisfaction with reducing the season bag limit from four birds to three birds, and 68% reported some level of satisfaction with prohibiting harvest of juvenile males.

COVID-19 did not affect hunters' opinions about whether there were enough turkeys to allow ample opportunity to harvest a bird (median = 2 [no]; $x^2 = 1.70$, df = 2, $P = 0.43$; Table 2) and whether the turkey population had changed over the past 5 yr (median = 3 [decreased]; $x^2 = 23.72$, df = 3, $P = 0.30$). When respondents were asked if they knew about the decline in harvest prior to reading this survey, 81% of all respondents answered "yes," and COVID-19 did not affect this ($x^2 = 2.54$, df = 1, $P = 0.11$). Ninety-seven percent of respondents reported some level of concern over declining turkey harvest, and this did not differ between before (median = 4 [extremely concerned]) and during (median = 4) COVID-19 ($x^2 = 3.64$, df = 3, $P = 0.30$). However, despite expressing concern over declining turkey populations, 70% of respondents reported they would not stop turkey hunting even if turkey populations continued to decline.

Average hunter effort during the spring hunting season did not differ before (31.0 h) and during (31.6 h) COVID-19 ($F_{3,\ 816.5} = 2.11$, $P = 0.70$; Table 3). Average hunter effort per harvested bird among successful hunters during the spring hunting season also did not differ before (26.6 h) and during (25.4 h) COVID-19 ($F_{3,\ 423.4} = 0.67$, $P = 0.62$). Successful hunters harvested an average of 1.5 birds per year during the spring hunting season before and

Table 1. Summary of hunter satisfaction (% of respondents) with current (year the survey was sent) hunting season quality and current and proposed hunting season regulations reported by turkey hunters in Bedford, Giles, Lawrence, Maury, and Wayne counties, south-central Tennessee, 2017–2020. Data were collected on Likert scales.

	Before COVID-19 (2017–2019)					During COVID-19 (2020)				
	1	2	3	4	5	1	2	3	4	5
Satisfaction with current hunting season[a]	25.1	19.6	10.2	29.2	15.9	23.8	24.2	6.2	28.2	17.6
Quality of current hunting season compared to 5 yr ago[b]	26.6	38.9	23.3	10.0	1.2	19.1	34.7	26.7	16.4	3.1
Satisfaction with current hunting season length	6.9	8.8	18.4	29.5	36.4	8.5	10.3	21.4	25.9	33.9
Satisfaction with current hunting season opening and closing dates	10.2	10.4	23.0	27.5	28.9	10.2	18.7	20.5	25.3	25.3
Satisfaction with current hunting season daily bag limit (1 bearded bird)	12.1	8.7	15.0	19.5	44.7	8.5	7.6	17.9	19.6	46.4
Satisfaction with current hunting season bag limit (4 bearded birds)	19.0	12.2	16.5	21.9	30.4	23.9	9.3	18.1	20.4	28.3
Satisfaction with proposed hunting season bag limit (3 bearded birds)	13.8	5.1	16.0	20.2	44.9	8.9	6.6	15.5	23.9	45.1
Satisfaction with proposal of removing immature males from harvest (except for youth hunts)	7.9	7.1	14.4	23.0	47.6	15.0	10.2	18.1	18.6	38.1

a. Scale for all questions except quality of current hunting season: 1 = very dissatisfied, 2 = somewhat dissatisfied, 3 = neither satisfied nor dissatisfied, 4 = somewhat satisfied, 5 = very satisfied.

b. 1 = much worse, 2 = worse, 3 = same, 4 = better, 5 = much better.

Table 2. Summary of hunter opinion and behavior (% of respondents) reported by wild turkey hunters in Bedford, Giles, Lawrence, Maury, and Wayne counties, south-central Tennessee, 2017–2020.

	Before COVID-19 (2017–2019)	During COVID-19 (2020)
Enough turkeys to allow for ample harvest		
Yes	42.5	46.9
No	50.9	46.0
Don't know	6.6	7.1
Seen a turkey population change over the past 5 yr		
Increased	8.7	17.6
Stayed the same	16.2	21.6
Decreased	72.6	58.2
Don't know	2.5	2.6
Knew about harvest decline prior to this survey		
Yes	82.3	76.7
No	17.7	23.3
Concerned about harvest decline		
Not concerned	3.3	3.1
Somewhat concerned	11.2	14.7
Moderately concerned	23.7	26.7
Extremely concerned	61.8	55.5
If population declined where you hunt, would you continue to hunt there		
Yes	68.3	78.0
No	31.7	22.0

Table 3. Average hunter effort reported by turkey hunters before and during COVID-19 in Bedford, Giles, Lawrence, Maury, and Wayne counties, south-central Tennessee, 2017–2020.

	Before COVID-19 (2017–2019)			During COVID-19 (2020)		
	n	Mean	SE	*n*	Mean	SE
Hunter effort (h) for all hunters	1112	31.0	1.1	214	31.6	1.1
Hunter effort (h) per harvested bird for successful hunters	546	26.6	1.1	114	25.4	1.1
Average birds harvested for successful hunters	544	1.5	1.0	113	1.5	1.1
Take per unit effort for all hunters	1094	0.11	0.01	209	0.11	0.01
Average days hunted for all hunters	1099	7.3	1.0	210	7.6	1.1

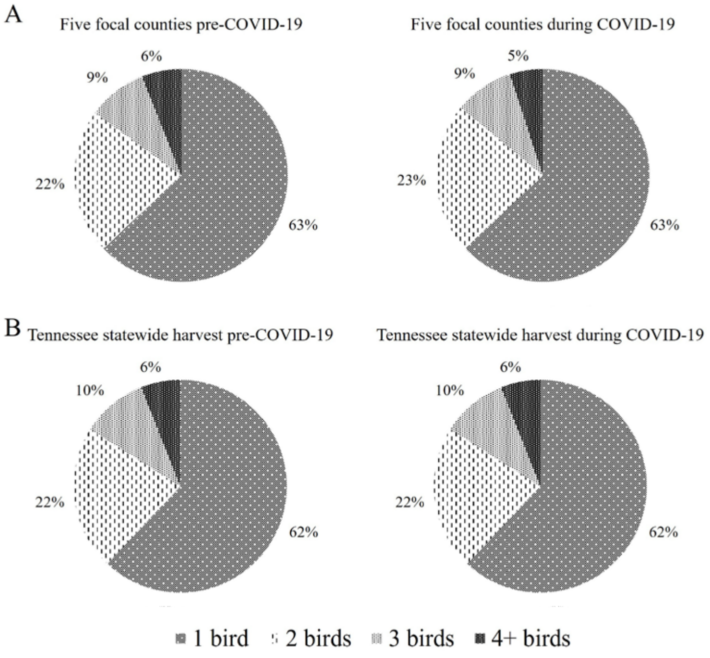

Figure 3. Proportion of hunters that harvested 1, 2, 3, or 4+ birds in A) five focal counties (Bedford, Giles, Lawrence, Maury, and Wayne) pre-COVID-19 and during COVID-19 and B) statewide pre-COVID-19 and during COVID-19 in Tennessee, 2017–2020.

during COVID-19 ($F_{3,\ 482.0} = 0.23$, $P = 0.53$). Take per unit effort during the spring hunting season also did not differ before and during COVID-19 ($F_{3,\ 883.7} = 1.0$, $P = 0.39$). Hunters reported hunting 7.3 days before COVID-19 and 7.6 days during COVID-19 ($F_{3,\ 775.7} = 0.83$, $P = 0.37$) during the spring hunting season. Based on reported harvest in the mail surveys, the proportion of individuals who reported killing 1, 2, 3, or 4+ birds during the spring hunting season was similar before and during COVID-19 (Figure 3A). The Tennessee statewide harvest exhibited the same harvest pattern as well (Figure 3B).

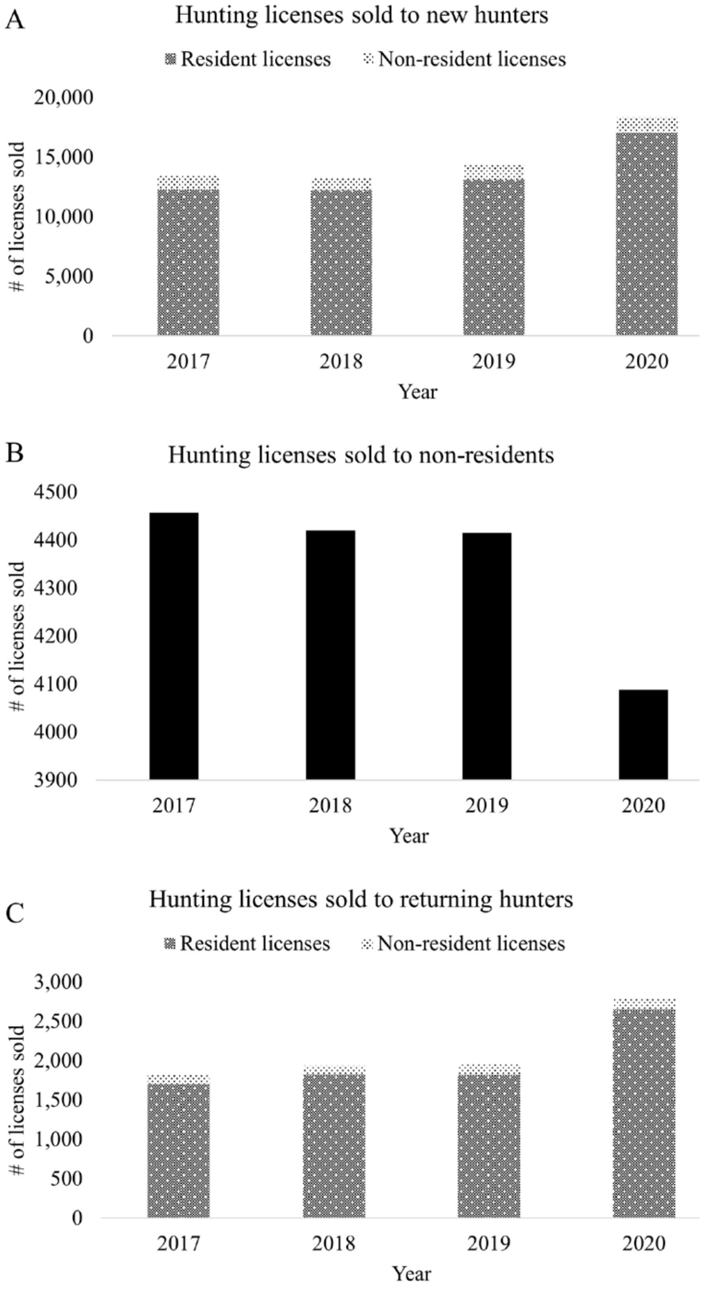

Figure 4. Number of Tennessee hunting licenses sold, 2017–2020, to Tennessee resident and non-Tennessee resident new hunters (A) and returning hunters (C), and overall non-Tennessee resident hunters (B).

During COVID-19, survey respondents were asked, "Because of the COVID-19 pandemic, my wild turkey hunting in the five focal counties has: a) decreased by _____ trips, b) remained about the same, or c) increased by _____ trips." Of the hunters who answered this question ($n = 275$), 75% reported their effort did not change, 16% reported their effort increased, and 9% reported their effort decreased. We note that for hunters who responded to the survey over multiple years, this reported change in effort by hunters was only a perceived change, as only 37% of respondents' hunting effort during the spring hunting season prior to and during COVID-19 accurately reflected their reported change.

Despite reporting yearly turkey harvest values prior to 2017, we only report license sale information from 2017–2020 because of a change in the TWRA system responsible for handling the sale of hunting licenses between 2016 and 2017. The sale of new hunting licenses (resident and non-resident) peaked in 2020 (Figure 4A), whereas the sale of non-resident hunting licenses was at a 4-yr low in 2020 (Figure 4B). The sale of hunting licenses to resident and non-resident returning hunters increased from the previous 3-yr average by 47% in 2020 (Figure 4C).

The original model developed for the path analysis (Figure 2) did not satisfy the goodness-of-fit tests (chi-square summary statistic or CFI) for the spring hunting season either before or during COVID-19. Therefore, additional models were developed using model modification by removing insignificant or unsupported model parameters (Suhr 2008). Before COVID-19 ($x^2 = 159.38$, df = 18, $P < 0.001$), hunter effort during the spring hunting season was more likely to be positively influenced by harvest during the current hunting season ($P < 0.001$) or previous hunting season ($P < 0.001$) compared to the number of gobbles heard ($P = 0.02$) (Figure 5A). Hunter effort during the spring hunting season was negatively related to hunting on public land ($P = 0.01$; Figure 5A). During COVID-19 ($x^2 = 56.3$, df = 31, $P = 0.004$), hunter effort during the spring hunting season was positively influenced by the distance individuals drove to hunt ($P = 0.02$), which was positively influenced by the number of people in their hunting party ($P = 0.03$; Figure 5B). Hunter effort during the spring hunting season also was positively influenced by the previous hunting season harvest ($P = 0.004$; Figure 5B).

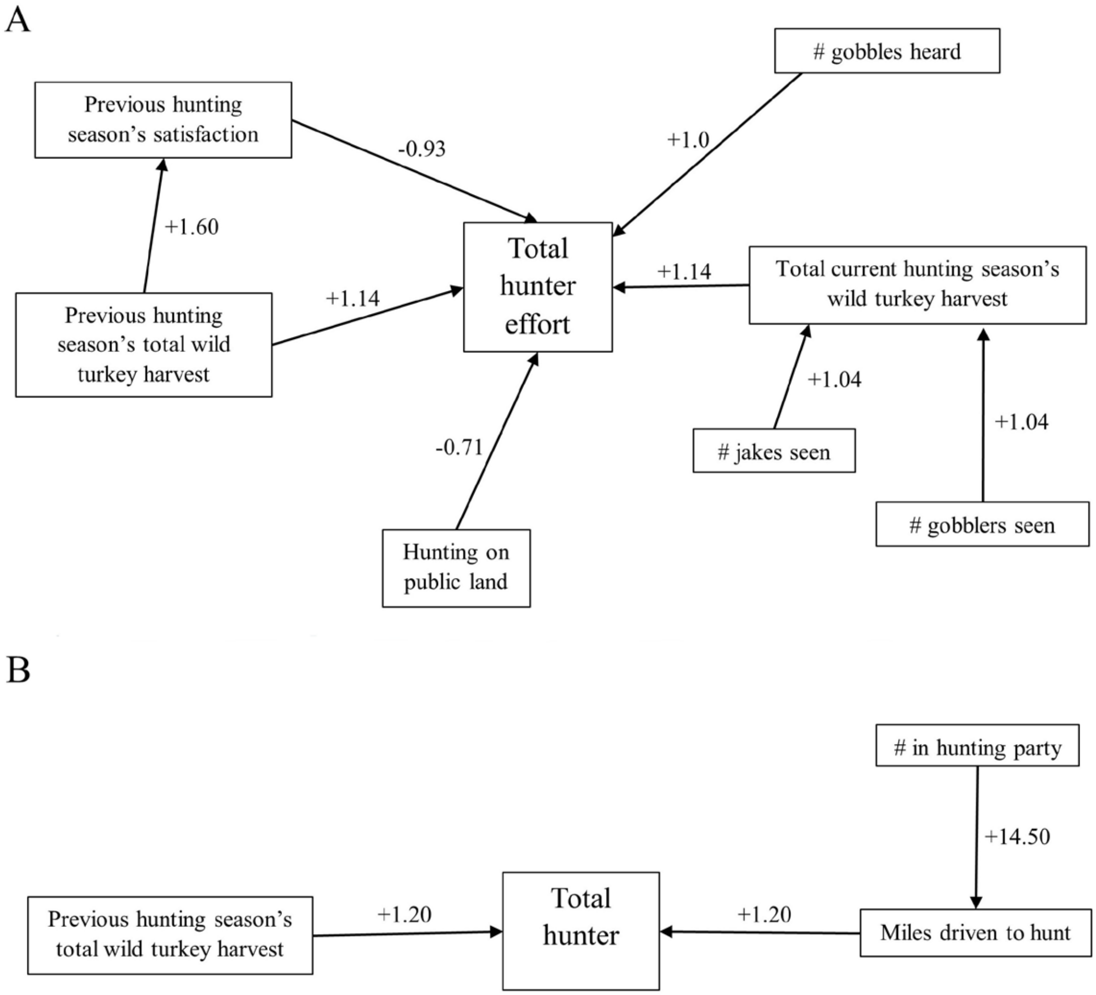

Figure 5. The final path analysis models showing significant ($P < 0.05$) causal relationships for A) before COVID-19 (2017–2019) and B) during COVID-19 (2020) between the variables included in the turkey hunter effort survey and hunter effort, Tennessee, 2017–2020. The direction and power (+ or -) of the causal relationships are indicated by the direction of the arrows and their associated signs.

Discussion

Hunter Satisfaction and Behavior in Response to COVID-19

The increased turkey harvest in Tennessee during COVID-19 (2020) was caused by an influx of ~25,000 new and returning hunters, not increased effort of every-year hunters because of more time resulting from lockdown restrictions. The influx of new and returning hunters in 2020 resulted in a 26.1% increase in license sales above the 3-yr license sale average (2017–2019), which equated to a 27.8% increase in the 2020 harvest above the 3-yr harvest average (2017–2019). Overall hunter effort, success, take per unit effort, and days afield of existing hunters in south-central Tennessee during the spring hunting season did not change during COVID-19. In contrast to our results, Danks et al. (2022) reported a nationwide decrease in take per unit effort for turkey hunters, suggesting increases in harvest in 2020 were a result of lockdown protocols. Chizinski et al. (2021) reported a reduction in non-resident turkey hunters in Nebraska because the state suspended the sale of non-resident licenses attempting to minimize travel and the spread of COVID-19. This contradiction highlights the variation among states and regions, emphasizing the importance of conducting local studies.

Some turkey researchers expected hunter effort to increase because of the COVID-19 lockdown protocols (Goldman 2020, Chizinski et al. 2021, Danks et al. 2022). The every-year hunters in our study shared this expectation. However, such changes in hunter effort were only perceived by hunters and not actually reflected in the overall hunter effort survey responses. This perceived change is most likely a result of the high level of news and social media coverage of the COVID-19 lockdown protocols that repeatedly highlighted the unusual amount of free time that some individuals suddenly had and the desire to occupy this time with more solitary, outdoor activities.

Although there were no significant changes in hunter satisfaction or behavior during the spring hunting season in Tennessee resulting from COVID-19, there was a shift in hunter motivation. Prior to COVID-19, hunter effort during the spring hunting season was driven by measurable hunting standards—the number of gobbles heard, current and previous season harvest, and land type hunted (public or private). During COVID-19, the only measurable hunting standard influencing hunter effort during the spring hunting season was the hunter's previous hunting season harvest. In addition to the previous season harvest, total miles driven to hunt positively influenced hunter effort during COVID-19. This shift in drivers of hunter effort highlights a change in the mindset of hunters during COVID-19. During COVID-19, hunters were possibly hunting more out of a desire to spend time outdoors and be active, rather than the more traditional goal of harvesting a turkey.

If the hypothesis was true that during COVID-19 hunters spent more time hunting and that directly translated into more birds being harvested, we would have expected an increase in the proportion of hunters who harvested 3 or 4+ birds compared to previous years, as individual hunters should have harvested more birds with their extra time to hunt. However, the proportion of hunters who killed 1, 2, 3, or 4+ turkeys during COVID-19 was identical to previous years. While it could be argued that these proportions did not change because the availability of turkeys to harvest did not change (i.e., turkey populations were not increasing; Chizinski et al. 2021), we believe the proportions did not change because the high influx of new and returning hunters entering the sport of turkey hunting apparently were as successful in harvesting turkeys as the existing hunters were. The increase of successful new and returning hunters is important for turkey hunting as it has been shown that seeing and successfully harvesting an animal increases hunter satisfaction, and hunters with higher satisfaction are more likely to continue in the sport (Gigliotti 2008, Mehmood 2011).

There was concern that the elevated harvest in 2020 may have contributed to further population decline. However, the Tennessee turkey harvest during 2021, 2022, and 2023 indicated the 2020 harvest did not adversely affect the population of males. In Tennessee, 32,770 birds were harvested in 2021, 30,000 birds were harvested in 2022, and 31,912 birds were harvested in 2023. The average harvest of these years was greater than the 3- and 5-yr pre-COVID-19 harvest averages. These data indicate that despite a concern about declining turkey populations, the turkey population in Tennessee was robust enough to withstand a record-high harvest without immediate negative repercussions. The data also indicate the increased harvest in 2020 was positive for the sport of turkey hunting. Multiple studies have reported declining hunter population (Larson et al. 2014, USFWS and USCB 2018, RM/NSSF 2017, Bakner et al. 2022). Additional time resulting from COVID-19 lockdowns may have stimulated new and returning hunters that otherwise would not have participated in hunting or purchased a license. In Tennessee, the increase in hunter numbers that was seen during COVID-19 was maintained throughout the 2021 and 2022 hunting seasons (TWRA, unpublished data).

Our survey indicated hunters in south-central Tennessee were concerned about the declining turkey harvest, and the possibility that the declining harvest was the result of turkey population decline. Despite these concerns, hunters' willingness to support a change in season regulations or to change their own hunting activities was minimal. Hunters were supportive of lowering bag limits, but over two-thirds reported they would not stop turkey hunting even if turkey populations declined. This response suggests hunters place more value on the act or challenge of hunting and being in nature than successfully harvesting a turkey. Watkins et al. (2018) reported approximately 50% of hunters in Tennessee could be classified as "social harvesters" who put more importance on the overall challenge of hunting and knowing their peers also are hunting. Wynveen et al. (2005) reported interacting with wildlife (turkey and other wildlife species) while hunting was a top predictor of overall hunt quality. If state wildlife agencies wish to maintain hunter participation in the sport and hunter trust in the agency, they should use this information when setting hunting season regulations.

Management Implications

The turkey population in Tennessee was robust enough to withstand increased harvest during COVID-19 as hunter-reported harvest returned to pre-COVID-19 levels in 2021–2023. State wildlife agencies should continue to carefully consider potential emergency hunting season modifications in response to these unusual situations. State wildlife agencies should work to balance hunter safety and health with the resources being impacted and the money (agency and community) generated from that hunting season. Our survey indicates hunter attitudes and levels of satisfaction may differ from those in other regions, and this difference likely is strongly influenced by differences in turkey populations and harvest rates. Ideally, state wildlife agencies should rely on data collected in their state and region when responding to unusual societal situations that may affect hunting seasons.

Acknowledgments

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Travel Distance and Habitat Selection by Female Wild Turkeys on the First Day of Egg Laying

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Abstract: Nest site selection has a critical effect on nest success for eastern wild turkeys (*Meleagris gallopavo silvestris*), yet the underlying drivers of nest site selection are often misrepresented in the literature. Early works typically focused on evaluating behavioral ecology of female wild turkeys before nest initiation, under the assumption that female wild turkeys sought out nest sites well in advance of nest initiation. However, recent work has clearly found no evidence of nest site search behavior before the day of nest initiation, thus increasing the need to focus evaluations of resource selection on the day when nest site selection occurs (i.e., the first day of laying). Our objective was to determine if differential selection for landcover characteristics was occurring on the first day of an egg was laid (e.g., date of nest site selection). We determined movement paths from the roost to the nest on the first day of egg laying (i.e., laying path) using global positioning system data from 164 female wild turkeys in west-central Louisiana during 2014 to 2021. We compared the landcover characteristics used along laying paths to available landcover characteristics. We found that female wild turkeys showed no clear selection of any landcover characteristics along paths they traveled on the day of nest initiation. Our results suggest that nest site selection was not driven by landcover characteristics and that perhaps selection is driven by other, finer-scale environmental factors or alternatively, may have no clear pattern.

Key words: landcover characteristics, Louisiana, nest site selection, *Meleagris gallopavo silvestris*

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Understanding resource selection is critical to assessing avian behavior, as resource selection influences survival and fecundity (Holt 1984, Dunning et al. 1992, Martin 1995). During the reproductive period, resource selection is thought to underlie nest success in avian species (Pulliam et al. 1992, Martin 1995, Devers et al. 2007, Johnson 2007), as resource selection is related to nest site selection, which can affect demographics (Clark and Shutler 1999, Jones 2001, Fontaine and Martin 2006, Lima 2009). Along with energy considerations, nest site selection is also thought to be driven by predator avoidance (Dunning et al. 1992, Martin 1998, Conway and Martin 2000) and by abiotic factors (Martin 2001).

Eastern wild turkeys (*Meleagris gallopavo silvestris*, hereinafter, wild turkeys) are a ground-nesting Galliform distributed generally east of the Great Plains in the U.S. and in parts of southeastern Canada (Chamberlain et al. 2022). Wild turkey populations have declined during the last several decades in the southeastern U.S. and long-term declines have been noted in nearly all reproductive indices such as nest success and poults per hen (Byrne et al. 2015, Crawford et al. 2021, Chamberlain et al. 2022, Clawson et al. 2022). Thus, furthering our understanding of how resource selection may influence wild turkey reproduction is needed to inform management for ensuring sustainable wild turkey populations.

Reproduction drives population trajectories for wild turkeys, so previous research has often focused on resource selection during the breeding season. In the southeastern U.S., female wild turkeys will select for landscapes containing mature pine or open mixed hardwood-pine (*Pinus* spp.) forests during the breeding season (Miller et al. 1999, Chamberlain and Leopold 2000, Thogmartin 2001, Miller and Conner 2007). Research has also shown nest site selection for areas near roads (Wood et al. 2018), areas that have been burned within the previous three years (Yeldell et al. 2017), and an avoidance of flooded or low-lying areas (Byrne and Chamberlain 2013). At the nest site, visual obstruction, percent ground cover, and vegetation density are thought to play a role in site selection and nest success (Fuller et al. 2013, Yeldell et al. 2017). However, there is considerable variation throughout the extant literature in the strength of selection and the effect of vegetation characteristics on nest success (Yeldell et al. 2017, Wood et al. 2019, Crawford et al. 2021).

Nest sites are rarely visited by hens before laying begins (Conley

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et al. 2016, Collier et al. 2019), thus selection of nest sites prior to the breeding season as posited by Badyaev et al. (1996) is likely not occurring. Conversely, emerging evidence suggests that selection of nest sites could only occur on the day the first egg is laid. As such, Schofield (2019) evaluated microhabitat conditions visited by females on the day the first egg was laid, finding that vegetation characteristics associated with nest sites were readily available along paths used by females to access the nest site (Martin 1993) and that nest site vegetation had little effect on nest success.

To better understand potential mechanisms for nest site selection by wild turkeys, our objective was to evaluate selection of landcover characteristics by female wild turkeys along the path that females used on the day they initiated their first nest. We hypothesized that females would exhibit selection for particular landcover characteristics along paths as they approached the nest sites. We predicted that females would select areas with a greater proportion of roads and recently burned areas, greater proportions of upland pine and pine-hardwood, and a lesser proportion of wetland areas.

Study Area

We conducted our research on the Kisatchie National Forest (KNF), Peason Ridge Wildlife Management Area (PRWMA), and Fort Polk WMA (FPWMA) in west-central Louisiana (Figure 1). Our study area experienced a subtropical climate, with mean daily temperatures of 10 C in January and 28 C in July and mean annual rainfall of approximately 151 cm (NOAA 2023). The KNF was managed by the U.S. Forest Service (USFS) and was separated into five ranger districts (RD), from which our work was conducted on the Kisatchie RD (41,453 ha), Winn RD (67,408 ha), Catahoula RD (49,169 ha), and the Vernon Unit of the Calcasieu RD (33,994 ha) located in Natchitoches, Winn, Grant, and Vernon Parishes, respectively. The northern portion of the FPWMA and all of PRWMA were managed by the U.S. Army, and the southern portion was managed by the USFS as part of the Vernon RD. Each of our study areas had similar forest characteristics and land management and were considered one unit for this study. Our study area was composed of pine-dominated forests, hardwood riparian zones, and forested wetlands with forest openings, food plots, pipelines, and forest roads throughout. Overstory trees included loblolly pine (*Pinus taeda*), longleaf pine (*P. palustris*), shortleaf pine (*P. echinata*), slash pine (*P. elliottii*), sweetgum (*Liquidambar styraciflua*), oaks (*Quercus* spp.), hickories (*Carya* spp.), and red maple (*Acer rubrum*). Understory species included yaupon (*Ilex vomitoria*), American beautyberry (*Callicarpa americana*), blackberry (*Rubus* spp.), greenbrier (*Smilax* spp.), wild grape (*Vitis* spp.), broomsedge (*Andropogon virginicus*), woodoats (*Chasmanthium* spp.), and panic grasses (*Panicum* spp. and *Dichanthelium* spp.). Privately owned properties surrounding the public land was predominately even-aged loblolly pine stands primarily managed for wood fiber production, small homesites, pastures, hardwood-dominated wetlands, and agricultural fields. For additional details of the study area see Yeldell et al. (2017).

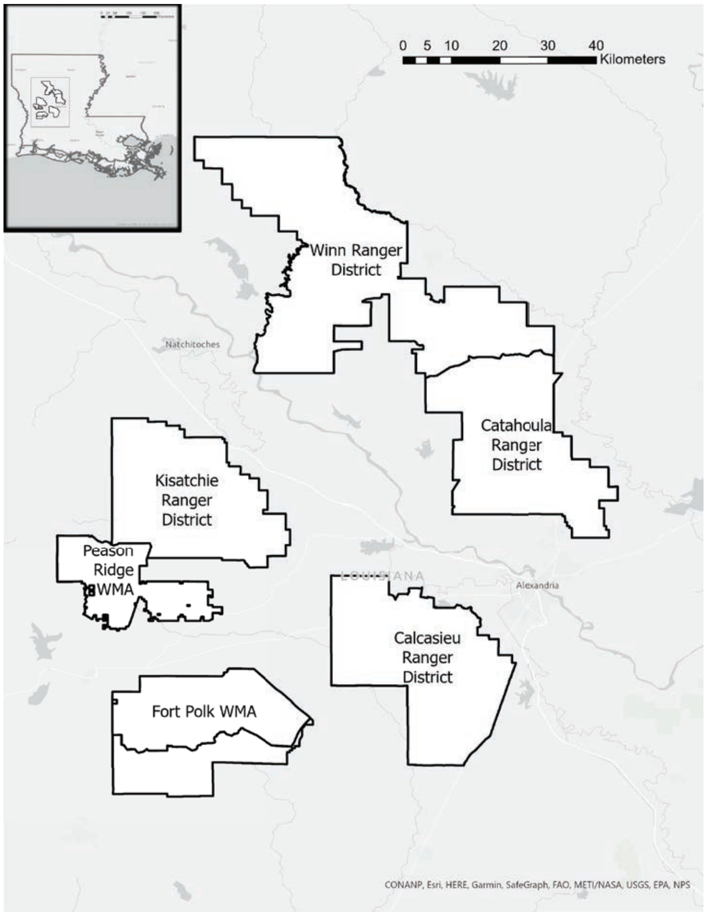

Figure 1. Study areas for evaluating resource selection by female eastern wild turkeys during the first day of egg laying, which included the Fort Polk Wildlife Management Area, four ranger districts of the Kisatchie National Forest (Calcasieu, Catahoula, Kisatchie, and Winn), and Peason Ridge Wildlife Management Area, Louisiana, 2014–2021.

Methods

We captured female wild turkeys using rocket nets from January–March, 2014–2021. We classified females as juveniles or adults based on barring on the 9th and 10th primaries (Pelham and Dickson 1992). We fitted each female with a riveted, uniquely numbered, tarsal aluminum band and a global positioning system (GPS) transmitter equipped with a very high frequency (VHF) emitter (88 g; Lotek Minitrack Backpack, Lotek PinPoint Backpack; Lotek Wireless, Newmarket, Ontario, Canada). We released all individuals at the capture site after processing. All wild turkey capture, handling, and marking procedures were approved by the

Institutional Animal Care and Use Committee at Louisiana State University AgCenter (protocols A2014-013 and A2015-07 and A2018-13).

We programmed GPS transmitters to collect a location hourly from 0500 to 2000 h daily with one roost location at 23:59:58. We used handheld Yagi antennas and a VHF/ultra-high frequency (UHF) PinPoint Commander unit (Lotek Wireless) to download GPS data ≥ 1 time per week throughout the study period. We determined date and time of nest initiation (i.e., beginning of egg laying) and nest incubation following methods from Conley et al. (2015), Bakner et al. (2019), and Lohr et al. (2020), where nest sites were confirmed via VHF telemetry and GPS data evaluation and used the date of the female's earliest GPS fix within a 50-m radius of that nest site as the date of nest initiation.

To create a behavioral trajectory, we drew lines between each GPS point starting at the roost location the night before the first egg was laid and ending at the nest site. Then, to encompass the area the female likely used between each GPS point, we created a 100-m buffer for each female's line using the rgeos package (Bivand et al. 2021) in R (R Core Team 2022), which we defined as the laying path. For each nest attempt, we then exactly replicated each laying path five times and rotated those replicates in random directions originating at the roost location from the night before laying began (Figure 2) to create a set of available but unused paths (hereinafter, random paths) which allowed for evaluation of resource selection relative to the actual laying path given what was available around the roost location (Thogmartin 1999, Fuller et al. 2013, Wood et al. 2019, Schofield 2019).

To create metrics for landcover characteristics, we used 30-m resolution National Land Cover Database (NLCD) imagery from the U.S. Geological Survey (USGS) (Homer et al. 2015). We used 2016 and 2019 NLCD imagery for GPS data on females during 2014–2016 and 2017–2021, respectively. We reclassified the NLCD landcover classes into eight landcover metrics (woody wetlands, herbaceous, shrub/scrub, mixed forest, evergreen forest, deciduous forest, road [developed open, developed low], and infrastructure [developed medium, developed high]) previously indicated to be influential during the reproductive period (Thogmartin 1999, Byrne and Chamberlain 2013, Kilburg et al. 2015, Crawford et al. 2021). For each landcover type, we assigned a value between 0 and 1 based on the proportion of that landcover type within each laying or random path.

We created a normalized difference vegetation index (NDVI) from Sentinel-2 satellite imagery data (10 m-resolution) from 2016 to 2021 (Pettorelli et al. 2005). To create NDVI data for 2014–2015, we used Landsat 7 satellite imagery data (15-m resolution) from USGS (Irons et al. 2012). We selected imagery with <10% cloud cover near the median laying date each year (30 April to 1 May). We separated the imagery into two bands and estimated NDVI in ArcMap 10.8 (ESRI, Redlands, California) as:

$$\text{NDVI} = (\text{Near-Infrared} - \text{Red}) \div (\text{Near-Infrared} + \text{Red})$$

for the entire study area (Ulrey et al. 2022). We estimated the average NDVI for each laying and random path, with the value being between –1 and 1, and used those values for modeling. To estimate forest cover, we used satellite imagery from the U.S. Department of Agriculture's National Agriculture Imagery Program (NAIP), which has a 1-m resolution per pixel. We then used Earth Resources Data Analysis System (ERDAS) Imagine 2020 software (Hexagon AB, Stockholm, Sweden) to recategorize each pixel into two general vegetation categories, forested or open, to calculate the proportion of forested cover (between 0 and 1) for each laying and random path. For each landcover metric, we estimated the proportion of each that fell within the laying path and used those proportions as explanatory covariates in our selection modeling.

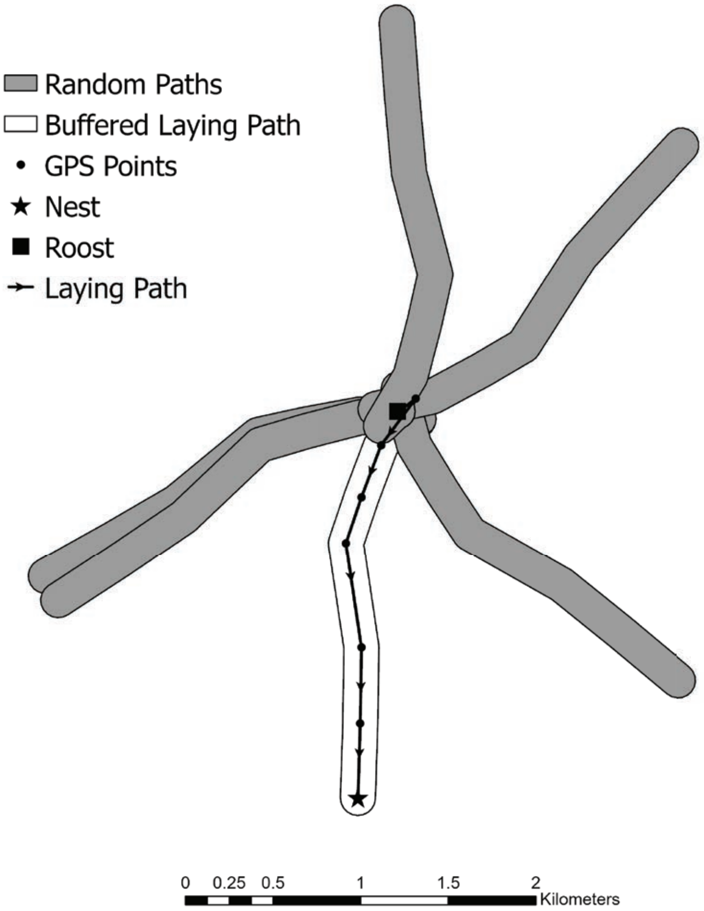

Figure 2. Used laying path (clear) and randomly rotated unused paths (gray) for a female eastern wild turkey monitored in west-central Louisiana during 2014–2021. The roost (square) and the nest (star) identify the start and ending locations of the laying path, respectively.

Additionally, we used spatial data provided by the USFS and U.S. Army to identify if each laying path had been subjected to any prescribed fires or timber harvest (i.e., thinning and clearcuts; 1 = yes, 0 = no; burn or logging, respectively) within the previous three years (Yeldell et al. 2017, Sullivan et al. 2020; Table 1).

We evaluated each landscape metrics' effect (Table 1) on selection by individual female along laying paths using logistic regression in R (R Core Team 2022). We used a Pearson correlation test to determine if potentially correlated covariates should be removed ($|r| \geq 0.6$) (Dormann et al. 2018). We developed a candidate model set based on the proportion of each landcover type, burned, logged, NDVI, and forest cover (along with relevant interactions between covariates; Table 1), with the models we used being based on what was seen as important in previous research (Thogmartin 1999, Byrne and Chamberlain 2013, Kilburg et al. 2015, Yeldell et al. 2017, Sullivan et al. 2020, Crawford et al. 2021). From these, we also created a global logistic regression model including all covariates. We compared laying paths (used) to five identical random paths (available). Five identical random paths are sufficient to estimate ecologically relevant availability for our wild turkey females, as being identically shaped to the original laying path accounts for individual female movement patterns, and five random paths in five random directions most often covered a wide range of possible directions while allowing for some overlap between our estimations of used and available laying paths (Wisz et al. 2008, Benson 2013, Street et al. 2021). For our analyses, we used the Akaike Information Criteria (AIC_c) value to determine model support relative to all models, including the null model (Burnham et al. 2011). Models with an evidence ratio ≤ 2 based on the AIC weight of the lowest AIC model best explained the variation in laying path versus random path (Burnham and Anderson 2002, Dick 2004).

Results

We captured 304 female wild turkeys from 2014 to 2021 (270 adults, 34 juveniles). Fifty-eight females died or had transmitter failure before nesting season began (51 adults, 7 juveniles) and 39 did not attempt to nest (24 adults and 15 juveniles), for an estimated nesting rate of 89% for adults ($n = 219$) and 44% for juveniles ($n = 27$; 84% overall). We observed 197 first nest attempts, but we censored 33 due to two or more missed GPS locations along the laying path, which left 164 unique laying paths. Nest initiation dates ranged from 14 March to 26 May ($\bar{x} = 13$ April, SE = 1 day). Mean total distance traveled along laying paths was 1690 m (SE = 85; range = 90–7676; Figure 3). The linear distance between roost sites the night before laying began and nest sites on the first day of laying was on average 956 m (SE = 65, range = 24–7085) and the median speed per time step (two consecutive GPS locations) was 198 m hour^{-1} (SE = 9, range = 4–1990).

We found no correlation between covariates ($|r| < 0.6$). We observed no evidence that the covariates we evaluated influenced selection to the point of biological relevance along laying paths (Table 2). Our results did indicate that laying paths were less likely to contain woody wetlands ($\beta = -1.214$; $CI = -2.427 - -0.188$; Figure 4) when compared to random paths.

Table 1. List of covariates and data sources used to define landcover characteristics contained within each laying and random path for female eastern wild turkeys in west-central Louisiana during 2014–2021. See text for more information about data sources. Each covariate's value is either a percentage based on its proportion within each laying or random path (%; continuous; all NAIP- or NLCD-source covariates), a number between -1 and 1 for each path (continuous; NDVI), or a binomial 0 or 1 based on its presence or absence for each path (categorical; Burn and Logging). Definitions for NLCD covariates are simplified from the USGS definitions.

Covariate	Source[a]	Definition
Forested	NAIP	Identification of trees by pixel color using Earth Resources Data Analysis System (ERDAS) Imagine 2020 software.
Open	NAIP	Identification of a lack of trees by pixel color using ERDAS Imagine 2020 software.
Woody wetlands	NLCD	Forest or shrubland vegetation are > 20% of cover with the soil or substrate being periodically saturated or covered with water.
Herbaceous	NLCD	Graminoid or herbaceous vegetation cover > 80% of the pixel.
Shrub/scrub	NLCD	Shrubs < 5 m tall cover > 20% of the pixel. Includes true shrubs and young/stunted trees.
Evergreen forest	NLCD	Trees > 5 m tall cover > 20% of the pixel. > 75% of tree species maintain leaves throughout the year, with the canopy never being without green foliage.
Deciduous forest	NLCD	Trees > 5 m tall cover > 20% of the pixel. > 75% of tree species shed foliage seasonally.
Mixed forest	NLCD	Trees > 5 m tall cover > 20% of the pixel. Neither deciduous nor evergreen species comprised > 75% of total tree cover.
Roads	NLCD	Combination of NLCD classes "Developed, Open Space" and "Low Intensity." Impervious surfaces accounted for 10–49% of total pixel.
Infrastructure	NLCD	Combination of NLCD classes "Developed, Medium Intensity" and "High Intensity." Impervious surfaces accounted for 50–100% of total pixel area.
NDVI	ESA/USGS	Quantification of vegetation by measuring the difference between near-infrared and red-light reflections.
Burn	USFS/Army	Areas burned within the previous 3 yr.
Logging	USFS	Areas thinned or clearcut within the previous 3 yr.

a. NAIP: National Agriculture Imagery Program; NLCD: National Land Cover Database; ESA: European Space Agency; USGS; USFS: U.S. Forest Service; Army: U.S. Army.

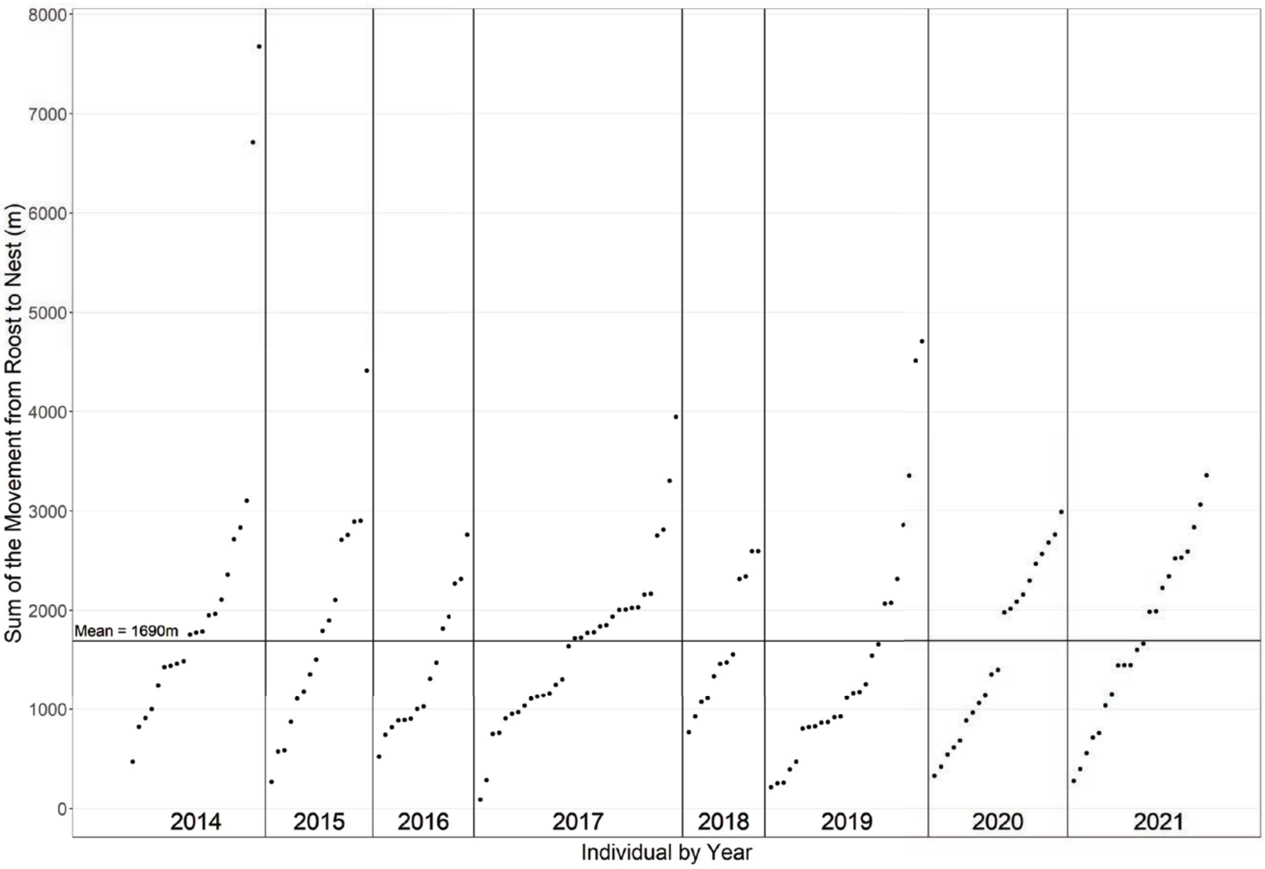

Figure 3. Total distance moved from the roost to the nest on the first day of laying for female eastern wild turkeys in west-central Louisiana during 2014–2021.

Table 2. Logistic regression model selection with matched-pairs case-control sampling, where the used laying path were cases and five random paths were controls, to show selection of landcover types along paths used prior to laying the first egg in the first nest of female eastern wild turkeys in west-central Louisiana during 2014–2021. Model selection was based on Akaike's Information Criterion for each potential model (AIC_c), number of parameters (K), ΔAIC_c, the Akaike weight of evidence (w_i), and the evidence ratio based on the lowest AIC_c model (ER). See Table 1 for covariate definitions and data sources.

Model	K	AIC_c	ΔAIC_c	w_i	ER
Woody wetlands	2	879.77	0.00	0.43	1.0
Evergreen forest × Woody wetlands	4	882.59	2.82	0.11	3.9
Herbaceous	2	882.69	2.92	0.10	4.3
Null	1	883.30	3.53	0.07	6.1
Infrastructure	2	883.37	3.60	0.07	6.1
Forested	2	884.07	4.30	0.05	8.6
Roads	2	884.10	4.33	0.05	8.6
Deciduous forest	2	884.14	4.37	0.05	8.6
Evergreen forest	2	884.26	4.49	0.05	8.6
Mixed forest	2	884.91	5.14	0.03	14.3
Mean NDVI	2	884.95	5.18	0.03	14.3
Logging	2	885.13	5.35	0.03	14.3
Shrub/scrub	2	885.16	5.39	0.03	14.3
Open	2	885.18	5.41	0.03	14.3
Burn	2	885.23	5.46	0.03	14.3
Evergreen forest × Deciduous forest	4	886.70	6.93	0.01	43.0
Forested × Open	4	886.96	7.19	0.01	43.0
Mixed forest × Deciduous forest	4	887.40	7.63	0.01	43.0
Global	13	896.45	16.68	0.00	>100

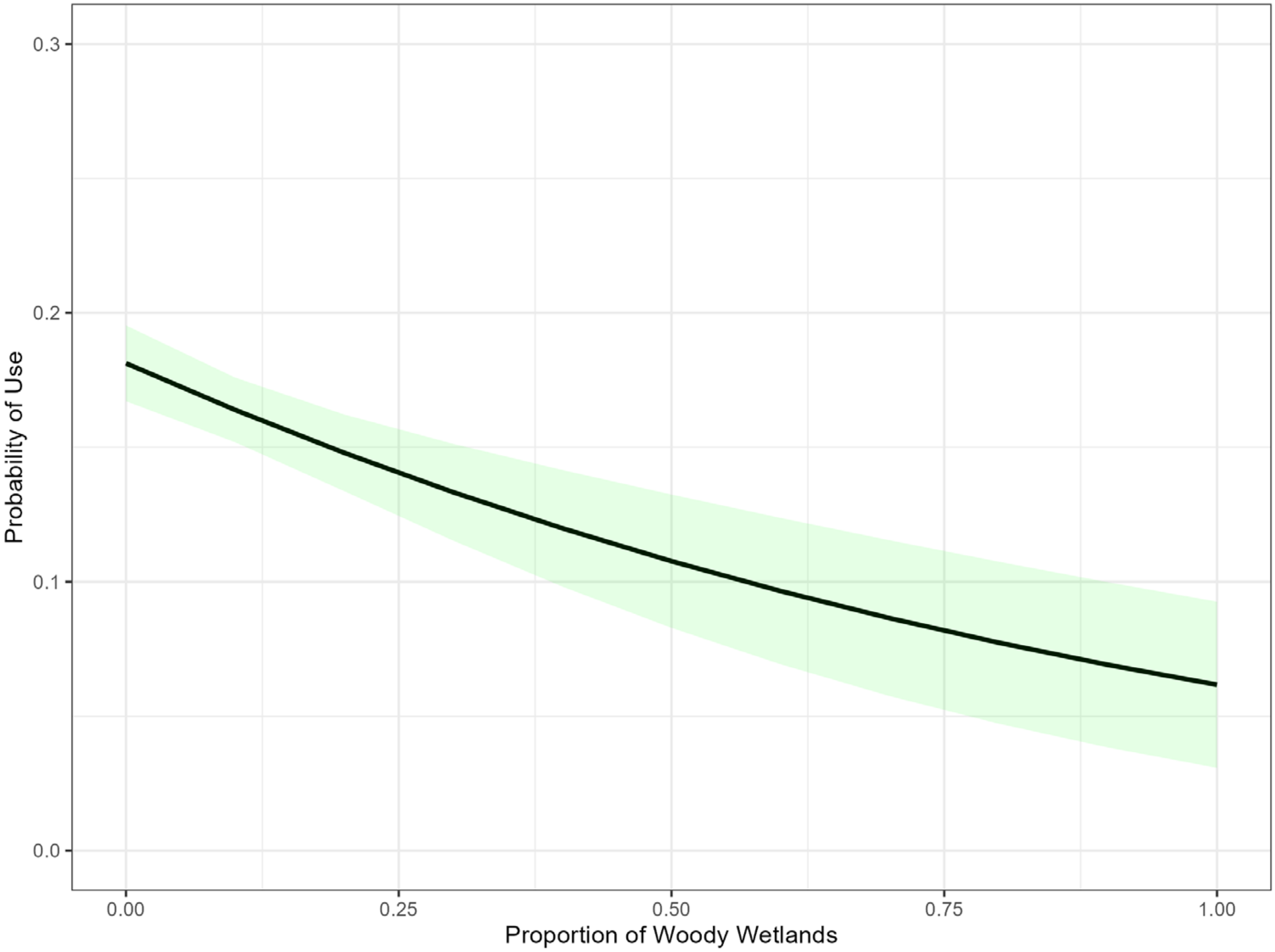

Figure 4. Predicted probability of use for woody wetlands as female eastern wild turkeys moved from the roost to the nest on the first day of laying in west-central Louisiana during 2014–2021.

Discussion

Wild turkey resource selection during the reproductive period is thought to have consequences for both female survival and reproductive success (Chamberlain and Leopold 1998, Thogmartin 1999, Kilburg et al. 2015, Lohr et al. 2020). Using GPS-based movement data for female wild turkeys on the day of nest initiation, we determined that landscape metrics commonly used to evaluate resource selection within ranges or around nest sites (Sullivan et al. 2020, Crawford et al. 2021, Keever et al. 2023) did not play a biologically significant role in habitat selection on the day of nest initiation. The only statistically significant effect was the avoidance of wetlands, which represent areas typically not used by wild turkeys for nesting (Crawford et al. 2021). Additionally, female wild turkeys showed no selection for burned areas or presence of roads along laying paths, which differs from previous studies on resource selection by wild turkeys during the reproductive period (Thogmartin 1999, Miller and Conner 2007, Martin et al. 2012, Yeldell et al. 2017, Cohen et al. 2019). Our results indicate that landcover metrics provide little insight into selection criteria used by wild turkeys on the day of nest initiation in pine-dominated landscapes, like those seen across most of the southeastern U.S.

Female wild turkeys likely have enough behavioral plasticity to use all landcover types we considered in our analyses during the nesting period, which could possibly explain lack of selection for or against most landcover types. Recent work by Schofield (2019) indicated that female wild turkeys increased daily movements during egg laying, but that increase occurred concomitant with a decrease in space use, which is indicative of a lack of site familiarity (Conley et al. 2016). Schofield (2019) hypothesized that during the egg laying period, female movements were more akin to prospecting areas within a reduced range where nesting activity would ultimately occur. Thus, female movements were used presumably to identify and assess resource availability and distribution, as opposed to already having garnered that information prior to the onset of breeding as suggested by Badyaev et al. (1996). As such, resource selection along the laying path during nest site selection is generally indistinguishable from selection during movements by females throughout the reproductive period.

The relationships between behavioral decisions made by female wild turkeys and subsequent demographic consequences are poorly understood (Conley et al. 2015, Conley et al. 2016). Contemporary research across the southeastern U.S. noted that landcover type and nest site vegetation were not primary drivers of wild turkey nest success (Crawford et al. 2021, Keever et al. 2023). Similarly, our results suggest that landcover used on the day of nest initiation did not influence nest site selection other than females avoiding wetland areas. Although resource selection by reproductively active female wild turkeys has been discussed exhaustively in wild turkey literature, researchers have collectively been unable to identify clear patterns in resource selection and their consequences on population productivity (Crawford et al. 2021, Keever et al. 2023).

We suggest that future work evaluating drivers of wild turkey resource selection during nesting takes a more holistic approach that includes behavior ecology, conspecific activities, and predator-prey interactions, rather than purely focusing on the effects of vegetation characteristics. Our understanding of the behavioral ecology of wild turkeys during the reproductive period has increased via access to GPS technology (Collier and Chamberlain 2011) which offers a clearer picture of behaviors across a broad range of study sites relative to previous direct observations of individual wild turkey flocks (Watts and Stokes 1971, Healy 1992). By shifting focus to evaluating how individual wild turkey behaviors and their social effects change throughout the reproductive season, researchers may be able to provide more rigorous assessments of factors driving reproductive success (Bakner et al. 2019, Lohr et al. 2020, Ulrey 2021, Ulrey et al. 2022). When paired with understanding the links between predators and wild turkeys and the ties that vegetation characteristics could have with all these social, behavioral, and ecosystem effects, research can more accurately inform land managers whose only tool to increase wild turkey populations is to target specific vegetation characteristics with habitat improvements. Habitat improvements will always play a role in supporting wild turkey populations, but they cannot be used as a panacea to improve wild turkey nest success.

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Lesser Prairie-Chicken Brood Ecology on the Southern High Plains of Texas

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Abstract: The lesser prairie-chicken (*Tympanuchus pallidicinctus*) has declined precipitously in abundance and currently occupies a substantially reduced portion of its historic range. Within the sand shinnery oak (*Quercus havardii*) prairies at the southwestern extent of the lesser prairie-chicken's contemporary range, efforts to conserve the species have been constrained by limited information on how land management practices influence habitat quality, and subsequently, affect lesser prairie-chicken recruitment. From 2008–2011, we captured and radio-tagged hen lesser prairie-chickens to monitor broods during four breeding seasons in western Texas. We evaluated influences of vegetation structure and composition, insect availability, and weather on brood ecology on private lands with continuous cattle grazing but no recent herbicide treatment to control shrubs. We located 32 nests from 50 hens captured. Of these nests, 16 produced broods, with 69% of broods lost within the first 14 days. Brood survival was low, and few if any chicks monitored survived to adulthood. Brood sites were dominated by shrub cover and percentages of grass and forb cover were low compared to those reported from other studies. Mean vegetation cover percentages, insect abundance, richness, order, and families did not differ between brood and random sites. Insect abundance was negatively influenced by increased visual obstruction and grass cover, but positively influenced by increased litter, forb cover, and winter precipitation. As found in other studies, chick survival, especially within 14 days post-hatch, is the main limiting factor for population viability. Therefore, lesser prairie-chicken populations throughout the Sand Shinnery Oak Prairie Ecoregion will be largely dependent on management practices that restore healthy prairies, including reduced shrub cover and greater herbaceous groundcover.

Key words: grazing, habitat use, insects, sand shinnery oak, *Tympanuchus pallidicinctus*

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The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is a prairie grouse presumed to have been widely distributed throughout the western portions of the U.S. Central and Southern Great Plains historically. However, in the past century the species has declined precipitously in abundance and currently occupies a substantially reduced portion of its historic range due to conversion of native prairies to row-crop agriculture, energy development, unmanaged cattle grazing (e.g., high stocking densities and long grazing durations), woody-plant encroachment, and periods of intense drought (Giesen 1998, Hagen et al. 2004, Grisham et al. 2013, Ross et al. 2016). Collectively, these factors have likely decreased lesser prairie-chicken survival and impacted reproductive effort.

Lesser prairie-chickens occur in four ecoregions among varying temperature and precipitation gradients (Grisham et al. 2016). Across all ecoregions, in 2022 the total range-wide population size was estimated at 26,591 individuals (90% CL: 16,321, 38,259; Nasman et al. 2022). Within the Southern High Plains of Texas and New Mexico, lesser prairie-chickens occur in the Sand Shinnery Oak (*Quercus havardii*) Prairie Ecoregion (Timmer et al. 2013). These prairies represent the extreme southwestern portion of lesser prairie-chicken distribution, where the population is geographically and genetically disconnected from other ecoregions (Hagen and Giesen 2005, Oyler-McCance et al. 2016). Populations occupying sand shinnery oak prairies remain dynamic, having decreased from 2967 (90% CL: 1119, 5016) individuals in 2012 to as few as 519 (179, 934) individuals in 2015 (Nasman et al. 2022).

Sand shinnery oak prairies were historically shaped by fire, precipitation, and grazing (Peterson and Boyd 1998, Grisham et al.

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2014). These ecological drivers created prairies that were a matrix of bunchgrasses, shrubs, and forbs (Smythe and Haukos 2009, Zavaleta et al. 2016), but their interplay has largely been altered due to land use changes and climate change. Fire suppression started during European settlement and remains common; reintroduction of fire may be the most important land management action to facilitate conservation efforts (Hagen and Elmore 2016). Precipitation directly influences plant and insect community structure, but on the Southern High Plains recurring intensive droughts are common and increasing in frequency. Extended periods of drought can drastically alter habitat quality, and subsequently, reduce lesser prairie-chicken reproductive output and recruitment (Grisham et al. 2014, Fritts et al. 2018). Precipitation is the most difficult ecological driver to address through management, and the Southern High Plains are forecasted to become drier with more frequent extreme heat events and fewer precipitation events (Grisham et al. 2013). Additionally, sand shinnery oak prairies were historically maintained in part by seasonal grazing by native mammals (Peterson and Boyd 1998). However, native grazers have mostly been replaced with domestic cattle that often graze continuously and at greater intensities than historical nomadic species.

Nest and brood survival have been documented as the main demographic parameters affecting lesser prairie-chicken population persistence (Wisdom and Mills 1997, Hagen et al. 2009, Fritts et al. 2018, Ross et al. 2018). Using a sensitivity analysis, Hagen et al. (2009) found that the effect of chick survival on population growth rate was 1.7–2.1 times greater than the effect on any other demographic rate. Hence, effective management is best based on habitat management strategies that increase fecundity. Moreover, efforts that simultaneously increase nest success and chick survival are predicted to yield a greater effect on population growth rate than increasing female survival. Therefore, understanding brood-rearing ecology is critical to informing sand shinnery oak prairie management and restoration efforts to maintain viable populations of lesser prairie-chickens (Davis 2009).

Despite the importance of brood-rearing ecology for the persistence of lesser prairie-chickens, little is known about brood habitat use within sand shinnery oak-grassland communities (Riley and Davis 1993, Bell et al. 2010). Factors influencing lesser prairie-chicken brood survival appear to be synergistic among temperature and precipitation, concealment cover, ease of locomotion, and food availability (Merchant 1982). Fields et al. (2006) demonstrated that chick survival decreased as temperatures increased during drought periods and was greater when nests were initiated earlier in the nesting season, allowing chicks time to develop and self-thermoregulate prior to the onset of hotter summer temperatures. During periods of hotter temperatures, especially thermal extremes, overhead vegetation structure provides important cover to avoid desiccation. Bell et al. (2010) reported hens with broods used areas that were warmer than random locations when temperatures were cool and used cooler locations when temperatures were warm, shifting depending on the time of day and diurnal variation in temperature. Therefore, retaining patches of dense shrub cover for thermal refugia is an important management consideration. Prairies with diverse plant communities, especially with abundant grasses and forbs, also support high insect biomass, critical components of lesser prairie-chicken brood-rearing foraging habitat. Conversely, areas with shrub monocultures, particularly those with mismanaged cattle grazing and lack of fire, limit habitat conditions for insects and therefore may result in malnutrition or starvation. Travel corridors are also important for chicks to easily navigate to feed and escape predation (Jones 1963, Riley et al. 1993).

Efforts to conserve lesser prairie-chicken throughout the Sand Shinnery Oak Prairie Ecoregion have been constrained by limited information on how land management practices influence habitat quality, and subsequently, affect lesser prairie-chicken recruitment. Therefore, to address these information gaps, we sought to assess the effects of prairie condition on brood-rearing ecology on privately owned lands in Texas. Our objectives were to evaluate: 1) brood survival on prairies experiencing continuous cattle grazing; 2) brood site selection and area; and 3) food availability for chicks including the influence of ground cover and weather on insect abundance and richness.

Study Area

Our research was conducted on 25,293 ha of privately owned lands in Cochran, Hockley, Terry, and Yoakum counties, Texas from 2008 to 2011. Most land use for this study area included cattle production, intensive row-crop agriculture, especially cotton and grain sorghum, and oil production (Haukos and Smith 1989, Grisham et al. 2014). Management records were incomplete, but the last reported herbicide treatment of sand shinnery oaks was between 1979 and 1983 (Olawsky and Smith 1991). Prairies throughout the entire study area were grazed continuously through the study period.

The landscape was composed of a matrix of rangeland, cropland, and gently undulating sandhills dominated by sand shinnery oak and sand sagebrush (*Artemisia filifolia*) with mixed grasses and forbs. Mesquite (*Prosopis glandulosa*) was encroaching on the periphery of sand shinnery oak grasslands (Hagen et al. 2004). Soils in the area included Brownfield and Tivoli series characterized by deep, loose, light colored, neutral sandy soils and deep, loose, light-colored sands that occur as dunes that were 2–5 m high with slopes as much as 30%, respectively (Newman 1964). Precipitation for the study area averaged 45.9 cm, mostly occurring from May to October (Newman 1964). Temperatures ranged –33 to 44° C with minimum temperatures during January ($\bar{x}$ = 2.4 C) and maximum temperatures during July ($\bar{x}$ = 25 C; Newman 1964).

Methods

We captured lesser prairie-chickens on leks during late winter (February) and spring (March–April) annually using walk-in funnel traps (Haukos et al. 1989, Schroder and Braun 1991) and magnetic drop-nets (Wildlife Capture Services, Flagstaff, Arizona). Upon capture, we used plumage characteristics (Copelin 1963) to sex and age birds. We banded hens with a uniquely numbered aluminum blunt-end leg band and fit those individuals with a radio-transmitter (9-g necklace style; American Wildlife Enterprises, Florida) equipped with an 8-hr mortality sensor. We released all individuals at their capture location. We located radio-tagged hens once daily throughout the breeding season (February–August) to monitor nesting activity and hatch date of successful nests (Grisham et al. 2014). All methods were approved under Texas Tech University Institutional Care and Use Protocol 1052-08. Capture and handling practices followed guidelines outlined by the Ornithological Council (Fair et al. 2010).

We located radio-tagged hens using a hand-held three-element Yagi antenna and receiver (R-2000; Advanced Telemetry Systems, Ashanti, Minnesota). We triangulated hens daily but waited to conduct flush counts until 14 days post-hatch (i.e., when chicks can fly) to minimize disturbance, then flushed broods to count the number of chicks at 7-day intervals until 60 days post-hatch (Hagen et al. 2005, Pitman et al. 2006a). Broods were flushed at daybreak and areas were thoroughly searched until we were confident all chicks had been located. We excluded hens from future sampling if they flushed >400 m with no evidence of chicks, were with other adult lesser prairie-chickens, or made continuous long-distance flights post-flush for two consecutive flush intervals. If hens made short-distance flights (i.e., <20 m) when flushed (a brooding behavior) and no chicks were located, we again flushed at the next interval to confirm brood loss (Pitman et al. 2006a).

We estimated ground cover at the location of the brooding hen and 7.5-m away along two perpendicular lines (one north-south, one east-west) emanating from the brood location (Hagen et al. 2005). We collected vegetation and insect samples immediately after determining fate status of the hen and chicks (see below) to reduce sampling bias and to minimize vegetation disturbance. We visually estimated the percentage of litter, bare ground, and canopy cover classes of grass, forb, and woody vegetation using a 20 × 50-cm frame, for a total of five frames per brood location. Additionally, we recorded visual obstruction readings (hereinafter, VOR; Robel et al. 1970) from a 4-m distance and 1-m eye height at each cardinal direction at the center location and each 7.5-m interval (n = 20 VOR readings per plot). To assess how lesser prairie-chickens used areas specific to vegetation structure, we used the same protocol to measure vegetation at paired-random locations within 360 m of the brood location in a random direction, consistent with observed renesting distance radii within sand shinnery oak-grassland communities by Grisham (2012). Random locations were sampled immediately after sampling brood locations.

We used a 30-cm insect net to sample insects at brood hen locations and corresponding random locations. We sampled four parallel lines 10 m apart with 20 sweeps per line. Insects were frozen at –17.5 C until each sample was sorted, counted, and identified to order and family. We obtained wet mass for each sample to account for water content given chicks' risk of dehydration. We summed all insects collected across orders to represent insect abundance and used the number of insect orders to represent insect richness.

We obtained 5-min averages of temperature and precipitation from the West Texas Mesonet's Sundown Station and used these data to develop weather variables unique to each season and brood. We selected seasonal weather parameters that influence vegetation cover, affect insect populations as food resources for chicks, and relate to physiological tolerance (Branson 2008, Grisham et al. 2013, Hovick et al. 2014). Weather variables included precipitation annually and during the previous winter (1 December to 28/29 February), and precipitation and maximum temperatures during the first 2 wk after a brood hatched (or for the number of days a brood survived if less than 14 days) and during the entire period for a brood (i.e., hatch until the last time known alive).

Statistical Analyses

We used the nest survival data type in Program MARK to estimate brood survival (White and Burnham 1999). We developed eight *a priori* models to model brood survival including: 1) a null model, and subsequent models incorporating temporal trends for broods known to be alive, including 2) daily survival; 3) weekly survival; 4) days post hatch grouped as early (0–3 days), pre-flight (4–10 days), mid (11–35 days), and late (36–71 days); 5) a linear relationship of brood survival increasing with brood age; 6) a quadratic relationship of brood survival increasing with brood age to an apex and then digressing; 7) brood hen age, and; 8) number of chicks at hatch (Fields et al. 2006, Pitman et al. 2006a).

To characterize brood areas and selection cues, we tested for differences in vegetation and insect abundance and richness between brood and paired random locations. We used logistic regression models with brood or random location as the response variable (1 and 0, respectively) and each vegetation and insect covariate as predictors. To differentiate food availability for chicks between brood areas and random locations, we used generalized linear mixed-effects models with the R package lme4 (Bates et al. 2015) with brood identification as a random effect and a Poisson distribution for insect abundance and richness. We explored models with multiple variables, but limited our candidate set to single variables to better assess relative importance. First, we evaluated effects of vegetation covariates on insect abundance and richness by combining brood and paired random locations to understand insect availability for broods across the landscape. Second, with combined brood and random locations, we evaluated insect abundance in relation to weather parameters. We did not evaluate relationships between insect richness and weather parameters because of collinearity in fixed effects. Third, we assessed whether insect orders or families differed between brood and random locations. Fourth, we used a *t*-test to assess wet mass and differences in number of individual insects between brood and random locations. Lastly, we calculated the minimum boundary geometry using convex hulls in QGIS V3.32.0 (QGIS Development Team 2023) to estimate brood habitat area for the 13 hens and broods we located. To reduce biases from small sample sizes (birds with <15 relocations), we report area estimates for the eight brood-rearing hens whose broods survived the longest.

For all analyses, we *z*-standardized all continuous predictor variables (hereinafter, covariates) to improve model convergence. We examined relationships among covariates and retained one of a pair when the absolute value of their Pearson's correlation coefficient was >0.70. We evaluated influences of covariates on response variables using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Akaike 1973). We considered covariates significant if 95% Confidence Limits (CL) on their regression coefficient (β) did not overlap zero.

Results

We captured and radio-tagged 50 hens and located 36 nests (14 in 2008, 9 in 2009, 10 in 2010, 3 in 2011) from 2008–2011, including renest attempts. Sixteen hens had broods during our study period, and we obtained locations of these hens throughout the brood-rearing period. Eleven (69%) of the broods were lost (i.e., all chicks died or otherwise could not be located) before the first flush date. The remaining five broods were monitored at 7-day intervals until they were lost or considered a successful brood at 49 days post-hatch. Only one brood may have been successful, but the hen dropped her radio-transmitter between days 42 and 49 in 2010. The brood-survival model that incorporated a quadratic time trend received the most support (Table 1). According to this model, the probability of a brood surviving increased as the brood aged, and then decreased as the brood approached flock break-up. The probability of broods surviving the duration of the study was 0.002 (SE 0.004, 95% CL = 0.0001, 0.063).

We collected 23 vegetation samples from the brood-rearing hens whose broods survived beyond the first flush at 14 days post-hatch (Pitman et al 2006a) Most samples were collected at first flush and up to 28 days post hatch. None of our vegetation covariates differed between brood sites and paired random locations with litter, shrub, and bare ground coverages most common among all sites followed by grass and forbs and relatively low VOR (Table 2). Space use of the eight brood rearing hens averaged 156.8 ha, but was highly variable (minimum = 37.0 ha, maximum = 385.5 ha, SD = 126.8 ha). Of 13 hens and broods we located through daily triangulation and flushing, we found two brooding areas to overlap, each having only one location within the area used by the other (Figure 1).

We sampled insects at 23 brood and 22 random locations (one random location sample was lost) from brood-rearing hens. We collected an average of 0.48 (SD = 0.29) insects per sweep. There were 9 and 10 insect orders collected at brood and random locations, respectively (Table 3). Short-horned grasshoppers (Order Orthoptera, Family Acrididae) were the most abundant insect collected at brood and random locations. We found no differences

Table 1. *A priori* candidate models used to estimate brood survival rates for lesser prairie-chickens (*Tympanuchus pallidicinctus*) in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011. K = number of parameters; AIC = Akaike's Information Criterion (AIC_c); w_i = AIC model weight.

Model	K	AIC_c	ΔAIC_c	w_i	Deviance
Quadratic	3	41.68	0.00	0.58	35.52
Hen age	2	44.81	3.13	0.12	40.72
Early, Mid, Late	4	45.34	3.66	0.09	39.18
Null	1	46.10	4.42	0.06	44.08
Weekly	4	46.94	5.25	0.04	38.67
Linear	2	47.13	5.45	0.03	43.05
Brood age	2	47.97	6.26	0.02	43.89
# Chicks	2	48.13	6.45	0.02	44.04

Table 2. Mean (SD) percentage of vegetation variables measured at lesser prairie-chicken (*Tympanuchus pallidicinctus*) brood locations and paired random points. Surveys were conducted in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011.

Survey method	Variable	Overall	Brood	Random
Ground cover	% grass	17.2 (11.1)	16.9 (10.7)	17.4 (11.8)
	% forb	3.7 (4.7)	2.8 (2.5)	4.6 (6.1)
	% bare ground	21.4 (12.4)	23 (13.9)	19.8 (10.8)
	% litter	33.6 (13.8)	31.6 (11)	35.7 (16.1)
	% woody	24.3 (10.1)	26 (10.6)	22.5 (9.4)
Visual obstruction reading	Decimeters	1.4 (0.8)	1.3 (0.9)	1.4 (0.7)

between insect abundance, richness, order, or families between brood and random points. Wet mass also did not differ between brood ($\bar{x} = 5.10$ g, SE = 1.14, 95% CL = 2.74, 7.46) and random points ($\bar{x} = 2.94$ g, SE = 2.11, 95% CL = 2.05, 3.84; $P = 0.08$).

Insect abundance increased with decreasing VOR (Tables 4, 5). Less grass coverage with greater litter and forb coverage were positively associated with insect abundance, but associated models had weak model weights (Tables 4, 5). Insect richness did not vary by vegetation covariates with our null model ranking first followed by all other models with minimal differences among weak model weights and CLs overlapping 0 (Tables 4, 5). Only one weather covariate, winter precipitation, influenced insect abundance, having a positive influence (Tables 4, 5).

Table 3. Insect orders and abundance (mean and SE) for lesser prairie-chicken (*Tympanuchus pallidicinctus*) brood and random locations. Surveys were conducted on private lands with no recent herbicide treatment and continuous grazing in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011.

		Brood (*n* = 23)		Random (*n* = 22)	
Order	Family	Mean	SE	Mean	SE
Blattodea	Blattidae	0.04	0.04	0.04	0.04
Carabidae	Carabidae	0.82	0.42	0.26	0.11
Coleoptera	Brentidae	0	0	0.08	0.08
Coleoptera	Cantharidae	0	0	0.08	0.04
Coleoptera	Chrysomelidae	0.34	0.13	0.34	0.17
Coleoptera	Coccinellidae	0.04	0.04	0.21	0.13
Coleoptera	Curculionidae	0.13	0.13	0.08	0.06
Coleoptera	Cycloneda	0	0	0.04	0.04
Coleoptera	Dryophthoridae	0.3	0.3	0.08	0.06
Coleoptera	Scarabaeidae	0.04	0.09	0.04	0.04
Coleoptera	Tenebrionidae	0	0	0.04	0.04
Diptera	Bombyliidea	0.26	0.09	0.04	0.2
Diptera	Muscidae	0.3	0.13	0.26	0.12
Diptera	Simuliidae	0	0	0.21	0.21
Diptera	Stratiomyidae	0.17	0.17	0	0
Hemiptera	Cicadellidae	3.36	0.94	3.5	1.06
Hemiptera	Cicadidae	0.17	0.13	0	0
Hemiptera	Miridae	0.13	0.07	0.34	0.16
Hemiptera	Pentatomidae	0.08	0.08	0	0
Hymenoptera	Formicidae	9.34	2.88	12.73	4.03
Hymenoptera	Halictidae	0	0	0.04	0.04
Hymenoptera	Sphecidae	0.13	0.07	0.08	0.06
Mantodea	Mantidae	0.69	0.2	0.26	0.09
Neuroptera	Chrysopidae	0	0	0.08	0.06
Neuroptera	Myrmeleontidae	0.04	0.04	0.04	0.04
Orthoptera	Acrididae	21.86	3.88	18.08	2.1
Phasmida	Heteronemiidae	0.08	0.08	0.17	0.08

Table 4. *A priori* candidate models used to assess influences of vegetation structure and cover and weather variables on insect abundance and insect richness. Surveys were conducted in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011. K = number of parameters; AIC = Akaike's Information Criterion (AIC$_c$); w_i = AIC model weight, LL = Log-likelihood.

Analysis	Model	K	AIC$_c$	ΔAIC$_c$	w_i	LL
Abundance	Visual Obstruction Reading	3	728.033	0.000	0.980	−360.731
	Grass ground cover	3	735.879	7.846	0.019	−364.654
	Litter	3	742.006	13.973	0.001	−367.717
	Forb ground cover	3	749.112	21.079	0.000	−371.270
	Null	2	756.023	27.990	0.000	−375.872
	Woody ground cover	3	757.252	29.219	0.000	−375.341
	Bare ground	3	758.081	30.047	0.000	−375.755
Richness	Null	2	166.732	0.000	0.253	−81.226
	Forb ground cover	3	167.202	0.471	0.200	−80.316
	Bare ground	3	167.727	0.996	0.154	−80.578
	Grass ground cover	3	168.244	1.512	0.119	−80.836
	Visual Obstruction Reading	3	168.449	1.717	0.107	−80.939
	Woody ground cover	3	168.886	2.154	0.086	−81.157
	Litter	3	169.014	2.283	0.081	−81.221
Abundance	Winter precipitation	3	753.080	0.000	0.683	−373.254
	Null	2	756.023	2.943	0.157	−375.872
	Max. temp. – first 2 wk of a brood	3	756.891	3.811	0.102	−375.160
	Precipitation – brood-rearing	3	757.984	4.903	0.059	−375.706

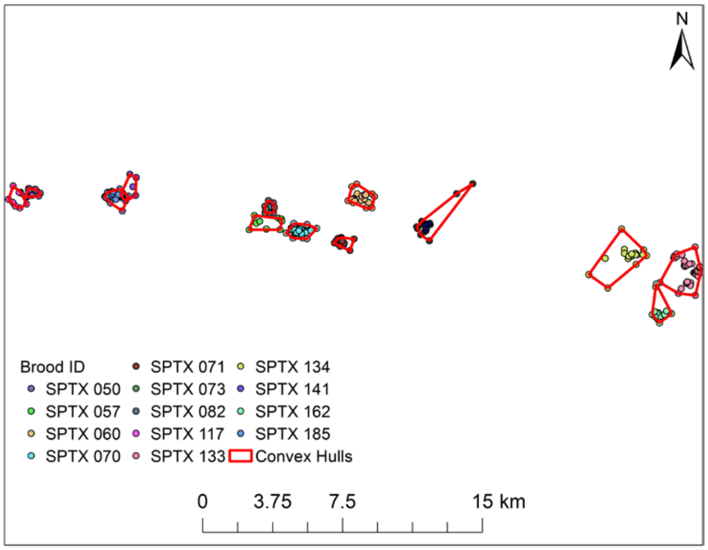

Figure 1. Point locations and convex hulls of 13 lesser prairie-chicken (*Tympanuchus pallidicinctus*) broods located to evaluate brood survival. Surveys were conducted in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011. Spatial data are accurate and precise, but scale/scope presented in figure have been modified to protect sensitive geospatial data.

Table 5. Estimates of beta coefficients (β), standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits, z-value, corresponding *P*-values of vegetation and weather covariates used to assess influences on insect abundance and insect richness, a primary food source for lesser prairie-chicken (*Tympanuchus pallidicinctus*) chicks. Surveys were conducted in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011.

Analysis	Covariate	β	SE	LCL	UCL	z	P
Abundance	Intercept	4.192	0.126	3.939	4.446	32.411	<0.001
	Visual Obstruction Reading	–0.190	0.032	–0.255	–0.125	5.741	<0.001
	Grass ground cover	–0.144	0.028	–0.201	–0.087	4.943	<0.001
	Litter ground cover	0.119	0.026	0.067	0.171	4.460	<0.001
	Forb ground cover	0.071	0.020	0.030	0.112	3.380	<0.001
	Woody ground cover	–0.028	0.025	–0.078	0.021	1.123	0.262
	Bare ground	–0.016	0.025	–0.066	0.034	0.621	0.534
Richness	Intercept	1.356	0.092	1.171	1.541	15.210	<0.001
	Forb ground cover	–0.110	0.085	–0.281	0.061	1.265	0.206
	Bare ground	0.085	0.074	–0.064	0.233	1.119	0.263
	Grass ground cover	–0.069	0.080	–0.230	0.091	0.845	0.398
	Visual Obstruction Reading	–0.074	0.099	–0.273	0.126	0.725	0.469
	Woody ground cover	0.028	0.076	–0.125	0.181	0.361	0.718
	Litter ground cover	–0.008	0.076	–0.161	0.146	0.096	0.924
Abundance	Intercept	3.677	0.086	3.503	3.850	41.531	<0.001
	Winter precipitation	0.206	0.075	0.054	0.357	2.666	0.008
	Max. temp. – first 2 wk of a brood	–0.116	0.094	–0.305	0.072	1.209	0.227
	Precipitation – brood-rearing	–0.070	0.120	–0.311	0.172	0.565	0.572

Discussion

Lesser prairie-chicken brood survival in the Sand Shinnery Oak Ecoregion during our study was extremely low, suggesting that population level reproduction was also low. Chick survival was least during the first 2 wk post-hatch but increased weekly thereafter. Compared to populations at the northern extent of their range, adults in the Southern High Plains must invest more in survival and less in reproduction, maximizing reproductive efforts when environmental conditions are optimal (Patten et al. 2005, Hagen et al. 2009, Grisham et al. 2014). Moreover, lesser prairie-chickens in sand shinnery oak-grassland communities exhibit a boom-bust fecundity pattern, tied closely to recurring droughts (Merchant 1982, Fritts et al. 2018). The combination of these factors, in concert with their low population abundance and few days that most broods survived, makes conservation challenging, particularly in the sand shinnery oak prairies (e.g., Hagen et al. 2005). Despite these challenges, our results provide important baseline information regarding brood ecology of the species within the Sand Shinnery Oak Prairie Ecoregion.

In our study, 69% of the broods were lost before the first flush (<14 days). It is possible chicks moved away from the hen or became part of an amalgamated brood with another hen during surveys (Pitman et al. 2006b, Dahlgren et al. 2010, Orange et al. 2016). Nonetheless, if our assessments were correct, then of the 50 radio-tagged hens and 32 nests laid, there was little evidence that chicks successfully reached independence. Brood loss within 14 days of hatching likely has been a key vital rate influencing species' decline (Wisdom and Mills 1997, Pitman et al. 2006a, Davis 2009, Hagen et al. 2009). In Kansas, Fields et al. (2006) reported 28% of broods had at least one chick 60 days post-hatch and estimated the probability of a brood surviving to 60 days was 49% and 5% for those reared by adults and subadults, respectively. Also in Kansas, Pitman et al. (2006a) suggested overall chick survival for early brood-rearing (hatch to 14 days post-hatch) was 48%, 37% for the late period (15 to 60 days post-hatch), and 18% for the entire brood-rearing period of hatch to 60 days post-hatch. Estimates reported from the Southern High Plains are substantially lower than those from the northern populations. In the northeastern Texas panhandle, Holt (2012) estimated 63-day chick survival as 10%, while during a 2-yr study in New Mexico, Merchant (1982) reported yearly estimates of 0% and 27% for hens that produced a brood that survived until independence.

Herbaceous vegetation structure is closely tied to precipitation, where above-average rainfall in the spring and summer maximizes vegetation growth, and tall, dense residual vegetation cover from the previous growing season contributes to quality nesting, and subsequently brood-rearing habitat conditions (Bailey et al. 2000, Grisham 2012). During the 2010 season, following the most winter precipitation during our study (study area average = 11.56 cm), nest initiation occurred earlier (mean Julian date = 114) compared to other years (mean Julian dates = 129–144), and broods survived longer. Conversely, the 2011 season represented the other extreme of the precipitation gradient with an intense La Niña event and subsequent drought affecting lesser prairie-chicken reproductive ecology (Nielsen-Gammon 2012). In 2011, only 3 of 15 (20%) radio-tagged hens nested; however, all nests were abandoned within two days of initiation. The drought of 2011 was so severe that sand shinnery oak and grasses on our study sites did not leaf out, leaving no substantial cover for lesser prairie-chickens. Only 2.46 cm of precipitation occurred from 15 October 2010 to 31 August 2011, constituting the worst drought on record and warmest La Niña event in the area since 1950. Our study area had 56 days with temperatures >38 C, and at the time, made 2011 the hottest summer on record for the area (Grisham et al. 2016).

Habitat use by brood-rearing hens did not appear to be linked to specific structural vegetation variables. We found no differences between used and random locations, which may have been attributed to a true lack of selection or from small sample sizes that likely limited our ability to fully evaluate heterogeneity in habitat quality. The lack of differences between brood and random locations in our study differed from previous findings (Ahlborn 1980, Hagen et al. 2004, Bell et al. 2010). The overall uniformity and extent of shrub cover resulting from constant, unmanaged cattle grazing likely contributed to the low percentage of grass and forb cover and subsequently, decreased the quality of brood-rearing habitat. At brood sites, forb coverage was less (approximately 3%) than the 13–15% reported in other studies (Jones 1963, Hagen et al. 2004, Hagen et al. 2005). Lesser prairie-chicken brood-rearing habitat in the Sand Shinnery Oak Prairie Ecoregion should consist of approximately 50% of total overhead cover, with relatively equal proportions of shrub (20–25%), herbaceous cover (18–26%), and ground litter (38–44%; Hagen et al. 2013).

Increased precipitation prior to brood-rearing during winter and spring maximizes vegetation growth, promotes forb growth, and supports greater insect abundance (Noy-Meir 1973, Kingsolver 1998, Fields et al. 2006, Wenninger and Inouye 2008). Lesser prairie-chicken chick survival is positively correlated with insect availability, especially during the first 2 wk of life (Hagen et al. 2005). Davis et al. (1980) reported foods of chicks and young juveniles in New Mexico were 99–100% insects, especially short-horned (80.4%) and long-horned (7.7%) grasshoppers. We found grasshoppers (Order Orthoptera) and leafhoppers (Order Hemiptera) were the most common insects available for possible consumption. While we found a positive significant relationship between winter precipitation and insect abundance, insects appeared to be limited even in years when precipitation was near average (e.g., 2008 = 41.1 cm).

Low heterogeneity in vegetation composition may have contributed to the lower insect availability, and possibly, lower brood survival due to malnutrition or starvation. Our sand shinnery oak dominated stands lacked sufficient forb cover to support insect communities and may be the underlying reason why chicks failed to survive the first 14 days post hatch. This is further supported by the negative relationship between insect abundance and visual obstruction, which was mostly related to shrub cover. Additionally, while maximum temperature was not a good predictor of food availability in our study and may not be a good predictor of brood survival (Fields et al. 2006), it may lead to decreased survival if chicks must decrease feeding time to seek shade during periods of higher temperatures (Ahlborn 1980).

We found no evidence that chicks born in our study survived to adulthood. We acknowledge that repeated disturbances via flushing may have contributed to low brood survival probabilities. Beyond this, chick survival in our study was a clearly affected by synergistic effects of severe drought and unmanaged cattle grazing with high stocking densities that resulted in poor prairie conditions. Shrub-dominated prairies at our study site, and likely elsewhere, may not support properly interspersed brood-rearing habitat in relation to lekking and nesting habitat. Long-term survival of lesser prairie-chickens in the Sand Shinnery Oak Prairie Ecoregion will be largely dependent on management practices that promote healthy prairies. When possible, it would be prudent for land managers to employ practices such as short duration, low intensity grazing that mimic native grazers, and prescribed burning and herbicide treatments to reduce woody shrub cover and promote conditions for grass and forb cover, and subsequently, support greater food resources for chicks.

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Rapid Yield Estimation Methods for Unharvested Rice Cultivated for Migrating and Wintering Waterfowl

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Abstract: Land managers in the southeastern United States cultivate rice (*Oryza sativa*) to provide calorie-dense forage for autumn-migrating and wintering waterfowl and other migratory birds. Conservation planners require accurate yield estimates for rice and other energy-rich croplands to parameterize bioenergetic models and support data-driven, adaptive resource management efforts. We developed a rapid method to efficiently estimate rice yield and quantified associated precision, accuracy, sampling time, and operating costs in the Lower Mississippi Alluvial Valley ($n = 16$ fields). We compared a visual index of seed-head size and density using ocular scores (1–10; i.e., rapid assessment) to 1-m^2 harvested plots within each field. We regressed our visual index against known rice yield estimates (kg [dry] ha^{-1}) and related our yield estimates to rice cultivation practices to inform management actions that maximize yield and cost efficiency for wildlife management. Our model ($R^2_{adj} = 0.80$) reliably estimated rice seed yield within 20–40 min per field. We found that yield was positively correlated with input cost, but that 125–180 kg ha^{-1} of post-emergence nitrogen and at least one herbicide application seemed to balance yield production while minimizing costs (US$900–1200 ha^{-1}). We suggest our rapid visual index method be incorporated into resource monitoring protocols to improve conservation planning initiatives.

Key words: bioenergetics, carrying capacity, National Wildlife Refuge, *Oryza sativa*, sampling

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Migratory waterfowl spend 7–9 months in migration and wintering areas where habitat resource management activities focus on production of natural and agricultural food to support energetic needs (Nelms et al. 2007). Many conservation planners in these regions use bioenergetic models as planning tools based on some evidence for cross-seasonal effects (Sedinger and Alisauskas 2014, Osnas et al. 2016). Some agencies also use bioenergetic models to set objectives for land management tracts (e.g., U.S. Fish and Wildlife Service [USFWS] National Wildlife Refuges; Hagy et al. 2021b) and to help quantify contributions to the North American Waterfowl Management Plan (NAWMP; USFWS and CWS 1986, Williams et al. 2014, USFWS and CWS 2018). The NAWMP established Migratory Bird Joint Ventures (JV) in 1986 which are cooperative, regional, public-private partnerships that work to conserve migratory bird habitat (USFWS and CWS 1986, 2018). Many JVs located within non-breeding season geographies step-down continental waterfowl population objectives to their respective regions and use bioenergetic models to translate regional population goals into foraging habitat objectives (Wilson and Esslinger 2002, Lower Mississippi Valley JV [LMVJV] 2015). Provision of high-energy foraging resources for migrating and wintering waterfowl are critically important to meeting habitat objectives in many geographies (LMVJV 2015, Brasher et al. 2018, Hagy et al. 2021b).

Rice (*Oryza sativa*) is a major agricultural commodity and critical food resource for wintering waterfowl in the Mississippi Flyway, Texas Gulf Coast, and California's Central Valley (Petrie et al. 2014, LMVJV 2015, Marty et al. 2015). Indeed, over 800,000 ha^{-1} are cultivated in rice throughout the Mississippi Alluvial Valley (MAV), >200,000 ha^{-1} in the Gulf Coast Prairies of Louisiana and Texas, and >200,000 ha^{-1} in California's Central Valley annually (Petrie et al. 2014). Waste-grain and unharvested rice seeds

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account for approximately 12% of the estimated wintering wetland forage needed to support target waterfowl population objectives within the LMVJV and 42% within the Gulf Coast JV region (Petrie et al. 2014). However, more efficient farming techniques and earlier planting and harvest dates continue to reduce waste-grain rice available for waterfowl (Manley et al. 2004, Stafford et al. 2006). State, federal, and private land managers increasingly cultivate rice and leave it unharvested and flooded to efficiently meet habitat resource management goals (LMVJV 2015). Unharvested rice can provide 45 times greater energy biomass compared to harvested rice (Hagy et al. 2021a). Given the importance of unharvested rice to waterfowl and its increasing use by waterfowl and wetland managers, accurate biomass estimates are needed to parameterize bioenergetic models for conservation planning and implementation (Petrie et al. 2014, Williams et al. 2014, Marty et al 2015, Hagy et al. 2021b).

Biomass of harvested rice historically has been estimated using soil cores (Manley et al. 2004, Stafford et al. 2005, Havens et al. 2009, Marty et al. 2015). In unharvested fields, harvested samples known as crop-cuts have been used (Fermont and Benson 2011, Sapkota et al. 2016). However, both soil cores and crop-cuts are labor intense and typically cost-prohibitive for operational monitoring (Low and Bellrose 1944, Gray et al. 1999, Sapkota et al. 2016). Therefore, our goal was to design a rapid assessment methodology based on visual assessments of rice density and quality with acceptable levels of precision (coefficient of variation [CV] = 15–20%; Stafford et al. 2006). Specifically, we sought to: (1) quantify precision and accuracy of multiple methods to estimate rice seed production within the Mississippi Alluvial Valley; (2) assess speed, bias, and precision trade-offs among different rapid assessment variants; (3) evaluate unharvested rice yields relative to total input costs and fertilizer and herbicide applications; and (4) recommend the most appropriate rapid assessment method(s) and optimal input costs, nutrient, and chemical applications to wetland biologists and managers.

Study Area

Our study fields were located in two states within the MAV at three USFWS National Wildlife Refuges (NWR) and one Tennessee Wildlife Resource Agency (TWRA) refuge. Specifically, fields were in Overflow NWR (N 34.3575, W 91.1211) and Dale Bumpers White River NWR (N 33.0791, W 91.6664) in Arkansas, and Hatchie NWR (N 35.4983, W 89.2631) and Hop-in Refuge (N 36.2511, W 88.9709) in Tennessee. Unharvested rice fields were bounded by levees and infrastructure for hydrological management within each impoundment to control weeds during the growing season and capture or flood impoundments during the non-growing season. Unharvested rice fields were planted with a seed drill or broadcaster during summer (i.e., May–July) after fields were brought to adequate nutrient and pH levels. After germination, shallow intermediate flooding schedules and sometimes herbicides were used to control weeds. Concurrently, some fields had post-planting fertilizers applied, typically in the form of urea, to provide nitrogen. Some years insecticide applications were also required to prevent crop destruction (Hardke 2021).

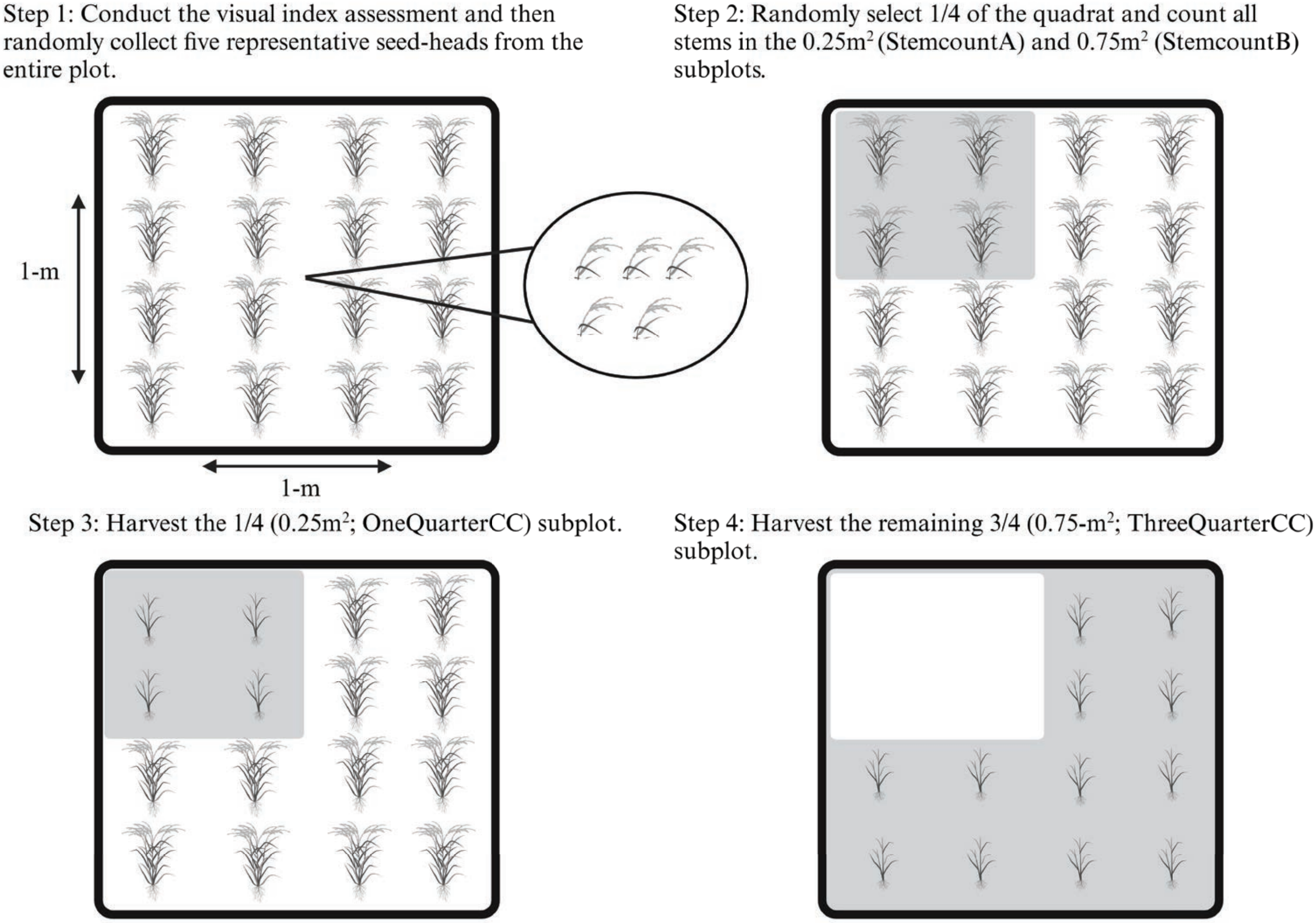
Methods

Field Sampling of Rapid Methods

We sampled unharvested rice in October 2020–2022 within a 1-m^2 quadrat among five locations along a systematic random transect spanning an entire rice field to capture any heterogeneity of rice production within each field (Martin et al. 2022, Highway 2022). We entered each field at a random location and placed our first quadrat 10–50 m from the field edge to establish our first sampling location (Sapkota et al. 2016). The four subsequent sample locations were spaced evenly along the transect to encompass the entire field using a systematic-random design (Martin et al. 2022, Highway 2022). If rice levees were present and dividing the field into sections, we used multiple transects to distribute plots across different paddies within each field. At each sample location, we used the following methods described below to estimate rice seed production (Figure 1).

We developed a qualitative visual index (VI) to estimate seed production based on ocular seed-head size and density scores. We estimated seed-head size and density scores on a 1 to 10 scale within each 1-m^2 quadrat where 1 represented the lowest score and 10 the highest, for a total possible score of 20. Lower scores of 1–4 indicated low quality, potentially dirty (mixed with moist-soil plants) or ratoon rice, while high scores, such as 8–10, were near commercial rice production grade. We conducted VI scoring at each sampling location preceding all other rapid assessment methods.

Following the VI method, we randomly collected five seed heads from each quadrat. Next, we divided the quadrat into four, 0.25-m^2 subplots. We randomly selected one of the four subplots and counted all stems within that subplot (0.25 m^2; StemcountA). Then we counted all stems in the remaining subplots collectively (0.75 m^2; StemcountB). We summed stem counts of the one and three quarter subplot samples for the total number of stems within the entire 1-m^2 plot (StemcountC). Following stem counts, we sequentially hand-harvested all seed heads from the randomly selected subplot first (0.25 m^2; OneQuarterCC), followed by harvesting all seed heads from the remaining three quarter subplots (0.75 m^2; ThreeQuarterCC). We stored all seeds in separate paper bags for each sampling method to allow them to dry.


Step 1: Conduct the visual index assessment and then randomly collect five representative seed-heads from the entire plot.

Step 2: Randomly select 1/4 of the quadrat and count all stems in the 0.25m^2 (StemcountA) and 0.75m^2 (StemcountB) subplots.

Step 3: Harvest the 1/4 (0.25m^2; OneQuarterCC) subplot.

Step 4: Harvest the remaining 3/4 (0.75-m^2; ThreeQuarterCC) subplot.

Figure 1. During October 2020, 2021, and 2022, we sampled unharvested rice grown for migrating and wintering waterfowl in the Mississippi Alluvial Valley to evaluate a series of rapid assessment methods that estimated rice seed yield. This is a graphical interpretation of rapid assessment methodologies created with Biorender.com demonstrating rice seed sampling using a visual assessment of the entire 1-m^2 plot, stem count methods, and crop-cut methods.

Laboratory Methods

All seed heads were air dried at room temperature in paper bags for ≥1 wk, then thrashed from their panicles leaving only the seeds, and weighed to the nearest 0.1 g (Sapkota et al. 2016). For the crop-cut methods, we used a mechanical seed thrasher in 2020 and 2021 and hand thrashed samples in 2022. All seed heads collected for the stem count methods were hand thrashed. For each individual sample, we randomly selected 20 dried seeds and recorded the number of blank seeds to develop a correction factor for the number of blank seeds in each sample so we did not overestimate rice yield. Blank seeds are caused by sterile florets that do not produce a functional seed and are primarily the hull. The prevalence of blank seeds can be affected by rice variety, planting dates, soil temperature, irrigation before seed heading, excessive fertilization, and irrigation using cold water (Board and Peterson 1980). After samples were weighed, we combined biomass estimates from the 0.25-m^2 subplot and the 0.75-m^2 subplot to calculate seed biomass (g [dry]) across the entire quadrat (WholeCC). The WholeCC biomass was assumed to be the true biomass for each quadrat on which we compared rapid assessment methods.

To correct for sampling loss, processing loss, and blank seeds, we calculated correction factors to adjust our measured weight. First, we assumed a 3% loss of seed weight during sampling, collecting, sorting, and weighing of all samples regardless of method based on Hagy et al. (2011). Next, we collected samples of seeds lost (i.e., discarded by the mechanical thrasher) during the thrashing of the crop-cut samples (OneQuaterCC, ThreeQuarterCC, WholeCC). The stem count samples were hand thrashed in such small batches no seeds were lost. Thus, no thrashing correction factors were needed. Then, we randomly selected and weighed 50 blank and 50 whole seeds to the nearest 0.1 g and calculated mean weights which gave us a factor to adjust mass based on the number of blank seeds in each sample. Last, to account for excess weight from chaff (rice plant stems or parts of seed heads that are not actual grains), we collected eight samples of seeds after they were thrashed and weighed them before and after a thorough cleaning. Adjusting our measured weights accordingly with these corrections, we could then extrapolate rice seed density (kg ha^{-1}). We gathered information about agricultural practices and financial costs regarding rice cultivation for each field from state and federal wetland managers. Specifically, we collected total input cost, fertilizer rates (kg ha^{-1}), and number of herbicide applications (1–2+).

Statistical Analysis

The WholeCC (1 m^2) represented true seed biomass (kg ha^{-1}). Therefore, we compared estimated rice yield derived from rapid methods to the WholeCC (Sapkota et al. 2016). We first applied our correction factors at the subplot-level and then extrapolated subplot samples to estimate rice seed biomass (kg ha^{-1}). For the stem count methods, we calculated average weight of the five randomly selected seed heads from each quadrat and multiplied mean weight by the stem density (g m^{-2}) and converted estimates to kg ha^{-1}.

We estimated rice yield for the VI by regressing WholeCC biomass (i.e., true biomass [kg ha^{-1}]) on our VI Total scores (i.e., whole-plot estimate (kg ha^{-1}; Naylor et al. 2005). We calculated adjusted marginal coefficient of determination (R^2_{adj}) to estimate variance in total biomass explained by the visual estimation method. We calculated 95% confidence (CI) and prediction intervals (PI) because both estimates of variance may be of interest to conservation planners and biologists. Confidence intervals are most useful to conservation planners to predict average seed yield across many rice fields in a landscape; PIs may be more useful to biologists measuring variance of predictions within single units (Naylor et al. 2005). Last, we compared mean precision and bias across each method. We used ANOVA to compare rapid yield estimation methods to our WholeCC method and set $\alpha = 0.1$ (Tacha et al. 1982). Non-significant results would indicate no detectable difference in yield estimation and thus a more efficient and comparable method. Additionally, we estimated the bias for each method assuming WholeCC estimates represented true biomass (i.e., Bias = [method estimate – WholeCC estimate] ÷ WholeCC estimate) and compared bias among methods with linear regression. All statistical analyses were performed in program R (R Core Team 2022).

We evaluated rice yield relative to financial input costs and agricultural practices. First, we assumed US$222 ha^{-1} for irrigation costs when these costs were unavailable (MSU 2021). We used a logarithmic regression to assess how yield from our WholeCC biomass related to input cost (i.e., WholeCC (kg ha^{-1}) regressed on log (input cost [$] ha^{-1}). We calculated adjusted marginal coefficient of determination (R^2_{adj}) to estimate variance in total biomass explained by the input cost and calculated 95% CI. For fertilizer rates, we standardized nitrogen applications (kg ha^{-1}) among fields post-planting by calculating kg ha^{-1} based on the known percentage of nitrogen in urea and ammonium sulfate. We separated these fields based on natural breaks in nitrogen applications into <50, 50–100, 125–155, 155–180 and >180 kg ha^{-1} groups ($n = 3$, 3, 3, 6, 1 respectively). We also evaluated the number of herbicide applications and grouped fields into 0, 1, or 2 applications. We then calculated mean and SE of rice yield relative to fertilizer rate and application.

Results

Yield Estimates and Comparisons

Blank seeds weighed 16.67% of whole seeds. Thus, we deflated seed mass by multiplying the percentage of blanks in each sample by 0.1667. We found the mechanical thrasher expelled 2.1% and 15.7% of whole seeds in 2020 and 2021, respectively. Hand-thrashing in 2022 expelled only 0.2% of whole seeds when thrashing crop-cut samples. We inflated seed yield by expelled seed-thrashing correction factors annually and only to crop-cut estimates because of their greater sample sizes. Last, we found that chaff created a 0.74% bias and thus corrected for this effect.

Yield estimates among all methods, years, and fields ranged from 1200–15,036 kg ha^{-1} (SE = 0.0–3584; 23–298 bu ac^{-1}). Within each year, rice yield averaged 5757 kg ha^{-1} (SE = 1320; 114 bu ac^{-1}) in 2020, 5520 kg ha^{-1} (SE = 838; 109 bu ac^{-1}) in 2021, and 6360 kg ha^{-1} (SE = 1325; 126 bu ac^{-1}) in 2022 (Table 1). Our visual index explained 80% of the variation in total rice seed biomass ($R^2_{adj} = 0.80$; Figure 2). In addition, the visual index only overestimated true yield by 1.2% ($P = 0.858$). We found differences in yield estimates among rapid assessment methods ($F_{6,105} = 1.90$, $P = 0.087$; Figure 3). The stem count methods overestimated rice production by 29% using StemcountA ($P = 0.006$), 37% using StemcountB ($P < 0.001$), and 34% using StemCountC ($P = 0.001$; Figure 3); whereas, crop cuts did not (QuarterCC, $P = 0.784$; ThreeQuaterCC, $P = 0.897$). Lastly, each method yielded similar precision of mean CVs ranging from 24.7–35.0% across all five methods. The VI had the greatest precision (CV = 24.7%; Figures 2 and 3).

Table 1. Yield in both kilograms per hectare (kg ha^{-1}, with SE) and bushels per acre (bu ac^{-1}) of fields sampled with unharvested rice grown for wintering waterfowl to evaluate methods to estimate rice yield on four refuges in Arkansas (Overflow National Wildlife Refuge [NWR] and Dale Bumpers White River [DBWR] NWR) and Tennessee (Hatchie NWR and Hop-in Refuge [state refuge]), 2020–2022.

		2020 Yield			2021 Yield			2022 Yield		
Refuge	Field	kg ha^{-1}	SE	bu ac^{-1}	kg ha^{-1}	SE	bu ac^{-1}	kg ha^{-1}	SE	bu ac^{-1}
Overflow NWR	Jackson	3171.2	1115.1	62.9						
	Middle Long	1592.6	320.8	31.6	4722.1	260.4	93.6			
	North Long	2972.0	205.9	101.9	5141.1	335.8	101.9			
	North Flat Slough				4420.1	781.5	87.6			
DBWR NWR	Powerline				6872.9	289.6	136.3			
	Simmons 40	8306.9	428.8	164.7	8510.1	762.0	168.7	9657.8	451.6	191.5
	Simmons 11							6572.8	989.1	130.3
	Turner East	9141.4	536.8	181.2						
	Turner North	7817.7	328.1	155.0						
Hatchie NWR	Triangle				3456.7	627.1	68.5			
Hop-in Refuge	North							4460.2	639.0	88.4
	South							4747.1	844.1	94.1

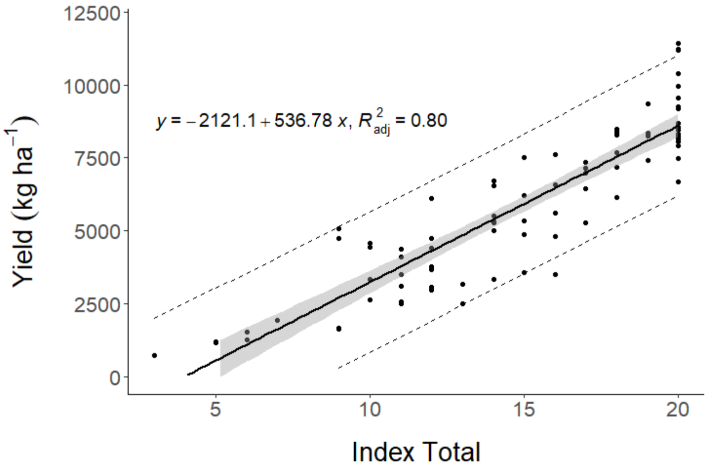


Figure 2. Linear relationship and associated 95% confidence (gray shade) and prediction intervals (dashed lines) between unharvested rice yield estimates (kg ha^{-1}) from whole-plot crop-cuts (i.e., true biomass) and estimated Visual Index Scores (seed density + quality indexed from 1–10 for each metric) from fields in the Mississippi Alluvial Valley, October 2020, 2021, and 2022. Black dots are individual data points collected across 16 rice fields.

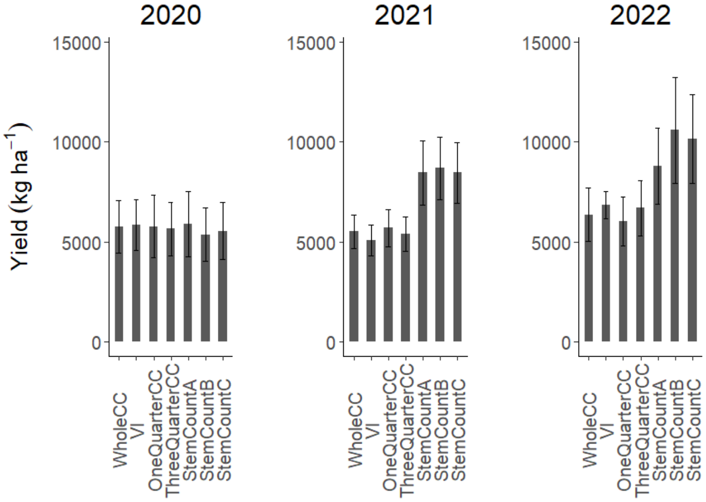


Figure 3. Comparison of unharvested rice yield (kg ha^{-1}) in 2020, 2021, and 2022 for each rapid assessment method conducted on 16 fields in the Mississippi Alluvial Valley. Sampled include included 1-m^2 whole plot crop-cut (WholeCC), visual index (VI), 0.25-m^2 quarter plot crop-cut (OneQuarterCC), 0.75-m^2 crop-cut (ThreeQuarterCC), stem count method with quarter plot stem counts (0.25 m^2; StemCountA), three-quarter plot stem counts (0.75 m^2; StemCountB), and whole plot stem counts (1 m^2; StemCountC). Error bars are ± 1 SE.

Agricultural Practices

In general, input cost was positively corelated to yield (95% CI: 2729.5–5540.4) explaining 74% of the variation in total rice seed biomass ($R^2_{adj} = 0.74$, $F_{1,13} = 40.4$, $P < 0.001$; Figure 4). Managers that applied <50 kg ha^{-1} post-planting nitrogen fertilizer yielded 2579 (SE = 496) kg ha^{-1} of rice seed. However, levels greater than 180 kg ha^{-1} (i.e., 432 kg ha^{-1}) of post-planting nitrogen yielded similar production of 3457 kg ha^{-1}. Other than one field, greater amounts of post-planting fertilizer increased rice seed production. Managers that applied 50–100 kg ha^{-1} of post-plant nitrogen fertilizer produced 4761 (SE = 209) kg ha^{-1} of rice on average compared to applications of 125–155 kg ha^{-1} producing 5675 (SE = 1075) kg ha^{-1} and applications of 155–180 kg ha^{-1} producing 8177 (SE = 501) kg ha^{-1} of rice. Similarly, as managers increased the number of

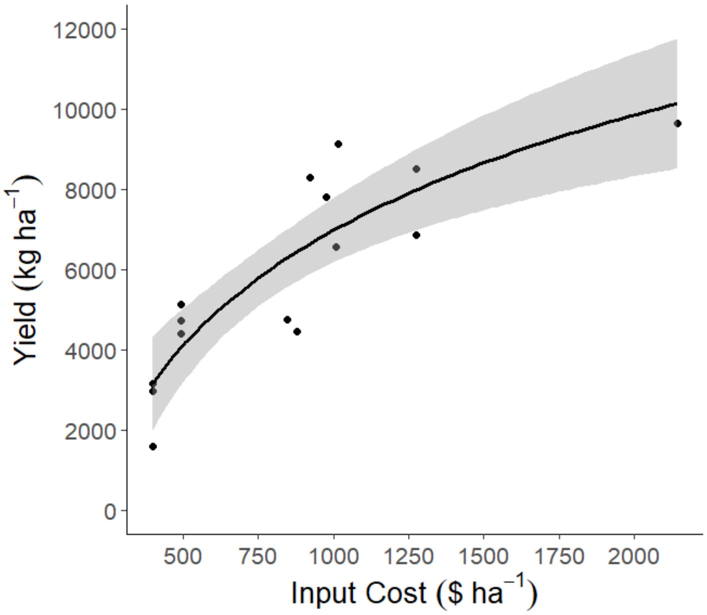


Figure 4. Logarithmic regression of the estimated unharvested rice yield (kg ha^{-1}) on the associated input cost (US$ ha^{-1}; estimated based on information from field managers) with the 95% CI (gray shade) for 16 fields in the Mississippi Alluvial Valley, October 2020, 2021, and 2022.

herbicide applications, their yields also increased. Mangers that applied no herbicide produced the least yield at 2579 (SE = 496) kg ha^{-1}. Subsequently, managers that applied one herbicide application produced 5978 (SE = 646) kg ha^{-1}, and managers that applied two herbicide applications produced the greatest yields averaging 8016 (SE = 896) kg ha^{-1}.

Discussion

Given the importance of unharvested rice to waterfowl and its increasing use by waterfowl and wetland managers, we evaluated rapid assessment methods to estimate rice seed production to assess trade-offs among estimated accuracy, precision, and speed. Our visual index and smaller crop-cut size estimates were generally similar to inaugural whole-plot crop-cut estimates. While we did observe high levels of variability in some instances, we believe much of this was due to the variability of production within our sampled fields, especially when yields were low. The time saved using our visual index cannot be understated when compared to crop-cuts and stem count methods. No physical samples are required, which greatly increased in-field efficiency and eliminated post-processing. Combined with minimal calculations and an automated data processing application, we demonstrated accurate yield estimates can be obtained before even leaving the field.

We found no trade-off in precision vs. bias across crop-cut plot sizes, suggesting managers can use subsampled 0.25-m^2 crop-cuts and obtain similar yield estimates, thus increasing harvesting and post-processing efficiency. We acknowledge, however, that crop-cuts required mechanical seed-thrashing (which expelled >10% of whole seeds) or large amounts of time for hand thrashing. We believe that the large amounts of seed expelled during mechanical thrashing was a result of different seed weights due to drying times. We strongly advise managers using mechanical thrashers to dry rice seeds for at least 1 wk first and then use our correction factor for seed loss from 2020.

The stem count method overestimated rice yield compared to the whole-plot crop-cut. Five seed heads may also not be a large enough sample to precisely estimate seed mass compared to average mass across the entire plot. Sapkota et al. (2016) showed the use of smaller sample sizes when using crop-cuts could lead to the overestimation of wheat yield. Conversely, observer bias may have been injected when selecting random seed heads and thus unknowingly but consistently larger or heavier seed heads were selected compared to the plot average. Similar observer biases have been demonstrated with moist-soil vegetation rapid assessment methods (Martin et al. 2022). Therefore, we do not recommend the stem count method or its variants because of overestimation properties which could result in positive bias of foraging energetic carrying capacities.

Importantly, the visual index method required no harvesting or post-processing and estimated rice yield most precisely and accurately. This visual estimation method required 20–40 min per field and explained 80% of variation in rice production. Therefore, we recommend the visual index scoring system to be used over all other methods. We acknowledge our regresion model predicts negative rice yields at low index scores, similar to moist-soil rapid assessment methods (e.g., Martin et al. 2022); yet, negative yields are impossible. Therefore, we suggest any negative yields be treated as zeros. One drawback to the visual index is observers must be familiar with the variability of rice growth, seed sizes, and densities in their region to accurately assign visual quality scores. Therefore, similarly encouraged by researchers developing moist-soil rapid assessment methods, we suggest annual training on rice variability and scoring to standardize estimates regionally (Naylor et al. 2005, Martin et al. 2022). We also advocate for the fewest number of observers across fields with established sampling protocols to reduce likely observer biases. Last, we recommend using applications that build in examples for observers paired with application-based data management and analysis.

In rice fields with predictably high yield and low variation, seed density and size scores could be reasonably estimated at the field level by traversing randomized transects encompassing the entire variability of a field. Exploring this relationship, regressing yield and infield variation, we found that yields exceeding 297 kg ha^{-1}

(120 bu ac^{-1}) had a CV < 20%. Thus, yields exceeding this threshold will appear homogeneous to observers and could be sampled with a single transect. This will increase the efficiency of the method with little to no effect on yield estimates. Similar variations to Naylor et al. (2005) to estimate moist-soil seed production have been used successfully thereby significantly reducing time in the field (Martin et al. 2022). Conversely, if in-field variation is high, established plots are likely necessary to obtain precise yield estimates.

Unsurprisingly, generally greater input costs produce greater rice yield (MSU 2021); however, there appears to be a threshold at which input costs will be at a diminishing rate of return. In other words, managers can expect a greater yield with higher input cost, but at a lower rate of return as the yield per additional cost decreases. Based on total input cost (seed, contracted services, fertilizer, herbicide, insecticide, and irrigation) for each field, we determined an optimal cost range and recommended managers target \$865–1235 ha^{-1} (\$350–500 ac^{-1}; MSU 2021). Once a field has reached adequate pre-planting conditions, greatest benefits of post-planting nitrogen inputs appeared around 125 kg ha^{-1} (112 lbs ac^{-1}) and benefits diminished when inputs exceeded 180 kg ha^{-1} (160 lbs ac^{-1}). Lastly, herbicide applications always increased yield, so at least one application is prudent to limit weed competition that can dramatically reduce yield. Federal and state lands are generally located on marginal to low soil production capacity from an agricultural standpoint; thus, providing adequate growing conditions through fertilization and controlling herbaceous competition is necessary if greater than marginal yields are to be expected.

Management Implications

From our evaluation of agricultural inputs and yields, we have identified several key practices to maximize production efficiency. Our visual index score is a cost-effective and time-efficient method to estimate unharvested rice yield accurately and precisely. Public and private land managers are constrained by time and personnel; therefore, our method promotes the monitoring of rice yields at local and landscape scales because it is accurate, efficient, and thus not burdensome on wetland biologists and managers. Effectively and efficiently monitoring yields in these energy-rich croplands will accomplish two goals: (1) provide wetland managers with needed monitoring so they may adapt annual agricultural practices to increase rice yield while reducing input costs (Rains and Thomas 2009); and (2) allow conservation planners to most accurately step-down NAWMP habitat resource goals to inform wetland management at the JV, regional, and wetland complex scales (LMVJV 2015, Hagy et al. 2021a).

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Nonbreeding Waterfowl Behavioral Response to Crewed and Uncrewed Aerial Surveys on Conservation Areas in Missouri

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Abstract: Monitoring waterfowl populations provides the basis for improving habitat quantity and quality, establishing harvest regulations, and ensuring sustainable waterfowl populations through appropriate management. Waterfowl biologists currently use a variety of population and habitat monitoring methods ranging from informal ground observations to low-level occupied aircraft surveys. Unoccupied aerial systems (UAS) may provide safer and more precise alternatives to traditional aerial survey techniques that are less disturbing to waterfowl, but there is limited information on how waterfowl in winter respond to UAS. Therefore, we compared the behavioral responses of waterfowl to helicopters and UAS on Missouri Department of Conservation wetland conservation areas October–February 2021–2022. Helicopter surveys were flown using an Airbus H125 helicopter at heights of 100–350 m, with UAS surveys flown using a DJI Mavic 2 Pro UAS at 15–90 m. Waterfowl behavior was categorized as alert, swim, fly, or abandonment using flock-scan surveys recorded for 10-min periods before, during, and after the surveys. The percentage of time flocks spent in each behavior during- or post-survey were compared to time spent in those behaviors pre-survey. Waterfowl increased time spent swimming, flying, and abandonment in response to helicopter flights, whereas UAS flights did not influence overall waterfowl behavior. Additionally, waterfowl did not change behavior in response to UAS flights regardless of waterfowl guild (mallard, other ducks, or goose) or hunting season (open or closed). Waterfowl did increase flight behavior during UAS flights at 30 m, however, there was no change in behavior at all other UAS survey altitudes. Use of UAS may be a good alternative to traditional waterfowl survey methods and is not likely to affect waterfowl distributions or energy expenditures during the survey periods.

Key words: aerial survey, disturbance, drone, duck, goose

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Information collected from waterfowl surveys is used to monitor waterfowl populations, establish harvest regulations, inform management decisions, provide the basis for improving waterfowl habitat quantity and quality, and ensure the sustainability of the resource for the future (Williams et al. 1996, Johnson and Williams 1999, Nichols et al. 2007, Soulliere et al. 2013). Localized surveys allow wetland managers to evaluate waterfowl response to habitat conservation and management decisions as a form of Adaptive Resource Management (Williams et al. 1996, Johnson and Williams 1999, Nichols et al. 2007). Waterfowl biologists use a variety of population monitoring methods ranging from informal ground observations to more systematic approaches, including low-level crewed aerial surveys and structured ground counts (Stancill and Leslie 1990). Historical and existing methods for monitoring waterfowl abundance are expensive, risk crew safety, and contain logistical and observational challenges that can result in inaccurate or imprecise abundance estimates (Martinson 1967, Stancill and Leslie 1990, Smith 1995, Pagano and Arnold 2009). Observational challenges during ground surveys include visual obstructions, such as standing vegetation, and high abundances of birds that make accurate counting difficult (Martinson 1967, Pagano and Arnold 2009). Aerial surveys often result in imprecise estimates due to challenges with estimating density of birds from the air and limited time for counting tens of thousands of birds in the short time they are in view of the aircraft (Martinson 1967, Pagano and Arnold 2009). Aerial surveys conducted from fixed-wing aircraft

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are also expensive, flown at extremely low altitudes (<150 m) and inherently dangerous, making them the leading cause of work-related mortalities among wildlife biologists (Sasse 2003).

Current low-level aerial surveys impact resting waterfowl, causing disturbance and increasing energetic expenditure (Pease et al. 2005, Gilbert et al. 2020). Lesser snow, Ross', and greater white-fronted geese (*Anser caerulescens, Anser rossii, and Anser albifrons*, respectively) may abandon the survey area even prior to arrival of the aircraft (Soulliere et al. 2013, Wang et al. 2019, Gilbert et al. 2020). Harlequin ducks (*Histrionicus histrionicus*) increase disturbance-related behaviors and decrease comfort behaviors during exposure to aircraft (Goudie 2006). Previous research found that survey methodology (crewed aircraft versus ground surveys) did not result in different rates of disturbance, including wetland abandonment, with both methods resulting in approximately 14% of waterfowl disturbed and 3% of individuals abandoning the wetland and with geese exhibiting more disturbance behaviors than ducks (Gilbert et al. 2020). Refuge status, or lack of hunting pressure, can also impact waterfowl response to aerial surveys, with ducks and geese showing 2.2 times greater response to aircraft disturbance on areas closed to hunting (Hagy et al. 2017, Gilbert et al. 2020). Disturbance level of harlequin ducks differs depending on the type of aircraft (military jets, single-engine fixed-wing, and helicopter), indicating smaller and quieter aerial systems such as unoccupied aerial systems (UAS) may cause lower disturbance than crewed aircraft (Goudie 2006, Wang et al. 2019).

In recent years, UAS have emerged as a new technology for monitoring wildlife populations that may provide a safer alternative to current ground and low-level aerial survey techniques (Linchant et al. 2015, Pimm et al. 2015, Lyons et al. 2019, Elmore et al. 2023). Over time, aerial platforms have increased in technological ability and versatility, including improvements in sensor quality and capabilities, and the price of data acquisition and processing has decreased, allowing broader use of UAS to monitor wildlife populations (Linchant et al. 2015, Pimm et al. 2015, Lyons et al. 2019, Elmore et al. 2023). In many cases, UAS are more cost-efficient and provide more flexibility in use than traditional methods, and may allow the integration of technology to monitor and inform daily management decisions in real time (Marchowski 2021). Although UAS have been demonstrated as effective in wildlife monitoring and population surveys, there is limited research on the effect of UAS on non-breeding avifauna (Marchowski 2021, de Leija et al. 2023). Disturbance levels among wildlife may vary based on UAS shape, size, color, noise-level produced, and flight pattern design, with smaller, quieter UAS flown at steady altitudes and speeds generally causing less disturbance (McEvoy et al. 2016, Mulero-Pázmány et al. 2017, de Leija et al. 2023). Overall, UAS may provide less disturbance to wildlife than traditional ground and aerial surveys. For example, limited disturbance of colonial-nesting waterbirds was observed with UAS flown at or above 50 m above ground (Barnas et al. 2018, Barr et al. 2020, de Leija et al. 2023). Several studies have evaluated the ability of UAS to identify nesting waterfowl and the disturbance of UAS surveys on nesting avifauna, but more research is needed to determine disturbance impacts to waterfowl during non-breeding seasons (McEvoy et al. 2016, Barnas et al. 2018, Barr et al. 2020, Ryckman et al. 2022, Elmore et al. 2023). Thus, objectives of this study were to (1) evaluate the impacts of UAS compared to crewed aircraft on waterfowl behavior during non-breeding season surveys, and (2) identify factors influencing behavioral response of waterfowl to UAS surveys to reduce potential bias due to waterfowl response to the surveys.

Study Area

We conducted waterfowl observations at ten intensively managed wetland Conservation Areas (hereinafter, areas) within the Upper Mississippi River Conservation Priority Area across Missouri from October 2021 through January 2022 (Figure 1). Areas were Missouri Department of Conservation (MDC) properties, all with a management emphasis of providing migrating waterfowl

Figure 1. Study sites located on intensively managed wetland conservation areas in Missouri where we conducted waterfowl behavior response surveys to helicopter and unoccupied aerial system surveys during October–February 2021–2022.

habitat and hunting opportunities, ranging from 1518 to 5637 ha. All areas contained portions of waterfowl refuge that were closed to any form of human recreational use 15 October–1 March, with the remaining portions of the areas open to waterfowl hunting during the state hunting season through a controlled lottery system or available for walk-in hunting. The areas all contained water pumping capabilities and various water-control structures, which allowed water levels to be managed in smaller units or pools (approximately 40–160 ha) within the larger conservation areas. Vegetation cover types present in refuge and hunting pools included moist-soil vegetation (smartweeds [*Persicaria* spp.], millets [*Echinochloa* spp. and *Leptochloa* spp.], and others), open water, shrub-scrub (buttonbush [*Cephalanthus occidentalis*], black willow [*Salix nigra*], and swamp privet [*Foresteria acuminata*]), wooded (oak species [*Quercus* spp.], bald cypress [*Taxodium distichum*], water tupelo [*Nyssa aquatica*]), flooded harvested crop (corn [*Zea mays*], soybeans [*Glycine max*], and wheat [*Triticum* spp.]), and flooded standing crop (corn, soybeans, and wheat). Waterfowl numbers on the areas ranged from approximately 25,000 to 200,000 ducks, with up to an additional 50,000 geese during peak times of migration.

Methods

Waterfowl Surveys

MDC personnel conducted waterfowl abundance surveys using an Airbus H125 helicopter (Airbus, Leiden, Netherlands) at altitudes of 100–350 m above ground level (AGL) from October 2021–January 2022. Helicopter surveys were flown weekly by region, surveying three to five areas during each flight, resulting in 12 observed helicopter flights. For each flight, one wetland pool within the survey was selected for monitoring waterfowl behavior based on waterfowl abundance, species present, and viewing capabilities. We conducted UAS surveys with a DJI Mavic Pro 2 (Da-Jiang Innovations, Shenzhen, Guangdong, China), a multi-rotor style UAS, using software developed in-house and installed on a DJI Smart Controller (Da-Jiang Innovations) for automated flight path planning in a lawnmower transect flight pattern. We flew UAS surveys over the same wetland pool as was monitored during the helicopter flight. UAS surveys were initiated on the backside of the levee, 50–500 m from the perimeter of the wetland, so that waterfowl behavior was not influenced by the takeoff and landing portions of the surveys (Barnas et al. 2018). The UAS surveys were flown at ground speeds of 10 m sec^{-1} for flights at 60 and 90 m AGL and 5 m sec^{-1} at flights at 15 and 30 m AGL, to reduce image blurriness due to flight speed and simulate actual flight conditions of UAS abundance surveys (Tang et al. 2021). Image overlaps were set to 30% frontal overlap and 10% side (horizontal) overlap. UAS surveys were spatially and temporally paired with each helicopter survey and occurred ≥30 min before or after completion of the helicopter flight, to allow recovery time for birds following any potential response to the helicopter flight (McEvoy et al. 2016, Barnas et al. 2018, Barr et al. 2020). Additional UAS surveys were flown twice weekly (weather permitting) October 2021–January 2022 at areas selected based on waterfowl abundance, species present, weather conditions, and vegetation cover type present. All UAS flights were conducted under a Special Use Permit from the Missouri Department of Conservation and followed the regulations set forth in 14 Code of Federal Regulations Part 107 Small Unmanned Aircraft Systems (14 CFR Part 107).

All surveys (UAS and helicopter) were flown over pools designated as refuge and closed to any anthropogenic activity, starting no earlier than 2 h after sunrise and ending by 1300 h. We randomized UAS survey altitude (15, 30, 60, and 90 m) order and terminated any flight in which the waterfowl flushed and left the pool (abandonment). We included a 30-min rest/recovery period between UAS flights at different altitudes to allow recovery time for birds following any potential response to the previous UAS flight (McEvoy et al. 2016, Barnas et al. 2018, Barr et al. 2020).

Monitoring Waterfowl Behavior

We recorded waterfowl behavior using a Canon T2i camera (Canon Inc., Tokyo, Japan) on video recording mode attached to a Vortex Skyline 80ED (20–60x80) spotting scope (Vortex Optics, Barneveld, Wisconsin) from a vantage point >100 m from the flock under observation, allowing us to view a portion of birds in a visible portion of the wetland with enough detail to identify individual bird behaviors while not impacting behavior (Barr et al. 2020, Ryckman et al. 2022, de Leija et al. 2023). We defined the beginning of a survey as the time the UAS took flight, or the helicopter entered auditory range and the end of a survey as when the UAS landed, or the helicopter exited auditory range. Video recordings began 10 min prior to each survey (pre-survey behavior), continued for the duration of the survey (during survey behavior), and ended 10 min after the survey ended (post-survey behavior). The time at which the UAS or helicopter was directly over the waterfowl flock in the video frame was also recorded during surveys. The period beginning up to 5 min before through up to 5 min after the helicopter or UAS was directly over the portion of birds under observation was extracted for the survey time period. Thus, each survey consisted of 3 parts, each 10 min long: pre-survey, survey, and post-survey. The pre-survey period allowed us to establish baseline behavior, whereas the post-survey period allowed us to examine any residual effects surveys had on waterfowl flock behavior.

Videos were reviewed by a single observer in Windows Media

Player (Microsoft, Seattle, Washington), and waterfowl were classified into one of three taxonomic guilds: geese (Canada [*Branta canadensis*], greater-whited fronted, lesser snow, and Ross' geese), mallards (*Anas platyrhynchos*), and other ducks (northern pintail [*Anas acuta*], northern shoveler [*Spatula clypeata*], American wigeon [*Mareca americana*], gadwall [*Mareca strepera*], American green-winged teal [*Anas crecca carolinensis*], and ring-necked ducks [*Aythya collaris*]). Although our study areas contain many mixed-species flocks, we were uncertain if one species response in a mixed-species flock would be independent of the response of other waterfowl species present in the flock. Unlike mallards, which were encountered in flocks not containing other species, we did not encounter individual species flocks of species in the other duck guild to analyze these species individually. Therefore, we analyzed the combination of all species in that flock as one guild, (i.e., other duck). The same was true for geese, in that we did not encounter them enough in individual species flocks but using mixed-species flocks we had a large enough sample to analyze them as a separate guild. Each video was assigned a time of year, either before, during, or after hunting season, depending on the date of the survey and season dates for that conservation area.

While reviewing videos, we recorded the greatest disturbance behavior most exhibited by the waterfowl flock at the beginning of the video (i.e., if birds were alert but also swimming, their behavior was recorded as swimming). When the behavior most exhibited by the flock changed, the new behavior and time was recorded. We classified waterfowl flock behavior into one of seven behavioral categories as defined in Barr et al. (2020) and Ryckman et al. (2022): abandonment, flight, swim, alert, maintenance, courtship, aggression, resting, and feeding/foraging. These seven behaviors were then condensed to five disturbance response categories for analysis: none (maintenance, courtship, aggression, resting, and feeding/foraging), alert, swim, fly (flight), and abandonment, with the assumption that these behaviors represented a continuum of increasing disturbance response from none to abandonment.

Evaluating Waterfowl Response

To analyze waterfowl disturbance response to survey method, all waterfowl guilds, UAS altitudes, and times of year were analyzed together, and waterfowl flock was used as the sampling unit (McEvoy et al. 2016, Barr et al. 2020). We calculated the percentage of time a flock spent in each behavior before, during, and after a survey. Most of the flock frequently exhibited no behavior in one or all disturbance categories during behavioral observations, creating zero-inflated data. We fit zero-inflated Bayesian beta regression models using Markov Chain Monte Carlo (MCMC) approaches in R (R Core Team 2022) through package zoib (Liu and Kong 2015). We generated Bayesian posterior distributions of estimates for each waterfowl flock disturbance behavior to identify differences in percentages of time the flock spent in each behavior in response to survey period and aircraft type (before, during helicopter or UAS survey, and after) in a before-treatment-after design. The distribution of the percentages of time a flock spent in each behavior pre-survey was used as a moderately informative prior for the Bayesian analysis (McCarthy and Masters 2005, Choy et al. 2009). We also fit zero-inflated Bayesian beta regression models to evaluate differences in waterfowl flock response based on waterfowl guild, UAS survey height, and time of year. We ran all models on two chains for 150,000 iterations with a burn-in period of 50,000 iterations and a thinning interval of 10 (McGrath et al. 2018, Weston et al. 2020). MCMC chain plots were then visually inspected for model convergence and biological significance was determined using the 95% credible intervals derived from MCMC estimates of model coefficient beta estimates, where parameters with intervals not crossing zero were considered significantly different from pre-survey waterfowl behavior (McGrath et al. 2018, Weston et al. 2020). All models included wetland pool as a random effect, nested within area.

Results

Behavioral observations were collected for 12 helicopter flights with 48 paired UAS flights ($n = 12$ flights per UAS altitude) and 86 additional unpaired UAS flights. Across all 134 UAS surveys, we observed 11 species of waterfowl during behavior observations with sample sizes of 72 mallard surveys, 51 other duck surveys, and 11 goose surveys. While evaluating waterfowl responses to UAS surveys, we did not observe abandonment as a response during pre-survey, during, or post-survey and thus excluded abandonment from the analyses evaluating responses to UAS surveys.

Waterfowl Behavioral Response to Survey Method

Waterfowl exhibited behavioral responses to helicopter surveys, with differences detected in percentage of time spent in all disturbance behaviors (alert, swim, fly, and abandonment) between the pre-survey and survey periods (Figure 2). We also observed differences in the percentage of time waterfowl spent in alert and swimming behaviors during the pre-survey and post-survey periods for helicopter surveys (Figure 2). Compared to the pre-survey period, mean percent of time alert decreased during (5.6 ± 4.2% [SE]) and post (10.2 ± 5.9%) helicopter surveys, whereas mean percent of time swimming (44.7 ± 6.6%), flying (29.4 ± 6.5%), and abandonment (12.9 ± 7.5%) increased during the helicopter surveys (Table 1; Figure 2). Percentage of time the flock exhibited swimming behavior in response to helicopter surveys only differed between pre-survey and post-survey periods, with flocks spending a greater percent of time swimming during the post-survey period (38.1 ± 5.2%; Table 1; Figure 2). For UAS surveys, we observed no difference in the percentage of time ducks spent in any disturbance behaviors during pre-survey, survey, and post-survey periods, indicating that they were not disturbed by the UAS surveys (Figure 2).

Waterfowl Behavioral Response to UAS Surveys

Waterfowl did not exhibit a behavioral response to UAS surveys, with no differences in percentage of time spent in disturbance behaviors during the different survey periods. There were no differences in the behaviors of combined duck species (mallards plus other ducks) during any survey period at UAS survey altitudes of 15, 60, and 90 m, except percent of time spent in flight behavior increased (9.5 ± 1.5%) during surveys at 30 m compared to the percentage of time the flock spent in pre-survey flight behavior (Table 2; Figure 3). We found no difference in behaviors of any waterfowl guild (mallard, other duck, and geese) in the pre-survey, survey, or post-survey periods (Table 3; Figure 4). We also observed no difference in the waterfowl response to UAS surveys among time periods relative to hunting season (pre-hunting season, during hunting season, or after the close of hunting season; Table 4; Figure 5).

Table 1. Mean (± SE) proportion of time waterfowl spent in each disturbance-behavior category (alert, swim, fly, abandonment) for the pre-, survey, and post-survey periods for unoccupied aerial system (UAS) and helicopter surveys conducted October–February 2021–2022 at intensively managed wetland conservation areas in Missouri. All means with asterisks (*) have 95% beta coefficient credible intervals that do not overlap mean pre-survey behavior and therefore can be interpreted as biologically significant.

Disturbance Behavior	Pre-Survey		Helicopter Survey		Post Helicopter Survey		UAS Survey		Post UAS Survey	
Alert	0.12	±0.03	*0.06	±0.04	*0.10	±0.06	0.19	±0.05	0.17	±0.06
Swim	0.27	±0.03	*0.45	±0.07	*0.38	±0.05	0.28	±0.04	0.31	±0.04
Fly	0.08	±0.01	*0.30	±0.07	0.02	±0.01	0.03	±0.02	0.02	±0.02
Abandonment	not observed		*0.13	±0.08	0.01	±0.03	not observed		not observed	

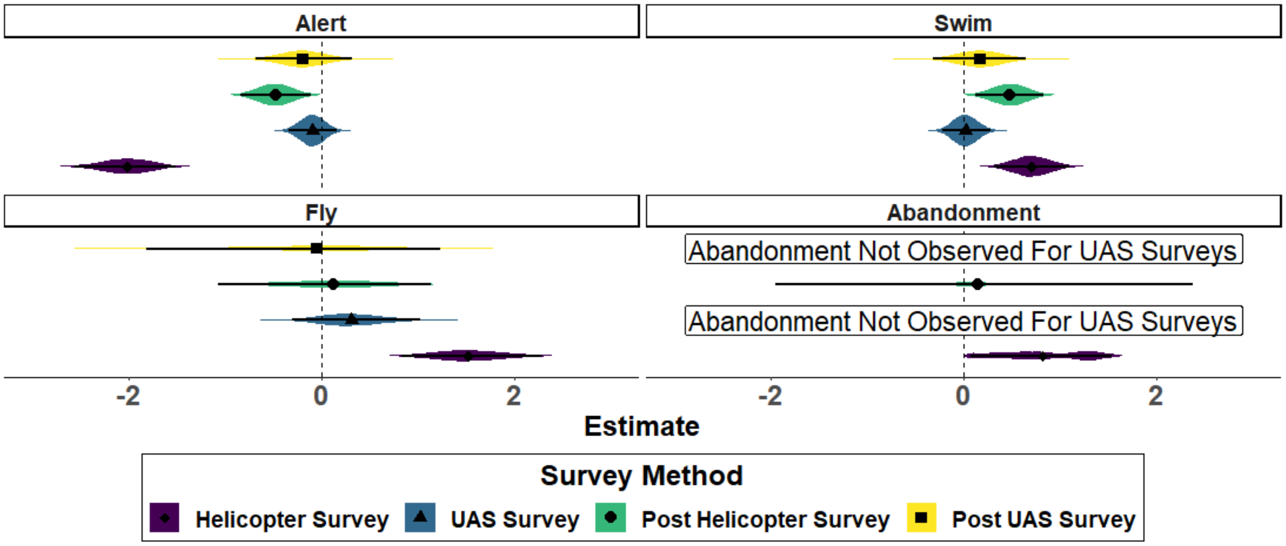

Figure 2. Beta coefficient estimates for percentage of time waterfowl flocks spent in disturbance behaviors (alert, swim, fly, and abandonment) in response to survey methodology (unoccupied aerial system [UAS] survey, post-UAS survey, helicopter survey, and post-helicopter survey). Data were collected from wetland conservation areas in Missouri, October–February 2021–2022, and analyzed using Bayesian generalized linear mixed models. The vertical dashed line ($x = 0$) represents percentage of time spent in behavior pre-survey with the 95% credible intervals represented for during- and post-survey estimates; 95% credible interval not crossing 0 was deemed significant.

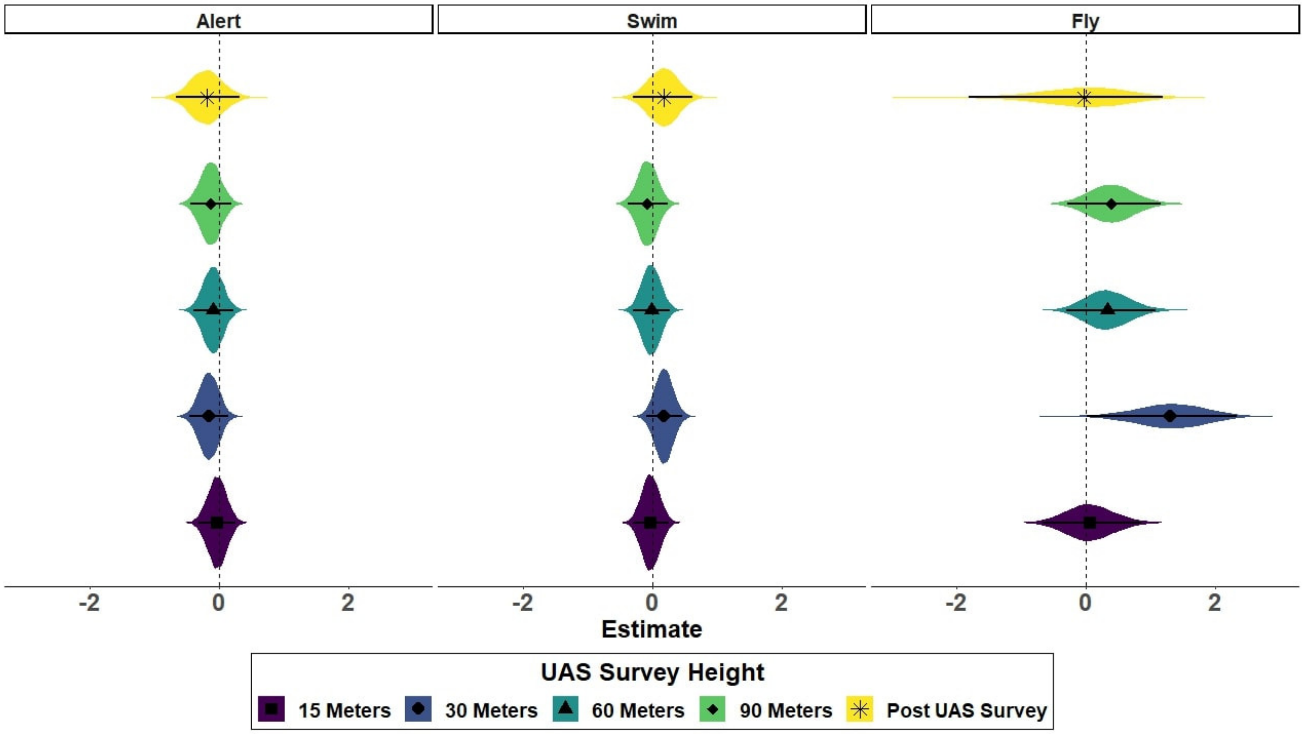

Figure 3. Beta coefficient estimates for the percentage of time waterfowl flocks spent in disturbance behaviors (alert, swim, and fly) in response to unoccupied aerial system (UAS) survey height (15, 30, 60, and 90 m). Data were collected from wetland conservation areas in Missouri, October–February 2021–2022, and analyzed using Bayesian generalized linear mixed models. The vertical dashed line ($x = 0$) represents percentage of time spent in behavior pre-survey with the 95% credible intervals represented for during- and post-survey percentages in behaviors; 95% credible interval not crossing 0 was deemed significant.

Table 2. Mean (± SE) proportion of time waterfowl spent in each disturbance-behavior category (alert, swim, fly) for the pre-survey, unoccupied aerial system (UAS) survey, and post-survey periods for different UAS survey heights conducted October–February 2021–2022 at intensively managed wetland conservation areas in Missouri. All means with asterisks (*) have 95% beta coefficient credible intervals that do not overlap mean pre-survey behavior and therefore can be interpreted as biologically significant.

Survey Method and Height	Alert		Swim		Fly	
Pre-survey	0.172	±0.029	0.265	±0.023	0.017	±0.010
UAS 15 m	0.101	±0.051	0.272	±0.040	0.028	±0.024
UAS 30 m	0.177	±0.041	0.313	±0.037	*0.095	±0.015
UAS 60 m	0.192	±0.037	0.273	±0.038	0.050	±0.020
UAS 90 m	0.179	±0.051	0.268	±0.047	0.053	±0.026
Post-survey	0.170	±0.055	0.309	±0.040	0.021	±0.017

Table 3. Mean (± SE) proportion of time spent in each disturbance-behavior category (alert, swim, fly) for the pre-survey, unoccupied aerial system (UAS) survey, and post-survey periods for different waterfowl guilds (geese, mallard, and other ducks) conducted October–February 2021–2022 at intensively managed wetland conservation areas in Missouri.

Disturbance Behavior	Survey Method	Geese		Mallard		Other Ducks	
Alert	Pre-survey	0.181	±0.019	0.190	±0.032	0.125	±0.023
	UAS survey	0.174	±0.061	0.182	±0.043	0.100	±0.049
	Post-survey	0.196	±0.027	0.125	±0.076	0.116	±0.025
Swim	Pre-survey	0.220	±0.019	0.291	±0.024	0.235	±0.020
	UAS survey	0.289	±0.051	0.290	±0.040	0.267	±0.042
	Post-survey	0.304	±0.027	0.338	±0.053	0.280	±0.027
Fly	Pre-survey	0.023	±0.018	0.020	±0.011	0.013	±0.010
	UAS survey	0.038	±0.024	0.028	±0.020	0.045	±0.027
	Post-survey	0.043	±0.021	0.038	±0.024	0.034	±0.023

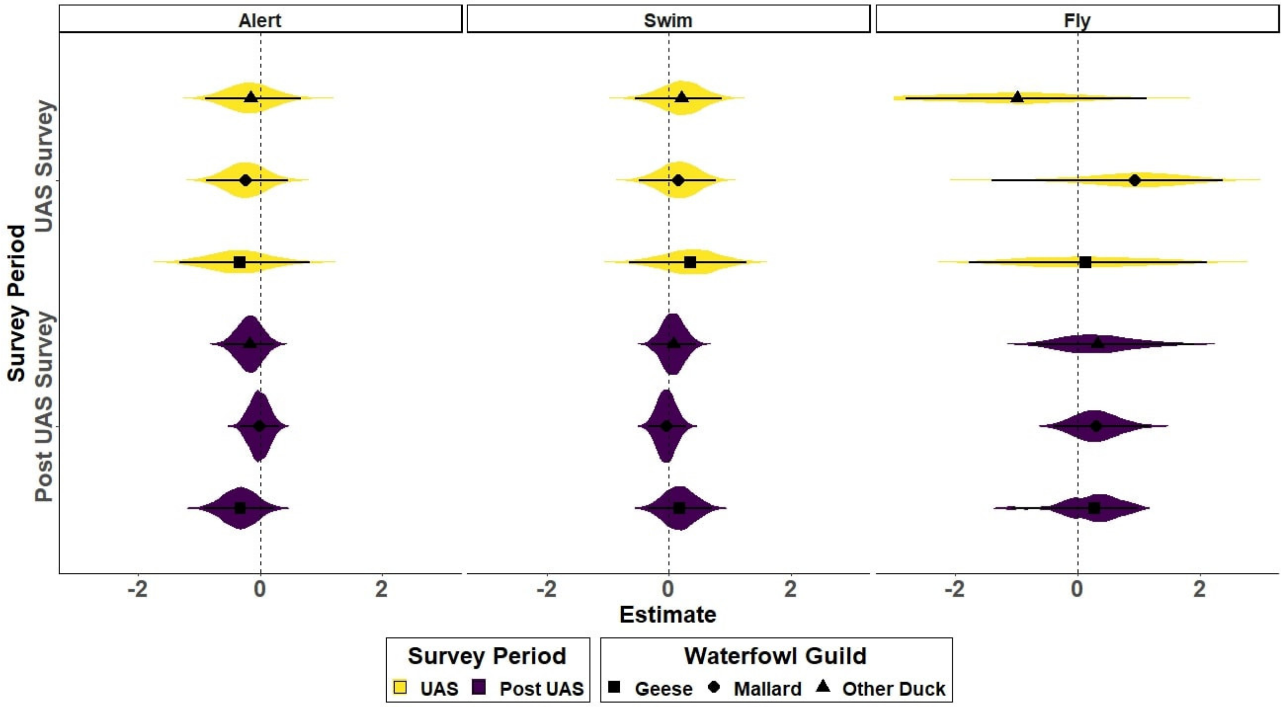

Figure 4. Beta coefficient estimates for the percentage of time waterfowl flocks spent in disturbance behaviors (alert, swim, and fly) in response to unoccupied aerial system (UAS) surveys dependent on waterfowl guild (geese, mallard, or other ducks). Data were collected from wetland conservation areas in Missouri, October–February 2021–2022, and analyzed using Bayesian generalized linear mixed models. The vertical dashed line ($x = 0$) represents percentage of time spent in behavior pre-survey with the 95% credible intervals represented for during- and post-survey percentages in behaviors; 95% credible interval not crossing 0 was deemed significant.

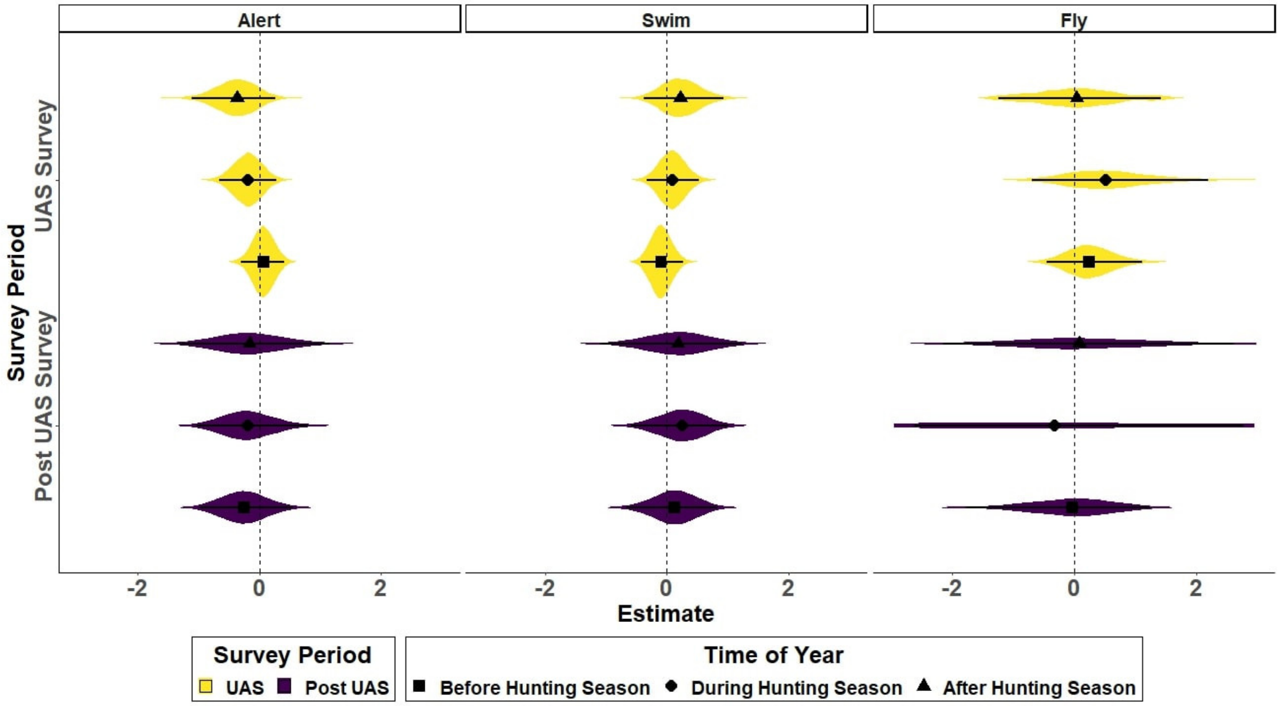

Figure 5. Beta coefficient estimates for the percentage of time waterfowl flocks spent in disturbance behaviors (alert, swim, and fly) in response to unoccupied aerial system (UAS) surveys dependent on time of year with hunting season (before, during, and after). Data were collected from wetland conservation areas in Missouri, October–February 2021–2022, and analyzed using Bayesian generalized linear mixed models. The vertical dashed line ($x = 0$) represents percentage of time spent in behavior pre-survey with the 95% credible intervals represented for during- and post-survey percentages in behaviors; 95% credible interval not crossing 0 was deemed significant.

Table 4. Mean (± SE) proportion of time waterfowl spent in each disturbance-behavior category (alert, swim, fly) for the pre-survey, unoccupied aerial system (UAS) survey, and post-survey periods for different hunting season periods (before, during, and after) conducted October–February 2021–2022 at intensively managed wetland conservation areas in Missouri.

Disturbance Behavior	Survey Method	Before Hunting Season		During Hunting Season		After Hunting Season	
Alert	Pre-survey	0.184	±0.032	0.142	±0.025	0.164	±0.024
	UAS survey	0.194	±0.044	0.188	±0.049	0.170	±0.048
	Post-survey	0.110	±0.091	0.196	±0.027	0.123	±0.032
Swim	Pre-survey	0.289	±0.024	0.248	±0.022	0.236	±0.024
	UAS survey	0.278	±0.041	0.282	±0.040	0.295	±0.042
	Post-survey	0.334	±0.065	0.304	±0.027	0.278	±0.032
Fly	Pre-survey	0.027	±0.013	0.011	±0.009	0.041	±0.024
	UAS survey	0.036	±0.024	0.030	±0.022	0.035	±0.024
	Post-survey	0.056	±0.026	0.042	±0.027	0.052	±0.034

Discussion

Numerous studies on occupied and unoccupied aircraft disturbance reported a range of factors can influence waterfowl, including aircraft type, speed, altitude, vegetation characteristics, refuge status, and individual breeding status (Goudie 2006, Brisson-Curadeau et al. 2017, Mulero-Pázmány et al. 2017). Avifauna during the breeding season are more easily disturbed by rotorcraft-type aircraft at lower altitudes over areas with less dense vegetation, however, it is unclear whether and to what extent results of these studies apply to avifauna responses during the non-breeding season (Goudie 2006, Mulero-Pázmány et al. 2017, de Leija et al. 2023). One study found that non-breeding waterfowl exhibit similar responses as breeding waterfowl, but non-breeding waterfowl were less responsive to rotor-type aircraft than fixed-wing aircraft (McEvoy et al. 2016). Although numerous studies have demonstrated crewed aircraft surveys disturb waterfowl during all times of the year, our results indicate nonbreeding waterfowl behavioral response to UAS are minimal and that UAS surveys result in substantially less disturbance to waterfowl than those conducted by helicopter. Anecdotally, the response of the waterfowl during the helicopter surveys was abrupt and drastic, particularly for geese, with most waterfowl responding before or right as the helicopter entered human aural range and before it was visually accessible (typically approaching from behind trees). Geese would commonly abandon wetland pools before the helicopter was in visual line-of-sight, suggesting that the helicopter produced sufficient noise to be perceived as a threat even prior to visual detection by birds. Those birds that had not abandoned the wetland prior to the helicopter's arrival would often abandon or fly once the helicopter entered visual range, suggesting that they were responding to combination of auditory and visual cues.

Unoccupied aerial systems that mimic raptors may cause more disturbance to small avifauna, such as waterfowl, compared to UAS which do not resemble raptors or appear to exhibit raptor-like behaviors (McEvoy et al. 2016, Mulero-Pázmány et al. 2017). Although the UAS used in our study and the flight patterns did not resemble raptors, we did observe a slight increase in the frequency of waterfowl flight behaviors during UAS surveys conducted at 30 m AGL. Previous studies found birds engage in alert behaviors in response to raptor overflights and UASs, however, the time spent in these behaviors is usually a small percentage of time and biologically insignificant even if time spent in alert behaviors increases (Barnas et al. 2018, Ryckman et al. 2022). Compared to other studies, we found that waterfowl spent a greater percentage of time in alert behaviors during the pre-survey period (10–18% in our study vs. < 1–6%; Barnas et al. 2018, Ryckman et al. 2022). This alert behavior may be due to the numerous (50–250) bald eagles (*Haliaeetus leucocephalus*) present at our study sites, which may have affected the behavior of waterfowl. This may also explain the increase in flight behavior in waterfowl at survey altitudes of 30 m, as eagles may hunt waterfowl at this height, and objects flying at this altitude may cause waterfowl to flee due to a perceived predation threat (Dekker 1984, Folk 1992).

Previous research found differences in behavioral response to UAS among avifauna species, hypothesizing that differences in behavioral response was due to different life history traits and strategies, with greater responses observed in species that were hunted or heavily targeted compared to those that were not hunted (McGrath et al. 2018, de Leija et al. 2023). We found no difference in the behavioral response among waterfowl guilds to UAS surveys in our study, potentially because waterfowl species tend to show more similar life history traits and strategies during the non-breeding season, aggregating in the large mixed-species flocks that we observed (Anderson and Batt 1983, Ackerman et al. 2006). Most surprisingly, we found no behavioral response among geese to our UAS surveys while previous studies found that geese were most responsive to disturbance, particularly during aerial surveys, including UAS surveys (Barnas et al. 2018, Gilbert et al. 2020). Most studies evaluating waterfowl species-specific behavioral response to UAS primarily occurred during the breeding season, whereas our study occurred during the non-breeding season, and we saw an overall lower behavioral response to UAS surveys than in the previous UAS breeding studies (Brisson-Curadeau et al. 2017, Barr et al. 2020, Ryckman et al. 2022). Avifauna have been shown to exhibit different responses to predators and disturbance during different life-history stages, with more response exhibited during the breeding season, possibly to protect eggs or teach young escape techniques, and this may explain why geese were less responsive during our study (Piratelli et al. 2015, Mikula et al. 2018). Additionally, we may have found differences in response to UAS surveys in our study compared to those on the breeding grounds due to many mixed-species flocks comprised of over 50,000 birds. Previous work on the non-breeding grounds found that larger flock sizes typically reduced responses to UAS flights (McEvoy et al. 2016, Brisson-Curadeau et al. 2017, Gilbert et al. 2020, Weston et al. 2020, de Leija et al. 2023).

The presence of refuge has been shown to decrease avifauna response to UAS or other aerial survey methods, and while most previous studies have focused on breeding avifauna, limited studies have shown that the same disturbance patterns occur in avifauna during the non-breeding season (Mulero-Pázmány et al. 2017, McGrath et al. 2018, Gilbert et al. 2020). We hypothesized that waterfowl disturbance would be greater on refuges during the non-hunting season than during the hunting season due to the perceived higher risk of mortality from birds leaving the refuge than tolerating the UAS. However, our results showed that there were no behavioral differences in response to UAS before, during, or after the hunting season. This finding suggests that waterfowl did not perceive the UAS as a substantial threat and that the energetic costs of avoiding or moving away from the UAS may have exceeded the risk imposed by the UAS. The perceived risk of the UAS by waterfowl may have also been reduced due knowledge of the refuge areas from previous years and perceived hunting pressure (regardless of the opening or closing of seasons) on the surrounding areas (Hagy et al. 2017, McGrath et al. 2018, Gilbert et al. 2020). We consider it unlikely that the reduction in disturbance was due to habituation of disturbance from UAS or other anthropogenic sources, as the refuges in our study were closed to all anthropogenic use and waterfowl response did not decrease throughout the year as additional UAS flights were conducted.

Management Implications

Our study was designed to increase the understanding of the feasibility of using UAS as a tool for monitoring non-breeding waterfowl abundance and the impacts of UAS surveys on waterfowl disturbance behavior. By comparing the percentage of time spent in seven behavioral categories prior to, during, and post-survey, we determined that there was no change in behavior during or post-survey period with UAS surveys, indicating UAS are unlikely to result in disturbance responses that could lead to an inherent bias in abundance survey estimates (Ryckman et al. 2022, de Leija et al. 2023). Although most birds in the flock did not respond negatively to the UAS during our observations, we only recorded the behavior exhibited by most of the flock. While the flock as a majority did not respond to the UAS surveys, some individuals may have responded negatively to the UAS. However, we did not observe instances in which the behaviors of a few birds were drastically different than most of the flock. Our results suggest that the appropriate combination of aerial platform and survey altitude may allow for use of UAS to monitor non-breeding waterfowl abundance with minimal disturbance. Additional work across other UAS platforms and target fauna for planned surveys would allow evaluation of the level of disturbance or impacts that may be expected prior to launching full implementation of surveys.

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Impact of Invasive Wild Pig on White-Tailed Deer and Eastern Wild Turkeys in Southwest Georgia

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Abstract: Wild pigs (*Sus scrofa*) are a highly destructive invasive species and reported to be present in 77% of counties in the southeastern U.S. Wild pigs may negatively affect white-tailed deer (*Odocoileus virginianus*; hereinafter, deer) and eastern wild turkeys (*Meleagris gallopavo silvestris*; hereinafter, turkey) via competition over forage or exclusion from preferred areas. To explore effects of wild pigs on spatial distribution of these species within a mixed agriculture-forest landscape, we developed models predicting camera trap detections of deer and turkeys as a function of landcover, calendar season, and wild pig presence. We deployed 147 passive camera traps and collected data for one month during each calendar season during 2020 to 2022 in southwestern Georgia (32,760 camera nights). We observed a negative association between turkeys and wild pigs during summer and within mixed forests, and a negative association between deer and wild pigs in pecan (*Carya illinoinensis*) orchards during summer, fall and winter. However, there was a positive association between deer and wild pigs in forested wetlands and mixed forests during fall and winter. The negative relationships between turkeys and wild pigs or deer and wild pigs may be from adverse interactions or simply species-specific landcover preferences. Similarly, the positive correlations with deer are likely the result of common landcover preferences, as it seems highly unlikely that deer benefit from wild pigs. Our results highlight how the relationship between invasive species and native species may be confounded by differences in land cover preferences and suggest further, manipulative experiments, may be necessary to better assess the effects of wild pigs on native wildlife.

Keywords: camera traps, habitat selection, invasive species, *Meleagris gallopavo, Odocoileus virginianus, Sus scrofa*

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Introduced (i.e., non-native) species can compete aggressively with native species, prey on native species, and alter natural disturbance regimes resulting in altered community composition and, in some cases, native species extinction (Mack and D'Antonio 1998, Wilcove et al. 1998, Gurevitch and Padilla 2004, Kass et al. 2020). Characteristics of successful invasive species that allow them to compete with native species include high fertility and fecundity, generalist and opportunistic diets, early reproductive maturity, and the ability to quickly exploit vacant niches via range expansion and competitive behavior (Wilcove et al. 1998, Sakai et al. 2001). Native species often avoid invasive species and exhibit behavioral changes more frequently than the invasive species (Ruland and Jeschke 2020).

Wild pigs (*Sus scrofa;* also known as wild boar, feral swine, wild hog, feral hog, and feral pig; hereinafter referred to as wild pig; Keiter et al. 2016) are globally invasive and particularly damaging outside of their native range. Invasive wild pigs are linked with the extinction of 14 species and are considered a threat to 672 endangered or critically endangered species worldwide (345 flora and 327 fauna; Risch et al. 2021). An estimated 6.9 million wild pigs are now found in 31 states in the U.S., with the greatest concentrations in the southeastern U.S. where wild pigs occupy approximately 77% of counties in Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, Missouri, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, Virginia, and West Virginia (Lewis et al. 2019, USDA APHIS 2020, USDA APHIS 2022). While there is extensive literature available on wild pig economic costs (Pimentel 2007, Mengak 2016, Anderson et al. 2019, McKee et al. 2020), diet (Yarrow 1987, Taylor and Hellgren 1997, Elston and Hewitt 2010, Ballari and Barrios-Garcia 2014), and population expansion (Wood and Barrett 1979, Graves 1984, McClure et al. 2018, Lewis et al. 2019), there is less empirical evidence of their effects on native species, especially economically valuable game species (McDonough et al. 2022, Walters and Osborne 2022).

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Existing research of effects of wild pigs on native species is largely observational (McDonough et al. 2022). Studies of wild pig interactions with native wildlife has focused on potential competition by quantifying dietary overlap (Yarrow 1987, Taylor and Hellgren 1997, Elston and Hewitt 2010) or nest depredation by wild pigs (Tolleson et al. 1993, Sanders et al. 2020). However, there is recent research on effects of wild pigs on the spatial distribution of white-tailed deer (*Odocoileus virginianus*) and eastern wild turkey (*Meleagris gallapovo*; Keever 2014, O'Brien et al. 2019, Lewis 2020, Garabedian et al. 2022, Walters and Osborne 2022, Dykstra et al. 2023, McDonough 2023), and these studies have generally found negative or neutral associations. White-tailed deer and eastern wild turkey (hereinafter deer and turkey, respectively) are the most popular game animals in the U.S., pursued by 8.1 and 2.0 million hunters, respectively (USFWS and USCB 2018), and deer hunting is the most important source of funds for state wildlife agencies in the Southeast (Duda et al. 2022). Although evidence suggests wild pigs may compete with and prey upon turkey and deer, there is little evidence of population-level effects of wild pigs on these species. However, given the importance of deer and turkeys, it is imperative to understand how wild pigs may affect these game species.

In this study, we explored effects of wild pig relative abundance on detection rates of deer and turkey across a mixed agricultural-forest landscape in southwestern Georgia. To examine potential effects, we collected passive camera trapping data for one month during each calendar season from 2020 to 2022. We predicted that the relative abundance of wild pigs, accounting for the interaction of season and landcover types, would have a negative effect on both deer and turkey detection rates.

Methods

Study Area

Our study occurred on private property in Calhoun County, Georgia (Figure 1) with an historically abundant wild pig population. The 92.44-km^2 study area consisted of row crops (39%), wetlands (32%), pine forests comprised of longleaf (*Pinus palustris*) and loblolly pine (*P. taeda*; 13%), pecan (*Carya illinoinensis*) orchards (10%), and mixed hardwood-pine interspersed with live oak (*Quercus virginiana*; 3%), with the remaining 3% consisting of wildlife food plots and narrow riparian areas. Row crops were planted in late spring and harvested in late summer or early fall, with crops consisting of corn (*Zea mays*), cotton (*Gossypium* spp.), and peanuts (*Arachis hypogaea*). Daily temperatures average 34 C and 17 C in summer and winter months, respectively (U.S. Climate Data 2020). Monthly precipitation averages 150.6 mm in summer and 100.8 mm in winter (U.S. Climate Data 2020).

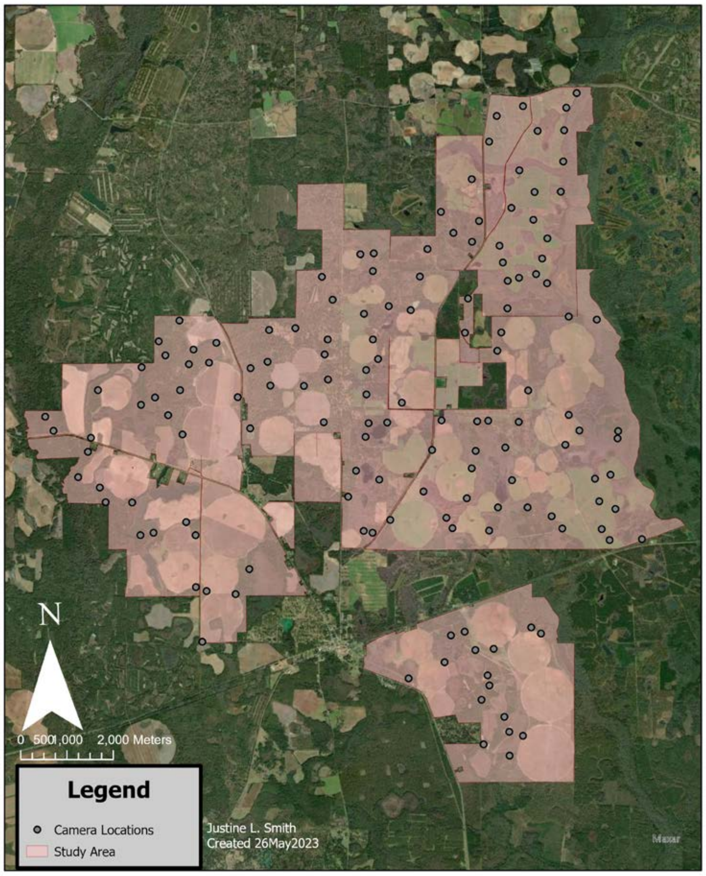

Figure 1. Study area in Calhoun County, Georgia with gray circles indicate camera locations ($n = 147$) used for assessing game species response to wild pig presence.

Data Collection

We used Browning Strike Force HD Pro X (Browning Trail Cameras, Morgan, Utah) trail cameras for passive camera trapping surveys. We used ArcGIS 10.8.1 (ESRI 2020) to determine locations by overlaying 40-ha grid cells over the study area. We placed one camera trap within each cell approximately 1.5 m away from a wildlife trail and 1.0 m above the ground. We used the 2019 National Land Cover Data (NLCD, 30-m resolution; Dewitz and U.S. Geological Survey 2021) to determine landcover at each camera trap location. We excluded cells that fell entirely within row crops to avoid camera damage associated with farming activity. Overall, we deployed 60 cameras in evergreen forests, 49 cameras in forested wetlands, 23 cameras in pecan orchards, and 15 cameras in mixed forests. Of the cover types included in sampling (i.e., excluding row crops), evergreen forests, pecan orchards, and mixed forests were over-sampled relative to their availability. Forested wetlands were under-sampled relative to their availability due to accessibility, as we avoided placing cameras in areas that were prone to flooding. When able, we placed cameras in forested wetlands above the flood line.

We programmed cameras to capture one image upon motion trigger with a 30 sec delay between photos. We conducted camera surveys for one month each calendar season for two years, using months with solstices or equinoxes (i.e., March = spring, June = summer, September = fall, December = winter). We sampled two seasons in 2020 (fall and winter), all four seasons in 2021, and two seasons in 2022 (spring and summer) for a total of eight seasons.

We partitioned detections for each species (deer, turkey, and wild pig) within each season quantified as detections camera^{-1} day^{-1}. We avoided double counting individuals by withholding detections occurring within 15 min of a prior detection at a given camera when group size remained the same or decreased. However, if the group size of a detection event increased relative to the detection event immediately preceding, and within the 15-min window, we retained the detections of the larger group size.

Statistical Analysis

We estimated deer, turkey, and wild pig detections camera^{-1} day^{-1} from spatiotemporal predictors using a zero-inflated Poisson regression (ZIPR) model and the pscl package (Zeileis et al. 2008) in R (R Core Team 2021). We used a ZIPR model because deer, turkey, and wild pig detections camera^{-1} day^{-1} primarily consisted of zeroes (66.4%, 98.2%, and 93.3% respectively). We included landcover data (evergreen forests, mixed forests, pecan orchards, forested wetlands) and season (spring, summer, fall, winter) as predictor variables. For each species, we developed a null model, models for each predictor, and a global model including the two-way interaction of predictors. We calculated the Akaike Information Criteria (AIC) and delta AIC (ΔAIC) using the 'AICmodavg' package (Mazerolle 2023) in R and identified the most parsimonious spatiotemporal model using an information-theoretic approach. We considered models within 2 ΔAIC as competing models and used model averaging for parameter estimates if presented with competing models (Burnham and Anderson 2002). We identified the most parsimonious spatiotemporal model to understand how each species (deer, turkey, and wild pigs) used different landcover types throughout calendar seasons. Upon identifying the most parsimonious spatiotemporal model for deer and turkeys, we included the original wild pig detections camera^{-1} day^{-1} as a main effect and associated interactions as predictor variables to determine if adding wild pig detection rates improved model predictions using an information-theoretic approach (i.e., reduced AIC score). We considered any predictors informative when their 95% confidence intervals did not overlap zero.

Results

We monitored 147 camera traps across eight seasons for 32,760 camera days. We detected deer at all camera locations ($n = 147$), wild pigs at 86% ($n = 126$), and turkey at 63% of locations ($n = 93$). We detected deer most (1.07 deer detections camera^{-1} day^{-1}) during winter 2020 and least (0.48 deer detections camera^{-1} day^{-1}) during spring 2021. Wild pigs were detected most (0.20 wild pig detections camera^{-1} day^{-1}) during fall 2021 and least (0.07 wild pig detections camera^{-1} day^{-1}) during spring 2022. Turkey detection rates were greatest during spring 2021 (0.06 turkey detections camera^{-1} day^{-1}) and least during summer 2021 (0.03 turkey detections camera^{-1} day^{-1}).

For wild pigs, turkeys, and deer, our global spatiotemporal model received the most support. There were no competing models (i.e., second-best models had ΔAIC = 282.84, 137.99, and 266.48 for wild pigs, turkey, and deer, respectively). The pig model suggested that their detection rates increased in pecan orchards during fall and winter and forested wetlands during winter but declined in mixed forests during summer (Table 1).

Including wild pig detections camera^{-1} day^{-1} and associated interactions reduced AIC for the turkey model by 25.22 and the deer model by 126.99, markedly improving both deer and turkey models. Models that only considered wild pig detections camera^{-1} day^{-1} as an additive predictor (i.e., no predictors interacting with wild pig detections) were not competitive with models including

Table 1. Combinations of predictor variables used in the count component of the zero-inflated Poisson regression to predict wild pig detections camera^{-1} day^{-1}. All coefficients are relative to a model using Evergreen Forests and March as the referent condition and estimated using data collected from 147 camera surveys deployed in Calhoun County, Georgia from 2020–2022. Asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Coefficients	β	SE	P
Reference Condition	0.639	0.070	<0.01***
Summer	–0.067	0.098	0.50
Fall	–0.026	0.088	0.77
Winter	–0.258	0.095	<0.01**
Forested Wetlands	–0.081	0.097	0.41
Mixed Forests	–0.240	0.128	0.06
Pecan Orchards	–0.637	0.260	0.01*
Summer × Forested Wetlands	–0.001	0.138	0.99
Fall × Forested Wetlands	–0.179	0.121	0.14
Winter × Forested Wetlands	0.527	0.124	<0.01***
Summer × Mixed Forests	–0.486	0.241	0.04*
Fall × Mixed Forests	–0.198	0.160	0.21
Winter × Mixed Forests	0.211	0.166	0.20
Summer × Pecan Orchards	0.310	0.323	0.33
Fall × Pecan Orchards	0.753	0.283	0.01**
Winter × Pecan Orchards	0.837	0.305	0.01**

interactions $\Delta \mathrm{AIC} = 113.84$ for the deer model and 6.73 for the turkey model. The three-way interaction in the deer model was informative (Table 2). In the presence of wild pigs, deer detection rates declined in pecan orchards during summer, fall, and winter but increased in forested wetlands and mixed forests during fall and winter (Figure 2). The three-way interaction associated with the turkey model was not estimable. Therefore, we only included two-way interactions in our modeling efforts for turkeys (Table 3). Relative to the reference condition, turkey detection rates declined in forested wetlands during summer, mixed forests during fall and winter, and pecan orchards during winter and increased in pecan orchards during summer (Table 3). Turkey detections showed a significant negative association with wild pigs during summer (Figure 3A) and in mixed forests (Figure 3B).

Table 2. Combinations of predictor variables used in the count component of the zero-inflated Poisson regression to predict white-tailed deer detections camera^{-1} day^{-1}. All coefficients are relative to a model using Evergreen Forests and March as the referent condition and estimated using data collected from 147 camera surveys deployed in Calhoun County, Georgia from 2020–2022. Asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Coefficients	*β*	SE	*P*
Reference Condition	0.603	0.026	<0.01***
Pig	0.117	0.024	<0.01***
Summer	−0.296	0.040	<0.01***
Fall	0.077	0.036	0.03*
Winter	−0.089	0.036	0.01*
Forested Wetlands	−0.100	0.043	0.03*
Mixed Forests	0.142	0.057	0.01*
Pecan Orchards	0.052	0.049	0.29
Pig × Summer	−0.023	0.044	0.60
Pig × Fall	−0.020	0.055	<0.01***
Pig × Winter	−0.019	0.047	<0.01***
Pig × Forested Wetlands	−0.138	0.072	0.05*
Pig × Mixed Forests	−0.609	0.213	<0.01***
Pig × Pecan Orchards	0.591	0.182	<0.01**
Summer × Forested Wetlands	0.090	0.063	0.16
Fall × Forested Wetlands	−0.899	0.059	0.13
Winter × Forested Wetlands	0.020	0.057	0.72
Summer × Mixed Forests	0.048	0.083	0.56
Fall × Mixed Forests	−0.185	0.080	0.02*
Winter × Mixed Forests	−0.252	0.080	<0.01**
Summer × Pecan Orchards	−0.293	0.090	<0.01**
Fall × Pecan Orchards	−0.110	0.072	0.13
Winter × Pecan Orchards	−0.025	0.065	0.70
Pig × Summer × Forested Wetlands	−0.083	0.103	0.42
Pig × Fall × Forested Wetlands	0.220	0.096	0.02*
Pig × Winter × Forested Wetlands	0.226	0.083	<0.01**
Pig × Summer × Mixed Forests	−0.881	0.731	0.23
Pig × Fall × Mixed Forests	0.863	0.220	<0.01***
Pig × Winter × Mixed Forests	0.528	0.236	0.03*
Pig × Summer × Pecan Orchards	−1.602	0.489	<0.01**
Pig × Fall × Pecan Orchards	−0.553	0.193	<0.01**
Pig × Winter × Pecan Orchards	−0.535	0.190	<0.01**

Table 3. Combinations of predictor variables used in the count component of the zero-inflated Poisson regression to predict eastern wild turkey detections camera^{-1} day^{-1}. All coefficients are relative to a model using Evergreen Forests and March as the referent condition and estimated using data collected from 147 camera surveys deployed in Calhoun County, Georgia from 2020–2022. Asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Coefficients	*β*	SE	*P*
Reference Condition	0.488	0.091	<0.01***
Pig	−0.169	0.163	0.30
Summer	−0.046	0.166	0.78
Fall	0.404	0.155	0.01*
Winter	1.435	0.120	<0.01***
Forested Wetlands	0.204	0.125	0.10
Mixed Forests	0.453	0.186	0.01*
Pecan Orchards	−0.169	0.221	0.44
Pig × Summer	−0.967	0.327	<0.01**
Pig × Fall	0.085	0.154	0.58
Pig × Winter	−0.160	0.099	0.10
Pig × Forested Wetlands	0.221	0.135	0.10
Pig × Mixed Forests	−0.897	0.360	0.01*
Pig × Pecan Orchards	0.192	0.138	0.16
Summer × Forested Wetlands	−0.579	0.260	0.03*
Fall × Forested Wetlands	−0.185	0.206	0.37
Winter × Forested Wetlands	0.062	0.160	0.70
Summer × Mixed Forests	−1.001	0.452	0.03*
Fall × Mixed Forests	−1.751	0.606	<0.01**
Winter × Mixed Forests	−1.010	0.396	0.01*
Summer × Pecan Orchards	0.748	0.283	0.01*
Fall × Pecan Orchards	0.224	0.269	0.41
Winter × Pecan Orchards	−0.624	0.274	0.02*

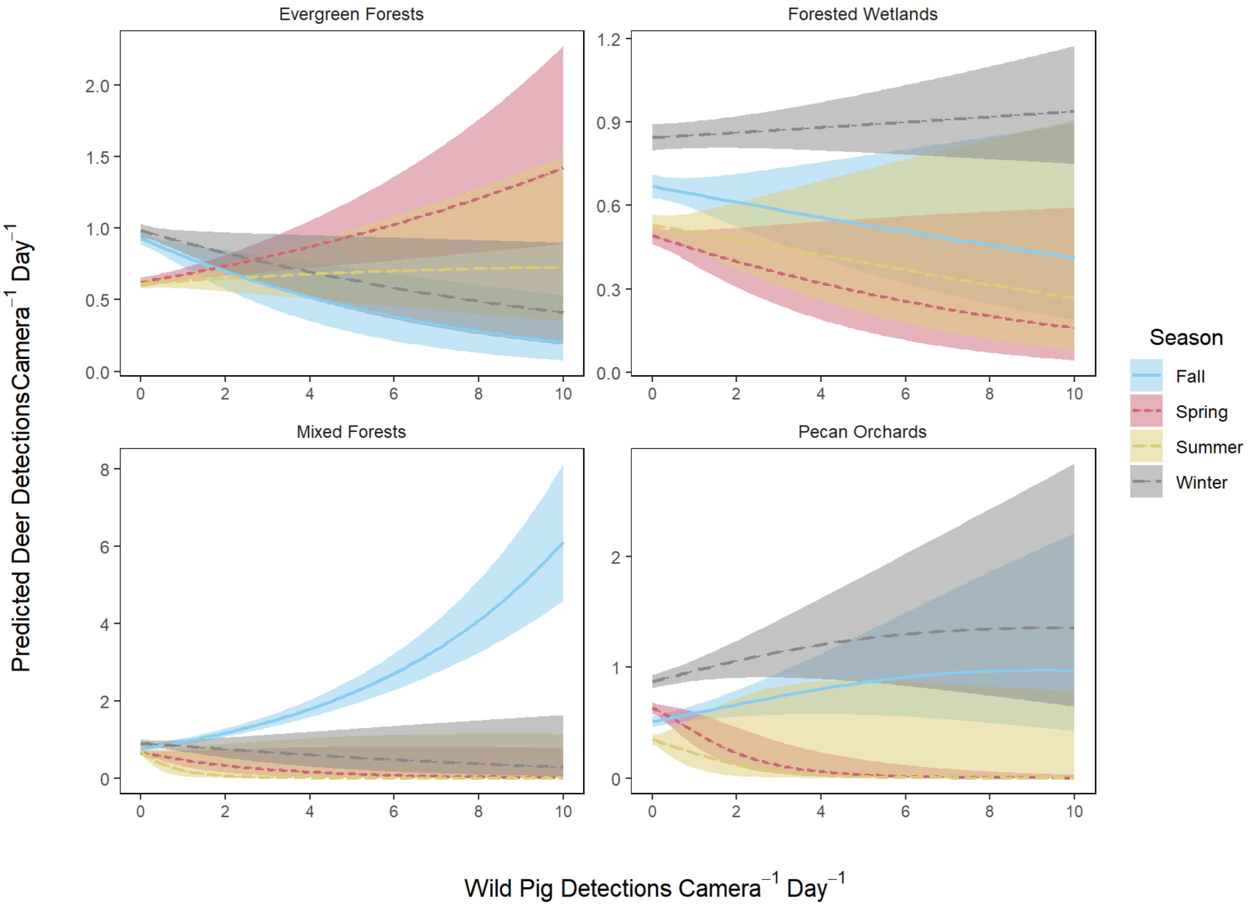

Figure 2. Predicted deer detections camera^{-1} day^{-1} across landcover types (evergreen forests, forested wetlands, mixed forests, and pecan orchards) during spring (pink), summer (yellow), fall (blue), and winter (gray) as wild pig detections camera^{-1} day^{-1} increases from a zero-inflated Poisson regression (ZIPR) model. Color lines indicate the predicted relationship paired with 95% confidence intervals (shaded ribbon).

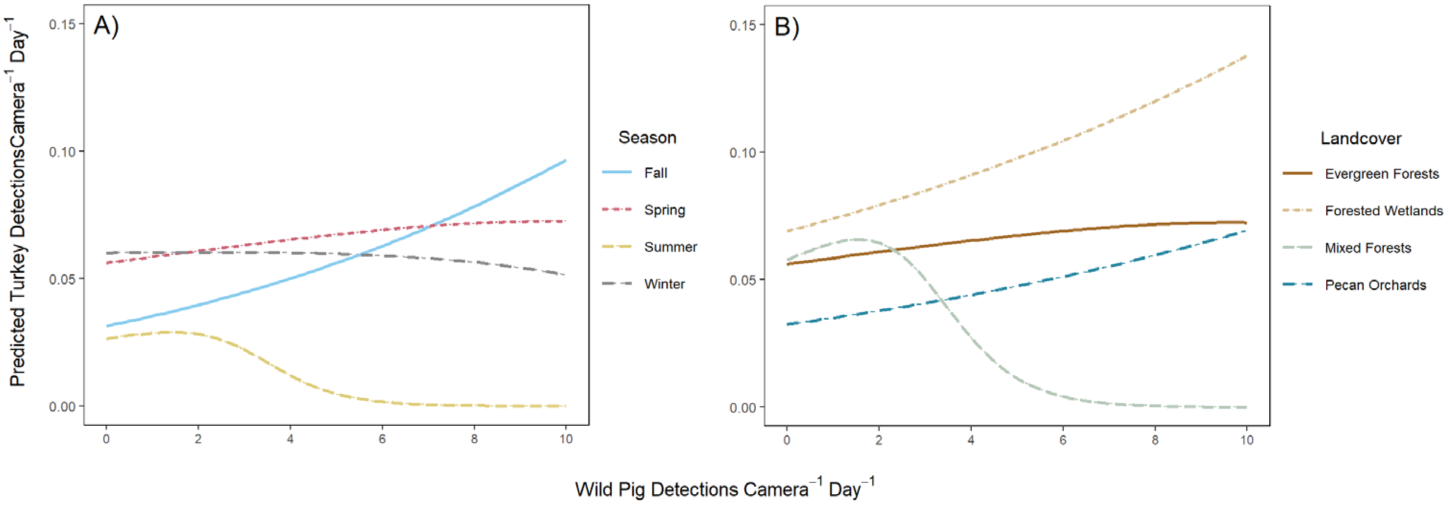

Figure 3. A) Predicted wild turkey detections camera^{-1} day^{-1} during spring (pink), summer (yellow), fall (blue), and winter (gray) as wild pig detections camera^{-1} day^{-1} increases from a zero-inflated Poisson regression (ZIPR) model. B) Predicted wild turkey detections camera^{-1} day^{-1} in evergreen forests (brown), forested wetlands (yellow), mixed forests (gray), and pecan orchards (blue) as wild pig detections camera^{-1} day^{-1} increases from a ZIPR model.

Discussion

Wild pigs are highly adaptable and thrive in heterogeneous landscapes (Morelle and Lejeune 2015, Lewis et al. 2017, Boyce et al. 2020). Previous studies have evaluated spatiotemporal associations between wild pigs and deer and/or turkey, so we interpret our findings in light of past empirical evidence. We did not anticipate a positive association between deer and wild pigs, as this does not align with previous research (Keever 2014, O'Brien et al. 2019, Lewis 2020, Garabedian et al. 2022, Dykstra et al. 2023, McDonough 2023). However, like earlier work (Lewis 2020, McDonough 2023), we found a negative association between wild pigs and turkeys.

Contrary to our prediction, we found a positive association between wild pig and deer detection rates. Nonetheless, there are studies indicating no association (Garabedian et al. 2022, Dykstra et al. 2023) or a negative association (Keever 2014, O'Brien et al. 2019, Lewis 2020, McDonough 2023) between wild pigs and deer. Deer and wild pig preference for forested areas is greater in fall and winter months associated with acorn production (Yarrow 1987, Taylor and Hellgren 1997, Elston and Hewitt 2010, Rose et al. 2011, Touzot et al. 2018) and is reflected in our modeling results. Because we cannot envision a scenario for increased wild pig detection rates causing increased deer detection rates, we suggest species-specific habitat preferences are responsible for the observed positive association.

Based on anecdotal observations, pigs exhibit aggressive behavior toward deer at baited sites (Tolleson et al. 1995, McDonough 2023) and we suspect a similar relationship may occur between pigs and deer in pecan orchards. Wild pig aggression is primarily exhibited in the presence of food (Vargas et al. 1987). We used passive camera trapping (i.e., without bait) and observed no aggressive encounters between wild pigs and deer as we did not observe either species within the same photo. Other research using passive camera trapping did not report aggressive behaviors of pigs toward deer (O'Brien et al. 2019, Dykstra et al. 2023), suggesting that baited camera surveys may trigger competition for pulse resources (Ozoga 1972, Vargas et al. 1987, Pimm et al. 1985, Theimer et al. 2015, Payne et al. 2017, Johnson et al. 2021). Pecans can be considered a pulse resource as harvesting occurs in the fall (Wells and Conner 2009) and pecans are consumed by some wildlife due to pecan's high fat and protein content (Shimada and Saitoh 2006, Atanasov et al. 2018). We propose aggressive behavior by wild pigs toward deer is a foraging-specific behavior, as there are no reports of active aggression at camera locations without bait (O'Brien et al. 2019, Dykstra et al. 2023). We suggest that passive camera trapping studies that record wild pig foraging behavior may provide additional information regarding the importance of available forage in mediating wild pig aggression toward other animals.

Predicted turkey detection rates declined when more than two wild pigs were detected per camera per day and approached zero when wild pig detections exceeded 6 detections camera^{-1} day^{-1} in mixed forests (Figure 3B). In contrast to our observations of negative associations between turkeys and pigs in mixed forest, Walters and Osborne (2022) found that turkeys were more likely to occupy camera sites where wild pigs were detected (59.4% occupancy when compared to 45.5% occupancy at sites with no wild pig detections). We suggest the negative association between wild pigs and turkeys within mixed forests is due to wild pigs temporarily displacing turkey from these areas (Taylor and Hellgren 1997, Elston and Hewitt 2010) and turkeys return to these locations when wild pigs are not present.

In southwest Georgia, turkey nesting typically begins mid-April with poults hatching after a 28-day incubation period (Little et al. 2014). Our first captured image of an adult female turkey with poults was recorded on 6 June 2021. Poult survival (i.e., nesting survival) strongly influences population reproductive success as poult mortality rate averages 48% with mammalian predators as the primary cause of mortality (Hubbard et al. 1999). Turkey populations respond behaviorally to predation risk (Wright 1914, Wynveen et al. 2005, Hughes and Lee 2015) and likely avoid areas with wild pigs to reduce exposing poults to potential predation, especially during nesting and when poults are young (Healy 1992, Bakner et al. 2022) as wild pigs are known nest predators (Tolleson et al. 1993, Sanders et al. 2020). Thus, we suggest the negative association between wild pig relative abundance and turkey detections during summer may be a mechanism to increase poult survival, but we cannot rule out differential species-specific habitat associations as an alternative explanation for our observations.

Our research, and that of others, indicate habitat overlap between wild pigs and deer (Lewis 2020, Garabedian et al. 2022, Dykstra et al. 2023) and wild pigs and turkeys (Lewis 2020, Walters and Osborne 2022). Dietary overlap among the three species (Yarrow 1987, Taylor and Hellgren 1997, Elston and Hewitt 2010), competition between wild pigs and deer (Lewis 2020, Garabedian et al. 2022, McDonough et al. 2022, Dykstra et al. 2023) and aggressive behavior exhibited by wild pigs toward deer have been observed (Tolleson et al. 1995, McDonough 2023). Furthermore, artificial nest studies indicate wild pigs may be a significant nest predator (Tolleson et al. 1993, Sanders et al. 2020). Our results support previous findings that there is a negative association between wild pigs and turkeys (Lewis 2020, McDonough 2023). However, we observed both positive and negative associations between deer and wild pig detections, depending on landcover and season. In contrast, prior studies observed either no association (Garabedian et al. 2022, Dykstra et al. 2023) or a negative association (Keever 2014, O'Brien et al. 2019, Lewis 2020, McDonough 2023) between deer and wild pigs. Our research contributes to the growing number of studies detecting negative impacts associated with wild pigs and suggests a need for better understanding factors that contribute to hypothesized interactions, i.e., competition and predation, between wild pigs and native wildlife.

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Size and Composition as a Proxy for Identification of Wild Pig Sounders

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Abstract: Management of wild pigs (*Sus scrofa*) typically employs some form of population survey methodology, and trail cameras are the most common tool for conducting these surveys. Identification of individual sounders is generally at the foundation of these population surveys. Pelage characteristics and relative age distribution of individuals within the sounder coupled with total sounder size are common characteristics used to identify unique sounders. However, in many populations, the pelage of many wild pigs is either black or wild/grizzled, making pelage characteristics unreliable for sounder identification. Consequently, our objective was to assess the potential of using sounder size and composition as a simple proxy for identification of individual sounders visiting a camera station. Specifically, we aimed to determine the probabilities of encountering two sounders of a specific size and composition at the same camera site. Our findings revealed that sounders comprised of two adult wild pigs were the most common to be found at the same camera site. Yet, sounders of unique size and composition with more than three adults had a very low frequency (<3.6%), and frequency showed a tendency to decrease as sounder size increased. Our data indicate that most sounder size/composition categories (88.8%) can be identified individually with high (>95%) confidence simply by counting the number of individuals and number of adults in the sounder. Only four sounder size/composition categories (sounder of two with zero adults, sounder of two with two adults, sounder of three with zero adults, and sounder of three with one adult) had probability of co-occurrence >0.10. Hence, our study suggests that using sounder size and composition as a proxy for sounder identification is suitable for population surveys and management purposes.

*Key words***:** camera survey, population survey, sounder size, sounder composition, *Sus scrofa*.

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Wild pigs (*Sus scrofa*) are known for their extensive geographic distribution (Lewis et al. 2017), and both native and invasive/introduced populations of this animal can cause extensive environmental damage (Mayer and Brisbin 2009, Barrios-Garcia and Ballari 2012). In the U.S., their populations have been rapidly expanding with damage estimates in the billions of dollars annually (Pimentel et al. 2005). Wild pigs are known for their destructive rooting and wallowing (Mayer and Brisbin 2009), ability to compete with native species for resources (Campbell and Long 2009, Barrios-Garcia and Ballari 2012, Fay et al. 2023), damage to crops (McKee et al. 2020, Carlisle et al. 2021), and transmission of diseases (Gortázar et al. 2007, Gaudreault et al. 2020). Wild pigs cause increased soil erosion (Gray et al. 2020), reduced water quality (Brooks et al. 2020, Bolds et al. 2021), and destruction to natural areas (Sweitzer and Van Vuren 2002, Mitchell et al. 2007). Ultimately, wild pigs have substantial negative impacts on biodiversity, ecosystem structure, and anthropogenic environments. With their expanding populations and increased societal awareness perpetuated by their impacts, greater emphasis has been placed on reduction or eradication of wild pig populations. However, despite recent advancements in wild pig management and research, robust methods for estimating population size are needed to guide management strategies and to assess outcomes of control operations.

Although a variety of approaches have been developed to estimate population size of wild pigs (Engeman et al. 2013), most methods rely upon data collected using trail cameras (Holtfreter et al. 2008, ENETWILD 2018, Massei et al. 2018, Schlichting et al. 2020). However, most developed techniques do not consider that wild pigs are highly social animals and generally found in groups (sounders), causing them to exist on the landscape in a clumped distribution. Some recent advances in population estimation (Emmet et al. 2022) suggest social dynamics of species such as wild pigs should be accounted for when estimating population size, and thus, identification of individual sounders should be incorporated into these estimates. Additionally, identification of individual sounders lies at the foundation of whole sounder removal (Lewis

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et al. 2022) and has been an important component of trapping approaches for quite some time (Sweitzer et al. 2000, Hanson et al. 2008, Hebeisen et al. 2008). Total number of individuals and the relative age distributions of members within a sounder (i.e., number of adults relative to juveniles) are measurable characteristics commonly used to uniquely identify a sounder. Additionally, variation in pelage coloration and pattern within a sounder can be considered when identifying unique sounders (Holtfreter et al. 2008, Fang et al. 2009, Keiter et al. 2017, Davis et al. 2020, Schlichting et al. 2020). However, in many areas of their range, a high percentage of individuals within a population have either black or wild/grizzled pelage (Mayer and Brisbin 2008, 2009). Thus, pelage coloration and pattern are sometimes unreliable for identifying unique sounders. To account for this limitation, some studies have incorporated assumptions to identify sounders by only counting images taken <10 min apart (Massei et al. 2018). However, these approaches are less than ideal and likely to introduce bias, leading to greater confidence intervals around density estimates.

Building upon our past experience using trail cameras to monitor wild pigs (Hanson et al. 2008, Holtfreter et al. 2008, Williams et al. 2011) and other wildlife (Mccoy et al. 2011, Price Tack et al. 2016, Elliott et al. 2022), we hypothesized wild pig sounders could be uniquely identified through certain aspects of their biology rather than with the use of pelage characteristics. Wild pig sounders are social groups comprised of related females and their offspring (Kaminski et al. 2005), and the individuals within these groups are fairly stable (Mayer and Brisbin 2008, Titus et al. 2022) during the short durations of camera surveys (usually less than 2 wk; Holtfreter et al. 2008, Kays et al. 2020). Additionally, wild pigs tend to show high site fidelity (Oliveira-Santos et al. 2016, Bastille-Rousseau et al. 2021), and in some cases exhibit territoriality (Gabor et al. 1999, Sparklin et al. 2009), so their spatial location is generally predictable. Based on these behavioral characteristics, we used the binomial distribution function to evaluate the potential for using sounder size as a simple proxy for identification of individual sounders, as well as sounder size and composition (number of adults and juveniles) in tandem. Specifically, we used data on sounder size and composition collected from several studies among four states to calculate the probabilities of two sounders of the same size and composition being found at the same camera site.

Methods

We estimated the relative frequency of wild pig sounders of variable size and composition across the landscape using data previously collected during other studies (Mayer 2021, McDonough 2023). These data were collected in Alabama, Florida, Georgia, and South Carolina. Land covers of the properties where these data were collected were common in the southeastern United States, including mixes of upland pine (*Pinus* spp.) interspersed with hardwood drains at interior sites, and both forested and non-forested wetlands for coastal sites.

Both Mayer (2021) and McDonough (2023) identified individual sounder sizes and compositions using different survey approaches (Table 1), and we combined both datasets for use in this study. Data generated in Florida, Georgia, and South Carolina were collected during all seasons (1982–2001) by Mayer (2021) using a simple count observational approach via vehicular and pedestrian diurnal surveys by a single observer. The numbers of adults and juveniles in each group were recorded. Mayer (2021) classified individuals as adults or juveniles based on body size (i.e., wild pigs estimated to be greater than 25–30 kg were classified as adults). Data generated in Alabama (2019–2021) were also collected during all seasons as part of ongoing research (Bolds et al. 2021, McDonough 2023) using Reconyx™ PC800 Hyperfire Professional IR Cameras (Reconyx Inc., Holmen, WI, USA), as described elsewhere (Lewis et al. 2022, McDonough 2023). Cameras were deployed across the study areas within a 1-km^2 grid and set in strategic areas with the greatest amount of wild pig signs. Cameras were programmed to take time lapse pictures every 4 min as well as in three-picture bursts 2 sec apart when triggered by motion with a 30-sec delay between motion activations. Once datasets were combined, we determined the total number of individuals in each sounder and classified each animal as either juvenile or adult based on body size similar to Mayer (2021). Any observations with uncertain counts or uncertain identification of all individuals present in the sounder were excluded from this study. The objective in combining these datasets was to generate a sample of sounder sizes and compositions that was generally representative of what is found on the landscape, rather than a sample that was representative of one area, and which could be influenced by habitat resources, management (e.g., trapping, etc.), or other factors.

The combined dataset from the above studies was used to develop a frequency matrix of sounder size (total number of wild pigs in the sounder) and composition (number of adults and juveniles) categories. Because occurrences of sounders with >10 adults were infrequent, we merged all instances of 10 or more adults into a single composition category. Because sounders are defined as a group of related females and their offspring (Kaminski et al. 2005, Titus et al. 2022), we considered the minimum sounder size to be two individuals. Because sounder sizes >20 were infrequent, all instances of sounders with ≥20 individuals were merged into a single sounder size category. To populate the matrix, we calculated the relative frequency of each combination of sounder size

Table 1. Summary of the sounder size/composition datasets gather from Mayer (2021) and McDonough (2023).

State	Study site	Sounder size metrics		Survey method	Number of unique sounders identified	Reference
		Mean ± SE	Range			
Florida	Immokalee Ranch	4.7 ± 0.1	2–19	Vehicular and pedestrian	219	Mayer 2021
Georgia	Ossabaw Island	3.8 ± 0.1	2–19	Vehicular and pedestrian	221	Mayer 2021
South Carolina	Savannah River Site	4.9 ± 0.2	2–22	Vehicular and pedestrian	209	Mayer 2021
Alabama	Control	8.6 ± 1.2	2–24	Camera	27	McDonough 2023
Alabama	Treatment 1	7.4 ± 0.6	2–41	Camera	92	McDonough 2023
Alabama	Treatment 2	6.6 ± 0.4	2–21	Camera	111	McDonough 2023
Alabama	Treatment 3	8.6 ± 0.7	2–23	Camera	49	McDonough 2023

and composition (i.e., number of adults) by dividing the number in each sounder size/composition category by the total number of sounders that were included in the combined dataset.

To determine the maximum number of sounders that have been found to overlap in space and time, we searched the literature for information on overlap of sounder home ranges. Using Web of Science and Google Scholar, we used combinations of "Sus scrofa" OR "wild boar" OR "wild hog" OR "wild pig" OR "feral pig" OR "feral swine" as interchangeable nomenclature with "overlap*" AND "sounder" to look for all available research that reported sounders overlapping in the same area. Based on information gathered from the literature review, the greatest number of sounders overlapping generally ranged from two to three (Boitani et al. 1994, Gabor et al. 1999, Sparklin et al. 2009, Kilgo et al. 2021, Lewis et al. 2022); therefore, we assumed that the maximum number of sounders that could overlap in space, and hence have the potential to be photographed at the same bait site, was three. Although on a few occasions Kilgo et al. (2021) identified more than three sounders overlapping in space, these observations occurred under unique circumstances (at a landfill). Thus, we felt these observations were generally anomalous for wild pigs in natural areas. To calculate the probability of at least two sounders of the same size and composition having the potential to be photographed at the same location, assuming that three sounders are using the same space at any particular time, we used the binomial distribution function: $1-(1-P)^x$; where P is the relative frequency of a sounder of a certain size and composition (i.e., the relative frequency calculated for each sounder size and composition), and x is the number of additional sounders overlapping with a given sounder (i.e., if three sounders are co-occurring, then $x = 2$).

Results

We were able to identify 928 sounders (comprising 4942 individual wild pigs) within our combined datasets and determine size and composition for each. Sounder sizes ranged from 2–41 with a mean of 5.3 ± 0.1 (SE) wild pigs. Composition of sounders ranged from all adults to all juveniles (Table 2). The sounder size/composition category that was most frequently detected contained two adult wild pigs (11.0%), followed by a sounder of two (8.0%) or three (7.5%) juveniles. In addition, sounders of three to five individuals with one adult (15.1%) had a frequency ≥5.0%. Sounders with greater than six individuals with at least three adults were the least common (each category >2.0%). Overall, most sounder sizes and compositions (83%) had a low probability (<0.02) of there being at least two of the same size and composition using the same site (Table 3). However, sounders that had less than five individuals with less than three adults had greater probabilities of co-occurrence (>0.05).

Table 2. Relative frequency of finding a wild pig sounder of a particular size and composition on the landscape. Numbers in bold indicate those sounder size/compositions that had relative frequencies ≥0.05.

Sounder size	Number of adults										
	0	1	2	3	4	5	6	7	8	9	10+
2	**0.080**	0.038	**0.110**								
3	**0.075**	**0.052**	0.022	0.041							
4	0.039	**0.050**	0.020	0.010	0.018						
5	0.011	**0.050**	0.026	0.005	0.001	0.011					
6	0.012	0.033	0.017	0.002	0.006	0.002	0.004				
7	0.003	0.020	0.016	0.006	0.002	0.002		0.003			
8	0.011	0.028	0.008	0.005	0.003	0.001	0.001	0.001	0.005		
9	0.002	0.013	0.008	0.001		0.002		0.001		0.002	
10	0.003	0.004	0.008	0.003	0.001	0.001	0.002	0.001			0.001
11	0.003	0.005	0.009	0.004	0.001	0.001	0.002				0.003
12	0.002		0.001	0.001	0.001	0.001			0.001		0.002
13	0.002		0.002	0.002				0.001		0.001	
14		0.002	0.002		0.002	0.001					
15	0.002		0.001	0.001	0.001		0.002	0.001	0.001		
16				0.001	0.001		0.002				
17			0.001	0.002							
18				0.001		0.001	0.002				
19				0.001	0.001	0.001	0.001	0.002			0.001
20+				0.004	0.002	0.001	0.001				0.001

Table 3. Probability that, given three wild pig sounders have overlapping home ranges, at least two of them have the same size and composition. Numbers in bold indicate those sounder/size compositions that had probability of occurrence ≥0.05.

Sounder size	Number of adults										
	0	1	2	3	4	5	6	7	8	9	10+
2	**0.153**	**0.074**	**0.208**								
3	**0.145**	**0.101**	0.043	**0.080**							
4	**0.076**	**0.097**	0.041	0.019	0.036						
5	0.021	**0.097**	**0.051**	0.011	0.002	0.021					
6	0.024	**0.066**	0.034	0.004	0.013	0.004	0.009				
7	0.006	0.041	0.032	0.013	0.004	0.004		0.006			
8	0.021	**0.055**	0.015	0.011	0.006	0.002	0.002	0.002	0.011		
9	0.004	0.026	0.015	0.002		0.004		0.002		0.004	
10	0.006	0.009	0.015	0.006	0.002	0.002	0.004	0.002			0.002
11	0.006	0.011	0.017	0.009	0.002	0.002	0.004				0.006
12	0.004		0.002	0.002	0.002	0.002			0.002		0.004
13	0.004		0.004	0.004				0.002		0.002	
14		0.004	0.004		0.004	0.002					
15	0.004		0.002	0.002	0.002		0.004	0.002	0.002		
16				0.002	0.002		0.004				
17			0.002	0.004							
18				0.002		0.002	0.004				
19				0.002	0.002	0.002	0.002	0.004			0.002
20+				0.009	0.004	0.002	0.002				0.002

Discussion

Our data suggest that when wild pig sounder size is greater than four with at least one adult, sounder identification using size and composition is a technique that can be employed with high confidence when conducting camera surveys for wild pigs. Most sounder size/composition combinations had very low probability of co-occurrence at the same camera location; only 12 size/composition categories (11.2% of represented categories) had co-occurrence probabilities >0.05. We would additionally argue that when sounder size is greater than two and at least one adult is present, excluding the unique category of a sounder composed of only two adults, this technique still has strong utility as almost all sounder/size compositions have probability of co-occurrence of less than 0.10. Finally, we emphasize that our calculated probabilities already assume that there are three sounders that co-occur at a site. Based on the information gathered from the literature review, the instances when three sounders co-occurred in the same area have been relatively low. Thus, the true probability that two or more sounders occupy the same area and have the same size and composition, is even less.

Our probability calculations are based solely on the size and composition of a sounder. However, there are several aspects of the biology of wild pigs that make this method even more reliable. Firstly, some populations of wild pigs are territorial (Gabor et al. 1999, Sparklin et al. 2009, Kilgo et al. 2021), indicating that the probability of overlap with any other sounder is often low. Thus, sounders can sometimes be identified simply based on location. Secondly, wild pigs are known to demonstrate high site fidelity (Oliveira-Santos et al. 2016, Bastille-Rousseau et al. 2021) and infrequently move outside of their established home range or territory. This, in turn, results in limited overlap between sounders of wild pigs (Boitani et al. 1994, Gabor et al. 1999, Sparklin et al. 2009, Lewis et al. 2022). Additionally, the presence of genetically related individuals within sounders reinforces their cohesive movement (Poteaux et al. 2009) and grouping behavior. Furthermore, effective baiting and conditioning have been shown to condition wild pigs to visit the same bait site at consistent times of the day (Snow et al. 2016, Snow and VerCauteren 2019, McRae et al. 2020, Snow et al. 2021). As a result, if multiple sounders inhabit a given area, they are likely to arrive at different times, further aiding in differentiation and identification of distinct groups. In sum, the combination of territorial behavior, high site fidelity, genetic relatedness, and movement behavior collectively fortify the effectiveness of our probability calculations, providing a robust framework for sounder identification.

Despite several behavioral characteristics of wild pigs enhancing the use of sounder size and composition as a proxy for unique identification of sounders, there are also a few behavioral aspects that weaken its potential utility. First, sounder size and composition can change during the farrowing period. When females approach parturition, they typically leave the sounder to give birth, and it is about 2–3 wk before they return with their offspring to re-join the sounder (Mauget 1982, Jensen 1986, Andersson et al. 2011). Additionally, sounders sometimes can experience dramatic changes in group composition due to merging or splitting (fission-fusion) of sounders (Ilse and Hellgren 1995, Gabor et al. 1999, Kaminski et al. 2005). Individual sounders can sometimes grow in numbers to the point where they split and form sub-groups, and it has been documented where small sounders or sub-groups of wild pigs have merged to form a larger sounder (Gabor et al. 1999). Although these behaviors do occur and have the potential to modify sounder size and composition, they have been reported more often during long-term studies (Truvé and Lemel 2003, Iacolina et al. 2009, Poteaux et al. 2009, McIlraith 2021) and most camera surveys for wild pigs last only 1–2 wk (Holtfreter et al. 2008, Williams et al. 2011, Risch et al. 2020). Thus, we can generally assume that sounders would be more stable within that time period.

We acknowledge that there are some sounder size/compositions that cannot be identified with the level of confidence (i.e., <0.05 probability of misidentification) that may be desired. Nevertheless, this tool can generally be applied with reasonably strong certainty. In those cases where sounder size and composition alone may not suffice for confident identification, physical characteristics such as pelage patterns, encompassing variation in color (i.e., black, red-brown, or white) and pattern (i.e., solid, spotted or mottled, belted, wild/grizzled, and combinations of these) can further aid in classifying and distinguishing individual sounders (Teton et al. 2020). Moreover, identifying sounders using other characteristics such as body mass, external dimensions, and hair morphology (Mayer and Brisbin 2008, 2009) would significantly enhance identification of individual sounders, particularly when dealing with smaller sounder sizes. Our study demonstrated the reliability of using sounder size and composition to identify individual sounders and provided the assurance that if one encounters a sounder with the same size/composition constantly in the same location, it will indeed be the same one. However, the possibility of incomplete observations, such as some individuals appearing in front of the camera while the rest of the sounder remains unseen, prompts the need for further investigation.

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Determining Body Mass of Wild Pigs from Body Measurements

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Abstract: Animal body mass can be used to estimate age, determine health status, or guide dosage when administering sedatives. Because it can be difficult to weigh live large animals, using morphometric measurements to estimate body mass is sometimes used in field studies. Several statistical models exist for estimating domestic pig mass from morphometric measurements, but models based on domestic animals are likely unreliable estimators of wild pig (*Sus scrofa*) body mass due to known hybridization between domestic and wild pigs, and variable environmental conditions. The goal of this project was to evaluate several easily obtainable morphometric measurements as predictors of wild pig body mass and compare our estimates with those of models developed from both wild and domestic pigs. We measured neck girth, heart girth, body length, and body mass from 127 wild pigs in Florida and Georgia, and 450 wild pigs in South Carolina. Our best-supported linear model included body length as the best predictor of wild pig body mass. Our body length and heart girth univariate models produced similar estimates to those of other published models using these attributes, providing evidence that these models may be broadly generalizable. We also compared estimates from our model to estimates from models derived from domestic pigs and found significant differences between our model and two of the models developed from domestic pigs. Thus, while body mass may be reliably estimated from simple morphometric measurements from wild pigs, our results suggest morphometric models produced for domestic pigs are not reliable predictors of wild pig body mass.

Key words: body mass estimation, domestic pigs, feral swine, morphometric measurements, *Sus scrofa*

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Direct measurement of large mammal body mass is often difficult in field settings. Obtaining animal body mass, though, is necessary for meeting many research objectives that include determining age, health status, or correct dosage for administering sedatives (Sweitzer et al. 1997, Fenati et al. 2008, Schlichting et al. 2015, Drimaj et al. 2019). Because it can be difficult to weigh live large animals, using easily obtainable morphometric measurements to estimate body mass is sometimes used in field studies (Bell et al. 1997, Amaral et al. 2010, Barrett et al. 2021, Baruzzi et al. 2023).

Wild pigs (*Sus scrofa*) can exceed 100 kg and therefore could be difficult to weigh in the field (Mayer et al. 2020). Equations that predict pig body mass from morphometric measurements are available; however, most of these equations were developed for commercial pig producers using domestic animals (Groesbeck et al. 2002, Mutua et al. 2011, Sungirai et al. 2014, Walugembe et al. 2014). Most wild pigs in the U.S. are hybrids with domestic and wild origins, and therefore retain some phenotypic and biological attributes of domestic pigs (Keiter et al. 2016, Smyser et al. 2020, Mayer 2021). However, there is often considerable phenotypic variability among wild and domestic pigs (Smyser et al. 2020), and it is likely that body mass-predicting equations developed for domestic pigs may be inappropriate for use with wild pigs. Domestic and wild pigs also differ in selective pressures, both of which directly influence growth rate and morphometric features (Pedone et al. 1995, Sungirai et al. 2014, Drimaj et al. 2019). For instance, domestic pigs are placed under favorable conditions (i.e., less selective pressures) that generally result in earlier maturity, larger litters, and heavier body mass than wild pigs, depending on their ancestry (Comer and Mayer 2009). These conditions have resulted in more vertebrae and faster growth rates for domestic pigs relative to wild pigs (Hammond 1962, Tohara 1967, Mikawa et al. 2011). In addition, domestic pigs are provided with veterinary care and ad libitum access to food and water, whereas wild pigs must opportunistically locate resources that fluctuate in availability and quality, thereby increasing their energetic demands.

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Despite the differences between domestic and wild pig morphometric characteristics, models developed for domestic pigs have been used to estimate body mass of wild pigs, perhaps because models that are explicitly developed for wild pigs have not been readily available until recently (Baruzzi et al. 2023). Therefore, models to predict body mass from morphometric measurements should be explicitly developed for wild pigs. Baruzzi et al. (2023) confirmed the validity of using morphometric measurements to predict body mass of wild pigs by generating models from six measurements for wild pigs in Mississippi. These models were validated across eight areas in Australia, Guam, and the U.S. using wild pigs of both sexes and a variety of sizes.

Given that wild pigs exhibit extensive morphometric variation both within and among populations across their invasive range (Mayer and Brisbin 2009), our objective for this study was to further evaluate the extent to which morphometric measurements can be used to estimate wild pig body mass across multiple populations within the southeastern U.S. In addition, we further explored our data to test the hypothesis that models developed for predicting body mass of domestic pigs would not be reliable for use in free ranging wild pig populations.

Study Area

We conducted our study on private and public lands in southwestern Georgia, northern Florida (hereafter SW GA/N FL due to proximity to each other), and central South Carolina. Properties in SW GA/N FL ranged in elevation from 52 m to 82 m and were dominated by agricultural fields of corn (*Zea mays*), cotton (*Gossypium* spp.), peanut (*Arachis hypogaea*), and pecan (*Carya illinoinensis*) or upland landscapes dominated by loblolly pine (*Pinus taeda*), longleaf pine (*P. palustris*), and shortleaf pine (*P. echinata*). Mean annual temperature across the SW GA/N FL properties was 19–20 C, and mean annual precipitation was 134–145 cm (NOAA 2022). All samples from South Carolina were obtained from the Savannah River Site (SRS), a 780 km^2 U.S. Department of Energy property located in the upper coastal plain (Mayer and Brisbin 2009). The SRS ranged in elevation from 20 m to 130 m and was dominated by managed upland pine forests (i.e., loblolly, longleaf, and shortleaf pine), riparian landscapes, and forested swamp land. No agricultural lands were present on the SRS. Mean annual temperature was 18 C, and mean annual precipitation was 122.5 cm (Chinn et al. 2022).

Methods

Data Collection

On the SW GA/N FL properties, wild pigs were removed by U.S. Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) Wildlife Services personnel via trapping and ground shooting from May 2021 to June 2022. On SRS, wild pigs were captured and euthanized by SRS-contracted trappers or captured, anesthetized, processed, and released by University of Georgia personnel as part of ongoing research activities from April 2017 to May 2021. Trappers placed whole corn in areas with evidence of wild pig activity (e.g., tracks, wallows, rooting, rubbing) and erected remotely triggered, corral-style traps once the target pigs visited the bait for several nights. Detailed descriptions of capture and handling procedures for SRS can be found in Keiter et al. (2017) and Chinn et al. (2022). We euthanized or anesthetized captured wild pigs and measured neck girth (NG), heart girth (HG), and body length (BL) with a cloth measuring tape (Figure 1), and measured body mass using either a dial or digital scale. Handling of wild pigs in SW GA/N FL and SRS occurred under approved University of Georgia Institutional Animal Care and Use Committee (IACUC) protocols (A2020 04-028-R1, A2023 01-030-Y1-A0, A2015 12-017, A2015 05-004, A2019 01-012, A2018 06-024, A2021 12-001, and A2021 04-013).

Statistical Analysis

We used univariate linear models to predict wild pig body mass from morphometric measurements. Our models regressed ln-transformed body mass against ln-transformed NG, HG, and BL. We ln-transformed body mass and each morphometric predictor to meet linearity assumptions (James and McCulloch 1990, Dobson 1992) as evaluated by quantile-quantile plots in the 'stats' package in program R (R Core Team 2023). We focused analysis on univariate models to avoid multicollinearity issues due to our highly correlated predictors. Furthermore, univariate models require fewer field measurements and therefore more incentive to calculate wild pig body mass. We evaluated all univariate models

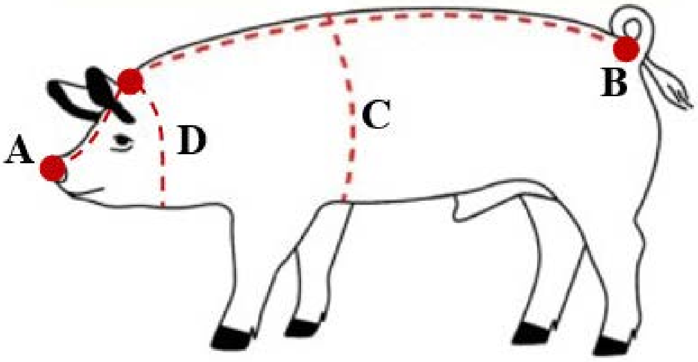

Figure 1. Diagram of the morphometric measurements taken on wild pigs (*Sus scrofa*) in central South Carolina and southwestern Georgia/northern Florida from April 2017 to June 2022. Measurements included body length (A-B), heart girth (C), and neck girth (D). Measurements were taken on wild pigs while in a lateral recumbent position. Diagram modified from Pater (2007).

(including a null model) using Akaike's Information Criterion adjusted for small sample size (AIC_c) using the 'AICcmodavg' package (Mazerolle 2020) in R (R Core Team 2023). We considered the model with the least AIC_c as the best model (Burnham and Anderson 2002). We used coefficient of determination (R^2) to assess the proportion of the variation in wild pig body mass that was explained by each model. We used the beta coefficients from the top model(s) to create equation(s) predicting body mass of wild pigs from their morphometric measurements.

We then evaluated models developed for wild and domestic pigs to determine how well each predicted body mass of wild pigs in our sample and compared the estimated body masses to those generated from our top model(s). We used our wild pig measurements to predict pig body mass using models from Groesbeck et al. (2002), Sungirai et al. (2014), and Baruzzi et al. (2023). The model produced by Walugembe et al. (2014) was based on domestic pigs <40 kg. Therefore, we tested this model using the wild pigs <40 kg ($n = 77$) available in our sample. The models developed from both wild pigs (Baruzzi et al. 2023) and domestic pigs (Groesbeck et al. 2002, Sungirai et al. 2014) used combinations of HG and BL to predict body mass and therefore could be applied to our wild pig data. The Baruzzi et al. (2023) models included:

$$\text{Body mass} = e^{(-9.56 + 2.82 \times \ln[\text{BL}])} \quad \text{and}$$

$$\text{Body mass} = e^{(-6.73 + 2.38 \times \ln[\text{HG}])},$$

where body mass was measured in kg, and BL and HG were measured in cm. Walugembe et al. (2014) used HG and length from the midpoint of the ears to the base of the tail to calculate body mass in domestic pigs. We collected the latter measurement on a subset of our wild pigs weighing <40 kg and used these data to include the Walugembe et al. (2014) model in our analysis. Although other models exist for domestic pigs, they could not be evaluated using our data because they incorporated different measurements (e.g., age; Ježek et al. 2011), were developed using larger pigs (mean: 116 ± 14.5 [SE] kg; Knauer and Wiegert 2017) than available in our data set, or because model coefficients were not provided (Mutua et al. 2011). We calculated the true differences and absolute value of the differences between the actual wild pig body mass and estimated body mass for each model, using the mean raw difference as a measure of bias and the mean absolute value of the differences as a measure of precision. We used an ANOVA and Tukey's honestly significant difference (HSD) test from the 'stats' R package (R Core Team 2023) to determine if there were differences ($P \leq 0.05$) among the estimated body masses generated from the alternative models and our wild pig model.

Results

We collected morphometric measurements from 127 wild pigs (62 males, 65 females) from SW GA/N FL and 450 wild pigs (89 males, 361 females) from the SRS. The mean body mass of wild pigs in our data set was 45.42 kg (SD = 22.71) and included 151 males and 426 females. Our best-supported model was the BL univariate model, which explained 94% of the variation in wild pig body mass (Table 1; Figure 2). This model was expressed as:

$$\text{Body mass} = e^{(-9.78 + 2.851 \times \ln[\text{BL}])}.$$

We evaluated five models developed for domestic and wild pigs using our wild pig data. The Groesbeck et al. (2002) model underestimated body mass for smaller pigs and slightly overestimated body mass for larger pigs (Figure 3A). Meanwhile, the Sungirai et al. (2014) model overestimated body mass for all pigs (Figure 3B), and the Walugembe et al. (2014) model slightly underestimated body mass for pigs <40 kg (Figure 3C). Both the BL and HG models from Baruzzi et al. (2023) produced body mass estimates similar to those of our best-supported model (Figure 4). Although our HG model received no support for being the best model based on AIC_c ranking ($\Delta AIC_c = 12.11$), we included it in comparisons with domestic and wild pig models (Figure 4B) because HG is commonly measured in field settings, and our HG model still explained 94% of the variation in wild pig body mass (Table 2). The HG model was expressed as:

$$\text{Body mass} = e^{(-7.671 + 2.599 \times \ln[\text{HG}[)}.$$

To facilitate use, we provided guides for estimating wild pig body mass with our BL and HG models (Table 2 and Table 3).

The absolute value of the differences (i.e., precision) of our best-supported wild pig model using BL differed ($P < 0.001$) from those of Groesbeck et al. (2002) and Sungirai et al. (2014; Figure 5). The Walugembe et al. (2014), our HG, Baruzzi et al. (2023) HG, and Baruzzi et al. (2023) BL models produced similar precision as our top wild pig model ($P = 0.891$, 0.994, 0.969, and 0.982,

Table 1. The univariate models used to evaluate wild pig (*Sus scrofa*) body mass in central South Carolina and southwestern Georgia/northern Florida. Wild pig body mass and morphometric measurements were collected between April 2017 and June 2022. Models include ln-transformed body mass regressed against ln-transformed body length (lnBL), heart girth (lnHG), and neck girth (lnNG). Included for each model are the number of parameters (K), sample-size adjusted Akaike's Information Criterion (AIC_c), Akaike differences (ΔAIC_c), the AIC_c model weight (*wi*), and the coefficient of determination (R^2).

Model	K	AIC_c	ΔAIC_c	*wi*	R^2
lnBL	3	–310.04	0.00	1.00	0.940
lnHG	3	–297.93	12.11	0.00	0.939
lnNG	3	133.45	443.48	0.00	0.871
Null	1	3146.82	3456.86	0.00	–

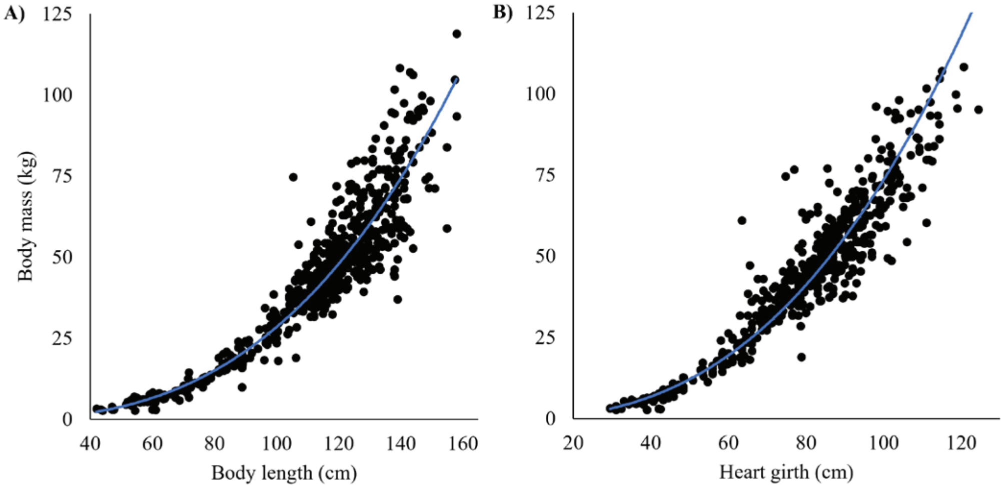

Figure 2. Relationship between wild pig (*Sus scrofa*) body mass (kg) to A) body length and B) heart girth, both measured in cm. Actual body mass is depicted with black points while estimated body mass is depicted with a blue line. Estimated body mass is from models developed from morphometric measurements taken on wild pigs (*Sus scrofa*) in central South Carolina and southwestern Georgia/northern Florida from April 2017 to June 2022.

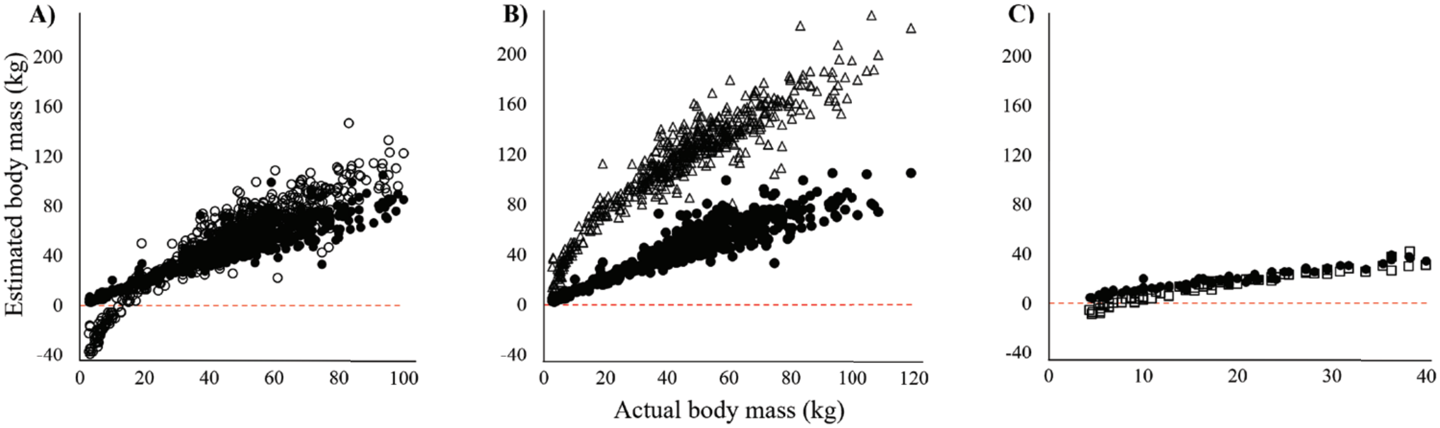

Figure 3. Comparison of actual wild pig (*Sus scrofa*) body mass (kg) and estimated body mass (kg) when using previously published models derived from domestic pig morphometric measurements. In each panel, our best-supported wild pig model is depicted with filled circles relative to models of: A) Groesbeck et al. (2002) with transparent circles; B) Sungirai et al. (2014) with transparent triangles; and C) Walugembe et al. (2014) with transparent squares. Note: Models in panel C only applied to pigs <40 kg.

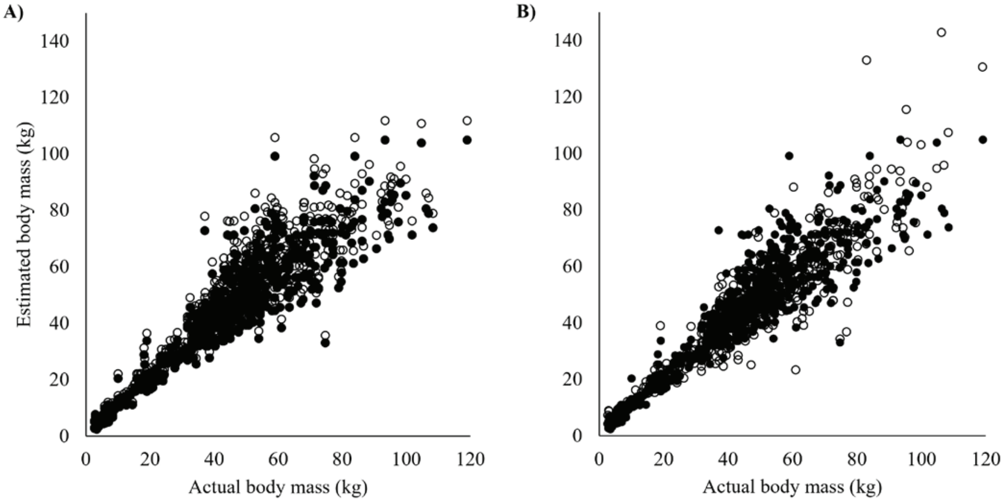

Figure 4. Comparison of actual wild pig (*Sus scrofa*) body mass (kg) and estimated body mass (kg) when using previously published models created from wild pig morphometric measurements. In each panel, our best-supported wild pig model (using body length as a predictor) is depicted with filled circles relative to: A) the body length and B) heart girth models from Baruzzi et al. (2023) with transparent circles.

Table 2. Wild pig (*Sus scrofa*) body mass estimated using the best-supported body length (BL) model generated from wild pig data in central South Carolina and southwestern Georgia/northern Florida. Body length is measured as the length from the tip of the snout to the base of the tail where the tail meets the body. Model: Weight (kg) = $e^{(-9.78 + 2.851 \times \ln[BL])}$, with BL in cm.

	Body length (cm)																													
	42	**46**	**50**	**54**	**58**	**62**	**66**	**70**	**74**	**78**	**82**	**86**	**90**	**94**	**98**	**102**	**106**	**110**	**114**	**118**	**122**	**126**	**130**	**134**	**138**	**142**	**146**	**150**	**154**	**158**
Weight (kg)	2	3	4	5	6	7	9	10	12	14	16	19	21	24	27	30	34	37	41	46	50	55	60	66	71	77	84	90	98	105

Table 3. Wild pig (*Sus scrofa*) body mass estimated using the heart girth (HG) model generated from wild pig data in central South Carolina and southwestern Georgia/northern Florida. Heart girth is measured as circumference of body just behind shoulder and forelegs. Model: Weight (kg) = $e^{(-7.671 + 2.599 \times \ln[HG])}$, with HG in cm.

	Heart Girth (cm)																										
	30	**34**	**38**	**42**	**46**	**50**	**54**	**58**	**62**	**66**	**70**	**74**	**78**	**82**	**86**	**90**	**94**	**98**	**102**	**106**	**110**	**114**	**118**	**122**	**126**	**130**	**134**
Weight (kg)	3	4	6	8	10	12	15	18	21	25	29	34	39	44	50	56	63	70	77	86	94	103	113	123	134	145	157

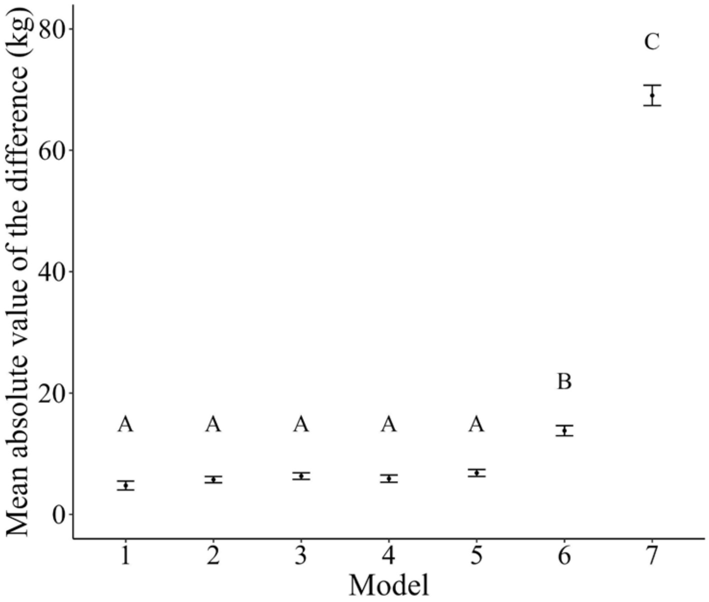

Figure 5. The mean and 95% CI of the absolute value of the difference between actual body mass and estimated body mass (used as an estimate of model precision) for each domestic and wild pig (*Sus scrofa*) model. Models are ordered as follows: 1 = Walugembe et al. (2014); 2 = heart girth model from Baruzzi et al. (2023); 3 = body length model from our study; 4 = heart girth model from our study; 5 = body length model from Baruzzi et al. (2023); 6 = Groesbeck et al. (2002); 7 = Sungiari et al. (2014). Black dots represent the means for each model. Models with unique letters are statistically different ($P < 0.05$).

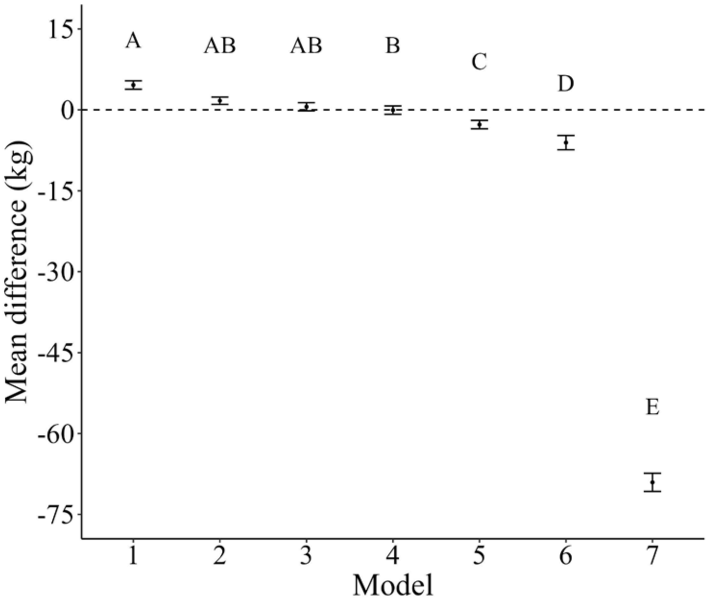

Figure 6. The mean difference and 95% CI between actual body mass and estimated body mass (used as an estimate of model accuracy or bias) for each domestic and wild pig (*Sus scrofa*) model. Models are ordered as follows: 1 = Walugembe et al. (2014); 2 = heart girth model from Baruzzi et al. (2023); 3 = body length model from our study; 4 = heart girth model from our study; 5 = body length model from Baruzzi et al. (2023); 6 = Groesbeck et al. (2002); 7 = Sungiari et al. (2014). Models are considered unbiased if their confidence intervals overlap with 0. Black dots represent the means for each model. Models with unique letters are statistically different ($P < 0.05$).

respectively). The true differences (i.e., accuracy or bias) of our best-supported wild pig model differed ($P < 0.001$) from those of Groesbeck et al. (2002), Sungirai et al. (2014), and Baruzzi et al. (2023) BL models (Figure 6). The Walugembe et al. (2014), our HG, and Baruzzi et al. (2023) HG models produced similar accuracy as our top wild pig model ($P = 0.116$, 0.981, and 0.740, respectively).

Discussion

Our results demonstrated that easily obtainable morphometric measurements can be used as precise and accurate predictors of wild pig body mass, and that models we developed using data from wild pigs can better estimate wild pig body mass than those developed using data from domestic pigs. Importantly, two of the three models developed using domestic pigs resulted in biased estimates of wild pig body mass. The Groesbeck et al. (2002) model overestimated overall body mass of larger wild pigs and underestimated body mass of smaller wild pigs, whereas the Sungirai et al. (2014) model consistently overestimated body mass. Overestimation of wild pig body mass by the Groesbeck et al. (2002) and Sungirai et al. (2014) models is likely attributed to differences in environmental characteristics among domestic and wild pigs. In contrast, the Walugembe et al. (2014) model underestimated wild pig body mass likely because this model only used data from domestic pigs <40 kg (Ježek et al. 2011). Magnitude of underestimation of wild pig body mass associated with the Groesbeck et al. (2002) and Walugembe et al. (2014) models is evidenced by negative predicted body mass for smaller wild pigs.

We determined that BL was the most informative predictor of wild pig body mass. This supports the findings of Baruzzi et al. (2023) who demonstrated that BL accounted for 96% of the variation in wild pig body mass. The coefficients of our BL model were very similar to the BL model of Baruzzi et al. (2023). We anticipated this result because the Baruzzi et al. (2023) BL model reliably estimated wild pig body mass across several locations such as Alabama, Australia, and Hawaii, illustrating the consistency of morphometric measurements in predicting body mass.

Our findings and those of Baruzzi et al. (2023) suggest body morphometrics can be used to precisely and accurately estimate wild pig body mass. Both modeling efforts yielded similar coefficients when using BL or HG, therefore we recommend using either of our models or those generated by Baruzzi et al. (2023) rather than models derived using domestic pigs when estimating wild pig body mass from morphometric measurements. There is more variability in body mass as wild pigs become heavier, possibly attributed to concomitant variation in reproductive status among female wild pigs which breed year-round throughout our study area. This variability was documented by the HG and BL models produced by both Baruzzi et al. (2023) and our study. Thus, there remains room for improvement when estimating the body mass of larger wild pigs. Morphometric measurements likely fluctuate less than body mass throughout the year due to environmental variation (Barrett 1978, Mayer 2021), and we encourage future research to evaluate how well our models generalize relative to seasonal variation of food and water availability.

Acknowledgments

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No Corn, No Problem: A Test for the Best Non-Grain Attractant for Wild Pigs

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Abstract: Grain-based attractants (e.g., corn) are standard among most wild pig (*Sus scrofa*) trapping and non-invasive sampling efforts (e.g., genetic spatial capture/recapture, camera trapping), but their use is not always feasible due to cost, deployment restrictions (e.g., difficulty of transporting grain into remote areas, property rules), and potential disease concerns associated with concentrating non-target species at bait sites. Attractant deployment and efficacy should be considered by biologists, private landowners, and researchers given the ultimate need to use attractants to attract wild pigs. To examine the efficacy of potential non-grain attractants, we used remote camera grids to identify attractant(s) that maximized wild pig visitation while minimizing non-target species visitation in a forested landscape in the southeastern United States. Further, we only considered non-grain attractants easy to carry (i.e., <0.5 kg and compact) and deploy (i.e., painted on tree trunks or activated scent wicks). Comparing eight non-grain attractants among food, non-food, and control (i.e., no attractant; $n = 11$ visitations) treatments, we found used cooking oil (i.e., fish fryer grease; $n = 38$ visitations), orange marmalade ($n = 36$ visitations), and caramel syrup ($n = 29$ visitations) were most attractive to wild pigs. Although also attractive to opossums (*Didelphis virginiana*; $n = 50$ visitations), used cooking oil was not a significant attractant among other non-target species. In contrast, orange marmalade was attractive to raccoons (*Procyon lotor*), opossums, and eastern gray squirrels (*Sciurus carolinensis*; $n = 188$ combined visitations), and caramel syrup was attractive to raccoons and opossums ($n = 137$ combined visitations). In our study, used cooking oil was the non-grain attractant most likely to maximize wild pig visitation while minimizing non-target species attraction, and increases the efficacy of sampling of remote areas considering its ease of distribution.

Keywords: camera trap, caramel syrup, cooking oil, non-target, orange marmalade

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Successful wildlife management and conservation depends on the ability to properly assess target species distribution, population size, and trends (Saracco et al. 2008, Kindberg et al. 2011). This is particularly important for exotic species as their distributions and populations may rapidly expand into new environments due to life history characteristics that often include a wide range of environmental tolerance, a broad or generalist diet, early sexual maturity, prolific reproduction, dispersal ability, and absence of natural enemies (Ricciardi and Rasmussen 1998, Sakai et al. 2001, Jeschke et al. 2012). The inconspicuous habits (e.g., nutria, *Myocastor coypus*; Witmer and Pitt 2012) along with human phobia (e.g., black rat, *Rattus rattus*; Phillips 2010) among mammalian exotics often make use of direct, invasive field methods laborious or otherwise logistically challenging (Van Rensburg et al. 1987). As a result, non-invasive methods are often used to assess distribution and population size, including those that benefit from the use of attractants (e.g., camera trapping, hair snaring, scent stations; Ferreras et al. 2018, Gurney et al. 2020, Holinda et al. 2020). Attractants have

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a variety of uses in wildlife management and research relating to exotic species including trapping (Reed et al. 2011), toxicant delivery (Engeman et al. 2006), and population abundance estimation (Amburgey et al. 2021). Although attracting a target species is critically important in each application, minimizing non-target visitation may be of equal or greater importance especially when lethal methods and/or sensitive species are involved (Glen et al. 2007).

Wild pigs (*Sus scrofa*) are tolerant and adaptable to various environmental conditions (Barrett and Birmingham 1994) and have a generalist omnivorous diet (Ditchkoff and Mayer 2009), early age of sexual maturity (Dzieciolowski et al. 1992), high reproductive capacity (Ditchkoff et al. 2012), and efficient dispersal ability (Snow et al. 2017), traits that facilitate population expansion and establishment. Although present in North America since the 1500s (Lewis et al. 2019), wild pigs have increasingly presented challenges to natural resource managers, biologists, and private landowners in recent decades as populations and distributions have continued to expand (Corn and Jordan 2017), leading to concomitant increases in agricultural damage and control costs (McKee et al. 2020). Management actions often include active removal methods (e.g., trapping, shooting, aerial gunning; Barrett and Birmingham 1994, Massei et al. 2011). However, research may also benefit from an improved understanding of attractant efficiencies. Grains (e.g., corn, wheat) are common baits (Lavelle et al. 2017) used in wild pig population assessments (Davis et al. 2020, Schlichting et al. 2020) and control efforts (Poche et al. 2018). However, grain loses appeal when considering its attractiveness to non-target species (a quality that can augment, for example, disease transmission; Miller et al. 2003), increased costs (Lavelle et al. 2017), and deployment feasibility in grain-restricted areas (e.g., national wildlife refuges, wildlife management areas, disease management zones) that harbor wild pig populations.

Non-grain attractants such as liquid domestic swine feed additives (e.g., apple and strawberry; Campbell and Long 2008) and orange flavoring (Karlin and Khan 2020) may provide alternatives for attracting wild pigs, especially when grain deployment is not an option, and have been shown to be effective in some cases. For example, use of orange flavoring with grain was shown to have greater visits from wild pigs and fewer visits from non-target species such as white-tailed deer (*Odocoileus virginianus*) and raccoon (*Procyon lotor*) relative to grain-only stations (Karlin and Khan 2020). However, non-grain attractants for wild pigs, even when used alone, can still attract non-target species (Campbell and Long 2008). When effective, non-grain attractants may aid in reducing costs and labor required to meet management and research objectives. For example, a non-grain attractant (e.g., jelly; Andelt and Woolley 1996) may represent a cost-efficient and less labor-intensive alternative that allows for a greater deployment range into remote or otherwise access-limited areas. However, while attractants may be effective in one region or ecotype, complementary investigations in new areas are warranted considering differences among non-target communities, local climatic conditions, and the availability of food resources.

Previous attractant studies have focused on wild pig populations and broader communities among countries (e.g., Australia; Elsworth et al. 2004), coastal islands (e.g., Ossabaw Island, Georgia, USA; Kavanaugh and Linhart 2000), private lands characterized by shrub rangelands (e.g., Texas; Campbell and Long 2008, Karlin and Khan 2020), and state-owned wildlife management areas with distinct wild pig hunting seasons (e.g., Alabama; Sandoval et al. 2019). While most studies focused on food-based attractants, investigation of urine-based attractants (Sandoval et al. 2019) may also be useful, particularly on public lands (e.g., national wildlife refuges) where food-based attractants may be precluded in certain areas due to baiting, feeding, hunting seasons, or access rules and restrictions. Our objective was to evaluate the effectiveness of eight commercially available, non-grain attractants for wild pigs within a forested landscape in the southeastern U.S. that would maximize attraction of wild pigs and minimize attraction of non-target species. We used both food and non-food non-grain alternatives to assess potential for implementation considering access, time, and grain baiting restriction challenges for stakeholders working on public lands.

Study Area

We tested attractants at the Sam D. Hamilton Noxubee National Wildlife Refuge (NWR) during summer (17 June–30 July) 2021. The study area encompassed 19,425 ha in east-central Mississippi (Figure 1) with bottomland hardwoods (i.e., woody wetlands; 52.2%) and upland forests (i.e., evergreen, deciduous, and mixed; 40.4%) collectively dominating the landscape, while remaining land cover types (e.g., water, developed) comprised the remaining 7.4% (Dewitz 2019). In addition to the presence of wild pigs since 2014, other mammals of interest included white-tailed deer, raccoon, bobcat (*Lynx rufus*), coyote (*Canis latrans*), nine-banded armadillo (*Dasypus novemcinctus*), Virginia opossum (*Didelphis virginiana*), and eastern gray squirrel (*Sciurus carolinensis*; hereinafter, gray squirrel). Annual precipitation totaled 162.6 cm, and average monthly low and high temperatures ranged 0.6–22.2 C and 12.2–32.8 C during the study year, respectively (NOAA 2023). During the study period, precipitation totaled 21.2 cm, and average low and high temperatures ranged 21.2–31.9 C, respectively (NOAA 2023). While public hunting pressure was relatively high for native mammals (e.g., white-tailed deer, gray squirrel) during

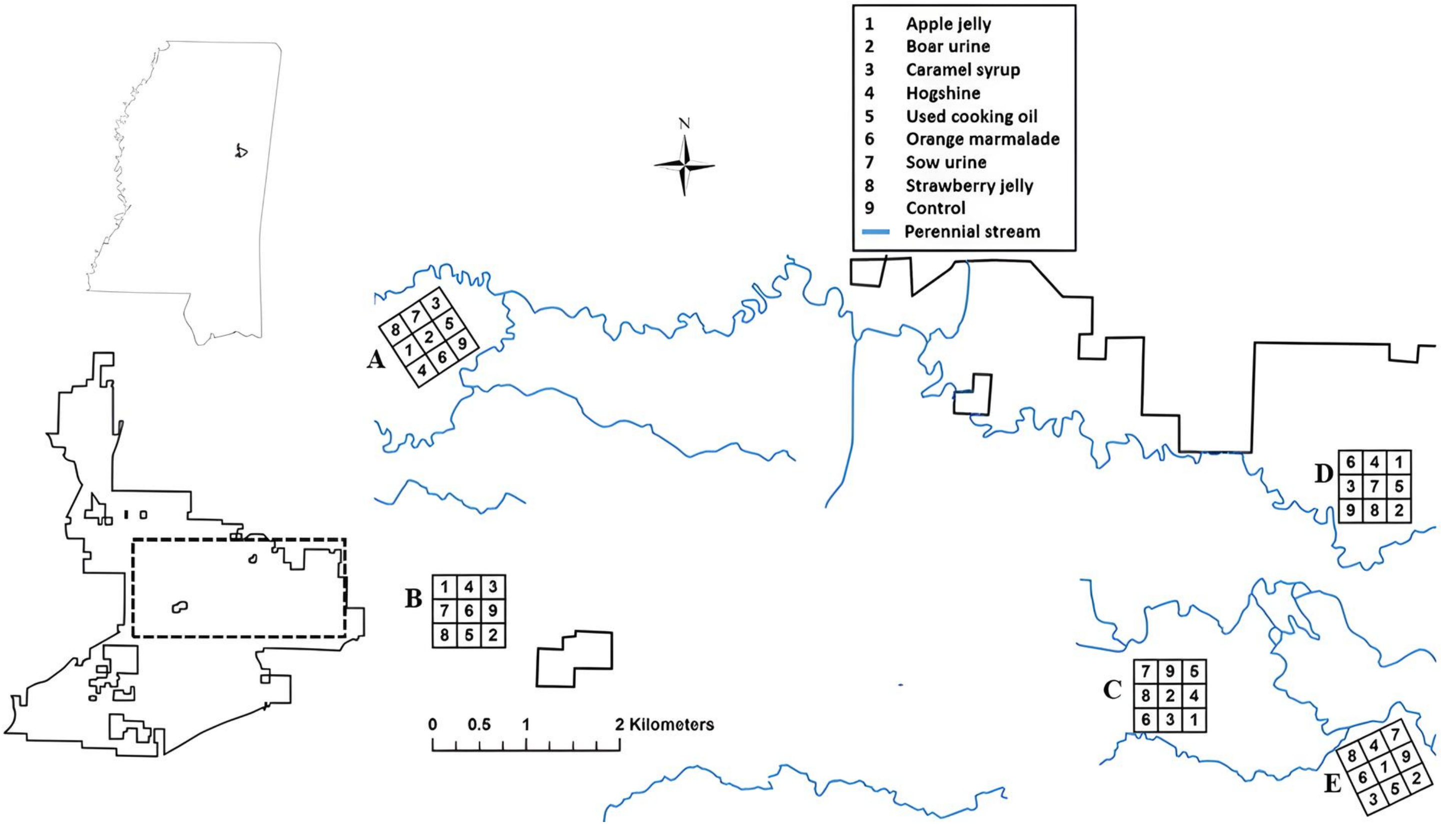

Figure 1. Location of the Sam D. Hamilton Noxubee National Wildlife Refuge in Noxubee, Oktibbeha, and Winston counties, Mississippi (top left), with sample area grid locations within the refuge (bottom left) and assigned treatments at grid locations (right) during an investigation of non-grain attractants for wild pigs (*Sus scrofa*).

respective hunting seasons, wild pig removal was limited to incidental take (i.e., approximately 100 wild pigs yr^{-1}, T. Carpenter, Sam D. Hamilton Noxubee NWR, pers. comm.) during native game hunting seasons. Although precise population estimates were not currently available, the wild pig distribution was primarily limited to the woody wetlands land cover type across the central region of the study area (Figure 1).

Methods

Sampling Design

We detected and GPS-marked rooting and wallowing areas during previous wild pig damage surveys in 2020–2021. Based on damage predominantly occurring within woody wetlands, we placed five attractant sampling areas (Figure 1) in damaged areas within this land cover type using ArcGIS (ESRI 2017). A 3 × 3 grid was overlayed in each area and a centroid location was generated in each cell to represent the location of each randomly assigned treatment (Figure 1). We used a grid size representing the smallest home range size reported for wild pigs in the region (0.6 km^2; Hartley et al. 2015) to ensure availability of each treatment to a given wild pig with enough separation (approximately 200 m spacing) among treatments to suggest an individual was attracted to that treatment and not an accidental "combination" of adjacent scents (Campbell and Long 2008). Grids were also oriented to avoid perennial streams, a potentially confounding variable (i.e., as streams provide travel corridors; Beasley et al. 2014). Although each grid was monitored for 14 days, monitoring periods were staggered (i.e., grids A and B: 17–30 June 2021, grid C: 2–15 July 2021, and grids D and E: 17–30 July 2021) due to the number of available cameras (see below).

Treatment Application and Monitoring

At each sampling grid centroid, we randomly assigned nine treatments for the duration of the monitoring period as follows: used cooking oil (i.e., fish fryer grease); orange marmalade (Great Value, Arkansas), strawberry jelly (Smuckers, Ohio), apple jelly (Smuckers), and caramel syrup (Smuckers); Hogshine, which is a commercial grain additive (Yawt Yawt, Mississippi); sow in heat urine (BoarMasters Wildlife Attractants, Idaho), dominant boar urine (BoarMasters Wildlife Attractants, Idaho); and a control (camera only; Figure 1). Non-urine treatments consisted of a weekly application to the same tree (i.e., 192 mL, equivalent to half standard jar per application), and urine treatments consisted of a weekly application to a key wick (Wildlife Research Center, Minnesota) hung from the same tree branch (i.e., 7 mL, the maximum amount that could be applied without exceeding wick absorption capacity). Initial applications and camera installations were completed on the day that preceded monitoring (i.e., day 1 started at midnight), and second applications and camera checks (i.e., battery checks and memory card changes) occurred on day 7. Monitoring of species visitation was conducted using a motion-sensing remote camera (FORCE-20; Spypoint, Quebec, Canada) located 5 m from the treatment with each camera set to capture three-image bursts at high sensitivity without delay. During the first monitoring period, cameras were placed 1 m above ground level; however, due to flash flooding concerns within woody wetlands, camera height was increased to 1.5 m on day 2 for all cameras. We maintained the adjusted height for the remainder of the study period in every grid. All procedures were in accordance with Sam D. Hamilton Noxubee NWR guidelines (U.S. Fish and Wildlife Service Permit #43620-20-013).

Statistical Analysis

Wild pigs in our study area are often uniform in coloration, and therefore, difficult or impossible to individually identify (Figure 2). Considering our inability to reliably identify individuals across all mammal species and our interest in visitations rather than abundance estimation (Kelly and Holub 2008), we defined a visitation event as a mammal species observation (regardless of number observed during the event) within the camera frame ≥10 min since the last observation of that species on camera (Karlin and Khan 2020). To reduce potential biases when processing remote camera images, we had the same two people review all images across all grids. Due to overdispersion of the species occurrence data from substantial non-detections, a negative binomial generalized linear model ('MASS' package; Venables and Ripley 2002) was fit for each species with ≥30 visitation events in R (R Core Team 2021). We used our finest scale count data (i.e., visits per day for each treatment in each grid; *n* = 5 replicates per treatment) as our response variable with attractant treatment as a predictor and the control treatment set as the base comparison. We determined statistical significance at α = 0.05.

Figure 2. Wild pig (*Sus scrofa*) sounder visiting a used cooking oil attractant in the Sam D. Hamilton Noxubee National Wildlife Refuge in Noxubee, Oktibbeha, and Winston counties, Mississippi, during an investigation of non-grain attractants for wild pigs (*Sus scrofa*).

Results

We observed no camera failures (e.g., due to dead batteries) during the duration of the study period. Flash flooding events were brief (i.e., <1 day) and did not appear to differentially impede wild pig or non-target visitation. We observed 1191 visitation events among 12 mammal species, five of which were used in our analysis including wild pig, opossum, raccoon, gray squirrel, and white-tailed deer (Table 1). Remaining species included nine-banded armadillo (*n* = 21 visits), gray fox (*Urocyon cinereoargenteus*; *n* = 13 visits), bobcat (*n* = 7 visits), fox squirrel (*Sciurus niger*; *n* = 5 visits), coyote (*n* = 4 visits), eastern cottontail (*Sylvilagus floridanus*;

Table 1. Total number of visitation events along with the mean number of visitation events (± standard error) per grid (*n* = 5) for each species and treatment during an investigation of non-grain attractants for wild pigs (*Sus scrofa*) between June and July 2021 in Noxubee, Oktibbeha, and Winston counties, Mississippi.

Attractant	Wild pig	Virginia opossum	Raccoon	Eastern gray squirrel	White-tailed deer
Used cooking oil	38 (7.6 ± 3.4)	50 (10.0 ± 4.0)	30 (6.0 ± 1.1)	14 (2.8 ± 1.6)	6 (1.2 ± 1.2)
Orange marmalade	36 (7.2 ± 3.8)	77 (15.4 ± 5.3)	73 (14.6 ± 3.6)	38 (7.6 ± 3.4)	3 (0.6 ± 0.4)
Caramel syrup	29 (5.8 ± 1.1)	89 (17.8 ± 4.5)	48 (9.6 ± 5.0)	21 (4.2 ± 1.2)	5 (1.0 ± 0.6)
Strawberry jelly	24 (4.8 ± 3.3)	52 (10.4 ± 4.3)	78 (15.6 ± 3.2)	30 (6.0 ± 3.3)	7 (1.4 ± 0.7)
Sow urine	23 (4.6 ± 1.9)	4 (0.8 ± 0.6)	38 (7.6 ± 3.2)	14 (2.8 ± 1.2)	5 (1.0 ± 0.4)
Boar urine	18 (3.6 ± 1.7)	23 (4.6 ± 4.6)	14 (2.8 ± 1.1)	13 (2.6 ± 0.9)	9 (1.8 ± 0.6)
Apple jelly	10 (2.0 ± 0.7)	39 (7.8 ± 3.8)	27 (5.4 ± 2.2)	21 (4.2 ± 0.7)	2 (0.4 ± 0.2)
Hogshine	9 (1.8 ± 1.3)	16 (3.2 ± 1.3)	22 (4.4 ± 2.0)	16 (3.2 ± 1.6)	10 (2.0 ± 0.9)
Control	11 (2.2 ± 0.8)	3 (0.6 ± 0.2)	24 (4.8 ± 3.3)	12 (2.4 ± 1.2)	5 (1.0 ± 0.4)

n = 2 visits), and unidentified Rodentia (families Cricetidae and possibly Muridae (*n* = 3 visits)). Among treatments, wild pig visitations were fewest for Hogshine and greatest for used cooking oil (Table 1; Figure 2). Used cooking oil, orange marmalade, and caramel syrup collectively maximized wild pig visitation, with these treatments being 1.24, 1.19, and 0.97 times more likely to be visited than the control, respectively (Table 2).

Among non-target species, opossums visited a variety of attractants including caramel syrup, orange marmalade, strawberry jelly, used cooking oil, apple jelly, boar urine, and Hogshine (Table 1) and were 1.67 to 3.39 times more likely to visit these attractants compared to the control (Table 2). Opossums did, however, have few visits to sow urine (Table 1). Raccoons had the greatest number of visits to strawberry jelly, orange marmalade, and caramel syrup and the least number of visits to boar urine (Table 1). Raccoons were 1.18, 1.11, and 0.69 times more likely to visit strawberry jelly, orange marmalade, and caramel syrup, respectively, compared to the control (Table 2). Gray squirrels had 1.15 times more visits to orange marmalade and 0.92 times more visits to strawberry jelly compared to the control (Table 1), with visits to other attractants not different from the control (Table 2). Finally, white-tailed deer showed no specific increase in attractant-specific visitation relative to the control (Table 1, Table 2).

Discussion

Examining diverse non-grain wild pig attractants allowed us to determine that used cooking oil was an effective attractant for wild pigs that minimized non-target species visitations. While orange marmalade demonstrated similar effectiveness in attracting wild pigs, it also attracted opossums, raccoons, and gray squirrels. Although each attractant has been shown to be successful while deployed concomitantly with grain (Higginbotham 2012, Karlin and Khan 2020), we showed that these attractants can also be effective when used independently, an especially important finding considering our preclusion to using grain in our study area. Used cooking oil and orange marmalade were generally effective in attracting wild pigs throughout our study duration (i.e., 31.4% and 30.0% of monitoring days with ≥1 visitation, respectively), but this effectiveness was most evident when comparing total visitations to those of other effective non-grain attractants identified elsewhere in the southeastern U.S. For example, used cooking oil (38 visits in 70 days = 0.54 visit day^{-1}) and orange marmalade (36 visits in 70 days = 0.51 visit day^{-1}) appeared to perform similarly well to strawberry (48 visits in 100 days = 0.48 visit day^{-1}) and apple scents (43 visits in 100 days = 0.43 visit day^{-1}; Campbell and Long 2008), and although study methodologies differed, this further demonstrates utility of alternative non-grain attractants when bait is restricted.

Table 2. Negative binomial generalized linear model *β*-coefficients with standard error (SE) and *Z*- and *P*-values for each species and treatment relative to the control treatment during an investigation of non-grain attractants (i.e., treatments) for wild pigs (*Sus scrofa*) in Noxubee, Oktibbeha, and Winston counties, Mississippi. *P*-values ≤0.05 for treatments are bolded.

Species	Treatment	β	SE	Z	P
Wild pig	Apple jelly	–0.10	0.49	–0.19	0.85
	Boar urine	0.49	0.45	1.11	0.28
	Caramel syrup	0.97	0.42	2.30	**0.021**
	Hogshine	–0.20	0.50	–0.40	0.69
	Used cooking oil	1.24	0.41	3.01	**0.003**
	Orange marmalade	1.19	0.41	2.87	**0.004**
	Sow urine	0.74	0.43	1.71	0.09
	Strawberry jelly	0.78	0.43	1.82	0.07
Virginia opossum	Apple jelly	2.57	0.64	4.01	**<0.001**
	Boar urine	2.04	0.65	3.11	**0.002**
	Caramel syrup	3.39	0.63	5.39	**<0.001**
	Hogshine	1.67	0.67	2.50	**0.012**
	Used cooking oil	2.81	0.64	4.42	**<0.001**
	Orange marmalade	3.25	0.63	5.15	**<0.001**
	Sow urine	0.29	0.80	0.36	0.72
	Strawberry jelly	2.85	0.64	4.49	**<0.001**
Raccoon	Apple jelly	0.12	0.33	0.36	0.72
	Boar urine	–0.54	0.38	–1.42	0.16
	Caramel syrup	0.69	0.31	2.26	**0.024**
	Hogshine	–0.09	0.34	–0.25	0.80
	Used cooking oil	0.22	0.33	0.69	0.49
	Orange marmalade	1.11	0.29	3.78	**<0.001**
	Sow urine	0.46	0.32	1.46	0.15
	Strawberry jelly	1.18	0.29	4.03	**<0.001**
Eastern gray squirrel	Apple jelly	0.56	0.41	1.37	0.17
	Boar urine	0.08	0.44	0.18	0.87
	Caramel syrup	0.56	0.41	1.37	0.17
	Hogshine	0.29	0.43	0.68	0.50
	Used cooking oil	0.15	0.44	0.35	0.72
	Orange marmalade	1.15	0.38	3.02	**0.003**
	Sow urine	0.15	0.44	0.35	0.72
	Strawberry jelly	0.92	0.39	2.35	**0.019**
White-tailed deer	Apple jelly	–0.92	0.87	–1.05	0.29
	Boar urine	0.59	0.61	0.96	0.34
	Caramel syrup	0.00	0.68	0.00	1.00
	Hogshine	0.69	0.60	1.15	0.25
	Used cooking oil	0.18	0.66	0.28	0.78
	Orange marmalade	–0.51	0.77	–0.66	0.51
	Sow urine	0.00	0.68	0.00	1.00
	Strawberry jelly	0.34	0.64	0.53	0.60

It was curious that other attractants used, such as strawberry and apple jelly, were ineffective in attracting wild pigs, considering their effectiveness elsewhere (e.g., Campbell and Long 2008). Although there is no definitive explanation for this disparity, local conditions and study design characteristics likely influenced wild pig preferences. For example, differences in ecoregions (South Texas Plains shrub rangeland vs. Blackland Prairie bottomland hardwood forests), climates (e.g., arid vs. humid), study timing (late summer/early spring vs. mid-summer), attractant type (commercial domestic swine additives vs. simple household items), deployment method (soaked cotton in polyvinyl capsules vs. direct application), duration between rebaiting (daily vs. weekly), and local wildlife community compositions, could have influenced wild pig choices. Our findings thus demonstrate the importance of understanding attractant efficacy at local scales, or within the context of the above listed considerations. Even our identification of orange marmalade as an effective wild pig attractant, while promising given its general consistency with other research, should be understood within local contexts (e.g., use in open landscapes vs. mock corral traps; Karlin and Khan 2020). Meanwhile, purely grain-based strategies seem more universal in attractiveness for both target and non-target species, which makes them valuable when allowed and feasibly deployed (Lavelle et al. 2017). We were also limited in our ability to identify individuals across all species examined, and therefore it is plausible to conclude that individual behaviors could lead to heterogeneity in visitations across all treatments, even within the same locality.

Attractants tested in this study represented those that performed well in other wild pig research or management applications, or those commercially produced for the purpose of attracting wild pigs. While attractant performance varied considerably for wild pigs, non-target visitation is also important to consider. Depending on objectives and the acceptable level of non-target species collateral damage (e.g., stress induced by trapping), attractant use will be accompanied by some level of risk, and we demonstrated that none of our attractants solely attracted wild pigs. However, if the aim of attractants is to support non-invasive research efforts, this obviously carries lesser direct risk to non-targets, even though indirect risks associated with congregating animals can persist, such as wildlife disease transmission (e.g., bovine tuberculosis; Cartensen et al. 2011; chronic wasting disease; Plummer et al. 2018).

Wild pig visitation with few visits by non-target species was best achieved with used cooking oil, a result unobtained by orange marmalade or caramel syrup which attracted primarily opossums and raccoons. While opossum visitation was also high for used cooking oil, raccoon visitation was not, an unexpected finding given associations between raccoons and fish-scented baits in oral pharmaceutical distributions (Campbell et al. 2006, Johnson et al. 2016) and the origin (i.e., fish-fryer) of our used cooking oil. Although we desired to identify an attractant which also minimized opossum visitation, this species was attracted to all treatments except sow urine, making minimizing opossum visitations potentially infeasible. Considering high levels of opossum visitation to other attractants (e.g., fishscent; Campbell et al. 2006, Johnson et al. 2016; molasses; Goodwin and Ten Houten 1991, chicken, catnip oil; Jordan and Lobb-Rabe 2015), and their generalist omnivorous diet (Walsh et al. 2017, Greenspan et al. 2018, Hart et al. 2019), this issue is not restricted to our study area, and other attractants will likely need to be investigated if the aim is to exclude opossums.

Our work continues to demonstrate the importance of investigating attractant preferences locally. While top attractants in the literature likely hold collective value when identifying or refining the suite of candidate attractants deployed, differences among local conditions and deployment characteristics, in addition to the generalist diet of wild pigs, may lead to variation in attractant efficacy. Although strategies may also benefit from concomitant use of non-grain attractants with grain baits, costs (e.g., US$7–10 per 22.7-kg bag of whole corn relative to $2–3 per standard jar of non-grain attractant), deployment feasibility (e.g., difficulty of transporting grain baits into remote areas), and potential drawbacks (e.g., disease risks associated with concentration of non-target species such as raccoon and white-tailed deer at grain bait sites, accelerated depletion of grain by non-targets), collectively undermine the value of deploying grain in many situations and suggest the need for non-grain alternatives. Combining or alternating non-grain attractants could increase visitation rates supporting various objectives including abundance estimation (e.g., via spatial capture-recapture methods), keeping sounders interested during trap construction, and attracting new individuals otherwise unattracted to non-grain attractants. Researchers and managers are encouraged to explore such combinations and evaluate effectiveness. In conclusion, this study effectively demonstrated the value of non-grain attractants in maximizing wild pig visitations, while also identifying attractants which can minimize non-target visitations, within bottomland hardwood forests.

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Effects of Trap Door Width on Wild Pig Entrance into Corral Traps

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Abstract: Wild pigs (*Sus scrofa*) are arguably one of the greatest wildlife management challenges facing natural resource professionals and landowners in the U.S., and lethal removal by trapping is often the most cost- and time-effective means for managing populations. Whereas numerous studies have examined the effects of trap type, trap activation designs, and baits on trapping effectiveness, no studies utilizing a conditioning period and accounting for unique individuals/sounders and wild pig social structure have examined the effects of trap door width on wild pig entrance into corral-style traps. Modifying trap door width may impact wild pig entrance rates into corral-style traps with wider doors better facilitating entrance. Our objective was to examine wild pig entry times into standard three-panel corral traps with wooden guillotine trap doors of either 0.8-m or 1.2-m widths. We placed these doors on 12 traps at a study site in east-central Alabama from June–September 2014 and 2015. We positioned a motion-sensitive game camera on each trap to record wild pig visitation behavior and then began baiting each trap. We recorded the time when wild pigs initially visited the trap site, time until the first wild pig entered the trap, and the time until 50% and 100% of the sounder had entered the trap. We used camera imagery data collected from 27 solitary individuals and 47 sounders to evaluate the effect of door width on the length of time that wild pigs took to enter traps. First entry time for sounders did not differ between 0.8-m and 1.2-m widths, nor did time until entry by 50% and 100% of sounders. However, first entry time was similar among solitary individuals. Our results suggest trap door width may not have as large of an impact on entrance rates into traps as previously thought.

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Wild pigs (*Sus scrofa*) are a non-native invasive species that are expanding in range and subsequent damage across North America. They are arguably one of the greatest wildlife management challenges facing natural resource managers today (Mayer and Brisbin 2009, VerCauteren et al. 2020). As wild pig populations continue to expand, so do the tools, techniques, and strategies used to reduce their populations. Because wild pigs are highly social and often travel in familial groups termed sounders, live trapping with baited corral-style traps followed by euthanasia is one of the most frequently used methods for managing wild pig populations (Choquenot 1993, Mayer and Johns 2009, Massei et al. 2011, Bodenchuk 2014, Higginbotham 2014). This technique is relatively inexpensive and can capture numerous wild pigs at each trapping event with less effort than other commonly used techniques such as shooting, recreational hunting, hunting with the aid of dogs, and shooting over bait (Ditchkoff and Bodenchuk 2020).

The development of science-based best management practices for trapping wild pigs is a critical step towards advancing cost- and time-effective removal strategies. Several studies have examined issues related to baits and scents (Campbell and Long 2007, 2009), trap activation design (Sweitzer et al. 1997, Williams et al. 2011b), and door type (e.g., saloon, rooting, and trainer; Smith et al. 2014). For example, when examining the addition of scent attractants to reduce the mean initial arrival time at baited camera sites, Sandoval et al. (2019) found that initial sounder visitation was faster when using a wild pig urine scent attractant, whereas Choquenot (1993) observed that a female wild pig in estrous was ineffective in attracting adult males to traps. Of 11 candidate attractants, Campbell and Long (2008) found that wild pigs had greatest visitation to apple and strawberry liquid feed additives placed in the field than control capsules in Texas. While there is a wide range of baits used to attract wild pigs into traps, Foster et al. (2023) demonstrated that whole-kernel corn (*Zea mays*) is highly preferred and effective. In addition to studies on bait preferences for toxicant delivery (Campbell et al. 2006, Campbell and Long 2009, Snow et al. 2016), Williams et al. (2011a) observed that wild pigs spent longer periods feeding at sites baited with dry whole-kernel corn compared to soured corn or a combination of soured and dry corn. Furthermore, Foster et al. (2023) found that corn was more preferred over other test baits, including soybeans (*Glycine max*), split peas

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(*Pisum sativum*), mealworms (*Tenebrio molitor*), peanuts (*Arachis hypogaea*), oats (*Avena sativa*), and acorns (*Quercus fusiformis*), with the exception of earthworms (*Dendrobaena veneta*). Several studies have examined the relative efficacies of trap and door activation designs. For instance, Williams et al. (2011b) found that corral traps had nearly four times greater capture rates than box traps, while Long and Campbell (2012) reported that box traps with rooter doors (gravity activated) captured more juvenile wild pigs than box traps with side-swing doors (spring-tension activated), suggesting that the latter were more difficult for younger wild pigs to activate. However, Gaskamp et al. (2021) reported greater removal rates (as a percentage of the population) using drop nets (85.7%) and suspended traps (88.1%) relative to corral traps (48.5%). When examining different door configurations (e.g., saloon, rooter) on corral traps, Smith et al. (2014) reported that only 5% of wild pigs pushed through continuous-catch doors after the trap door had initially closed.

Because conditioning wild pigs to enter a trap is a critical aspect of the trapping process, there still exists conflicting viewpoints regarding the appropriate trap door width to best facilitate wild pig trapping. Some professional trappers suggest wider doors (e.g., >1.2 m wide) enhance overall trapping effectiveness by reducing the time required to condition wild pigs to enter a trap, presumably because they believe wild pigs do not perceive the wider entrance as a potential risk. Conversely, others contend that door width is less important and that widths as narrow as 0.9 m are sufficient. Metcalf et al. (2014) evaluated a variety of door widths (i.e., 0.9 m, 1.2 m, 1.5 m, and 1.8 m) in Texas and found no differences in wild pig entrance. However, excluding the trap conditioning period from their data, not accounting for the population's social structure, and not distinguishing between unique sounders and solitary individuals made their conclusions less robust. Our objective was to uniquely identify wild pigs and determine if entry times into corral-style traps differ between 0.8-m and 1.2-m trap doors during trap conditioning and active periods.

Study Area

Our study was conducted on contiguous private lands owned by three landowners in Macon County, Alabama. The study area was 1716 ha and consisted predominantly of loblolly pine (*Pinus taeda*) plantations and bottomland hardwood forests of various oaks (*Quercus* spp.) and bald cypress (*Taxodium distichum*). Bughall Creek, a perennial stream, bordered the study area to the west. Elevation ranged 76.2–91.4 m above sea level, and the area received approximately 137.2 cm of annual precipitation (NOAA 2022). Non-forested areas consisted of recreational food plots, with a few small agricultural and fallow fields also scattered throughout each property. Prescribed fire was used in loblolly pine stands to manage the understory for white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris gallopavo*), and northern bobwhite (*Colinus virginianus*). The owners of the property were required to not hunt, trap, or otherwise harass wild pigs during the study, although some sporadic trapping and opportunistic shooting occurred prior to this study.

Methods

Trap Design and Data Collection

The study was conducted within the context of wild pig removal operations by the U.S. Department of Agriculture (USDA) Wildlife Services from April–September (2014) and June–September (2015) on the study area. Part of the operation was to condition wild pigs to enter corral traps to increase the probability of capturing entire sounders during initial trapping events. Game cameras (Moultrie Model M880i, Pradco Outdoor Brands, Alabama) were set for three-picture bursts, with 10 sec between pictures, and 1 min between bursts, during this conditioning period to determine how many solitary individuals and sounders were using the trap, and for post-removal monitoring. Game cameras remained running throughout the entire season. It was during this conditioning period, which lasted a single day to several weeks, that we monitored wild pig interactions with corral trap doors. Two door sizes (0.8 m and 1.2 m) were based on commonly used self-fabricated design plans whereby three 0.8-m or two 1.2-m doors could be cut from one sheet of treated plywood. The duration of each conditioning period depended on how soon wild pigs became conditioned to entering the trap, but in most cases (approximately 90%) lasted <3 wk. After this conditioning period, traps were activated and checked daily until wild pigs were captured and euthanized. After the euthanized wild pigs were removed from the trap, we reactivated the trap and began monitoring for the next solitary individual or sounder to begin using the trap.

To test the effects of door width on wild pig entry, we constructed 12 corral-style traps with wooden guillotine doors. Traps were constructed using three 1.5-m × 4.9-m galvanized wire panels with a 5.1-cm × 10.2-cm mesh, formed into an approximately 4.5-m diameter circular corral, which left an opening 1.0–1.4 m wide in which a door was placed. Metal 2.1-m T-posts (approximately 14) were placed at intervals of 0.9–1.2 m around the corral, and hammered into the ground approximately 0.5 m deep, allowing the panels to be secured using baling wire or rebar ties. We constructed trap doors from 1.2-m × 2.4-m × 1.3-cm sheets of treated plywood that were cut to either 0.8 m wide ($n = 9$) or 1.2 m wide ($n = 3$). Doors were set into a frame made from 5.1 cm × 10.2 cm and 5.1 cm × 5.1 cm treated lumber to form the door assembly.

Each assembly was fastened to the T-posts at each end of the trap opening, and we used a root stick or trip wire to trigger the door.

We placed traps in areas with known wild pig activity to maximize encounters. Traps were placed in forested areas along waterways or adjacent to permanent water sources such as ponds, natural food sources (e.g., mast-producing trees), and in areas where sign (i.e., trails, wallows, and rooting) had consistently been observed. In all but two cases, traps were located >900 m apart, with most traps accessible via unimproved private roads or trails. Once each trap was placed, the door was tied open and the interior was baited with 11.3 kg of whole kernel corn, with small amounts (approximately 0.11 kg) scattered in front of the door. For most traps (i.e., approximately 90%), we used hanging, battery-operated 18.9-L game feeders to dispense corn for approximately 30 sec daily, whereas traps without automatic feeders were checked on a 3–5-day interval to ensure bait was present. We placed a motion-sensitive game camera 4–8 m from each trap at 1–2 m above ground level facing the front of each trap door set to record three picture bursts with 10 sec between pictures, and 1 min between bursts. We began monitoring traps continuously as soon as each was baited.

Each week we visited traps, changed camera memory cards, replaced batteries as needed, and uploaded images. We visually inspected each image to identify individual wild pigs using combinations of pelage characteristics, relative size, sex, and other unique identifying marks (e.g., torn ear; Holtfreter et al. 2008). We also identified wild pigs as either solitary individuals or members of a sounder based on absence or presence of other wild pigs, respectively. Sounders were distinguished from other sounders based on combinations of total number observed, relative size (i.e., age), color, presence of unique pelage characteristics, and sex distribution within the sounder. There were no noticeable instances of individuals moving between sounders. This research was approved by the Auburn University Institutional Animal Care and Use Committee (IACUC Protocol #2015-2744).

Statistical Analysis

We defined a sounder as two or more wild pigs which we consistently observed across multiple observation periods. For sounders, we recorded first entry time, time required for 50% of the sounder to enter each trap type (i.e., 0.8-m or 1.2-m door width), and time required for 100% of the sounder to enter each trap type. We defined first entry as the elapsed time (in minutes) from the date and time any wild pig from a sounder was first observed on camera until one or more wild pigs from that sounder entered the trap. Time to 50% (in minutes) began on the initial date and time a sounder was first observed at the trap and continued until 50% of the sounder entered the trap. Similarly, time to 100% (in minutes) began from the initial date and time the sounder was first observed on camera until all members of the sounder had entered the trap at least once. We considered a wild pig to have entered a trap if the entire individual passed through the door. In many cases, cameras did not capture images until after some or all individuals had already entered the trap. For these instances, we assigned a zero for time to 50% or 100% if we observed the respective percentages of wild pigs within the trap. On rare occasions, we observed the same sounder at multiple traps of the same door width, and these were not reintroduced as "new" sounders in our dataset. We did not observe any instances in which a sounder entered traps of varying door widths. For solitary individuals, we only measured first entry time using the same criteria as above. We used linear mixed-effects models using package 'lme4' (Bates et al. 2015) in program R (R Core Development Team 2022) to evaluate differences between 0.8-m and 1.2-m door widths independently for first entry time, time to 50%, and time to 100% for sounders, and first entry time only for solitary individuals. To avoid potential pseudoreplication and to account for variation in multiple solitary individual/sounder observations at an individual trap, we included observations (i.e., distinct solitary individuals/sounders) nested within individual traps as a random effect. We converted response values (in minutes) to days for reporting. All tests were significant at $P<0.05$.

Results

From 2014–2015, we observed 27 solitary individuals and 47 sounders from >400,000 images. We recorded imagery from an average of 7 different solitary individuals and/or sounders (range = 2–10) per corral trap, while 9 solitary individuals and 3 sounders were observed outside of traps but never entered, regardless of door width. Our random effect of observations within individual traps was not statistically significant and therefore was not included in our models.

First entry time for sounders (Table 1) did not differ between 0.8-m ($\bar{x}=0.7$ days, SE = 0.4) and 1.2-m ($\bar{x}=3.3$ days, SE = 2.5) wide doors ($P=0.14$). Overall mean first entry time for sounders was 1.4 days (SE = 4.9). Likewise, first entry time for solitary

Table 1. First entry time (in days) for sounders and solitary individuals, and time until 50% and 100% of a sounder had entered through 0.8-m ($n=9$) and 1.2-m ($n=3$) wide doors on gates affixed to corral traps in Macon County, Alabama, 2014–2015.

	Sounder				Solitary individual			
	0.8 m		1.2 m		0.8 m		1.2 m	
Entry	Mean	SE	Mean	SE	Mean	SE	Mean	SE
First	0.7	0.4	3.3	2.5	7.2	3.7	12.5	9.1
50%	0.4	0.2	1.2	1.0				
100%	3.9	1.8	5.2	4.2				

individuals did not differ between 0.8-m ($\bar{x} = 7.2$ days, SE = 3.7) and 1.2-m ($\bar{x} = 12.5$ days, SE = 9.1) wide doors ($P = 0.59$). Time for 50% sounder entry did not differ between 0.8-m ($\bar{x} = 0.4$ days, SE = 0.2) and 1.2-m ($\bar{x} = 1.2$ days, SE = 1.0) wide doors ($P = 0.25$). Finally, time for 100% sounder entry did not differ between 0.8-m ($\bar{x} = 3.9$ days, SE = 1.8) and 1.2-m ($\bar{x} = 5.2$ days, SE = 4.2) wide doors ($P = 0.84$).

Discussion

Consistent with Metcalf et al. (2014), door width did not appear to influence the willingness of wild pigs to enter traps. Many sounders and solitary individuals readily entered traps soon after first being detected, regardless of door width. However, we noticed that larger (i.e., older) wild pigs tended to be more hesitant than smaller (i.e., younger) wild pigs in entering traps, a common observation which may relate to the perceived naivete of younger individuals. While we observed greater variation in mean entrance times through 1.2-m doors, this was likely a function of sample size and may have contributed to our inability to detect differences between door widths. Although we attempted to follow all sounders from initial observation until all members became conditioned to the trap, this was not always possible given camera failures, the practical need to remove wild pigs, and/or failure to communicate among researchers and field staff as to which sounders had been observed sufficiently and were available to be trapped and euthanized. Moreover, we did identify unique sounders and solitary individuals, but we did not have confidence in our ability to consistently assign sex and age to all individuals throughout all images collected during a sounder-trap interaction event. Because of this, we could not test the effects of age or sex on entry times, which has also been a point of contention among wild pig trappers. Therefore, further research is needed to explore potential differences that exist between sexes and ages of wild pigs and their respective willingness to enter traps.

Our research was limited in that we did not test door widths >1.2 m, and therefore, our results cannot be used to posit the effects of wider doors (e.g., 1.8 m, 2.4 m) that are also commercially common. We can only speculate that a notably greater door width will reduce trap entrance times. However, given first entry times of <1 wk for sounders in our study, which is consistent with other observations (Smith et al. 2014), any gains realized by using wider doors may be negligible. It is important to note that wild pigs in our study area were not actively managed by the landowners during the study and only received minimal management pressure in the two years preceding this study. Much of our research was also conducted during the summer months, a time of nutritional stress for wild pigs due to food availability and the energetic expenses of parturition and lactation (King and Williams 1984). As such, entry times observed in our study may be shorter than those observed in areas where wild pigs receive greater management pressure, or in relation to seasonal access to pulse resources (e.g., agricultural crops, hard mast). However, several solitary individuals and sounders never entered traps and only fed along trap edges. This observation may not relate to door width but instead to previous experiences these wild pigs may have had with traps in the area. Entry times were more variable and longer for solitary individuals than for sounders, which may have been a function of age (i.e., size as a proxy) and total number of individuals interacting with, and perhaps influencing, the likelihood of individuals entering a trap. Whereas most solitary individuals readily entered traps, one individual would not enter until 43 days after it was first detected on camera.

Corral trapping continues to be a common and, in many cases, a time- and cost-effective means for landowners and natural resource managers to reduce local wild pig populations. However, given the lack of apparent differences between sounders and solitary individuals during their interactions with varying trap door widths, trappers may want to emphasize other facets of the trapping process (e.g., trap placement, baiting, monitoring) that may provide more substantive effects on efficiency and effectiveness.

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Status of Historical Translocations of Gopher Tortoises Outside of Their Geographic Range in Central Alabama

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Abstract: The gopher tortoise (*Gopherus polyphemus*) is a species of concern in the southeastern United States, and its distribution is within the range of the longleaf pine (*Pinus palustris*). One conservation strategy within the state of Alabama has been translocation of adult tortoises to other areas with longleaf pine and sandy soils, including areas outside the current accepted species' range. Prior examples of such tortoise translocations occurred in two counties in central Alabama: one in the 1960s in Macon County and another in the 1980s in Autauga County. Both introductions occurred near the Coastal Plain fall-line, which is deemed the northernmost landmark designation that tortoises were historically presumed to reside. The status of these translocated tortoise populations had not been recently assessed. Therefore, we surveyed the two locations, captured individuals, and qualitatively examined the minimum known number of alive adult tortoises. We found populations of tortoises at both translocation sites, including evidence of reproduction and recruitment. Notably, we found two marked tortoises (one at each of the two relocation sites) from the original translocations, indicating that translocated tortoises survived in these new areas for 30 and 49–56 years, respectively. Although inference about translocation success is limited by overall low tortoise projected densities, our results suggest tortoise populations can persist in areas of Alabama outside their mapped geographic range, including on soil types not documented previously.

Key words: introduction, population density, reptile, relocation

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The gopher tortoise is a keystone species in the Coastal-Plain of the southeastern United States, having more than 330 commensal species documented using its burrows (Jackson and Milstrey 1989, Lips 1991, Kinlaw and Grasmueck 2012, Dziadzio and Smith 2016). Gopher tortoises prefer soft, sandy soils, with open canopies and an open understory dominated by herbaceous groundcover (Kaczor and Hartnett 1990). While gopher tortoises are mostly associated with mature, longleaf pine (*Pinus palustris*) forests within upland sandhill communities, they also occur in other cover types, including xeric hammocks and ruderal communities (Auffenberg and Franz 1982) and in areas highly fragmented by land use change (Noss 1995, Ashton and Burke 2007). Due to the effects of habitat loss and associated risks to the resulting small, isolated populations, such as disease prevalence (e.g., Upper Respiratory Tract Disease) and high nest mortality, the gopher tortoise is state-protected throughout its range and listed as federally threatened by the U.S. Fish and Wildlife Service in Louisiana, Mississippi, and in Alabama west of the Mobile and Tombigbee Rivers (TESII 1995).

To aid in gopher tortoise recovery efforts, translocations, or the relocation of individuals from one area to another (Berry 1986, IUCN 2013, Morris et al., 2021) have been used in many states as a strategy to establish populations in new areas (Tuberville et al. 2005, Soehren 2006). Post-release monitoring following translocation is important to assess the success of the translocation for newly released animals and can determine the presence of harmful effects from the move (Seddon and Armstrong 2016). Unfortunately, post-release monitoring has not been a common practice until more recently, especially with herpetofaunal species like the gopher tortoise, and thus the success of translocation efforts and their effects on recipient communities are often unknown (Dodd and Seigel 1991, Tuberville et al. 2005).

The documented range of gopher tortoise encompasses 25 counties in central and southern Alabama (Figure 1), occurring within the Coastal Plain and along its accompanying northern sandhill ridge in more northern counties (e.g., Speake 1986, Spillers and Speake 1993, Guyer and Bailey 1993, Patton 1996). At least 20 of these counties exhibit soils preferred by tortoises for burrowing, which is one of the habitat characteristics used to justify

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translocations (Guyer and Bailey 1993, Guyer et al. 2011). Translocation of gopher tortoises occurred in at least five documented conservation projects in Alabama since at least 1967, typically as attempts to preclude conservation status listings (Speake 1986, Speake 1987, Soehren 2006).

Information regarding these translocations and persistence of translocated populations has been limited to personal communications (D. Spillers, Fort Rucker, C. Guyer, Auburn University, B. Abbott, Alabama Department of Conservation and Natural Resources [ADCNR], and E. Shelton-Nix, ADCNR, personal communications), field notes (Patton 1996), or final research reports submitted to the ADCNR (Speake 1986, 1987). Between 1967 and 1986, multiple translocations of gopher tortoises were made by researchers from Auburn University to sites in Macon and Autauga counties (Figure 1), to areas where the species had not been documented. From 1967 to 1974, 30 adult tortoises of unknown sex were hard-released on private property in northeastern Macon County approximately 5.15 km north of Alabama Highway 80 (D.A. Speake, R.H. Mount, and K. Patton, Auburn University, personal communications; roughly 86.9–114.9 km north of the species range in either Bullock or Russell Counties, respectively). Individuals were marked with rounded drill bits along their marginal scutes (Figure 2a). At the time of release, no tortoise burrows were observed in the area (R.H. Mount and K. Patton, Auburn University, personal communications). On 1 April 1986, an additional 25 adult tortoises (10 females and 15 males) marked with rounded drill bits along their marginal scutes were hard-released in locations around Autauga County (specifically in or near the Autauga Wildlife Management Area, approximately 19 km northwest of Prattville; Speake 1986) approximately 105.25 km north of their geographic range.

To date, there have been two known attempts to assess the success of the Macon County translocation: Patton (1996) captured and marked nine adult tortoises in 1992 with a triangular file along the marginal carapace scutes (Figure 2b). In 1996, seven adult tortoises were captured, including three recaptures from 1992 near the same mapped burrow (Patton 1996). Juveniles were also noted during recaptures, indicating that tortoises reproduced in the

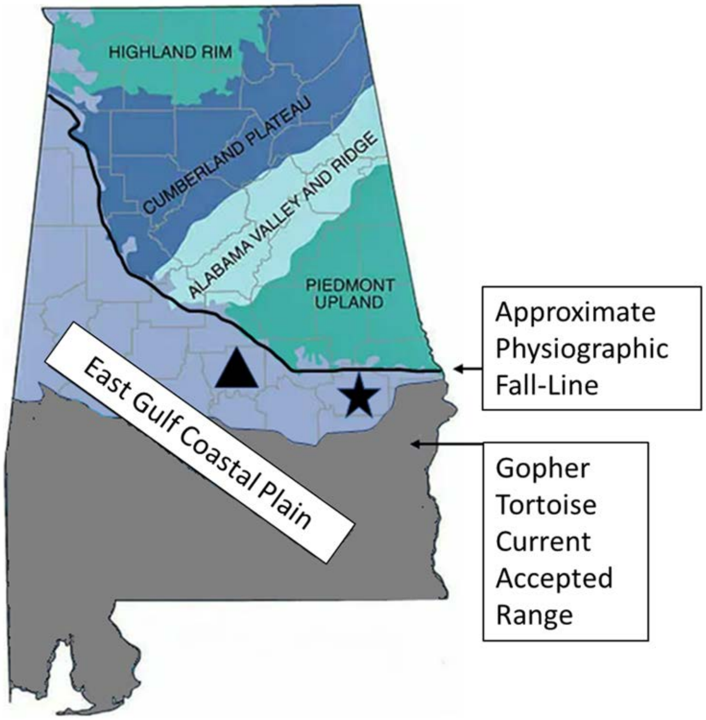

Figure 1. Survey sites of translocated gopher tortoise (*Gopherus polyphemus*) populations in Autauga (black triangle) and Macon (black star) counties, Alabama, June–July 2016. Colors represent the physiographic breakdown of the five major land formations in Alabama, including the East Gulf Coastal Plain, where the gopher tortoise naturally occurs (gray), occurring south of the fall-line.

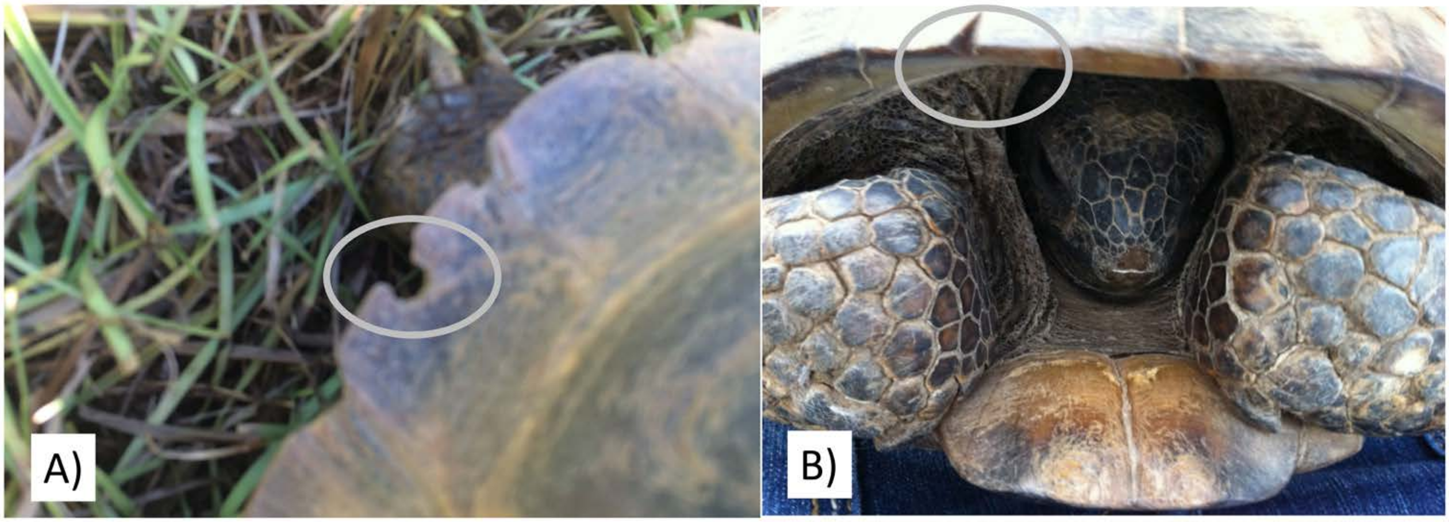

Figure 2: Tortoise carapace field marking methods: (A) Round filing on carapace is the older marking method from an Autauga County, Alabama, tortoise (originally released in 1986), and (B) triangular filing method of marking tortoise carapaces use in 2016 surveys.

translocated area, consistent with the reproduction of the original translocated individuals. However, no tortoises from the original release were captured during the surveys, and sex or age of the individuals was not recorded (Patton 1996). The Autauga County translocation effort was originally a study to assess gopher tortoise dispersal and habitat use in new areas, and the translocated individuals were initially monitored via radio telemetry to follow their movements. This translocated tortoise population was only resampled for mark-recapture individuals and number of burrows in 1987, one year after release, in which 19 of the originally released tortoises were recovered and signs of nesting were observed (Speake 1986, 1987).

Because gopher tortoise populations in Macon and Autauga counties have not been surveyed in decades, their status was unknown. Therefore, we sought to: (1) ascertain if the translocated gopher tortoise populations were still present, and (2) note any evidence of reproduction. Knowledge about the status of these translocated populations is valuable to conservation efforts for tortoises in Alabama and may provide valuable insights about the potential for future translocations of tortoises outside of their current range.

Study Area

We conducted surveys at two sites in Alabama: (1) 32.37 ha of privately owned land in southern Macon County and (2) 984 ha of Autauga County's Wildlife Management Area (AWMA, including the area of original tortoise translocation; Speake 1986) now owned by the ADCNR. Both sites had plant species composition characteristic of the longleaf pine ecosystem, including longleaf pine, turkey oak (*Quercus laevis*), winged sumac (*Rhus copallinum*), prickly pear cactus (*Opuntia humifusa*), loblolly pine (*Pinus taeda*), southern red oak (*Quercus falcata*), and a variety of grasses and forbs. In AWMA, soils included combinations of Troup-Blanton-Alaga and Troup-Shibuta-Bibb soils, which are sandy loam soils with intermittent clay components (Speake 1986, NRCS 2023), while the Macon County site included Uchee, Cowart, and Marvyn type soils, which are inherently more rocky and less sandy with varying proportions of loam (NRCS 2023).

Methods

During June–July 2016, we conducted 2-wk surveys at each site to locate tortoise burrows. Two to four viewers conducted a systematic scan for all burrows (active and inactive) at every site starting from a centralized location (Guyer et al. 2012). Surveys for burrows continued in a radiated fashion from each located burrow until no new burrows could be located within a minimum of 100 meters. Once a burrow was located, it was marked with flagging tape, given an identification number, and the GPS coordinates were recorded. Roads, rocky outcrops and montane areas, property boundaries, and densely wooded areas with thick canopies served as delimited areas excluded from surveys. We identified burrows as active or inactive, in which an active burrow was defined by fresh tortoise tracks, an unobstructed or freshly dug D-shaped opening, the sound of tortoise thumping inside the burrow, or other indicators of tortoise presence outside the burrow (e.g., feces, nail clippings, or the tortoise itself; Hermann et al. 2002, Styrsky et al. 2010). An inactive tortoise burrow had the same obvious D-shaped opening but with an obstructed entrance and no fresh tracking leading into or out of the burrow with possible leaf litter debris. Importantly, inactive burrows were not distinguished from potentially abandoned burrows.

We trapped all active adult burrows using Tomahawk (Tomahawk Live Trap, Hazelhurst, Wisconsin) live animal traps of various sizes (similar to and including Model 207) placed and set over the burrow opening. Traps were weighted down with dirt substrate and covered with burlap and vegetation for shade. We checked all traps at least twice daily over a 2-wk period. All captured animals were measured and sampled for blood unrelated to this study. Upon capture, tortoises were given a unique identification mark with a triangular file along the marginal scutes if they were not otherwise marked (Figure 2b). Because the number of captured tortoises differed from the number of active burrows, we indexed projected population density two ways: by using the observed number of tortoises captured (minimum number alive: MNA) and the observed number of burrows deemed active. Both methods have traditionally been used to assess gopher tortoise populations (McCoy and Mushinsky 1992, Hermann et al. 2002, Guyer et al. 2011, Guyer 2012). At each site, the number of active burrows and tortoises captured were divided by the number of hectares surveyed to obtain an index of burrow density and a tortoise density (Guyer et al. 2012). Only adult burrows were included in burrow density estimates. Burrow density was meant to be an index of tortoise activity or movement within the areas, whereas tortoise density was interpreted as an estimate of minimum potential population density at a given site, based on number of captured tortoises.

Results

During the 2016 surveys, we found 34 burrows (19 active, 9 inactive, and 6 juvenile) across the two sites. In Macon County, we found 12 adult burrows, with five being active. Approximately six hatchling/juvenile burrows were found but were difficult to assess for occupancy. At AWMA, 16 adult burrows were found, of which 14 were active. Hatchling and juvenile burrows were observed but were not counted.

Traps set at active adult burrows resulted in an 80% capture rate

Table 1. Summary results from surveys of two gopher tortoise translocated populations in Autauga and Macon counties, Alabama from June to July 2016.

Site	Active burrows	Inactive burrows	Juvenile burrows	Hectares surveyed	Tortoises captured	Burrows ha^{-1}	Tortoises ha^{-1}	Capture efficiency
Autauga	14	2	NA	984	7	0.02	0.007	50%
Macon	5	7	6	32.37	4	0.4	0.12	80%

in Macon County and 50% in AWMA (Table 1). Eleven adult tortoises were captured: seven at AWMA (three males; four females) and four at our Macon site (two males; two females; Table 1). We captured two male tortoises from the original translocations, identified by unique markings of rounded drilling on their carapace scutes (i.e., from the Patton 1996 study; Figure 2). One individual was at the AWMA site, approximately 30 years after its release, and the other at the Macon site, 49–56 years after its release. Both individuals had carapaces of nearly smooth scutes (e.g., barely any visible annuli to count rings for determining age). Burrow and tortoise densities were calculated at each site to be 0.4 burrows ha^{-1} and 0.12 tortoises ha^{-1} in Macon County, and 0.02 burrows ha^{-1} and 0.007 tortoises ha^{-1} in AWMA (Table 1). For the first time noted, tortoises were also found using Uchee and Cowart series soils in this study.

Discussion

In this study, we re-examined the presence and density of gopher tortoises translocated to two sites outside of their traditionally recognized range in central Alabama. We found adult, juvenile, and hatchling individuals and burrows at both central Alabama translocation sites, indicating the translocations were successful in establishing new populations. While naturally occurring gopher tortoise populations fall short of the Coastal Plain fall-line, results from this study suggests that the species can persist within this area and may be able to do so elsewhere within the northern extent of the East Gulf Coastal Plain. We observed gopher tortoises outside of the original translocation boundaries (and our study area), including on neighboring private properties at our Macon County site. Efforts to engage private landowners around our study area to gain permission to assess adult and juvenile tortoises not counted during this study could provide a more accurate regional population estimate and inform additional characteristics of habitat use.

Our recaptures of translocated individuals from both original release sites were unexpected. Given that only mature tortoises were originally translocated, the recaptured tortoise from Autauga County was likely older than 42 years of age and the recaptured tortoise from Macon County was likely at least 61 years old (i.e., if adult tortoises were released around the first year of sexual maturity, approximately 12 years of age or when the carapace exceeds 180 mm; McRae et al. 1981). However, the overall low projected tortoise densities from MNA at both sites calls into question the sustainability for long-term success of the translocations due to dispersal or mortality. One concerning caveat for these low densities is that small populations of gopher tortoise do well only when land is managed well for the species (Folt et al. 2021), but much of the original translocated area, like most gopher tortoise habitat (Wigley et al. 2012), was located on and around private property, in which land management practices have not always been conducted specifically to benefit the species. The highest projected tortoise density from our MNA index occurred at the Macon County site (0.12 tortoises hectare^{-1}). This projected estimate of tortoise density is similar to densities found in Conecuh National Forest (e.g., 0.14–0.32 tortoise ha^{-1}; Goessling et al. 2020), though our MNA is based on a much smaller area.

In the recognized gopher tortoise range, such as in southern Alabama, sandy-loam varieties of soil (i.e., Alaga, Blanton, and Troup soils) are common and considered priority gopher tortoise soils because they are >1.0 m in depth to facilitate deep burrow creation and digging. Other moderate or suitable tortoise soils are Florala and Shubuta soils (0.5–1.0 m in depth; Guyer et al. 2011; Guyer et al. 2012). AWMA had Troup-Blanton-Alaga and Troup-Shibuta-Bibb soils, similar to that of what is found in the southern Coastal Plain. Interestingly, even though AWMA had the lowest burrow and tortoise projected densities, priority and suitable soils of Troup-Blanton-Alaga and Troup-Shibuta-Bibb combinations were found commonly in a predominately sandy-loam distribution in areas where tortoises burrowed, suggesting that AWMA has soil characteristics conducive with supporting tortoises (Speake 1986, NRCS 2023). At the Macon County site, however, the most common soil types found were of the harder/rockier varieties of the Uchee and Cowart Series (UcB and UcE2; NRCS 2023). To our knowledge, this is the first study to document the use of Uchee or Cowart series soil-types by gopher tortoises. Since Uchee and Cowart sandy loam soils have not been ranked in terms of their usage by tortoises, future studies should examine these soils further, as well as soil impact on aggregated burrow distributions that may structure tortoise social interactions.

Our survey indicates that the translocations made in the 1960s and 1980s to an area outside the purported range of the gopher tortoise have created disjunct tortoise populations with reproduction occurring. Whether these translocations should have occurred outside of the tortoise's recognized range remains an open question. Though translocation may be an effective conservation strategy for the species, the subject is debated due to an insufficient understanding of translocation success from poor post-release monitoring and of how these translocations could affect other resident native species (Ricciardi and Simberloff 2009). Because we do not know if tortoises were ever native to this area (due to zero or limited documentation), this translocation should be viewed with caution. Future monitoring of translocation sites should also include impacts to all other wildlife (e.g., competition, disease, or other mechanisms) as well when surveying tortoises.

Given the long-term persistence of both translocated populations, we suggest that tortoises located in Macon and Autauga counties should be included in future statewide evaluations of tortoise conservation status and management planning. Despite the persistence of both populations, there is a need to assess population growth rates to determine whether these central Alabama populations are viable, and if not, whether efforts should be taken to bolster the populations. One limitation of our study is the limited data collected on hatchling and juvenile burrows. Another limitation is that we were only able to obtain permission from one of four landowners with tortoise presence in Macon County near the original translocation. Because we were only able to survey 32.37 of approximately 200 hectares of possible translocation terrain, the overall status of this population remains unknown. Therefore, we recommend additional engagement with private landowners to gain further insight into the extent of the spread of gopher tortoises in these areas due to migration and recruitment since their translocated release. Most importantly, this qualitative study shows that tortoises survive outside of the currently recognized habitat characteristics (e.g., soil types), even beyond that of their historically recognized range. This information is important to tortoise management going forward considering rapid urbanization and their ever-fragmenting habitat range in the southeastern U.S.

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Second Guessing the Maximum Likelihood Estimator Values for Bat Surveys

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Abstract: The U.S. Fish and Wildlife Service allows acoustical surveys and automated identification software to determine the presence of the endangered northern long-eared bat (*Myotis septentrionalis*) and Indiana bat (*Myotis sodalis*). Analytical software is required to assess presence probability on a site-night basis using a maximum likelihood estimator (MLE) that accounts for interspecific bat misclassification rates. The current standard for occupancy is a returned MLE P-value < 0.05 at the nightly level irrespective of the number of files identified as either northern long-eared bats or Indiana bats. These MLE P-values can vary based on presence of other bat species with similar calls and the relative proportions of all species recorded. Accordingly, there is concern that with few nightly northern long-eared bat or Indiana bat recordings or the presence of large numbers of high-frequency bats, false-negative findings from a swamping effect could result. Using data collected in 2020–2021 by the U.S. Fish and Wildlife Service to set nationwide acoustic monitoring guidelines, we examined the relationship of returned software MLE P-values from 4873 site-nights of acoustic detector data relative to nightly counts of northern long-eared bats and Indiana bats, overall counts of other high-frequency bats, and habitat cover type. For both northern long-eared bats and Indiana bats, nights with one or more echolocation pass files identified as either species but above the MLE P-value threshold largely occurred where nightly counts of the target species was <15 and their proportion to the count of high-frequency bat species was low. We followed this analysis with a simulation using a known call library and observed similar patterns. Accordingly, with few nightly echolocation passes, *post-hoc* visual assessment following automated software identification easily could be undertaken. Evidence of swamping by other high-frequency species causing positive file identification creating false-negative or false-positives of northern long-eared bats and Indiana bats was not apparent at nightly counts of either species > 10.

Key words: acoustic sampling, acoustic swamping, echolocation pass count, *Myotis septentrionalis*, *Myotis sodalis*

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After the advent and subsequent spread of white-nose syndrome (WNS) in the eastern United States, the U.S. Fish and Wildlife Service (USFWS) has shifted its reliance from mist-netting surveys to acoustical surveys for determining the presence or probable absence of the Federally Endangered northern long-eared bat (*Myotis septentrionalis*) and Indiana bat (*M. sodalis*; Armstrong et al. 2022, USFWS 2022). Current USFWS guidelines for acoustical monitoring acceptance specify use of automated bat identification software that employs a maximum likelihood estimator (MLE) scoring of software confidence of species presence on a nightly basis (Ford et al. 2023). Whereas all commercially available bat identification software programs provide a file-by-file call identification, assumed presence must account for known species misclassification rates (Britzke et al. 2002), i.e., high overlap of Indiana bats with little brown bats (*M. lucifugus*), to move from an ambiguous determination of presence of a given species to one with higher certainty (Nocera et al. 2019). Because of the regulatory and land management implications for false northern long-eared bat or Indiana bat presence, when not actually identified via physical capture (Vermont Fish and Wildlife Department 2009, Ford et al. 2016, Silvis et al. 2016, Schroder and Ward 2022), the USFWS has set a conservative nightly MLE threshold of $P < 0.05$ for accepting the presence of both these species (USFWS 2022). The MLE scoring at the nightly level is sensitive to the software user's input of possible species which may have different combinations of confusion matrix misclassification rates as well as to the admixtures of individual species files identified and the ratios of species noted therein (Britzke et al. 2013, Nocera et al. 2019). However, this

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stringent MLE scoring to prevent false positive outcomes could come at the cost of greater false negatives. For example, in many parts of the post-WNS landscape, one or two Indiana bat echolocation call files may not reach the USFWS MLE threshold in the presence of an equal or slightly greater number of little brown bat files or other high-frequency (>35 kHz) species such as eastern red bats (*Lasiurus borealis*; Britzke et al. 2011), resulting in false-absence determinations. Conversely, encountering high rates of acoustic activity near large, colonial day-roosts of little brown bats and gray bats (*M. grisescens*) or in areas with numerous eastern small-footed bats (*M. leibii*) conceivably could produce potentially significant MLE values for both false-negative or false-positive file identifications of northern long-eared bats and Indiana bats (Britzke et al. 2002, Janos 2013, Kaiser and O'Keefe 2015, Nocera et al. 2019).

Since 2017, the USFWS and numerous municipal, state, federal, and private organization cooperators have conducted summer acoustical sampling to develop metrics for the necessary level-of-effort (LOE) for regulatory clearance purposes. These surveys occurred within the historical distribution of the northern long-eared bat and Indiana bat and in close proximity to contemporary maternity colonies where presence is known (Barr et al. 2021, Armstrong et al. 2022). From data collected in 2020–2021, Ford et al. (2023) showed that when restricted to nightly counts with an MLE $P < 0.05$ for northern long-eared bats and Indiana bats, nightly echolocation passes were significantly greater at sites with confirmed maternity activity than sites simply within the historic distribution. Logically, these values provide a body of evidence that suggests acoustic results have the potential to be used as a screening tool to not only establish presence but also identify potential maternity colony locations in future survey efforts. Ford et al. (2023) used a conservative USFWS MLE threshold ($P < 0.05$), which excluded 56% and 51% of site-nights where individual northern long-eared bat and Indiana bat echolocation files were identified, respectively. However, assessments of the conditions and characteristics of when northern long-eared bat and Indiana bat echolocation passes are noted by identification software have not yet been addressed. Questions persist regarding MLE-induced false-negatives, which may occur on nights with low overall and/or target bat activity, or alternatively, from an acoustic "swamping" by high numbers of bat passes of species with overlapping echolocation characteristics that might cause MLE *P*-values to be errantly above the USFWS threshold when present or below the threshold when not present.

Using acoustic data from 12 states, collected during 2020–2021 (Armstrong et al. 2022), we modeled MLE *P*-values at known maternity colony areas based on pass counts of northern long-eared bats and Indiana bats when nonsignificant (MLE $P > 0.05$) presence statistics were returned. We predicted that low (<10) nightly pass counts of northern long-eared and Indiana bats would result in nonsignificant MLE determinations and therefore false-negative outcomes, largely irrespective of their ratio to other high-frequency bats. Conversely, we predicted that MLE uncertainty would increase when the ratio of northern long-eared bats and/or Indiana bats was low relative to high-frequency bats, even if nightly counts were higher (>10). Lastly, based on the findings of Ford et al. (2023), we predicted that identification swamping effects would be most associated with riparian areas where overall bat species richness and activity are highest.

Methods

We conducted acoustic surveys at 20 sites in 12 states (Alabama, Arkansas, Kentucky, Indiana, Illinois, Missouri, New Jersey, Ohio, Tennessee, Virginia, West Virginia, and Wisconsin) where maternity colonies of northern long-eared bats and Indiana bats were known to occur. These sites spanned the Appalachian Plateau, Central Lowlands, Coastal Plain, Interior Low Plateau, Piedmont, and Ozark Plateau physiographic provinces (Figure 1). For a more detailed study site description see Ford et al. (2023).

In these 12 states, we deployed acoustic detectors at 20 sites ($n = 64$ detectors) from 15 June–15 August 2020 and 15 May–15 August2021 to support the USFWS Range-wide Indiana Bat and Northern Long-eared Bat Survey Guidelines (USFWS 2022). The sites were selected based on recent (<5 yr) post-WNS records of maternity activity or proximity (8 km) to currently known maternity colonies where biologists generally would accept software results without subsequent visual vetting (Armstrong et al. 2022). Following the methods described by Barr et al. (2021), at each site, we placed 1–2 detectors in each of three broad cover types: forest, forest-field edge, and forested riparian following the site placement guidelines outlined by the USFWS guidelines (USFWS 2022). At each site, we cable-locked detectors to trees and mounted microphones on 3-m tall poles approximately 2–3 m from the bole of the tree. All detectors deployed were Wildlife Acoustic SM4 ZC with SMM U2 omni-directional microphones (Wildlife Acoustics Inc., Maynard, Massachusetts) except Ouachita-St. Francis National Forest in Arkansas where we used Anabat SD2s with "Stainless" directional microphones (Titley Scientific, Columbia, Missouri). We replaced detector batteries and downloaded data cards at 6-wk intervals at each site. Each detector was set to default settings per USFWS recommendations (USFWS 2022).

Following data collection and collation, we used the 4.2.0 classifier of Kaleidoscope (v. 5.1.0, Wildlife Acoustics) at the "0" setting to identify bat passes to species, record nightly pass counts, and calculate species-specific MLE probability of presence of known or potentially present bat species at each site (USFWS 2019). We used signal detection parameters of 8–120 kHz frequency range, 2–500 ms pulse length, 500 ms inter-syllable gap, and 5 pulses for species assignment (Ford et al. 2023). We proceeded without *post hoc* visual echolocation pass assessment because this identification package had been shown to be 100% accurate with regard to eliminating false negatives of northern long-eared bats and Indiana bats and 80–90% accurate with regard to eliminating false positives for both species (USFWS 2019). Additionally, we had high confidence in knowing the true status of maternity colony activity for both bat species from when these data were collected (Ford et al. 2023). For analyses, we retained all nights without precipitation at each site and detector location, as determined by site-specific or nearest Meteorological Terminal Aviation Routine records (Iowa Environmental Mesonet 2021). We also required that at least one nightly echolocation pass for an individual detector be identified as either northern long-eared bats, Indiana bats, or both, regardless of MLE *P*-value. We used a generalized linear model with a Poisson distribution and log-link function in SAS 9.4 (PROC GENMOD; SAS Inc. 2020) to assess the relationships of returned nightly MLE *P*-values for northern long-eared bats and Indiana bats, respectively, with: 1) the absolute count by detector night for either species; 2) the ratio of either northern long-eared bats or Indiana bats nightly echolocation passes to the sum of all high-frequency bat passes recorded on that night (eastern red bat, southeastern bat [*Myotis austroriparius*], gray bat, eastern small-footed bat, little brown bat, northern long-eared bat, Indiana bat, and tricolored bat [*Perimyotis subflavus*]); and 3) cover type. Because we anticipated that the ratio covariate would positively influence the MLE *P*-value response at low and high ratios, we entered it as a quadratic term. Following our test of field data, we created 800 simulated site-nights from the known bat species echolocation call library that is maintained to test the accuracy of automated identification software by creating the conditions observed from field data in terms of low to high counts of northern long-eared bats and Indiana bats and low to high ratios of counts therein relative to other high-frequency bat species (USFWS 2019). Our analysis of simulated data was the same as with field observations though without the inclusion of a cover type covariate. We checked each model for goodness-of-fit and over- and under-dispersion by examining residual plots.

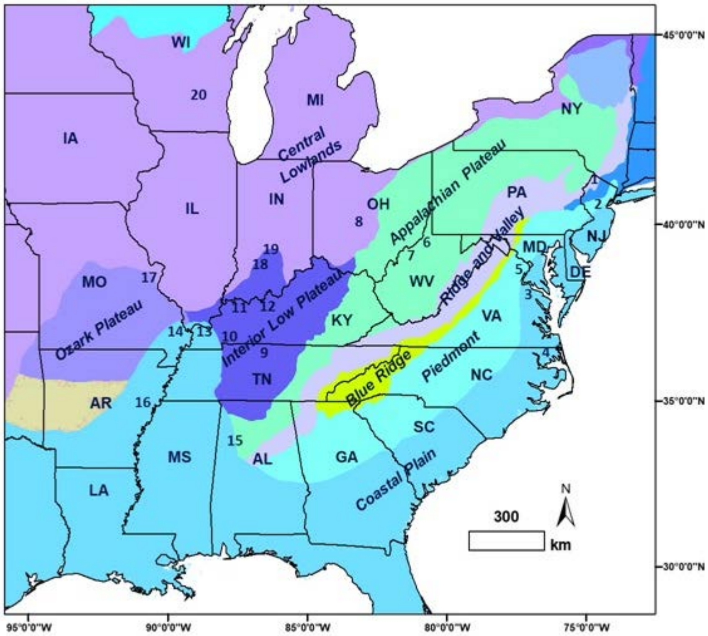

Figure 1. Acoustic survey sample sites (see text), 2020–2021 in the eastern U.S. across physiographic provinces (colors) by northern long-eared bat (*Myotis septentrionalis*) maternity colony (MYSE) and/or Indiana bat (*Myotis sodalis*) maternity colony (MYSO), 1. Wallkill National Wildlife Refuge (NWR), New Jersey (MYSE, MYSO), 2. Great Swamp NWR, New Jersey (MYSE), 3. Fort A.P. Hill Military Reservation (MR), Virginia (MYSO), 5. North River Gameland, North Carolina (MYSE), 5. Prince William Forest Park/Marine Corps Base-Quantico, Virginia (MYSE,), 6. Louis Wetzel Wildlife Management Area (WMA), West Virginia (MYSE), 7. The Jug WMA (MYSE), 8. Battelle Darby Metro Park, Galloway, Ohio (MYSO), 9. Wilson County Artificial Roost, Tennessee (MYSO), 10. Fort Campbell MR (MYSO), 11. Yellowbank WMA, Kentucky (MYSE, MYSO), 12. Fort Knox MR (MYSE, MYSO), 13. Ballard WMA, Kentucky (MYSE, MYSO), 14. Cypress Creek NWR, Illinois (MYSE, MYSO), 15. Oakmulgee WMA, Alabama (MYSE, MYSO), 16. Ouachita-St. Francis National Forest, Arkansas (MYSO), 17. Shaw Nature Center, Missouri (MYSO), 18. Beanblossom Bottoms Nature Preserve, Indiana (MYSE, MYSO), 19. Morgan-Monroe State Forest, Indiana (MYSE, MYSO), 20 Governor Dodge State Park, Wisconsin (MYSE).

Results

Over 2020–2021, for northern long-eared bats, we retained 2208 rain-free nights across 12 sites where maternity colonies were known present and at least one nightly echolocation pass was identified (Table 1), whereas for Indiana bats, we retained 2865 rain-free nights across 14 sites (Table 2). Mean nightly echolocation passes of northern long-eared bats were higher in forest and riparian cover types than in edge cover types when the MLE *P*-value was <0.05 (Table 1). However, mean nightly echolocation passes were low across all cover types when the MLE *P*-value was >0.05. Indiana bat activity was highest in the riparian cover type when the MLE *P*-value was <0.05, and similar to northern long-eared bats, also low across all cover types when the MLE *P*-value was >0.05 (Table 2). Nightly counts of all high-frequency bats were highest in riparian cover types when the MLE *P*-value was <0.05 for the target species (Tables 1 and 2). For both northern long-eared bats and Indiana bats, predicted MLE *P*-values were negatively related to the overall nightly echolocation pass count for either species as well as their respective ratios to the nightly count of all high-frequency bat echolocation pass counts (Tables 3 and 4; Figures 2 and 3). Higher MLE *P*-values were observed where northern long-eared bats were identified in edge cover types as opposed to forest and riparian cover types (Figure 2), whereas the forest cover type was most likely to display this condition compared to edge and riparian cover types for Indiana bats (Figure 3).

For both species, the predicted MLE *P*-value was >0.05 most often where each species' nightly echolocation pass counts were low and those identifications occurred in the context of far larger observed numbers of other high-frequency species. For northern long-eared bats, this species swamping occurred where the nightly count of northern long-eared bats was <10 and northern long-eared bat echolocation pass counts consisted of approximately 20% or less of the nightly total of all high-frequency bats (Figure 2). Results for Indiana bats were more variable, whereby at sites with nightly echolocation pass counts < 10, identified Indiana bat echolocation passes did not reach the MLE *P*-value < 0.05 threshold where the ratio to other high-frequency bats was less than 40% (Figure 3). Uncertainty for low Indiana bat count numbers increased where the species constituted ratios >90% of the entire high-frequency bat observations (Figure 3). For both species, nightly echolocation pass counts > 15 generally met the MLE *P*-value threshold irrespective of either target species counts, the ratio of those to all high-frequency bats, or cover type (Figures 2 and 3). Although model fit was less good, simulated data results followed the same trend as with observed data in that once either nightly counts of northern long-eared bats and Indiana bats reached > 10, the MLE *P*-value threshold was met and there was no strong evidence that high ratios of other high-frequency bat species relative to northern long-eared bats or Indiana bats would create false negative scenarios using the USFWS MLE acceptance standard (Tables 5 and 6; Figures 4 and 5) . Similarly, with the simulated data, uncertainty was greater when counts of either species were <5.

Table 1. Mean nightly echolocation passes of northern long-eared bats (*Myotis septentrionalis*) and all high-frequency bats (see text) at maternity colony areas (n = site-nights) in the eastern U.S., 2020–2021 by survey site, cover type (edge, forest, and riparian), and nightly maximum likelihood estimator (MLE) *P*-value (< 0.05 or > 0.05) of pass confidence from automated identification software.

		Northern Long-eared Bat			All High Frequency Bats		
	n	Mean	SE	Range	Mean	SE	Range
MLE < 0.05							
Edge	195	5.88	0.47	1–50	54.94	3.32	1–222
Forest	427	11.99	0.89	1–200	43.18	2.48	1–380
Riparian	420	22.85	2.19	1–507	174.47	13.91	1–2260
MLE > 0.05							
Edge	321	1.70	0.07	1–8	67.90	6.49	1–1,019
Forest	319	1.74	0.07	1–8	67.86	5.41	1–887
Riparian	526	2.63	0.11	1–16	124.34	6.37	1–1205

Table 2. Mean nightly echolocation passes of Indiana bats (*Myotis sodalis*) and all high-frequency bats (see text) at maternity colony areas (n = site-nights) in the eastern U.S., 2020–2021 by survey site, cover type (edge, forest, and riparian), and nightly maximum likelihood estimator (MLE) *P*-value (< 0.05 or > 0.05) of pass confidence from automated identification software.

		Indiana Bat			All High Frequency Bats		
	n	Mean	SE	Range	Mean	SE	Range
MLE < 0.05							
Edge	346	15.14	0.93	1–154	86.46	4.16	1–548
Forest	499	15.10	0.75	1–134	76.99	3.31	1–652
Riparian	646	48.20	4.92	1–1251	166.60	9.68	1–2260
MLE > 0.05							
Edge	460	2.20	0.08	1–11	59.89	3.40	1–514
Forest	481	2.20	0.09	1–17	82.87	7.27	1–1,072
Riparian	481	3.47	0.20	1–38	95.31	6.65	1–962

Table 3. Generalized linear model parameter estimates for predicted maximum likelihood estimator probability values of northern long-eared bat (*Myotis septentrionalis*) echolocation pass confidence from automated identification software at maternity colony areas ($n = 2208$ site-nights) in the eastern U.S., 2020–2021 by nightly count of northern long-eared bat echolocation passes, ratio of northern long-eared bats to other high-frequency bats (see text), and survey site cover type.

Parameter	β	SE	Wald χ^2	*P*
Intercept	0.32	0.08	17.53	0.0090
Count	−0.22	0.02	85.08	< 0.0001
Ratio	−11.91	1.05	127.44	< 0.0001
Ratio × Ratio	9.92	1.09	83.29	< 0.0001
Cover type[1]				
Edge	−0.27	0.10	7.98	0.0005
Forest	−0.09	0.10	0.79	0.3754

[1] Riparian was reference condition.

Table 4. Generalized linear model parameter estimates for predicted maximum likelihood estimator probability values of Indiana bat (*Myotis sodalis*) echolocation pass confidence from automated identification software at maternity colony areas ($n = 2865$ site-nights) in the eastern U.S., 2020–2021 by nightly count of Indiana bat echolocation passes, ratio of Indiana bats to other high-frequency bats (see text), and survey site cover type.

Parameter	β	SE	Wald χ^2	*P*
Intercept	0.34	0.08	16.95	< 0.0001
Count	−0.23	0.02	172.38	< 0.0001
Ratio	−6.88	0.67	107.10	< 0.0001
Ratio × Ratio	5.58	0.83	45.27	< 0.0001
Cover type[1]				
Edge	−0.08	0.08	0.81	0.3684
Forest	−0.25	0.09	7.53	0.0061

[1] Riparian was reference condition.

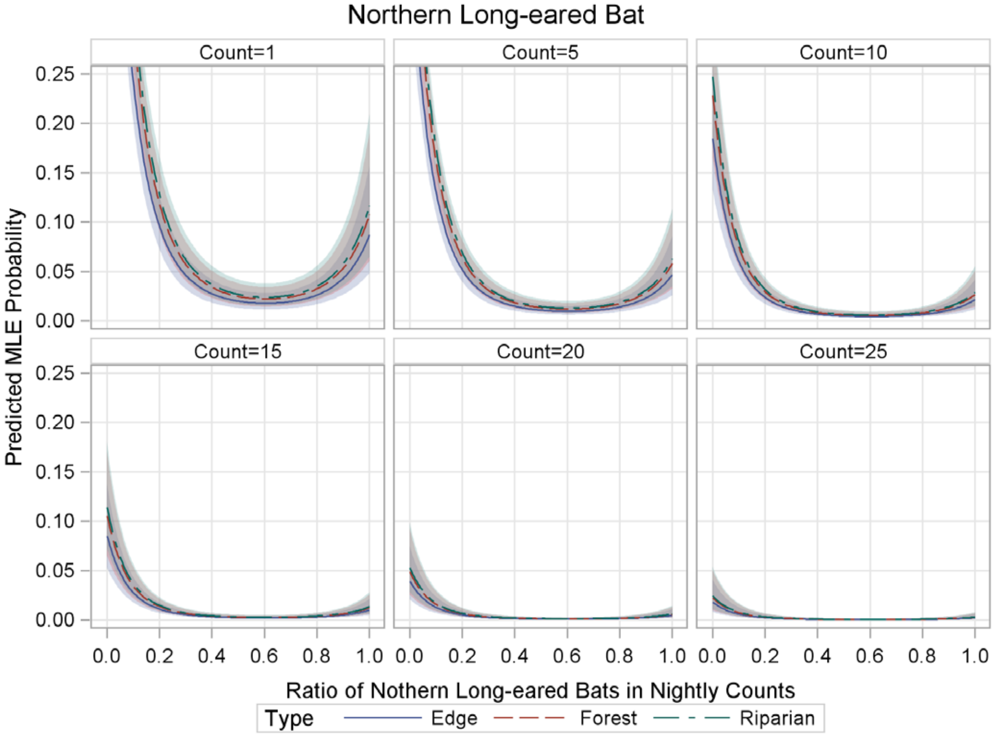

Figure 2. Mean and 95% confidence interval for predicted nightly maximum likelihood (MLE) *P*-values of northern long-eared bat (*Myotis septentrionalis*; $n = 2{,}208$ site-nights) echolocation pass confidence from automated identification software in the eastern U.S., 2020–2021 by nightly count of northern long-ear bat echolocation passes, ratio of northern long-eared bats to other high-frequency bats, and survey site cover type where at least one northern long-eared bat was identified at the echolocation pass file level.

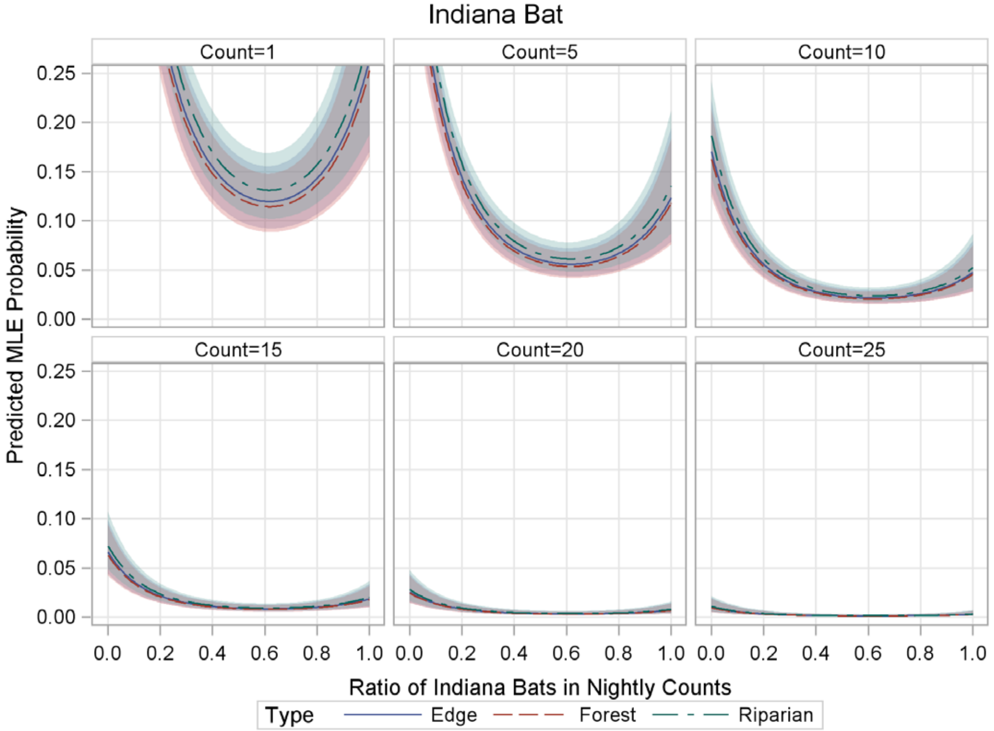

Figure 3. Mean and 95% confidence interval for predicted nightly maximum likelihood (MLE) *P*-values of Indiana bat (*Myotis sodalis*; $n = 2{,}865$ site-nights) echolocation pass confidence from automated identification software in the eastern U.S., 2020–2021 by nightly count of Indiana bat echolocation passes, ratio of Indiana bats to other high-frequency bats, and survey site cover type where at least one Indiana bat was identified at the echolocation pass file level.

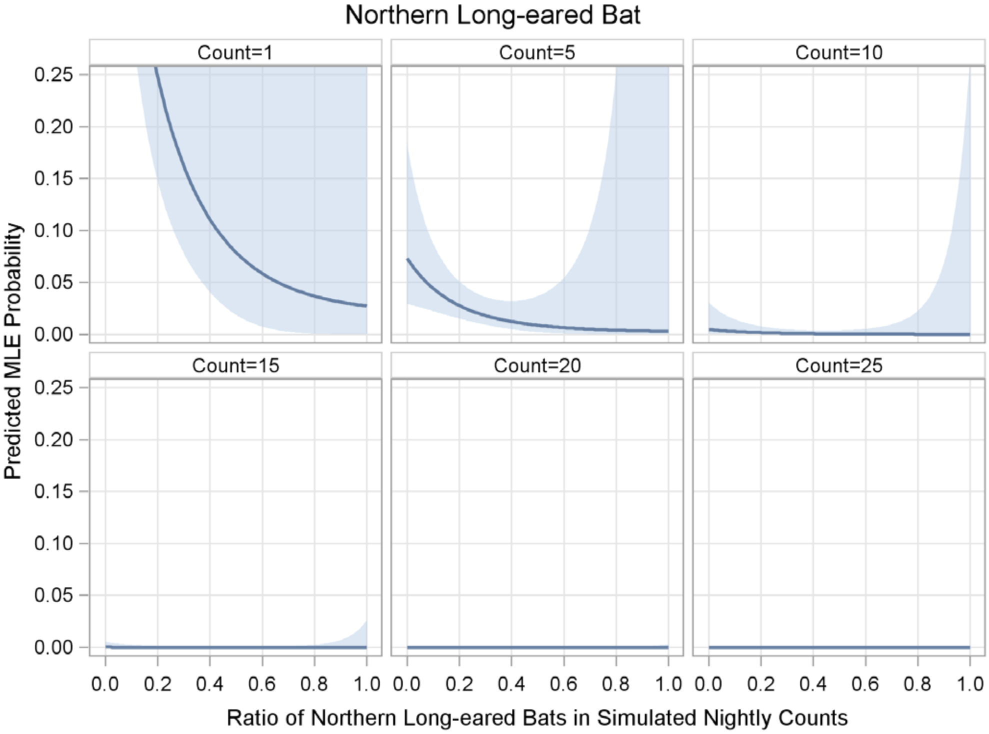

Figure 4. Mean and 95% confidence interval for predicted nightly maximum likelihood (MLE) *P*-values of northern long-eared bat (*Myotis septentrionalis*; $n = 800$ site-nights) echolocation pass confidence from automated identification software by simulated nightly count and ratio of northern long-eared bats to other high-frequency bats.

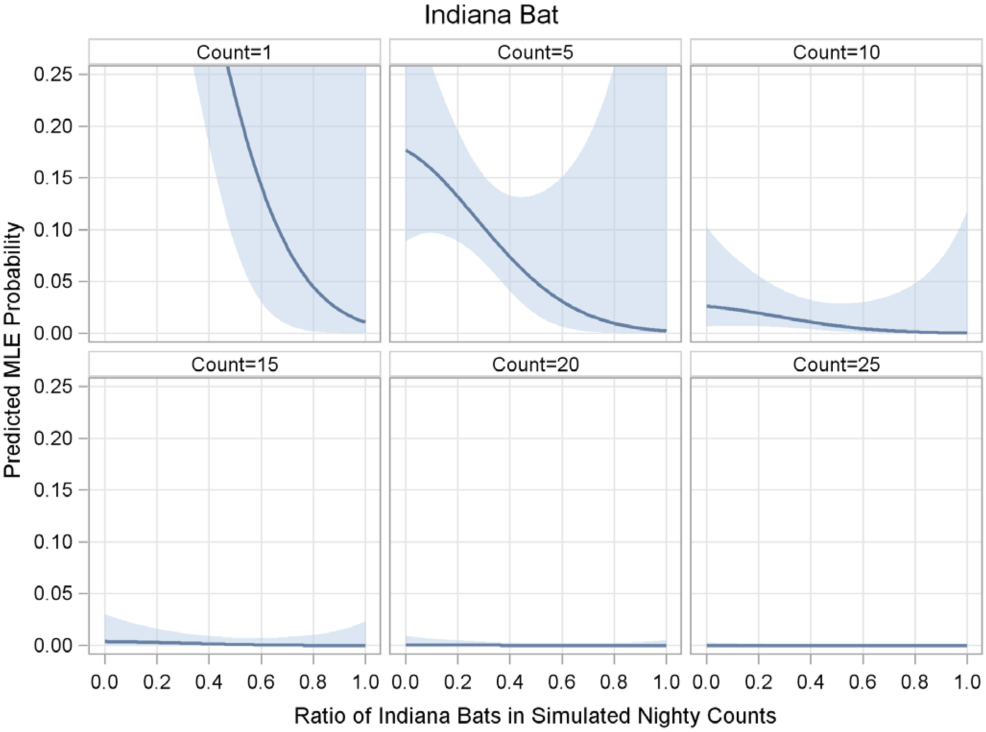

Figure 5. Mean and 95% confidence interval for predicted nightly maximum likelihood (MLE) *P*-values of Indiana bat (*Myotis sodalis*; $n = 800$ site-nights) echolocation pass confidence from automated identification software by simulated nightly count and ratio of northern long-eared bats to other high-frequency bats.

Table 5. Generalized linear model parameter estimates for predicted maximum likelihood estimator probability values of northern long-eared bat (*Myotis septentrionalis*) echolocation pass confidence from automated identification software from 800 simulated nightly counts and ratio of northern long-eared bats to other high-frequency bats.

Parameter	β	SE	Wald χ^2	P
Intercept	0.17	0.10	3.15	0.0761
Count	–0.38	0.07	30.51	< 0.0001
Ratio	–0.65	1.82	0.79	0.3748
Ratio × Ratio	–3.7	4.17	0.79	0.3748

Table 6. Generalized linear model parameter estimates for predicted maximum likelihood estimator probability values of Indiana bat (*Myotis sodalis*) echolocation pass confidence from automated identification software from 800 simulated nightly counts and ratio of Indiana bats to other high-frequency bats.

Parameter	β	SE	Wald χ^2	P
Intercept	0.13	0.08	3.10	0.0783
Count	–0.54	0.10	31.92	< 0.0001
Ratio	–5.51	2.39	5.31	0.0212
Ratio × Ratio	2.38	5.03	0.22	0.6355

Discussion

Confidence in USFWS acoustic monitoring protocols for northern long-eared bats and Indiana bats rests on the assumption that identified presence of either species at the nightly level is accurate. Although false-positives may result in unnecessary, but presumably beneficial conservation actions, false-negatives may lead to a lack of needed conservation measures (Ford et al. 2023). As such, two components of the USFWS's acoustic monitoring program seek to guard against false-positives and false-negatives within the context of assessing northern long-eared and Indiana bat presence at survey sites at the nightly level. First, to be considered present, the collective of northern long-eared bats or Indiana bats identified by automated software must display a MLE P-value ≤ 0.05 nightly (USFWS 2022). This restrictive α-level guards against a preponderance of false-positive designations. Secondly, automated identification software approved by the USFWS for monitoring northern long-eared bats and Indiana bats must return no false-negatives in 20 randomized tests and no more than 20% false-positives thereby adding additional confidence in accuracy (USFWS 2019).

In field settings, as demonstrated by our study, northern long-eared bats and Indiana bats individual echolocation passes clearly could be identified as such without reaching the nightly MLE P-value < 0.05 trigger. This uncertainty likely is due to other species being errantly identified as either northern long-eared bats or Indiana bats, as expected given misclassification rates (Nocera et al. 2019, Ford et al. 2023). For example, at our sites where we knew maternity colonies of one or both target species occurred and hence animals were locally abundant relative to most of the post-WNS landscape (Ford et al. 2023), positive identifications, but without sufficient relative numbers to overcome cross-species misclassification rates, did occur at the nightly level. However, in no instance did this occur over any multiple-night duration relative to the 2020–2021 USFWS required acoustical LOE (USFWS 2022). Conversely, automated software returned northern long-eared bat determinations from cluttered forested survey sites on the Eastern Shore of Virginia, where northern long-eared bats are exceedingly rare, occasionally meeting the nightly MLE P-value < 0.05 (Barr 2018), that were later qualitatively identified as eastern red bats.

Our results provide little evidence for a swamping effect except when nightly counts of the target species were very low in both the field collection dataset and our simulated dataset with known echolocation calls. However, the uncertainty associated with few recordings, presumably males or non-reproductive females as posited by Ford et al. (2023) suggests that target species in some instances may not occur in sufficient numbers to overcome misclassification rates with high probability. Contrary to our predictions, the speculated swamping phenomenon did not occur or at least did not show a clear trend relative to riparian cover types. This suggests that sampling riparian cover types may provide useful information about the Indiana bat but also the more upland forest obligate northern long-eared bat and other WNS-impacted species without as much risk of species misclassification as originally believed (Ford et al. 2005, Gorman et al. 2022). Although the Endangered Species Act does not distinguish between males and non-reproductive females versus maternity colonies of northern long-eared bats and Indiana bats (Ford et al. 2023), concerns about false-negatives stemming from rejecting a file-level identification that does not meet the MLE P-value standard and subsequent lack of conservation action remain valid. Our study indicates that this potential event generally occurs when few passes of the target bat species are recorded, typically on single nights, whereby qualitative visual examination of spectrograms may quickly mitigate false-negative error of solely relying on a non-significant MLE P-value.

Nonetheless, we urge caution in broadly applying our findings. For example, we examined the relationships of MLE P-values to nightly echolocation counts of northern long-eared bats and Indiana bats, their relative proportion of other high-frequency bats and cover types with only one of several approved automated software programs/versions. Moreover, we only used the "balanced" 0 sensitivity setting as opposed to the more sensitive or specific identification settings in Kaleidoscope Pro. Whether these relationships we observed are true for other approved versions of this or any other identification software or setting thereof are unknown. Results also could vary based on both the potential bat species selected for software to consider as possibly present, because misclassification rates change for and among bat species depending on the assemblage selection. For example, identification accuracy for Indiana bats would increase if little brown bats, when known to be absent at a site, were not selected for inclusion during software analysis. Still, because Nocera et al. (2019) only found strong agreement at the nightly level regarding species presence or absence using the USFWS MLE *P*-value threshold, as opposed to actual individual file agreement, additional testing with additional field datasets and simulations using known bat echolocation call libraries seems warranted.

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Seasonal Activity Patterns of Northern Long-eared Bats on the Coastal Mid-Atlantic

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Abstract: Conservation of bats declining from white-nose syndrome (WNS) impacts requires an understanding of both temporal and landscape-level habitat relationships. Traditionally, much of the research on bat ecology has focused on behavior of summer maternity colonies within species' distribution cores, including that of the endangered northern long-eared bat (*Myotis septentrionalis*). To further our knowledge of this species, we evaluated multi-season activity patterns in eastern North Carolina and Virginia, including areas where populations were recently discovered. We used passive acoustic monitoring to assess relative and probable activity of northern long-eared bats from October 2016 to August 2021. Northern long-eared bat relative activity was greatest in areas containing greater proportions of woody wetlands and upland pine-dominated evergreen forests. However, the likelihood of recording northern long-eared bats was associated with smaller proportions of woody wetlands and open water resources. Furthermore, we observed a higher probability of recording northern long-eared bats during non-winter seasons. Probable activity was greatest at temperatures between 10 and 25 C, potentially highlighting an optimal thermoneutral zone for the species regionally. Relative activity of northern long-eared bats on the Coastal Plain of Virginia and North Carolina was primarily driven by cover features, whereas probable activity was driven by a combination of cover features, seasonality, and temperature. Therefore, acoustical surveys for this species may be most effective when targeting woody wetlands adjacent to upland forests, particularly upland pine-dominated evergreen stands, during moderate temperatures of non-winter seasons (1 April–15 November). Moreover, conservation of a diverse mosaic of woody wetlands juxtaposed by upland forests may promote both roosting and overwintering habitat, thereby enhancing overwintering survival, maternity colony establishment, and ultimately, successful reproduction of northern long-eared bats.

Key words: *Myotis septentrionalis*, coastal, seasonal, activity

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Several North American bat species have experienced severe population declines as a result of the introduction of *Pseudogymnoascus destructans* (*Pd*), the fungal pathogen that causes white-nose syndrome (WNS; Cheng et al. 2021). In the Central and Southern Appalachians of the U.S., the northern long-eared bat (*Myotis septentrionalis*) was one of the most commonly occurring species pre-WNS (Ford et al. 2006, Rojas et al. 2017). In regions that experience harsh winters and lengthy hibernation periods, such as the High Allegheny Plateau of the Central Appalachians, northern long-eared bat populations precipitously decreased once *Pd* invaded karst hibernacula (Johnson et al. 2013, Ford et al. 2016, Austin et al. 2018). Additionally, the recently documented abandonment of maternity colony roosts and lack of juvenile captures in Virginia's Ridge and Valley and Blue Ridge Mountains (Figure 1) provide further evidence suggestive of population collapse (Kalen et al. 2022). These declines threaten the species with extinction (Cheng et al. 2021), contributing to a 2015 threatened listing under the U.S. Endangered Species Act of 1973 (USFWS 2015) and recent uplisting to endangered (USFWS 2022).

Despite widespread declines in the interior Northeast and Mid-Atlantic of the U.S. (Figure 1), isolated, remnant populations of northern long-eared bats appear to persist in coastal environments along the Eastern Seaboard (Jordan 2020, Deeley et al. 2021, De La Cruz et al. 2022b, Montgomery and Hogue 2022, Garcia

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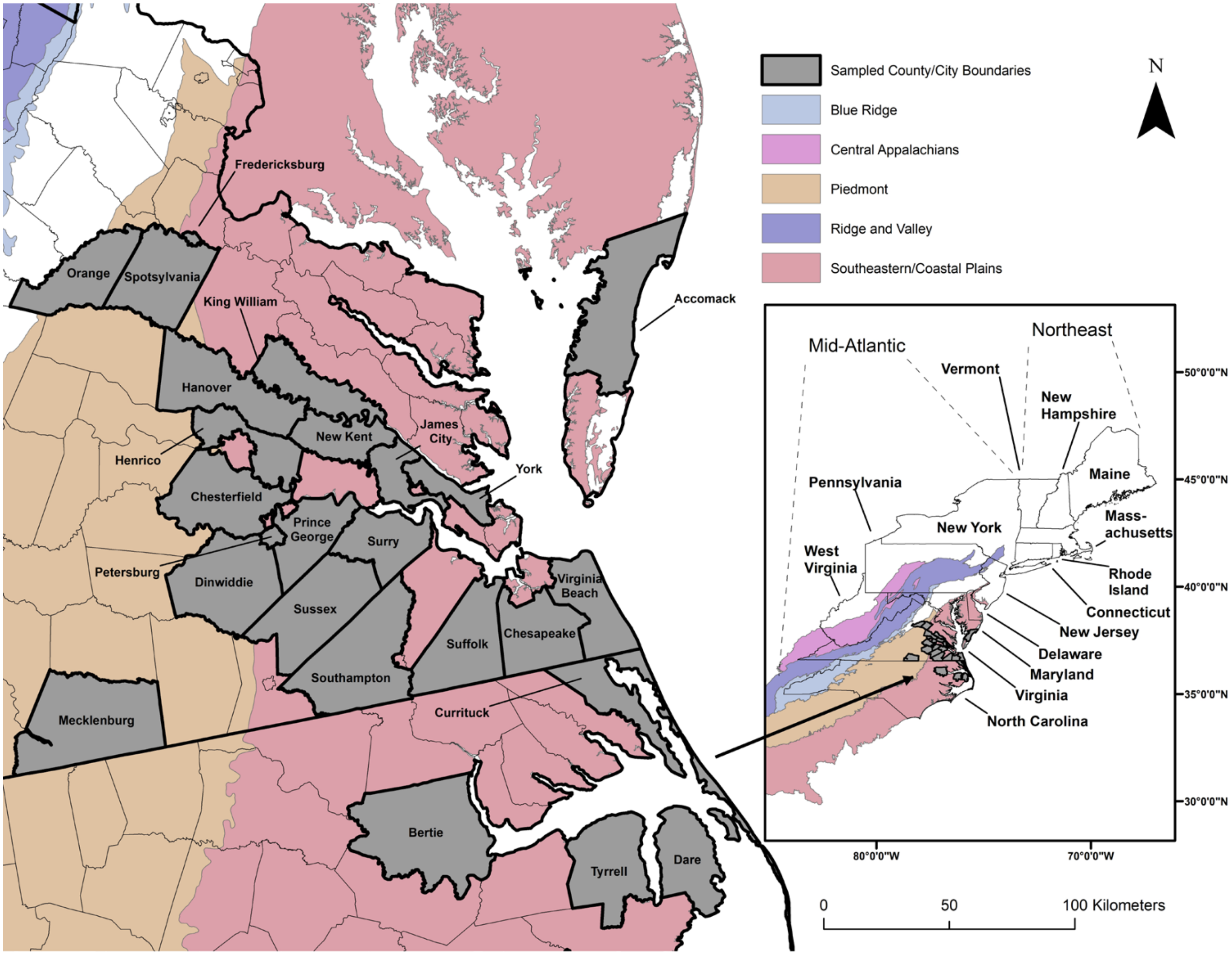

Figure 1. County and city boundaries in northeastern North Carolina and southeastern Virginia, containing 179 acoustic sites surveyed for northern long-eared bat (*Myotis septentrionalis*) calls, 2016–2021.

et al. 2023, Gorman et al. 2023, Hoff et al. 2023). Some of these populations have relied on the use of unique, sparsely occupied, and/or non-contaminated hibernacula as overwintering habitat. For example, in coastal Massachusetts, northern long-eared bats hibernate in the basements and crawlspaces of homes and military bunkers on Nantucket Island (Hoff et al. 2023). However, in coastal Virginia, male northern long-eared bats use woody wetlands and the intersection of these riparian forests and upland pine forests as overwintering habitat (De La Cruz et al. 2022b). Jordan (2020) documented the year-round presence of northern long-eared bats on the Coastal Plain of North Carolina. These bats largely used swamp tupelo (*Nyssa biflora*), water tupelo (*N. aquatica*), bald cypress (*Taxodium distichum*), and red maple (*Acer rubrum*) in contiguous tracts of woody wetlands as torpor sites during winter. Within the upper Gulf Coastal Plain of Louisiana, northern long-eared bats select tall, large-diameter pines with exfoliating bark as winter roosts (Garcia et al. 2023). In contrast, overwintering habitat in and adjacent to the Washington, D.C. metropolitan region (Deeley et al. 2021) may consist of a combination of alternative hibernacula such as mines (Lituma et al. 2021) and coastal forest torpor sites (Jordan 2020), or bats exhibit latitudinal migration, as observed in tricolored bats (*Perimyotis subflavus*; Fraser et al. 2012).

Historically, in the Mid-Atlantic, northern long-eared bats were assumed to range no farther south and east than the Great Dismal Swamp in southeastern Virginia (Morris et al. 2009). Furthermore, the species was also assumed to hibernate exclusively in cracks and crevices of caves or mines during winter (Caceres and Barclay 2000), features rare in the Coastal Plain. However, recent research has revealed both summer maternity colonies and overwintering populations of northern long-eared bats in southeastern Virginia (De La Cruz et al. 2022b) and eastern North Carolina (Jordan 2020). Specifically, populations were first discovered in the Coastal Plain of North Carolina in 2007 (Morris et al. 2009) and, as of 2020, 181 unique northern long-eared bats have been captured in this area (Jordan 2020). In Virginia and North Carolina, only in coastal areas have colonies remained cohesive and reproductively successful (Jordan 2020, De La Cruz et al. 2022a). Assuming continued declines of northern long-eared bat populations associated with inland hibernacula, these isolated, coastal populations may provide the last remaining refugia for the species in the Mid-Atlantic.

The persistence of northern long-eared bat populations in the coastal Mid-Atlantic underscores the need for a comprehensive understanding of their seasonal activity patterns in response to weather conditions to inform effective conservation efforts. In coastal North Carolina, northern long-eared bats were observed active throughout the winter but entered short bouts of torpor during periods of near-freezing weather (Jordan 2020). In coastal Massachusetts, the hibernation period of northern long-eared bats is shorter than mainland counterparts, likely due to more nights above freezing at coastal sites (Hoff et al. 2023). During summer in coastal New York, Gorman et al. (2021) found that northern long-eared bats were more active during warmer nights but that individuals were not deterred by precipitation events or excessive wind. Although a growing body of literature has examined northern long-eared bat ecology in coastal habitats of the Northeast and Mid-Atlantic (Jordan 2020, Gorman et al. 2021, Gorman et al. 2022, Gorman et al. 2023, De La Cruz et al. 2022a, Hoff et al. 2023), no research has evaluated the seasonal activity of northern long-eared bats using passive acoustic methods in northeastern North Carolina and southeastern Virginia. To examine this seasonal activity, we undertook a multi-season survey to assess relative (i.e., weekly counts of echolocational recordings) and probable (i.e., likelihood to collect ≥1 recording) activity of northern long-eared bats in relation to biotic and abiotic factors across southeastern Virginia and northeastern North Carolina. Our objectives were to use passive acoustic monitoring to 1) identify bat presence across the study area; 2) assess the effect of cover type covariates; 3) examine effects of weather and seasonality; 4) and identify potential conservation needs to enhance management efforts for northern long-eared bats within the region. We hypothesized that northern long-eared bat activity would be spatially concentrated and highest during the non-winter season (1 April–15 November), during warmer and drier weather, and in contiguous tracts of woody wetlands and upland forests. Additionally, we hypothesized that the likelihood to record northern long-eared bat activity would follow similar trends.

Study Area

Our study area encompassed 23 counties and 2 independent cities in the lower Piedmont and Coastal Plain of northeastern North Carolina and southeastern Virginia (Figure 1). The Piedmont is comprised of narrow to broad upland ridgetops ranging in elevation from 100 m to 400 m. The region experiences an average annual temperature of 12–18 C and receives 100–180 cm of precipitation per year. Pine stands (*Pinus* spp.), including loblolly pine (*P. taeda*) and shortleaf pine (*P. echinata*), are dominant on eroded sites, whereas hardwoods and mixed stands, often comprised of white oak (*Quercus alba*), red oak (*Q. rubra*), and sweetgum (*Liquidambar styraciflua*), occur on less eroded sites and bottomlands (USDA NRCS 2022). The Coastal Plain ranges in elevation from approximately 180 m at the Fall Line (i.e., boundary with Piedmont), where the landscape is characterized by short, steep slopes adjacent to bottomlands, to sea level at the Atlantic Ocean, where broad peneplains bisected by stream channels predominate. The Coastal Plain receives approximately 100–160 cm of precipitation and experiences an average annual temperature of 13–21 C (USDA NRCS 2022). Upland forests of the Coastal Plain are dominated by a mixed oak-hickory (*Carya* spp.)-pine community, which historically included a large component of longleaf pine (*P. palustris*). Periodically flooded forests adjacent to sediment-laden brownwater rivers that originate in the Appalachians or Piedmont are often comprised of swamp chestnut oak (*Q. michauxii*), cherrybark oak (*Q. pagoda*), shagbark hickory (*C. ovata*), and sweetgum (Fleming and Patterson 2017). Alluvial woody wetlands associated with acidic blackwater rivers that originate on the Coastal Plain are primarily composed of water tupelo, swamp tupelo, and bald cypress (Fleming and Patterson 2017). Large acreage of native forest and wetland habitats on the Coastal Plain of North Carolina and Virginia have been converted to agricultural fields and short-rotation pine plantations (Hefner et al. 1994, Hunter et al. 2001).

Methods

Acoustic Monitoring

We conducted acoustic monitoring at 179 sites from October 2016 to August 2021 (Figure 2). We deployed zero-crossing ultrasonic recorders (Song Meter 2 and Song Meter 4; Wildlife Acoustics, Maynard, Massachusetts), fitted with microphones (SMM-U1) to collect acoustic data. We attached recorders to trees at an approximate height of 1.5 m above the ground, ensuring

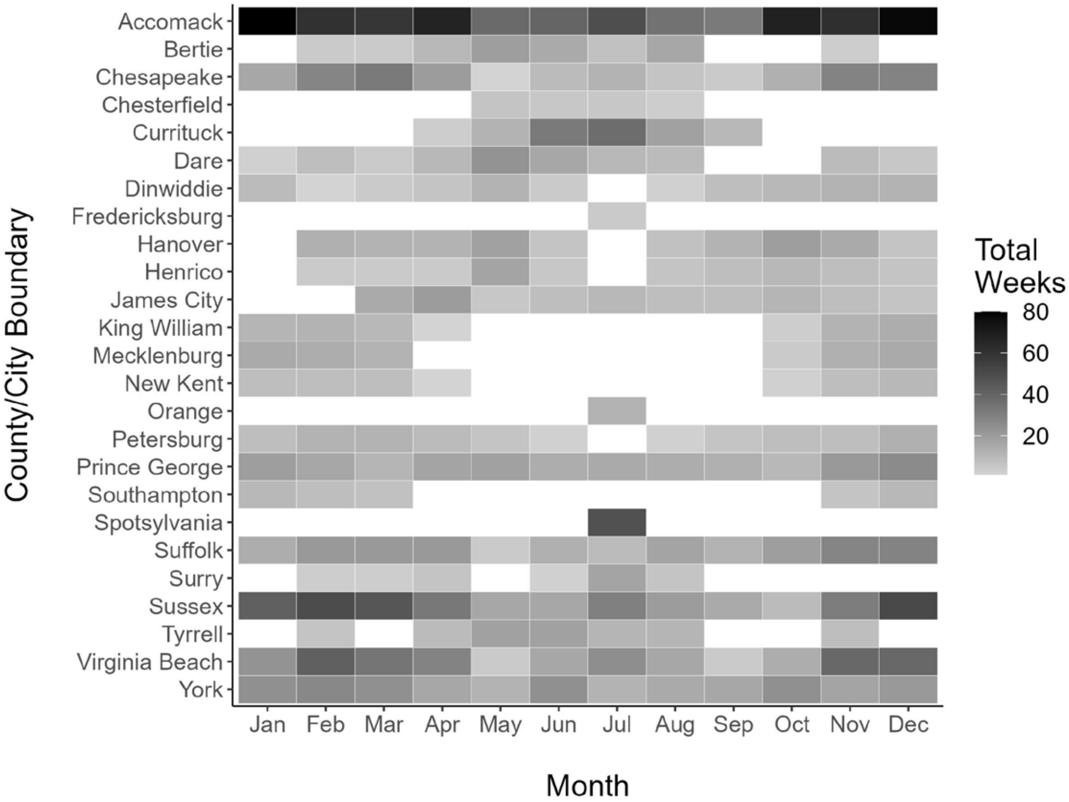

Figure 2. Sampling effort as represented by a monthly heatmap (white areas represent unsampled months) of the total number of acoustic monitoring weeks conducted in eastern North Carolina and Virginia, 2016–2021 (see Figure 1 for county/city locations).

microphones extended beyond the diameter of the bole, or on 3-m poles as dictated by site conditions (De La Cruz and Ward 2016). We deployed acoustic recorders near forest canopy openings, water sources, tree lines adjacent to large openings or that connected two larger blocks of forest, potential roost trees, and road and/or stream corridors with open tree canopies to assess both the relative and probable activity of northern long-eared bats (Britzke et al. 2010). To mitigate spatial autocorrelation, we deployed recorders at widely spaced sites, observing a median distance of 610 m between sampling sites. We programmed detectors to record from sunset to sunrise. We checked functionality of recorders and downloaded and processed data at approximately 30- to 60-day intervals. We identified echolocational recordings to species with automated acoustic software (Kaleidoscope Pro software; v. 5.4.7; Wildlife Acoustics), using default signal detection parameters and the 5.4.0 classifier set at 'Balanced/Neutral' (USFWS 2020). Based on geographical range extents (Reid 2006), we considered the following species for presence: Rafinesque's big-eared bats (*Corynorhinus rafinesquii*), big brown bats (*Eptesicus fuscus*), eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), silver-haired bats (*Lasionycteris noctivagans*), Southeastern myotis bats (*M. austroriparius*), little brown bats (*M. lucifugus*), evening bats (*Nycticeius humeralis*), and tricolored bats (*Perimyotis subflavus*). We also included Brazilian free-tailed bats (*Tadarida basiliensis*), Indiana bats (*M. sodalis*), northern long-eared bats, and Seminole bats (*Lasiurus seminolus*) due to recently documented range expansions into the Coastal Plain of Mid-Atlantic states (St. Germain et al. 2017, McCracken et al. 2018, Jordan 2020, True et al. 2021).

Predictor Variables

In response to recent research in the southeastern Coastal Plain (Jordan 2020, Stevens et al. 2020, De La Cruz et al. 2022a, Garcia et al. 2023), we assessed relative and probable activity of northern long-eared bats in relation to percent cover of woody wetlands (i.e., ≥20% forest/shrubland periodically saturated with water), evergreen forests (i.e., ≥20% forested area containing trees ≥5 m in height; ≥75% of foliage maintained all year), and open water (i.e., open water areas containing <25% vegetation or soil) resources using the 2019 National Land Cover Database (NLCD) raster dataset (Dewitz and USGS 2021). Additionally, we examined the effect of forest fragmentation on relative activity and the probability to record northern long-eared bat calls (De La Cruz et al. 2022a). To incorporate the availability of large core forests (>200 ha) in our models, we used a mapping tool (Landscape Fragmentation Tool in ArcGIS; Vogt et al. 2007) to characterize a forest/non-forest raster dataset derived from NLCD data. We also assessed canopy height (EROSC 2019), a known factor influencing seasonal and spatial habitat selection by northern long-eared bats (Perry and Thill 2007, De La Cruz et al. 2022a). We standardized all raster datasets to a 100-m resolution and, based on foraging dispersal estimates of northern long-eared bats (Silvis et al. 2016), calculated focal means of these raster data using a 500-m moving window analysis (De La Cruz et al. 2023). We also assessed the impact of weather variables on the relative and probable activity of northern long-eared bats. These variables included the weekly mean of daily total precipitation (mm) and, assuming upper thermal limits (Patriquin et al. 2016), the quadratic relationship of the weekly mean of daily average temperature (C). We obtained matching nightly weather data for sites from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) Data Explorer, using the inverse-distance squared weighting interpolation option for the standard 4 km PRISM grid cell (PRISM Climate Group 2022). Recognizing the high correlation between date and included quadratic temperature trends, we analyzed the simple effects of non-winter and winter seasons (1 April–15 November; 16 November–31 March) on northern long-eared bat activity.

Statistical Analysis

We assumed presence of northern long-eared bats for automated identification only if a statistically significant maximum likelihood estimate (MLE; $P < 0.05$) was observed for any given site-night, thereby accounting for known rates of misclassification and minimizing false positive and false negative errors (Britzke et al. 2002). We then aggregated these nightly data by site and year and totaled counts for northern long-eared bats across each corresponding week of the year (Straw et al. 2022). We used these counts (i.e., weekly relative activity) as the response variable in all modeling efforts. We used a Shapiro-Wilk test to assess weekly relative activity for non-normality and discovered that data were not ($P < 0.01$) normally distributed (R Core Team 2020). Consequently, we used zero-inflated negative binomial generalized linear mixed models (GLMMs) in the glmmTMB R package (Brooks et al. 2017) for all statistical analyses. All GLMMs included two sub-models: 1) a conditional count sub-model to model relative activity; and 2) a zero-inflation sub-model to model probable activity. Prior to modeling, we checked for collinearity across predictor variables using pairwise correlation (threshold = $|0.8|$) and scaled and centered continuous variables. In total, we compared eight GLMMs, including a null model. In our seven multivariate models, we matched predictor variables in the conditional and zero-inflation sub-models. We included in all models the spatial random effect of recorder site and temporal random effect of year (Carlin and Chalfoun 2021, Taylor et al. 2023); however, we excluded the random effects of site and year from all zero-inflation sub-models. To rank models, we used Akaike Information Criterion corrected for small sample size (i.e., AIC_c). We defined the top-ranking model as that which had no competing model within two ΔAIC units (Burnham and Anderson 2002). We used the DHARMa package in R to assess our top model for goodness-of-fit and over- and under-dispersion using a quantile-quantile plot, residual plot, and a one-sample Kolmogorov-Smirnov test (Hartig 2020). Furthermore, we investigated the ecological significance of our top model using the performance package in R to calculate the conditional (i.e., the proportion of variance explained by fixed and random factors) Nakagawa R^2 (Nakagawa and Schielzeth 2013, Lüdecke et al. 2021). We interpreted R^2 values as follows: ≤0.20, very low; 0.21–0.40, low; 0.41–0.60, medium; 0.61–0.80, high; and 0.81–1.00, as very high proportions of variance explained (Gorman et al. 2021, Hill et al. 2024, Torre et al. 2022). Finally, we investigated the relationship between relative and probable activity and significant predictor variables using partial effect plots.

Results

During 2016–2021, we sampled for 3312 weeks and collected 6,056,851 acoustic data files from 179 acoustic sampling sites in northeastern North Carolina and southeastern Virginia. Based on nights displaying a significant ($P < 0.05$) MLE, we identified 616,775 (10%) files to species, including 5273 (<1%) files identified as northern long-eared bats. We recorded northern long-eared bats in 72% of sampled county and city boundaries, including all counties in North Carolina. Our highest northern long-eared bat call totals were collected in Sussex ($n = 1676$; $\bar{x} = 140$ per site), Chesapeake ($n = 880$; $\bar{x} = 176$ per site), and Virginia Beach ($n = 298$; $\bar{x} = 37$ per site) counties, Virginia, and Currituck County ($n = 1525$; $\bar{x} = 169$ per site), North Carolina. We recorded no northern long-eared bats in Chesterfield, Henrico, King William, Mecklenburg, and Orange counties, Virginia, or within the cities of Fredericksburg and Petersburg, Virginia.

We had no competing models within two ΔAIC_c units and therefore consider our top-ranking model to be the best supported (Table 1). Our top model passed all DHARMa goodness-of-fit tests and explained a high proportion of variance ($R^2 = 0.69$), suggesting strong ecological relevance. We observed that northern long-eared bat weekly relative activity was greatest in areas containing larger proportions of woody wetlands and evergreen forests (Table 2;

Table 1. Variables included in both conditional count and zero-inflation sub-models of generalized linear mixed models, number of full-model parameters (K), Akaike's information criterion (AIC$_c$) units, ΔAIC$_c$ units, full-model weights (w_i), and full-model log-likelihood (LL), predicting weekly relative and probable activity of northern long-eared bats (*Myotis septentrionalis*) in northeastern North Carolina and southeastern Virginia, 2016–2021.

Model[a]	K[b]	AIC$_c$	ΔAIC$_c$	w_i	LL
TEMP + TEMP^2 + PRECIP + WOODY + EVER + WATER	19	3044.37	0.00	0.93	−1503.07
TEMP + TEMP^2 + PRECIP + WOODY + EVER + WATER + LARGE + CANOPY	23	3049.49	5.12	0.07	−1501.58
TEMP + TEMP^2 + PRECIP + LARGE + CANOPY	17	3058.83	14.46	0.00	−1512.32
TEMP + TEMP^2 + PRECIP	13	3061.97	17.6	0.00	−1517.93
WOODY + EVER + WATER	13	3079.15	34.78	0.00	−1526.52
WOODY + EVER + WATER + LARGE + CANOPY	17	3079.52	35.15	0.00	−1522.67
LARGE + CANOPY	11	3090.35	45.97	0.00	−1534.13
Null	3	3466.75	422.38	0.00	−1730.37

a. TEMP + TEMP^2: quadratic polynomial of the weekly mean of daily average temperature (C); PRECIP: weekly mean of daily total precipitation (mm); WOODY: percent woody wetlands; EVER: percent evergreen forests; WATER: percent open water; LARGE: percent core forest (>200 ha); CANOPY: canopy height (m).

b. All models included a single dispersion parameter and intercepts in both the conditional and zero-inflation sub-models. Excluding the Null model, each conditional count sub-model contained the fixed effect of season and random effects of site and year, while zero-inflation sub-models included only the fixed effect of season.

Table 2. Predictor variables, *β* and SE estimate, *z*-values, *P*-values, and lower (LCL) and upper confidence limits (UCL) for the top generalized linear mixed model predicting weekly relative (i.e., counts of echolocational recordings; conditional sub-model) and probable (i.e., likelihood to collect ≥1 recording; zero-inflation sub-model) activity of northern long-eared bats (*Myotis septentrionalis*) in northeastern North Carolina and southeastern Virginia, 2016–2021.

Sub-model	Term[a]	*β*	SE	*z*	*P*	LCL	UCL
Conditional	Intercept	−3.93	0.82	−4.82	<0.01	−5.53	−2.34
	TEMP	24.20	18.03	1.34	0.18	−11.13	59.53
	TEMP^2	−22.90	13.15	−1.74	0.08	−48.68	2.88
	PRECIP	−0.15	0.12	−1.22	0.22	−0.38	0.09
	WOODY	1.78	0.44	4.06	<0.01	0.92	2.63
	EVER	1.16	0.46	2.52	0.01	0.26	2.06
	WATER	−0.08	0.48	−0.18	0.86	−1.02	0.85
	SEASON – Winter	0.26	0.42	0.61	0.54	−0.57	1.08
Zero-inflation	Intercept	−0.69	0.30	−2.34	0.02	0.11	1.25
	TEMP	13.30	13.47	0.99	0.32	−38.26	13.78
	TEMP^2	−34.39	9.56	−3.60	<0.01	16.12	53.63
	PRECIP	−0.05	0.12	−0.39	0.69	−0.18	0.28
	WOODY	−0.28	0.14	−2.01	0.04	0.00	0.55
	EVER	−0.01	0.11	−0.12	0.90	−0.20	0.22
	WATER	−0.60	0.20	−3.02	<0.01	0.21	0.98
	SEASON – Winter	−0.79	0.38	−2.09	0.04	0.11	1.25

a. TEMP and TEMP^2: terms of the quadratic polynomial effects of weekly mean of daily average temperature (C); PRECIP: weekly mean of daily total precipitation (mm); WOODY: percent woody wetlands; EVER: percent evergreen forests; WATER: percent open water; SEASON – Winter: fixed effect of the winter season; the conditional sub-model contained the random effects of site location and year.

Figure 3). However, we observed no influence of temperature, precipitation, open water, or season on relative activity of the species (Table 2). Our results indicated that northern long-eared bat activity was more likely to be documented in non-winter seasons and during moderate temperature conditions (Table 2; Figure 4). We also observed that northern long-eared bats were more likely to be recorded in areas containing little open water and lesser amounts of woody wetland cover (Table 2; Figure 4). Finally, we observed

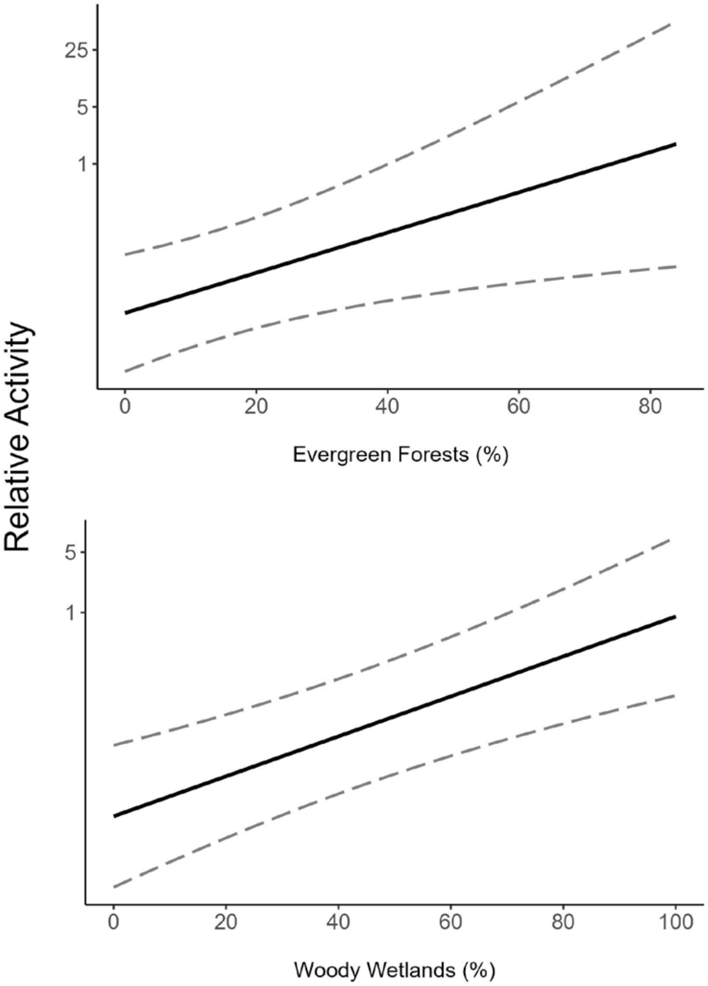

Figure 3. Partial effect plots of predicted weekly relative activity (and 95% CI) of northern long-eared bats (*Myotis septentrionalis*) in eastern North Carolina and Virginia, 2016–2021.

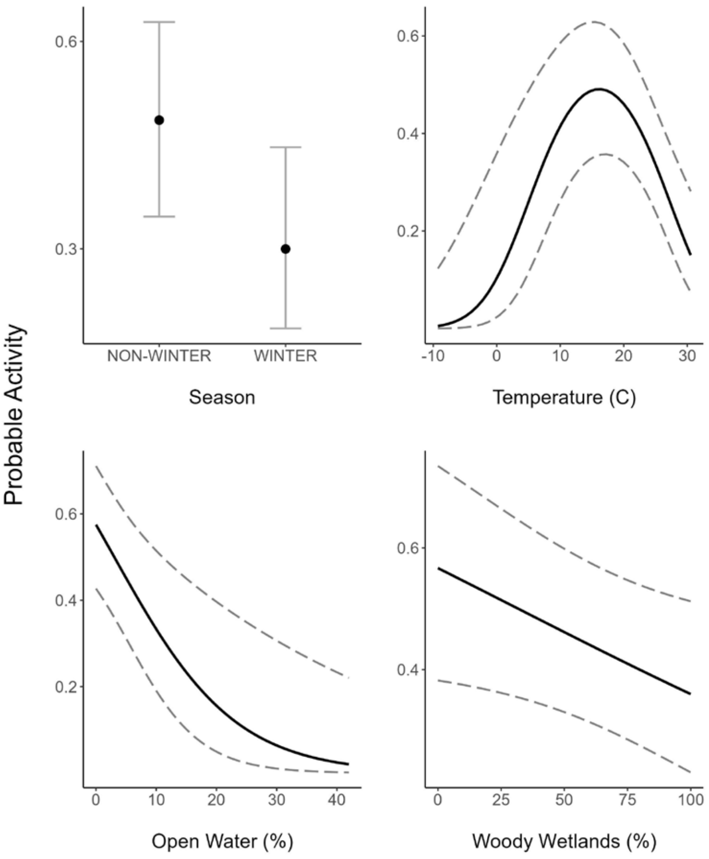

Figure 4. Partial effect plots of weekly predicted probability of activity (and 95% CI) of northern long-eared bats (*Myotis septentrionalis*) in eastern North Carolina and Virginia from 2016 to 2021 (non-winter = 1 April–15 November; winter = 16 November–31 March).

no relation between probable activity of northern long-eared bats and precipitation or evergreen forest cover (Table 2).

Discussion

Northern long-eared bats, widely regarded as a forest obligate, have been shown to select deciduous forests over pine forests across much of their range (Silvis et al. 2016). Our findings, however, indicate that northern long-eared bats in northeastern North Carolina and southeastern Virginia are more active in landscapes with higher proportions of woody wetlands and upland pine-dominated evergreen forests. However, probable activity decreased with increasing woody wetland cover and open water. Although northern long-eared bats do use woody wetlands for both roosting and foraging, our results suggest that northern long-eared bats may rely on those areas of woody wetlands more associated with upland forests rather than semi- or permanently inundated cover. For example, in the Coastal Plain of North Carolina, core and peripheral home ranges of reproductive female and volant juvenile northern long-eared bats were located nearer to both woody wetlands and upland forests than other cover types on the local landscape (De La Cruz et al. 2022a). Northern long-eared bats used riparian woody wetlands adjacent to upland pine-dominated evergreen forests at The Nature Conservancy's Piney Grove Preserve (PGP) in Sussex County, Virginia, as overwintering habitat (De La Cruz et al. 2022b). Although northern long-eared bats at the PGP were observed to roost in sweetgum, red maple, and tupelo, within or directly adjacent to woody wetlands, it may be that northern long-eared bats are actively selecting these sites due to proximity to pine stands. In Arkansas, northern long-eared bats were shown to prefer thinned, mature pine stands (Perry and Thill 2007). Additionally, research at the Kisatchie National Forest (KNF) on the upper Gulf Coastal Plain of Louisiana indicated that northern long-eared bats select pine as both summer and winter roosts (Garcia et al. 2023). Although northern long-eared bats largely overwintered in deciduous trees in the Croatan National Forest (CNF) on the Coastal Plain of North Carolina (Jordan 2020), the CNF contains a significant upland pine-dominated evergreen component. Minimally, our results support the conservation and management of a diverse mosaic of woody wetlands juxtaposed by upland forests, often characterized as pine-dominated evergreen forests. Beyond the simple association of this cover mosaic, it may be that northern long-eared bats use heterogenous forested areas created by active management such as prescribed fire. Intriguingly, the KNF, CNF, PGP, and Big Woods WMA are all dominated by a mosaic of woody wetland and pine-dominated evergreen forests, with upland pines often managed using prescribed fire (Watts and Harding 2007, Haywood 2012, Taillie et al. 2016). Specifically, we collected the greatest number of northern long-eared bat echolocation files at the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area (WMA), in Sussex County. Prescribed fire has been shown to enhance resource availability to northern long-eared bats at the intersection of cover types in other physiographic provinces (Johnson et al. 2009). It is possible that northern long-eared bats actively forage and roost proximal to the intersection of woody wetlands and upland forests, including fire-managed pines. Therefore, prescribed fire may be beneficial in promoting the continual formation of day-roosts and the variety of conditions needed for year-round use by this species in the region.

Northern long-eared bat activity was more likely to be documented in the non-winter than winter season, but total relative activity did not differ between seasons, supporting the observed year-round presence of northern long-eared bats in northeastern North Carolina and southeastern Virginia (Jordan 2020, De La Cruz et al. 2022b). Furthermore, while we observed that probable activity was highest between 10 and 25 C, we found no relationship between relative activity and temperature. Generally, bat activity is limited by prey availability and the thermoregulatory demands of foraging in lower ambient temperatures (Bernard and McCracken 2017). However, on the Coastal Plain, warmer winter temperatures (Grider et al. 2016) and year-round insect availability (Jordan 2020) likely decrease the obstacles to winter foraging. Locally, Whitaker et al. (1997) observed that eastern red bats in the Great Dismal Swamp of North Carolina and Virginia successfully foraged on Diptera (i.e., true flies) and Lepidoptera (i.e., moths) during winter. Similarly, in eastern and central Tennessee, Bernard et al. (2021) observed that bats, including northern long-eared bats, also foraged on true flies and moths during winter. Because we observed no variation in relative activity in relation to season or temperature, it seems likely that prey is readily available to northern long-eared bats even during winter. Interestingly, our results indicate that probable activity was highest during non-winter seasons at temperatures between 10 and 25 C. The upper thermoneutral zone for bats of the family Vespertilionidae is 30 C (Patriquin et al. 2016), suggesting our findings highlight the optimal temperature range for recording northern long-eared bat activity in the region. Jordan (2020) documented that northern long-eared bats enter torpor during temperatures approaching freezing on the Coastal Plain of North Carolina. Northern long-eared bat activity in coastal areas of the southeastern U.S. may be more influenced by short-term thermoregulatory requirements (e.g., decreased movement during extreme hot or cold periods) than seasonal resource availability.

Although prey availability (Bernard and McCracken 2017) and extreme weather events (Grider et al. 2016) undoubtedly alter bat activity, peak probable activity related to temperature may also be linked to the reproductive phenology of northern long-eared bats in northeastern North Carolina and southeastern Virginia. For example, De La Cruz et al. (2022a) observed that early volancy of juvenile northern long-eared bats on the Coastal Plain of North Carolina was linked to the early onset of the growing season in the region. Thermally stable roosts during the early growing season likely allow maternity colonies to remain normothermic, accelerate fetal growth, and produce consistent lactation earlier in the year (Burrell and Bergeson 2022). These conditions may then allow for early parturition and volancy, providing juvenile northern long-eared bats an extended developmental period to accumulate fat stores prior to winter hibernation or extended torpor (Geluso et al. 2019). However, researchers have also observed use of short, decayed, and highly shaded roosts by post-lactating adults and volant pups, likely indicating the reduced thermal requirements of colonies post-volancy (Perry and Thill 2007, Patriquin et al. 2016, De La Cruz et al. 2022a). Previously, it was assumed that the addition of newly volant pups onto the landscape would result in a spike of local acoustic activity (Ford et al. 2011). However, recent research indicates that for many species peak activity occurs during lactation rather than juvenile volancy (Deeley et al. 2022). Therefore, northern long-eared bat activity peaks prior to both juvenile volancy and the height of summer heat are likely coinciding with the high energy demands of lactation and the rearing of young. Furthermore, extreme weather events of coastal areas (Grider et al. 2016) may necessitate selection of contiguous tracts of woody wetlands and intersecting pine-dominated evergreen forests that provide adequate protection from inclement conditions during both maternity (Perry and Thill 2007, Patriquin et al. 2016) and non-maternity seasons (Jordan 2020).

Northern long-eared bats appear to be both reproductive and overwintering season residents of northeastern North Carolina (Jordan 2020) and southeastern Virginia (De La Cruz et al. 2022b). Despite documenting relatively consistent widespread northern long-eared bat activity, our highest call totals were localized to the Coastal Plain of Virginia and North Carolina. Additionally, call counts, particularly those collected during the spring and summer, may suggest that these areas contain multiple active northern long-eared bat maternity colonies (Ford et al. 2023). Future surveys to locate new reproductive populations of the species may benefit from targeting heterogenous forest sites, with emphasis on forest mosaics characterized by woody wetlands with associated upland pine-dominated evergreen forest, during warm (10–25 C) periods of non-winter seasons. Whereas northern long-eared bats require relatively large areas of contiguous woody wetlands and upland forests for both roosting and foraging on the Coastal Plain of North Carolina (Jordan 2020, De La Cruz et al. 2022a), the species also selects cover regularly subjected to small-scale disturbances that establish new roosts and improve conditions in existing roosts (Johnson et al. 2009, Ford et al. 2016). Specifically, northern long-eared bat activity appears to increase with increasing proportions of both woody wetlands and pine-dominated evergreen forests, possibly including pine stands managed using prescribed fire. Management of unique coastal cover, specifically a diverse mosaic of woody wetlands juxtaposed by upland forest and/or fire-managed pines, may provide habitat for both reproductively successful summer maternity colonies and overwintering populations of northern long-eared bats in the region. Our findings suggest that heterogenous coastal forests, specifically woody wetlands and associated upland pine stands, are likely important habitat for northern long-eared bats in the Mid-Atlantic. Implementing management strategies that maintain and enhance these unique habitats may support both maternity and overwintering population establishment of this endangered species.

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Seasonal Activity Patterns of Northern Long-eared Bats at Hibernacula in Western Virginia

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Abstract: Understanding the relationships of biotic and abiotic factors to seasonal activity at hibernacula is important for the conservation of bats impacted by white-nose syndrome (WNS). Research on the relative and probable activity patterns of the federally endangered northern long-eared bat (*Myotis septentrionalis*) primarily has focused on summer maternity colonies, whereas surveys at hibernacula have traditionally relied on external capture and internal counts. We used passive acoustic monitoring to assess the relative and probable activity of northern long-eared bats at 13 hibernacula in western Virginia, from August 2020 to May 2022. Northern long-eared bats were most active near hibernacula during warmer weeks of the fall swarm and spring emergence, when rainfall was low. Similarly, the probability of northern long-eared bat activity was highest near hibernacula during the spring/summer season. However, unlike relative activity, the likelihood of recording northern long-eared bats was associated with more heterogeneous, interior forests. Our results suggest that northern long-eared bat activity largely follows the described pre-WNS hibernation phenology of the species. Therefore, acoustical surveys to monitor northern long-eared bat populations at hibernacula should focus on entrances during peak activity periods (mid-April and early September), rather than the nearby landscape. Finally, management to promote resource-rich foraging habitat adjacent to hibernacula for use during swarming and emergence may increase survival during hibernation, fitness for spring migration, and ultimately, improve the reproductive success of northern long-eared bats in western Virginia.

Key words: *Myotis septentrionalis*, hibernacula, seasonal, activity

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Northern long-eared bats (*Myotis septentrionalis*) were recently listed as federally endangered (USFWS 2022) under the U.S. Endangered Species Act of 1973 due to extreme population declines resulting from the spread of white-nose syndrome (WNS) caused by the fungal pathogen *Pseudogymnoascus destructans* (*Pd*; Cheng et al. 2021). Northern long-eared bats, once among the most commonly captured species in the central Appalachians (Ford et al. 2006), have declined by 95% in total captures and limited reproductive success among surviving bats has been documented (Francl et al. 2012, Reynolds et al. 2016). Recent observation of maternity roosts in the Ridge and Valley and Blue Ridge Mountains of Virginia (Figure 1) provide evidence, based on early abandonment of roosts and absence of juvenile captures, for ongoing maternity colony collapse and failed recruitment (Kalen et al. 2022). Moreover, in the nearby High Appalachian Plateau of the Central Appalachians in West Virginia (Figure 1), an area characterized by colder winters with longer hibernation periods, northern long-eared bat populations declined rapidly after *Pd* invasion of karst hibernacula (Johnson et al. 2013, Ford et al. 2016, Austin et al. 2018).

The breakup of summer colonies often is associated with the conclusion of the summer reproductive season and departure of bats to hibernation sites (Pfeiffer and Mayer 2013). Preceding hibernation, northern long-eared bats, along with other hibernating species, engage in swarming behavior, gathering at cave and mine entrances to mate and select suitable hibernation sites (Caceres and Barclay 2000, Van Schaik et al. 2015, Fraser and McGuire 2023). During this period in the early fall, bats may enter their selected hibernaculum during the night to mate but exit to forage and then will typically roost in trees during the day (Caceres and

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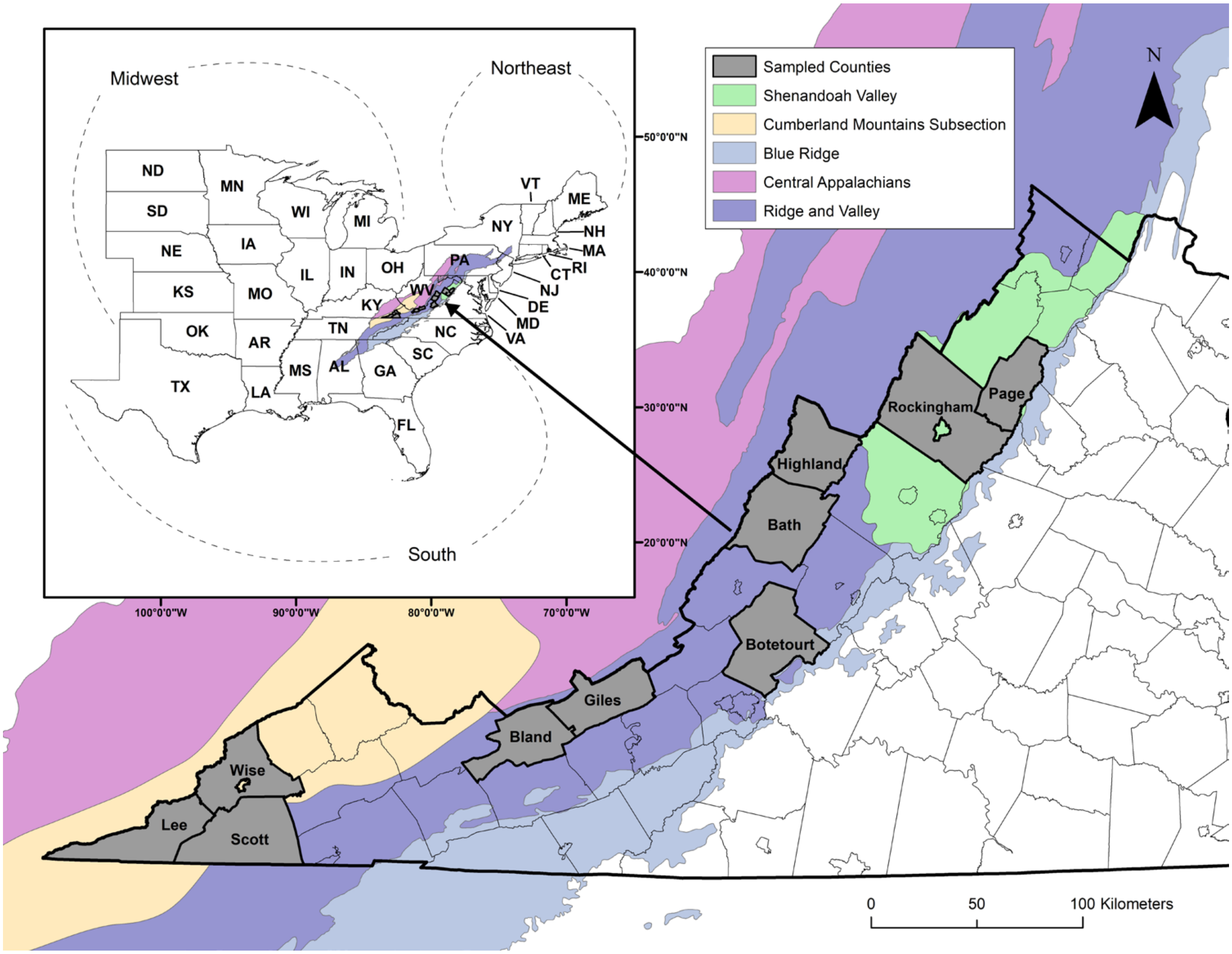

Figure 1. Ten county boundaries (gray fill denotes sampled area) for 13 hibernacula in western Virginia surveyed for northern long-eared bat (*Myotis septentrionalis*) calls, 2020–2022.

Barclay 2000). Successful foraging during the swarming period to increase fat deposits is essential for survival during hibernation, especially in the post-WNS era (Frick et al. 2017, Cheng et al. 2019, Cheng et al. 2021). This need is constrained by summer breeding, the energetic costs of fall migration, and mating (Fraser and McGuire 2023). Therefore, it is beneficial that bats select hibernacula near highly productive foraging habitat to promote fat deposition prior to hibernation (Jackson et al. 2022). The identification and management of high-quality habitat for fall roosting and foraging for many species remains a critical conservation data gap (Muthersbaugh et al. 2019). For example, prescribed fire near hibernacula may benefit northern long-eared bats by reducing forest clutter, increasing day-roost suitability, and enhancing foraging opportunities (Ford et al. 2016), thereby potentially leading to increased body mass going into hibernation (Lacki et al. 2015).

Following swarming, temperate zone bats may hibernate as long as 200 days (Speakman and Thomas 2003). Despite the high energetic costs (Thomas and Geiser 1997), northern long-eared bats frequently arouse during winter (Whitaker and Rissler 1992). Since the invasion of *Pd*, such episodes are thought to reduce bat susceptibility to *Pd* invasion, and therefore possibly disease related mortality (Bernard et al. 2017, Reynolds et al. 2017, Jackson et al. 2022). During these arousal events, bats may reduce *Pd* loads by grooming and therefore potentially increase the likelihood of survival so long as fat reserves are not dangerously depleted (Brownlee-Bouboulis and Reeder 2013, Reynolds et al. 2017).

Additionally, research in Tennessee has shown that some bats, including northern long-eared bats, are actively and successfully foraging on the winter landscape (Bernard et al. 2021), regardless of disease status (Bernard and McCracken 2017). It appears likely that the mild climate of the southeastern U.S. provides an insect prey base even during the hibernation period (Bernard et al. 2021). These conditions likely reduce both the physiological (e.g., weight loss) and disease (e.g., WNS severity) related stresses of hibernation compared to more northern regions (Bernard and McCracken 2017). Although arousal during hibernation may offer some survival benefits (e.g., grooming, foraging) for WNS-affected bats, abnormal behaviors such as daytime activity or excursions in subfreezing temperatures probably are detrimental to bats whether in the mild Southeast (Bernard and McCracken 2017) or colder areas of the Northeast (Reynolds et al. 2017) or Midwest (Langwig et al. 2021).

During the spring emergence period, northern long-eared bats leave hibernacula and disperse across the landscape (Caceres and Barclay 2000). During this time, reproductively active females undertake short- to mid-range (5–150 km), but energy-demanding, migrations from hibernation sites to summer roosting sites to form maternity colonies (Whitaker and Hamilton 1998, Gumbert et al. 2002). After emergence and an initial foraging session, bats may stage or begin migrating immediately, alternating thereafter between foraging bouts and migration flights (Roby et al. 2019). Conversely, male bats typically emerge after females (Cope and Humphrey 1977) and often remain near the hibernacula far into summer (Ford et al. 2005). Roby et al. (2019) found that bats reduce foraging or even cease migration when air temperatures drop below 10 C. Similarly, staging female northern long-eared bats in Kentucky utilized diurnal torpor while roosting on the landscape under adverse conditions (Thalken et al. 2018). While northern long-eared bats may use torpor to preserve energy reserves, prey availability and foraging efficiency near hibernacula during emergence are critical determinants of successful migration and reproduction (Meyer et al. 2016). However, successful foraging prior to migration is dictated not only by habitat availability and quality adjacent to hibernacula, but also by weather conditions at emergence (Meyer et al. 2016, Roby et al. 2019).

To assess the drivers of seasonal relative (i.e., weekly counts of echolocational recordings) and probable (i.e., likelihood to collect ≥1 recording) activity of northern long-eared bats at hibernacula, we initiated a multi-season survey in 2020 at 13 bat hibernacula in western Virginia. Our objectives were to use passive acoustic monitoring to evaluate the effect of 1) seasonality; 2) weather covariates; 3) proximity to hibernacula; and 4) habitat factors on relative and probable activity estimates of northern long-eared bats. We hypothesized that northern long-eared bat activity would be greatest during the fall swarm and spring emergence, nearer hibernacula, during warmer, dryer periods, and in interior portions of heterogenous forest habitats. Additionally, we hypothesized that the likelihood to record northern long-eared bat activity would follow similar trends.

Study Area

We collected acoustic data at hibernacula located in the Ridge and Valley and Appalachian Plateau physiographic regions of Bath, Bland, Botetourt, Giles, Highland, Lee, Page, Rockingham, Scott, and Wise counties in western Virginia (Figure 1). The Ridge and Valley is a series of long, narrow valleys and high ridges, with elevations ranging from 350 m to 1460 m. The Ridge and Valley has a temperate climate, with average annual temperatures ranging from 7–14 C in the north to 13–17 C in the south. Precipitation ranges from 80–150 cm therein (USDA NRCS 2022). The relatively dry climate of the Ridge and Valley supports xeric oak (*Quercus* spp.)-hickory (*Carya* spp.) or oak-pine (*Pinus* spp.) forests on ridges and side slopes. On mesic, north-facing slopes, yellow poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), and sugar maple (*Acer saccharum*) occur (Braun 1950). In the Cumberland Mountain subsection of the Appalachian Plateau, more mesic oaks, such as northern red oak (*Q. rubra*), typically dominate the diverse second- and third-growth side-slope forests, and rich, mixed mesophytic hardwood forests are present in sheltered coves and north-facing slopes (Braun 1950). Additionally, this region contains significant legacy below-ground coal mines, that can provide important overwintering sites for bats (Lituma et al. 2021). Regional topography here is characterized by steep slopes and narrow valleys ranging from approximately 240 m to 1130 m in elevation. The average annual temperature and precipitation of the Cumberland Mountain subsection are cooler and wetter than in the Ridge and Valley, at 13 C and 120 cm, respectively (USDA NRCS 2022).

Methods

Acoustic Monitoring

We conducted acoustic monitoring at 13 hibernacula (Big Salt, Breathing, Church Mountain, Cove Creek Mine, Cudjos, Hupmans Saltpeter, Kelly, New River, Newberry-Bane, Peerys, Rocky Hollow, Starr Chapel Saltpeter, and Woods Cave) within the 10 above-mentioned western Virginia counties from August 2020 to May 2022 (Figures 1, 2). We established on average $\bar{x} = 3 \pm 2$ (± SD) acoustic sampling sites at each hibernaculum, with recorders deployed near the opening feature to 550 m ($\bar{x} = 170 \pm 187$ m) beyond openings, to assess both relative and probable activity of northern long-eared bats. We used ultrasonic recorders to collect

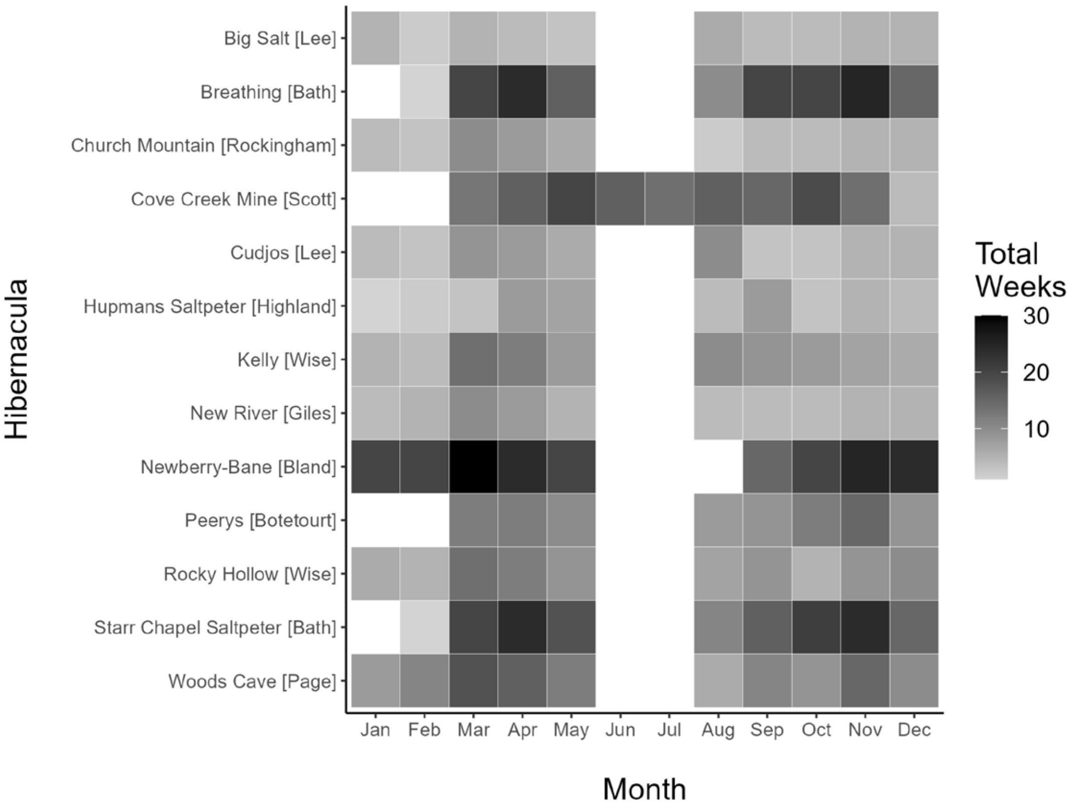

Figure 2. Sampling effort as represented by a monthly heatmap (white areas represent unsampled months) of the total number of acoustic monitoring weeks conducted at 13 hibernacula in western Virginia, 2020–2022 (county name in brackets; see Figure 1 for county locations).

acoustic data (Song Meter (SM) Mini, SMZC, and SM4; Wildlife Acoustics, Maynard, Massachusetts). We attached recorders to trees at an approximate height of 1.5 m above the ground, ensuring microphones extended beyond the diameter of the bole, or on 3-m poles as dictated by site conditions (Muthersbaugh et al. 2019). We deployed recorders perpendicular to hibernacula entrances and foraging/flyway features (e.g., forest roads/trails, streams, and rivers; Britzke et al. 2010). We programmed detectors to record from 1.5 hr prior to sunset to 1.5 hr after sunrise. We checked functionality of recorders and downloaded and processed data at approximately 30- to 60-day intervals. We used an automated acoustic software (Kaleidoscope Pro software; v. 5.4.7; Wildlife Acoustics) to identify echolocational recordings to species using default signal detection parameters and the 5.4.0 classifier set to 'Balanced/Neutral' (USFWS 2020). We categorized assemblages based on a north-south gradient, with a transition zone in Giles County. In southern sites, we examined data for 12 species: Virginia big-eared bats (*Corynorhinus townsendii virginianus*), big brown bats (*Eptesicus fuscus*), eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), silver-haired bats (*Lasionycteris noctivagans*), gray bats (*M. grisescens*), eastern small-footed bats (*M. leibii*), little brown bats (*M. lucifugus*), northern long-eared bats, Indiana bats (*M. sodalis*), evening bats (*Nycticeius humeralis*), and tri-colored bats (*Perimyotis subflavus*). In northern sites, we excluded gray and evening bats based on their limited distribution in the region. However, due to recent range expansions into the New River Valley, we included gray bats in Giles County (Reynolds and Fernald 2021, Taylor et al. 2023).

Predictor Variables

Following recent research in eastern West Virginia (De La Cruz et al. 2023), we examined relative and probable activity of northern long-eared bats in relation to landscape richness (i.e., total number of local cover types within a 500-m moving window) using the 2019 National Land Cover Database (NLCD) raster dataset (Dewitz and USGS 2021). Also using the NLCD layer, we incorporated a measure of distance from forest edge (0) into forest interior (–) and from forest edge into (+) non-forest cover (De La Cruz et al. 2023). This layer was created using forest/non-forest reclassifications of NLCD raster data and the distance function in the raster package in R (R Core Team 2020, Hijmans 2023). We standardized both our landscape richness and forest edge raster layers to a 100-m resolution. We also examined the effect of the weather variables weekly mean of daily average temperature (C) and weekly mean of daily total precipitation (mm; Muthersbaugh et al. 2019). We obtained matching nightly weather data for sites from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) Data Explorer, using the inverse-distance squared weighting interpolation option for the standard 4 km PRISM grid cell (PRISM Climate Group 2022). To account for likely bimodal activity patterns associated with swarming and emergence before and after hibernation, we incorporated a fourth-order polynomial of week of hibernation in models. Additionally, we assessed course temporal trends using seasonal (i.e., summer/fall, winter, and spring/summer) covariates (Muthersbaugh et al. 2019, Gorman et al. 2021, Deeley et al. 2022, Taylor et al. 2023). Finally, we evaluated the effect of proximity to hibernacula (≤200 m or >200 m; Muthersbaugh et al. 2019).

Statistical Analysis

To account for known rates of misclassification and to minimize false positive and false negative errors, we assumed presence of northern long-eared bats only if a statistically significant maximum likelihood estimate (MLE; $P < 0.05$) was returned for any given night/site (Britzke et al. 2002). We aggregated nightly data by hibernaculum, recording site, and year, then totaled counts for northern long-eared bats across each corresponding week of the year (Straw et al. 2022). We used these counts (i.e., weekly relative activity) as the response variable in all modeling efforts. We used a Shapiro-Wilk test to evaluate weekly relative activity totals for non-normality and found that the data were not normally distributed ($P < 0.01$). Therefore, we used zero-inflated negative binomial generalized linear mixed models (GLMMs) in the glmmTMB package of R (Brooks et al. 2017) for all statistical analyses. All GLMMs included two sub-models: 1) a conditional count sub-model to model relative activity; and 2) a zero-inflation sub-model to model probable activity. Prior to modeling, we assessed variables for collinearity using pairwise correlation (threshold = $|0.8|$) and centered and scaled continuous variables. We developed and compared seven multivariate GLMMs and a null model. We included in all conditional sub-models the random effect of hibernaculum location (Muthersbaugh et al. 2019, Taylor et al. 2023). We ranked models using Akaike Information Criterion corrected for small sample sizes (AIC_c) and considered models within two ΔAIC_c as competing (Burnham and Anderson 2002). We assessed goodness-of-fit and over- and under-dispersion of our top models using a quantile-quantile plot, residual plot, and a one-sample Kolmogorov-Smirnov test with the R DHARMa package (Hartig 2020). Additionally, we assessed ecological relevance of our top models by measure of conditional Nakagawa R^2 (i.e., proportion of variance explained by the fixed and random effects) using the performance package in R (Nakagawa and Schielzeth 2013, Lüdecke et al. 2021). We interpreted R^2 values as follows: ≤0.20, very low; 0.21–0.40, low; 0.41–0.60, medium; 0.61–0.80, high; and 0.81–1.00, as very high proportions of variance explained (Gorman et al. 2021, Hill et al. 2024, Torre et al. 2022). Finally, we created model-averaged partial effect plots using AIC_c weights to examine the relationship between relative and probable activity and predictor variables found to be significant.

Results

During 2020–2022, we sampled for 1267 weeks and collected 6,622,598 files of acoustic data from 13 hibernacula in western Virginia. A significant ($P < 0.05$) nightly MLE identified 712,221 (11%) files from our recordings to species, with 17,492 (2.4%) passes identified as northern long-eared bats. We recorded northern long-eared bats at all hibernacula sampled, with the greatest number of passes collected at Woods Cave ($n = 5031$; three sampling sites) and the least at Hupmans Saltpeter ($n = 58$; one sampling site; Figure 1).

We had two competing models within two ΔAIC_c units explaining drivers of relative and probable activity of northern long-eared bats (Table 1). Our top models passed all DHARMa goodness-of-fit tests and explained a medium proportion of variance (Model 1: $R^2 = 0.49$; Model 2: $R^2 = 0.47$), suggesting moderate ecological relevance. We observed that northern long-eared bat relative activity was greatest near hibernacula, and that activity was bimodal as expected, with distinct peaks related to the fall swarm (early-September) and spring (mid-April) emergence (Table 2; Figure 3). Furthermore, we found that northern long-eared bat relative activity was greatest during drier, warmer weeks (Table 2; Figure 3). However, we observed no influence of distance from forest edge (0) into forest interior (–) and from forest edge into (+) non-forest cover or total landscape richness on relative activity (Table 2). Our top-ranking models indicated that the probability for northern long-eared bat activity was highest near hibernacula during the spring/summer season (Table 2; Figure 4). However, results suggest that probable northern long-eared bat activity was highest in interior, heterogenous forest settings (Table 2; Figure 4). Finally, we observed no relation between probable activity of northern long-eared bats and the weekly mean of daily average temperature or precipitation (Table 2).

Discussion

We observed significant peaks in relative activity of northern long-eared bats coinciding with both fall swarming and spring

Table 1. Variables included in both conditional count and zero-inflation sub-models of generalized linear mixed models, number of full-model parameters (K), Akaike's information criterion (AIC_c) units, $\Delta\mathrm{AIC}_c$ units, full-model weights (w_i), and full-model log-likelihood (LL), predicting weekly relative and probable activity of northern long-eared bats (*Myotis septentrionalis*) at 13 hibernacula in western Virginia, 2020–2022.

Model[a]	K[b]	AIC_c	$\Delta\mathrm{AIC}_c$	w_i	LL
TEMP + PRECIP + PROX + FOREST + RICHNESS	20	5256.95	0.00	0.71	−2608.14
TEMP + PRECIP + PROX	16	5258.72	1.77	0.29	−2613.14
PROX	12	5274.10	17.15	0.00	−2624.92
DIST + FOREST + RICHNESS	16	5274.23	17.28	0.00	−2620.90
TEMP + PRECIP + FOREST + RICHNESS	18	5437.04	180.10	0.00	−2700.25
FOREST + RICHNESS	14	5450.65	193.70	0.00	−2711.16
TEMP + PRECIP	14	5487.72	230.78	0.00	−2729.69
Null	3	5704.79	447.84	0.00	−2849.39

a. TEMP: weekly mean of daily average temperature (C); PRECIP: weekly mean of daily total precipitation (mm); PROX: proximity to hibernacula (<200 m or >200 m); FOREST: distance from forest edge (0) into forest interior (–) and from forest edge into (+) non-forest cover (m); RICHNESS: number of local cover types.

b. All models include a single dispersion parameter and intercepts in both the conditional and zero-inflation sub-models. Excluding the Null model, each conditional sub-model contained the fourth-order polynomial effect of week of hibernation and random effects of hibernacula location, while zero-inflation sub-models contained the fixed effect of season.

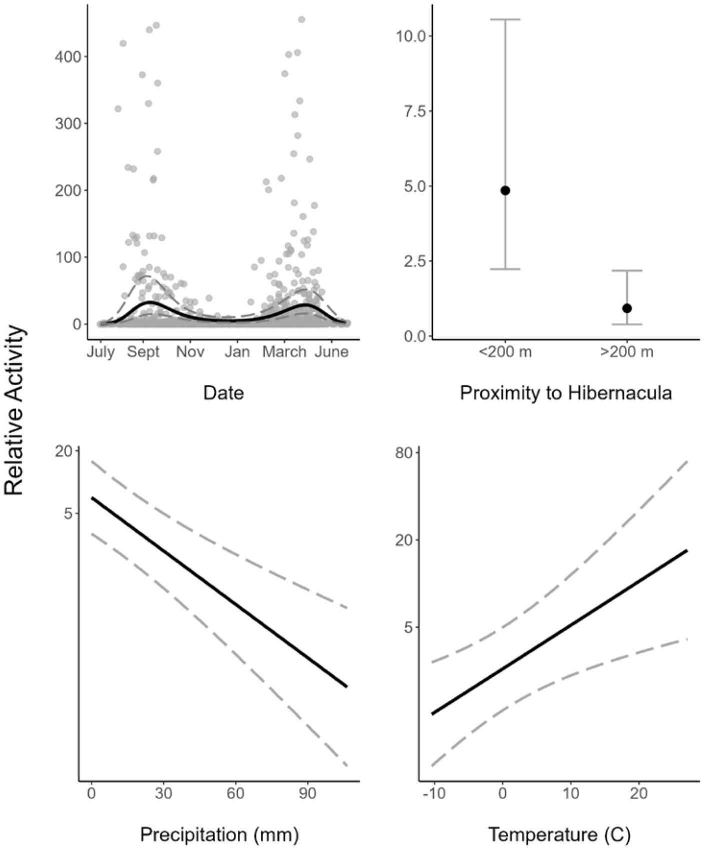

Figure 3. Model-averaged partial effect plots of predicted weekly relative activity (and 95% CI) of northern long-eared bats (*Myotis septentrionalis*) at 13 hibernacula in western Virginia, 2020–2022.

Table 2. Predictor variables, *β* estimates, and SE estimates for the top two generalized linear mixed models predicting weekly relative (i.e., counts of echolocational recordings; conditional sub-model) and probable (i.e., likelihood to collect ≥1 recording; zero-inflation sub-model) activity of northern long-eared bats (*Myotis septentrionalis*) at 13 hibernacula in western Virginia, 2020–2022.

		Model 1			Model 2		
Sub-model	Variable[a]	*β*	SE	*P*	*β*	SE	*P*
Conditional	Intercept	2.76	0.29	<0.01	2.34	0.31	<0.01
	TEMP	0.55	0.19	<0.01	0.65	0.20	<0.01
	PRECIP	−0.38	0.08	<0.01	−0.38	0.09	<0.01
	PROX – >200 m	−1.81	0.28	<0.01	−1.13	0.23	<0.01
	HIB	0.67	3.25	0.84	3.60	3.50	0.30
	HIB^2	7.22	5.64	0.20	5.27	6.15	0.39
	HIB^3	−1.96	2.95	0.51	−0.74	3.06	0.81
	HIB^4	−25.19	3.36	<0.01	−22.82	3.41	<0.01
	FOREST	0.62	0.34	0.07	–	–	–
	RICHNESS	−0.28	0.36	0.43	–	–	–
Zero-inflation	Intercept	0.89	0.27	<0.01	2.27	0.95	0.02
	TEMP	−0.20	0.16	0.20	−0.33	0.22	0.12
	PRECIP	−0.02	0.12	0.88	0.02	0.15	0.88
	PROX – >200 m	−1.69	0.23	<0.01	−2.90	0.82	<0.01
	SEASON – Winter	−0.25	0.34	0.47	−0.61	0.49	0.21
	SEASON – Spring/Summer	0.59	0.25	0.02	0.74	0.35	0.04
	FOREST	−0.55	0.16	<0.01	–	–	–
	RICHNESS	0.53	0.15	<0.01	–	–	–

a. TEMP: weekly mean of daily average temperature (C); PRECIP: weekly mean of daily total precipitation (mm); $\mathrm{HIB} + \mathrm{HIB}^2 + \mathrm{HIB}^3 + \mathrm{HIB}^4$: terms of fourth-order polynomial of week of hibernation; PROX: proximity to hibernacula (<200 m or >200 m); FOREST: distance from forest edge (0) into forest interior (–) and from forest edge into (+) non-forest cover (m); RICHNESS: number of local cover types; - denotes variables absent from model ; conditional sub-models contained the random effects of hibernacula location.

emergence, with activity concentrated near hibernacula entrances. Similarly, the probability of recording northern long-eared bats was highest near hibernacula during the spring/summer season and suggest that prioritizing sampling efforts at these entrances, rather than the broader landscape, could be a more efficient approach for monitoring northern long-eared bats at hibernacula. The increased likelihood of documenting northern long-eared bats during spring/summer raises questions about the composition and behavior of remnant populations. For example, an extended emergence period could be indicative of remnant populations represented by high proportions of resident males. However, similar to the varied emergence behavior observed in Indiana bats by Roby et al. (2019), some northern long-eared bats in our study may immediately migrate to summer maternity grounds whereas other individuals stage longer near hibernacula to replenish fat reserves and repair WNS-induced damage prior to migration. Additionally, we observed a higher probability to record northern long-eared bats in both interior forests and areas of greater landscape richness. This result, coupled with documented winter predation of insect prey (Bernard et al. 2021), may provide support for management that provides for the interspersion of high-quality foraging

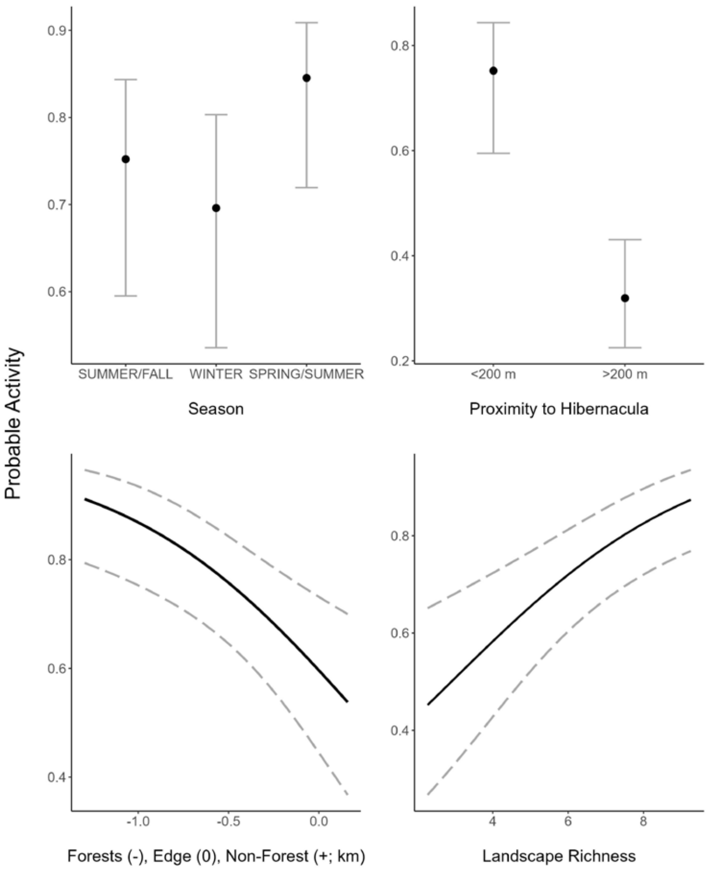

Figure 4. Model-averaged partial effect plots of weekly predicted probability of activity (and 95% CI) of northern long-eared bats (*Myotis septentrionalis*) at 13 hibernacula in western Virginia, 2020–2022.

habitat near hibernacula. Such management may improve the survival, migratory fitness, and ultimately, reproductive success of the northern long-eared bat.

Prior to our study, only Muthersbaugh et al. (2019) had assessed any facet of the post-WNS relative and probable activity of northern long-eared bats at hibernacula during the overwintering period in the Central Appalachians and our study was far more expansive in duration and sample-size. Still, our results are largely consistent with this previous work and suggest that northern long-eared bat activity at hibernacula is associated with the described phenology of the species, with bats arriving at hibernacula in the fall to mate and build fat stores before hibernation, and emerging in the spring to forage before migrating to summer roosting sites. Importantly, these results suggest that habitat alterations near hibernacula during specific timeframes (15 August–1 November and 15 March–15 May) may have a negative impact on northern long-eared bats, even within the context of the post-WNS landscape. Although relative activity estimates indicated peak periods during fall swarming and spring emergence, the probability of recording northern long-eared bat activity exceeded 50% during winter. This high probability for activity during winter, despite low relative activity, reveals that mid-winter arousal events are not uncommon. While these events may be partially driven by the detrimental impacts of WNS, causing bats to exit hibernacula under abnormal conditions (i.e., subfreezing temperatures, during daylight; Bernard and McCracken 2017), they also may be associated with active foraging, drinking, and grooming (Brownlee-Bouboulis and Reeder 2013, Reynolds et al. 2017, Bernard et al. 2021), roost switching within hibernacula (Ryan et al. 2019), or even movement between hibernacula (Langwig et al. 2021). Therefore, the persistence of northern long-eared bats in western Virginia may be due to their behavioral and physiological mitigation of advanced WNS, as evidenced by recent summer captures of the species in the Ridge and Valley of Virginia nearly 10 years post-WNS invasion (Kalen et al. 2022).

Our results indicate that weather also was a significant driver of northern long-eared bat activity at hibernacula in western Virginia. Specifically, relative activity increased with greater weekly means of daily average temperature; however, the probability of recording northern long-eared bats was not significantly impacted by temperature. Activity and temperature are typically linked to insectivorous prey availability and cost to an animal's energy budget to procure prey in cold weather (Bernard and McCracken 2017). The apparent decoupling of temperature for some species may signify WNS arousal, particularly for *Pd*-sensitive species such as northern long-eared bats. Our results support both observations. Northern long-eared bats in western Virginia were significantly more active during the warmer weeks of the year, when insect availability to bats is presumably greater. Nevertheless, the probability of recording the species remained relatively high despite low temperatures during winter, coinciding with the likely progression of WNS. Unlike Muthersbaugh et al. (2019), we observed a significant negative effect of weekly means of daily average precipitation on relative activity of northern long-eared bats. High precipitation may reduce hibernation arousals and exiting flights in northern long-eared bats in western Virginia, as the energy deficits from WNS and flight are unlikely to be offset by behavioral or physiological mechanisms. This hypothesis is supported by research showing that precipitation increases the energy cost of flight for bats (Voigt et al. 2011), maternity colonies avoid exposure to inclement weather (Patriquin et al. 2016), and torpor length in little brown bats is positively linked with precipitation totals (Dzal and Brigham 2013).

Our observed northern long-eared bat hibernacula associations derived from passive acoustic monitoring occasionally differ from those of site-specific internal counts conducted by the Virginia

Department of Wildlife Resources and the Virginia Department of Conservation and Recreation, Division of Natural Heritage. Although some automated acoustic misidentification of northern long-eared bats cannot be fully discounted (Nocera et al. 2019), this disparity may simply be attributed to roost selection within hibernacula, as the species often roosts in small clusters or singly in fissures and crevices of mines and caves that are overlooked or unapparent to observers during surveys (Caceres and Barclay 2000). Rather than using these sites simply as overwintering habitat, northern long-eared bats also may be attracted to hibernacula for short periods due to elevated social calls, for feeding opportunities, as migratory stopovers, and for mating (Lacki et al. 2015). Additionally, the seemingly high frequency of mid-winter arousals, potentially exacerbated by climate change-induced disruptions to normal hibernation periods (McClure et al. 2022), raises concerns about the adequacy of single-day internal surveys for monitoring of northern long-eared bats, given potential biases associated with imperfect detection (Cheng et al. 2021). Implementation of several methods (i.e., repeated external and internal surveys, long-term acoustic sampling) may increase monitoring confidence for northern long-eared bats at hibernacula in Virginia and elsewhere.

Northern long-eared bats appeared very active at Woods Cave. This cave, despite being farther north than other sampled hibernacula, is located in the Shenandoah Valley (Figure 1), which is significantly warmer during winter than the Ridge and Valley/Appalachian Plateau border to the west where northern long-eared bats were abundant pre-WNS (Johnson et al. 2013). Additionally, Woods Cave is in a mosaic of diverse forest types, moderately fragmented by agriculture, and is adjacent to the South Fork of the Shenandoah River. The post-WNS persistence of northern long-eared bat populations at Woods Cave may be attributed to the favorable combination of mild winter conditions and a diverse habitat assemblage characteristic of the Shenandoah Valley. Although Woods Cave and Hupmans Saltpeter, our most and least productive locations, respectively, are only 113 km apart, they may differ in their suitability for northern long-eared bats due to geophysical variation, suggesting that research assessing how factors such as elevation, structure, airflow, and ambient temperature affect northern long-eared populations post-WNS could be contributory. Additionally, because activity during winter may be associated with hibernacula switching, relating density of mine/cave openings near known hibernacula may be of value as well. Due to the relatively high probability of recording northern long-eared bats during winter that we observed, additional research related to prey availability and foraging of cave-hibernating bats in western Virginia may be warranted. Finally, the combination of passive monitoring and active capture may assist in acoustic monitoring validation and reveal whether relative activity correlates with trapping counts from the fall swarm and spring emergence (Whiting et al. 2022). Our research suggests that managers may benefit from scheduling active capture surveys for northern long-eared bats during periods of peak relative activity in spring (April) and early fall (September). Additionally, internal counts may benefit from multiple surveys between 28 October and 23 February, when activity was lowest, to mitigate bias associated with estimates of abundance and imperfect detection. Repeated hibernacula entry can negatively affect WNS-impacted species, however, research has shown that up to three surveys per year had no detectable impact on populations of Indiana bats, little brown bats, or tri-colored bats (Kilpatrick et al. 2020). Passive acoustics surveys may serve as either the basis for hibernacula surveys or, at minimum, provide useful additive information for inclusion in integrated models to support the management of rare, threatened, and endangered bats at hibernacula in western Virginia.

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Home Range Size and Resource Use by Eastern Spotted Skunks in Virginia

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Abstract. Throughout much of the eastern U.S., many forested ecosystems have lost large amounts of core forest areas due to land-use change, isolating wildlife in forest fragments. The eastern spotted skunk (*Spilogale putorius*) is considered a species of conservation concern in Virginia, where populations are restricted to spatially disjunct forest patches in the central Appalachian Mountains. We caught and radio-tagged eastern spotted skunks in the Appalachian Mountains of Virginia to assess whether current habitat fragmentation restricts skunk movements and hence distribution, potentially leading to isolation among habitat patches. Denning home range size (approximately 3.7 km^2) in our study was smaller than those in other studies of eastern spotted skunks and excursive movements were primarily limited to core forested areas (>2 km^2). Core forested areas were used more than non-forested and forest-edge areas. We conclude core forest area fragmentation limits eastern spotted skunk movement between mountain ridges. Increased forest patch connectivity may help prevent genetic and demographic isolation, reduce the likelihood of local extinctions, and facilitate colonization of suitable unoccupied areas.

Key words: compositional analysis, exploratory excursion, fragmentation, territoriality

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Many forest ecosystems have experienced fragmentation due to land conversion for agriculture or urban development (Bogaert et al. 2015). Size, shape, and degree of isolation of forest fragments can influence the distribution, demography, and genetic diversity of species (Schneider 2001, Devictor et al. 2008). When species' occurrences are limited to patches of habitat within a matrix of unsuitable conditions, an individual's home range may be limited within the habitat patch or it may make exploratory excursions to other patches but ultimately return to its home range area (Lidicker and Stenseth 1992, Kozakiewicz 1993). Understanding an animal's ability to traverse extra-home range environments is a key component of research involving movement patterns, migration rates, and resource use and intended to inform landscape management decisions. Excursions may allow an animal to elucidate the availability of resources outside of a familiar home range before dispersing (Lidicker and Stenseth 1992). If not identified as excursive during space-use studies, these movements can contribute to overestimations of home range size and lead to erroneous interpretations of resource use (Hodder et al. 1998). Home range size and excursive movements may be shaped by both resource availability and local population density. As density increases, animals may respond by using smaller home ranges which reduces range overlap, avoiding antagonistic interactions between individuals (Kozakiewicz 1985). Conversely, range overlap may increase, intensifying competition among individuals (Wolff 1985).

The eastern spotted skunk (*Spilogale putorius*; hereinafter, spotted skunk) has a global rank of Vulnerable on the IUCN Red List of Threatened Species (Gompper and Jachowski 2016) and a state rank of Vulnerable in Virginia (Chapman 2007). In the central Appalachian Mountains of Virginia, spotted skunks occupy small, disjunct forest patches throughout their historic range (Thorne et al. 2017). Spotted skunks are sexually dimorphic in body size which contributes to variation in home range size and resource use (Lesmeister et al. 2009). Physiological differences (e.g., reproductive condition) also may explain variation in movement patterns. Pregnant or kit-rearing females require more food, are vulnerable to predation, and may be restricted to smaller daily movements (Powell 1979). Restricted movements could have demographic and genetic consequences (Templeton et al. 1990), similar to those faced by Allegheny woodrats (*Neotoma magister*) in the region (Kanine 2013).

Our study objectives were to: identify patterns in exploratory excursions by spotted skunks; estimate site- and sex-specific differences in den home range size; assess sex- and site-specific patterns

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of den home range overlap; and assess within-study site and within-den home range resource use (second- and third-order selection, respectively; Johnson 1980). We predicted: 1) male spotted skunks would make more frequent and longer distance exploratory excursions to seek additional resources (Handley and Perrin 2007); 2) due to larger body size, potential territoriality, and mate-seeking behavior, male spotted skunks would occupy larger den home ranges (Clutton-Brock 1989) which would be greater at sites with larger core forest areas (Kozakiewicz 1985); 3) as a solitary carnivore species, spotted skunks would display little home range overlap with conspecifics, though more so between male-female dyads (Powell 1979); and 4) resource use would be associated with large core forest areas at lower elevations where complex forest structure may provide foraging and escape cover (Aebischer et al. 1993).

Study Area

We conducted our study within the Appalachian Mountains of Virginia in the Valley and Ridge and Blue Ridge physiographic provinces on or adjacent to the George Washington and Jefferson National Forests (Figure 1). This included Bald Mountain (BM) in Botetourt and Craig counties, Whitetop Mountain (WT) in Grayson County, and Wintergreen Resort (WG) in Nelson County. Elevation ranged from 350 to 1460 m. Forest composition varied by elevation and aspect but consisted predominately of Appalachian oak (*Quercus* spp.)–hickory (*Carya* spp.) association with cove hardwood in mesic ravines and north-facing slopes, yellow pine (*Pinus* spp.)–mountain laurel (*Kalmia latifolia*) associations on xeric ridgelines, and white pine (*P. strobus*), eastern hemlock (*Tsuga canadensis*), and rosebay rhododendron (*Rhododendron maximum*) along riparian zones. The high-elevation forest of the Mount Rogers National Recreation Area was dominated by northern hardwood and red spruce (*Picea rubens*) communities (Yarnell 1998). Annual precipitation was approximately 110 cm throughout most of the region but varied from north (less) to south (greater) and annual temperature ranged from –10.6 C in winter to 27.5 C in summer.

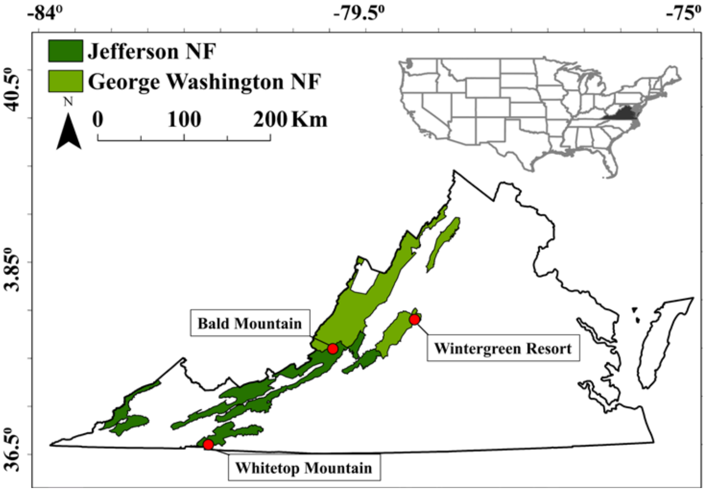

Figure 1. Eastern spotted skunk (*Spilogale putorius*) den home range study sites in Virginia, March 2016–November 2017.

Methods

Sampling Methods

To assess relationships between spotted skunk movement patterns, den home range size, and resource use, we initiated a radio telemetry study using very high frequency radio collars. During the winter seasons of 2016–2017, we deployed live traps (model 103, Tomahawk Live-Trap Co., Wisconsin) in three areas of high predicted spotted skunk occupancy (Thorne et al. 2017): BM, WG, and WT. Traps were baited with a mixture of peanut butter, bacon grease, and oats. Captured spotted skunks were removed from the traps and physically immobilized using a cloth handling bag. We sexed and weighed all captured individuals. We assessed age class (adult and juvenile) based on weight and tooth wear (Crabb 1944) and categorized individuals as juvenile (<350 g) and adult. Only adults were initially captured during winter months (February–May) and were all >350 g. Juveniles were only captured during summer (July–August) after emerging from their natal den and were not collared as body mass was too low (<200g) to support the use of a tracking collar.

We affixed a uniquely numbered ear tag to each captured individual and deployed 16-g radio collars (model M1740, Advanced Telemetry Systems Inc., Isanti, Minnesota) to adult individuals with a mass >350 g. These collars comprised approximately 2.3–4.6% of body weight of individuals with a mass of 350–700 g. Throughout the study, we attempted to recapture all collared individuals to replace collars prior to battery failure or remove collars at the conclusion of our fieldwork. We radio-collared and tracked individuals using TRX-1000S receivers and folding three-element Yagi antennas (Wildlife Materials Inc., Carbondale, Illinois) and attempted to locate each animal every four to seven days to prevent temporal autocorrelation. We tracked through all seasons until the individual was lost, expired, or the collar failed. Trapping and handling procedures were approved by the Virginia Polytechnic Institute and State University Institutional Animal Care and Use Committee (protocol number 13-119-FIW) and permitted by Virginia Department of Wildlife Resources.

Diurnal den locations were recorded using a hand-held GPS unit (model eTrex 20x, Garmin, Ltd., Olathe, Kansas). When field conditions prevented physical location of dens, we recorded three observer GPS coordinates and respective azimuth direction and used Program LOAS (Ecological Software Solutions, LLC, Sacramento, California) to triangulate an individual's estimated location. We estimated triangulation error by comparing the difference in distance between the actual and estimated location pairs following the methods of Lesmeister et al. (2009).

Data Analysis

We identified exploratory excursions using the Incremental Cluster Polygon method (Hodder et al. 1998). We compared number of excursions and excursion distance between sexes using Mann-Whitney U-Tests. We pooled non-excursive relocations of individuals to calculate den home range size and core-use area using 95% and 50% fixed-kernel density estimates with reference bandwidth, respectively (Worton 1989). Due to lost individuals, collar failures, and mortality, the threshold of 30–50 points per home range suggested for kernel density estimation was not achieved for all individuals (Seaman et al. 1999). Small sample sizes may lead to overestimation of home range size; however, estimates for simple home ranges, as in this study, may be less biased than complex ones (Seaman et al. 1999). Home range and habitat use information is important for spotted skunk conservation, thus we included individuals with ≥15 relocations to increase replications, understanding that estimates may be biased. We compared site- and sex-specific differences using Kruskal-Wallis tests (Kruskal 1952). We checked for correlation between number of relocations and den home range size using a Pearson's product moment correlation test. We calculated the volume of intersection (VI) to assess the degree of overlap (0 = no overlap, 1 = complete overlap) of the den home range and core area for sex-specific dyads. We then used a Kruskal-Wallis test for sex- and site-specific differences in VI of den home range and core areas.

We used compositional analysis to assess landscape characteristics and space use, or utilization distribution (UD; Millspaugh et al. 2006). Characteristics included land cover class, forest fragmentation, and elevation. We used the 2016 National Land Cover Database (NLCD) classification system (Yang et al. 2018) to categorize land cover types as hardwood forest, conifer forest, mixed hardwood-conifer forest, shrub-scrub, and non-forested (i.e., wildlife openings, oldfields, pasture and non-woody wetland areas). We derived a forest fragmentation map in ArcMap 10.2.2 (ESRI, Redlands, California) following methods of Vogt et al. (2007) to classify areas as core forest (>2 km^2 intact forest), forest-edge (boundaries around forest regions), patch forest (forest <2km^2), and perforated forest (boundaries between core forest and small forest perforations). We reclassified the 30-m National Elevation Dataset (Gesch et al. 2002) into 100-m intervals between 450 and 1050 m in elevation. However, due to limited observations at the highest and lowest elevations, we pooled observations <450 m, between 1050 and 1249, and >1249 m.

We estimated resource use at two levels according to the Johnson (1980) order of selection criteria following recommendations of Aebischer et al. (1993). We defined study areas using buffers equal to the mean radius of all home ranges at a site. We first summed the UD value of each landscape characteristic available within a den home range and divided by the total UD value of the den home range. We then used the weighted compositional analysis to assess within-home range resource use (third order selection). Next, we pooled UD values of each landscape characteristic for all individuals within a site and used the weighted compositional analysis to assess resource use (second order selection). We used the Wilk's lambda statistic to test the use of each landscape characteristic and performed a rank analysis on each resource class. All analyses were performed in R using the package 'adehabitatHR' (Calenge 2020) and R base package 'stats' (R Core Team 2014).

Results

We captured 27 spotted skunks including 18 adults (seven females, 11 males) and nine juveniles (two females, seven males). We collared and tracked all adult skunks but only collected ≥15 non-excursive relocations for 12 (seven males, five females; Table 1). Body mass of adult males ranged from 390–755 g ($\bar{x} = 566 \pm 15$ g) and adult females from 401–655 g ($\bar{x} = 470 \pm 26$ g). The 12 skunks with ≥15 relocations were tracked for an average of 296.4 ± 60.2 days and an average of 25.0 ± 2.5 relocations per individual were collected from March 2016–November 2017. Though tracking effort was generally even (1–2 tracking events per week per site), the number of relocations per individual varied across months and ranged from 1–5.8 ($\bar{x} = 2.5 \pm 2.3$). The greatest number of successful tracking attempts occurred during months immediately following live trapping and decreased to one or two from August through February. Triangulation estimate error was 0.9 ± 2.1 degree azimuth and 83.2 ± 15.1 m distance; points with an error polygon diameter greater than 115.5 m were not used. Of the 300 relocations included in the analyses, 61.3% were physically located and 38.7% were estimated from triangulation. We observed six mortality events during our study. At BM, two males were found dead during mating season (26 April 2017 and 28 Mar 2017) and three kit-rearing females were found dead (20 June 2016, 15 September 2016, and 1 August 2017). Three mortalities occurred within forest edge and two within core forest lacking understory cover. At WT, one female was found dead (11 June 2016) in forest-edge.

We observed five exploratory excursions by three males: one during mating season and four during early summer. Additionally, we observed six exploratory excursions by three females. All three females made at least one excursion during early pregnancy (April) and one female made two excursions post-partum (June and July). All excursions were observed at BM. Number of excursions varied ranged from 1–3 ($\bar{x} = 2.3 \pm 0.7$) and 1–4 ($\bar{x} = 2.0 \pm 1.0$) for males and females, respectively, and did not differ significantly between sexes ($W = 4.0$, $P = 1.0$). Excursion distance differed significantly between sexes and ranged from 0.4 km to 2.1 km ($\bar{x} = 1.1 \pm 0.3$ km) for males and 0.1 km to 0.75 km ($\bar{x} = 0.4 \pm 0.11$ km) for females. One excursion occurred within 200 m of forest-edge, and one occurred within forest-edge. All others occurred within core forest areas.

The number of relocations was not correlated with den home range size ($t_{10} = -1.58$, $P = 0.17$) or core area size ($t_{10} = -1.68$, $P = 0.12$). Mean den home range (95% KDE) size was 3.04 ± 0.63 km^2 for males and 3.96 ± 0.95 km^2 for females (Table 2). We found no difference in mean den home range size between sexes ($\chi^2 = 0.006$, $P = 0.94$) or among sites ($\chi^2 = 4.03$, $P = 0.13$). Similarly, core use area (50% KDE) did not differ between sexes ($\chi^2 = 0.007$, $P = 0.94$) or among study sites ($\chi^2 = 3.76$, $P = 0.15$; Table 2).

The VI of den home ranges was not influenced by sex dyad ($\chi^2 = 3.68$, df = 2, $P = 0.16$), and nearly differed by study site at the $\alpha = 0.05$ level ($\chi^2 = 5.72$, df = 2, $P = 0.06$, Figure 2). The VI was greatest at WT ($\bar{x} = 0.58$, SE = 0.07), followed by BM ($\bar{x} = 0.38$, SE = 0.03) and WG (no overlap). Mean core use area was not influenced by sex dyad ($\chi^2 = 2.96$, df = 2, $P = 0.23$), but differed among sites ($\chi^2 = 6.60$, df = 2, $P = 0.04$). The largest mean core area VI occurred at WT ($\bar{x} = 0.24$, SE = 0.05) followed by BM ($\bar{x} = 0.10$, SE = 0.02) and WG (no overlap).

Total area of each site was: BM = 28.9 km^2, WT = 25.5 km^2, and WG = 13.4 km^2. Use of cover types available within sites differed from random ($\lambda = 0.03$, $P = 0.001$), with greater use of mixed-hardwood-evergreen, followed by evergreen then hardwood (Table 3). Use of cover types within home ranges also differed from random ($\lambda = 0.07$, $P = 0.002$, Table 3). Spotted skunks used mixed-deciduous-evergreen most and avoided non-forested areas. Use of forest fragmentation type differed from random at both the second order ($\lambda = 0.02$, $P = 0.001$) and third order ($\lambda = 0.02$, $P = 0.001$, Table 4). Within-study site use of elevation differed significantly from random ($\lambda = 0.004$, $P = 0.003$, Table 5). Low elevations (between 549 and 650 m) and high elevations (above 1250 m) were used most, whereas mid-elevations were avoided. Third-order selection of elevation did not differ from random ($\lambda = 0.15$, $a = 0.05$, $P = 0.10$, Table 5).

Table 1. Number of relocations, unique den locations, triangulated locations, and reused dens for individual male (M) and female (F) eastern spotted skunks (*Spilogale putorius*) at three study sites in the central and southern Appalachian Mountains, Virginia, March 2016–November 2017.

Site	Skunk ID	Relocations	Unique dens	Triangulated	Reused
Bald Mountain	F009	46	34	10	2
	F012	16	7	8	1
	F018	19	9	10	0
	F029	34	22	12	0
	M008	25	19	6	0
	M010	29	20	18	1
	M011	21	11	10	0
Whitetop Mountain	F015	26	16	0	0
	M007	24	9	14	1
	M016	28	14	13	1
Wintergreen Mountain	M013	15	7	7	1
	M014	17	8	8	1

Table 2. Mean (SE) den home range (95% fixed kernel density estimator [KDE 95%]) and core-use area (50% fixed KDE) estimates of seven male and five female eastern spotted skunks (*Spilogale putorius*) in the central and southern Appalachian Mountains, Virginia, March 2016–November 2017.

	KDE 50%		KDE 95%	
Group	Mean (km^2)	SE	Mean (km^2)	SE
All sites				
Males ($n = 7$)	1.01	0.27	3.04	0.63
Females ($n = 5$)	0.87	0.15	3.96	0.96
Bald Mountain				
Males ($n = 3$)	1.11	0.33	3.78	0.13
Females ($n = 4$)	0.98	0.06	4.23	1.19
Whitetop Mountain				
Males ($n = 2$)	1.19	0.18	5.06	0.62
Females ($n = 1$)	0.62	–	2.87	–
Wintergreen Mountain				
Males ($n = 2$)	0.36	0.22	1.29	0.72

Table 3. Weighted composition analysis of within study-site den home range (second-order) and within home range relocation (third-order) use and ranking of land cover types by eastern spotted skunks (Spilogale putorius) in Virginia, March 2016–November 2017. Log-ratios indicate more (+) or less (-) use of cover type in row than in column. Significant divergence from random (P < 0.05) in bold. Lower ranks indicate higher level of use.

Cover type	Non-forested	Shrub-scrub	Evergreen	Mixed	Deciduous	Rank
Second order						
Non-forested		−2.43	**−5.57**	**−6.25**	**−3.47**	5
Shrub-scrub	2.43		**−3.14**	**−3.82**	−1.04	4
Evergreen	**5.57**	**3.14**		−0.68	**2.10**	2
Mixed	**6.25**	**3.82**	**0.68**		**2.78**	1
Deciduous	**3.47**	1.04	−2.10	−2.78		3
Third order						
Non-forested		−2.80	−5.92	−6.23	−7.31	5
Shrub-scrub	**2.80**		−3.61	−4.64	−4.28	4
Evergreen	**5.92**	**3.61**		−1.03	−0.67	2
Mixed	**6.23**	**4.64**	1.03		0.36	1
Deciduous	**7.31**	**4.28**	0.67	−0.36		3

Table 4. Weighted composition analysis of within study-site den home range (second-order) and within den home range relocation (third-order) use and ranking of forest fragmentation by eastern spotted skunks (*Spilogale putorius*) in Virginia, USA, March 2016–November 2017. Log-ratios indicate more (+) or less (-) use of forest fragmentation type in row than in column. Significant divergence from random ($P < 0.05$) in bold. Lower ranks indicate higher level of use.

Fragment type	NonForest	Patch	Edge	Perforated	SmallCore	LargeCore	Rank
Second order							
NonForest		−0.19	**−3.09**	−1.69	**−3.99**	**−3.39**	6
Patch	0.19		**−2.90**	**−1.50**	**−3.81**	**−3.21**	5
Edge	**3.09**	**2.90**		1.40	**−0.91**	−0.31	3
Perforated	1.69	**1.50**	−1.40		**−2.30**	**−1.70**	4
SmallCore	**3.99**	**3.81**	**0.91**	**2.30**		0.60	1
LargeCore	**3.39**	**3.21**	0.31	**1.70**	−0.61		2
Third order							
NonForest		−0.29	−0.43	−0.36	**−0.94**	**−0.46**	6
Patch	0.29		−0.14	−0.07	**−0.65**	−0.17	5
Edge	0.43	0.14		0.07	**−0.51**	−0.04	3
Perforated	0.36	0.07	−0.07		−0.58	−0.11	4
SmallCore	**0.94**	**0.65**	**0.51**	0.58		**0.47**	1
LargeCore	**0.46**	0.17	0.04	0.11	**−0.47**		2

Table 5. Weighted composition analysis of within study-site den range (second-order) and within den home range relocation (third-order) use and ranking of elevation by eastern spotted skunks (*Spilogale putorius*) in Virginia, March 2016–November 2017. Log-ratios indicate more (+) or less (-) use of elevation row than in column. Significant divergence from random ($P < 0.05$) in bold font. Lower ranks indicate higher level of use.

Elevation (m)	<450	450–549	550–649	650–749	750–849	850–949	950–1049	1050–1249	>1249	Rank
Second order										
<450		**−3.31**	**−2.32**	0.30	1.51	1.99	**3.52**	0.12	**−2.18**	4
450–549	**3.31**		**0.98**	**3.60**	**4.82**	**5.30**	**6.82**	**3.43**	**1.13**	1
550–649	**2.32**	**−0.98**		**2.62**	**3.83**	**4.31**	**5.84**	**2.44**	0.14	2
650–749	−0.30	**−3.60**	**−2.62**		1.21	1.69	**3.22**	−0.18	**−2.48**	6
750–849	−1.51	**−4.82**	**−3.83**	−1.21		0.48	**2.01**	−1.39	**−3.69**	7
850–949	−1.99	**−5.30**	**−4.31**	−1.69	−0.48		**1.53**	−1.87	**−4.17**	8
950–1049	**−3.52**	**−6.82**	**−5.84**	**−3.22**	**−2.01**	−1.53		**−3.40**	**−5.70**	9
1050–1249	−0.12	**−3.43**	**−2.44**	0.18	1.39	1.87	**3.40**		**−2.30**	5
>1249	**2.18**	**−1.13**	−0.14	**2.48**	**3.69**	**4.17**	**5.70**	**2.30**		3
Third order										
<450		−0.22	0.08	0.56	0.27	0.24	0.19	−0.82	−0.07	4
450–549	0.22		0.30	**0.78**	**0.48**	**0.46**	**0.41**	−0.61	**0.15**	2
550–649	−0.08	−0.30		**0.47**	0.18	0.15	0.11	−0.91	0.15	5
650–749	−0.56	**−0.78**	**−0.47**		−0.29	−0.32	−0.36	**−1.38**	−0.63	9
750–849	−0.27	**−0.48**	−0.18	0.29		−0.03	−0.07	**−1.09**	**−0.34**	8
850–949	−0.24	**−0.46**	−0.15	0.32	0.03		−0.04	**−1.06**	−0.31	7
950–1049	−0.19	**−0.41**	−0.11	0.36	0.07	−0.04		−1.02	−0.27	6
1050–1249	0.82	0.61	0.91	**1.38**	**1.09**	**1.06**	1.02		0.75	1
>1249	0.07	**−0.15**	0.15	0.63	**0.34**	0.31	0.27	−0.75		3

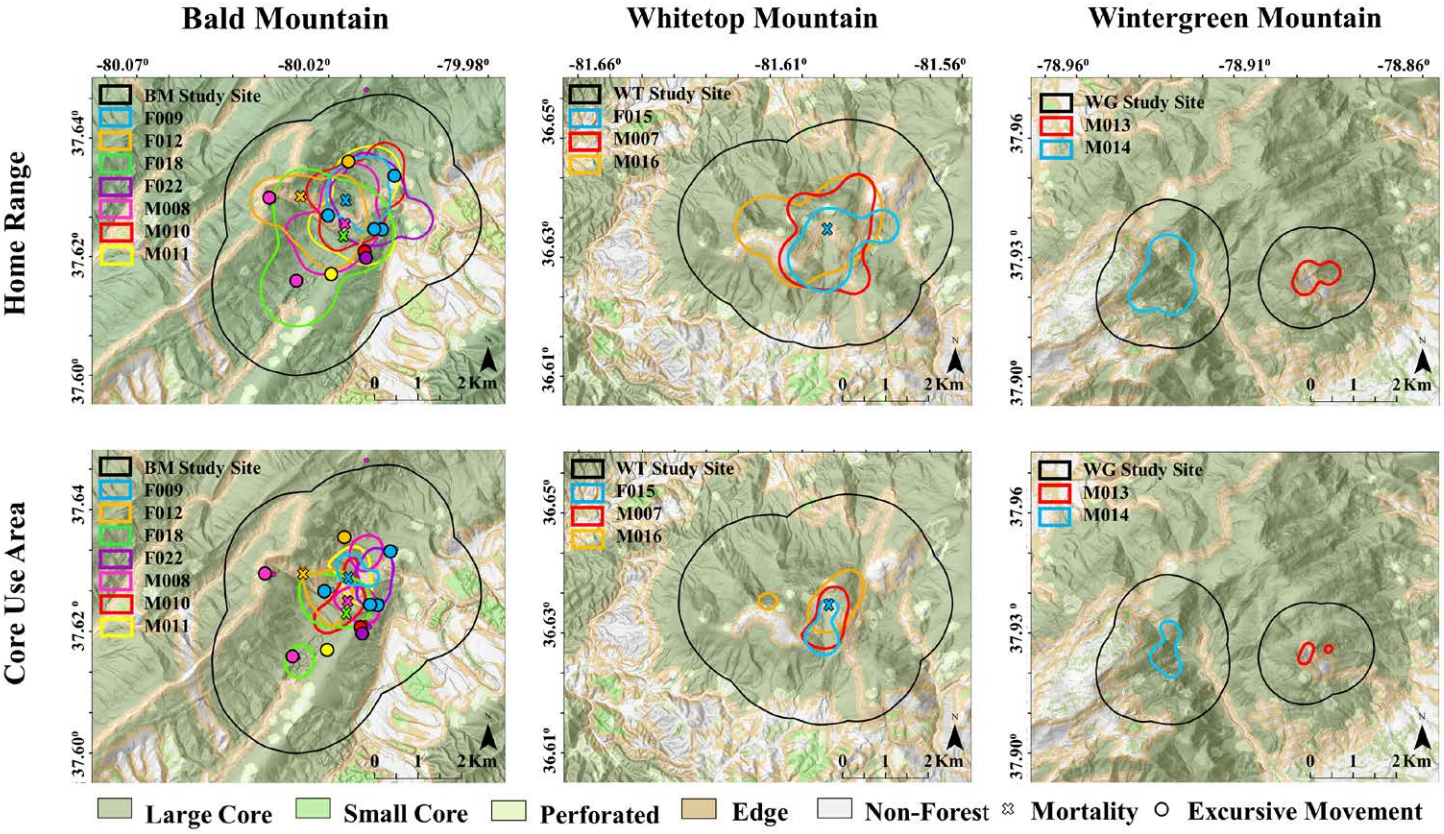

Figure 2. Eastern spotted skunk (*Spilogale putorius*) den home range (95% kernel density estimate [KDE]) and core use area (50% KDE) at three study sites in Virginia, March 2016–November 2017.

Discussion

Our first prediction that male spotted skunks would make more frequent excursions than females was not supported; however, we observed patterns of seasonality that differed between sexes. Male excursive movements occurred during mating season whereas female excursions occurred during pregnancy or kit-rearing. It is unclear why we only detected excursions at BM, however this site had the greatest number of spotted skunks. Also, we tracked individuals to diurnal den sites, thus, we potentially missed nocturnal excursive movements at BM and other sites.

Animals exploit known resources within their home ranges, while traversing novel landscapes risks higher energetic expenses with no guarantee of resource availability or increased fitness. At BM, male spotted skunks may have been avoiding intraspecific competition, seeking mating opportunities, or avoiding inbreeding. Excursive movements during the breeding season may act as a form of breeding (temporary) dispersal, as has been observed for other small carnivores (Cavallini 1996, Deuel et al. 2017). In contrast, pregnant and nursing females may be seeking food resources due to a greater energy demand (Rödel et al. 2016).

Animals often show behavioral plasticity related to dynamic environmental conditions (Komers 1997). During our study, a prescribed burn occurred at BM. We did not observe large movements by any of the skunks following the burn and tracked two individuals within the burned area immediately after the fire. Thus, the excursive movements observed in our study likely represented behavioral plasticity related to intrinsic condition (i.e., reproductive status).

Successful monitoring protocols and habitat restoration for conditional specialist species (Thorne and Ford 2022) requires consideration of seasonally appropriate cover types. For example, female spotted skunks prefer underground dens with ample cover when kit rearing (Thorne and Ford 2022). Female mortality was high in summer months when their excursive movements were greatest, supporting that escape cover is important. Conversely, tree cavities in brushy areas are used during mating season (Thorne and Ford 2022) when male excursive movements were most common. Both cover types support spotted skunk population growth and thus are important to consider when managing habitat. Few excursive relocations were detected within forest-edge areas and no relocations were detected outside of forested areas. This suggests spotted skunks in our study region may be limited to core forest patches, with non-forested areas serving as barriers to movement.

Our second prediction was not supported as male and female den home range size did not differ. In other studies, male spotted skunk home ranges were significantly larger than female home ranges (Lesmeister et al. 2013, Hassler et al. 2021). Although female den home range sizes in our study were similar to those found by Lesmeister et al. (2013) and Hassler et al. (2021), male ranges in our study were smaller. However, we did not include nocturnal and excursive movements which could explain differences between our estimates and other studies.

We also predicted den range overlap would be low, similar to other spotted skunk species (Jones et al. 2013). However, our estimates were more consistent with those of other species within Mephitidae, suggesting a similar solitary behavior with flexible territorial strategies. For example, striped skunks often come into contact and share dens with conspecifics suggesting overlap may not result in antagonism (Theimer et al. 2016). We did observe greater overlap at sites with smaller core forest areas, suggesting overlap could be affected by habitat quality. Though this difference was not statistically significant at the $\alpha = 0.05$ level, there is likely biological significance, a larger sample size may elucidate the relationship between core forest availability and home range overlap among conspecifics. We suggest future research assess how home range overlap and resource competition impacts spotted skunk vital rates. Additionally, social behavior studies may help determine if home range overlap and habitat quality precipitates hospitable or antagonistic interactions. Our high recapture rates of marked individuals at all three sites suggest nearly all animals were captured within site-years and our estimates of den home range distributions and overlap are representative of the population.

Our fourth prediction was supported as spotted skunks used cover types non-randomly. Mixed-hardwood-conifer was used more often than conifer or hardwood-dominated. Regionally, mixed forests often are associated with heavy understory cover, such as herbaceous ground cover and woody midstory shrub or tree cover, and may provide cover from predation and a variety of den resources (Menzel et al. 2002, 2004), an ideal combination for spotted skunks. Hardwood trees, particularly oaks, provide tree cavities used by spotted skunks in as den sites throughout their range (Lesmeister et al. 2008, Sprayberry and Edelman 2018, Eng and Jachowski 2019, Thorne et al. 2022). Moreover, evergreen species, such as conifer trees and ericaceous shrubs, provide year-round cover from avian predators in areas of more limited understory or ground cover (Lesmeister et al. 2010). We strongly suspect all mortalities documented in this study were due to avian predators, likely barred owls (*Strix varia*) or great horned owls (*Bubo virginianus*), as these species are known spotted skunk predators (Lesmeister et al. 2010, Hassler et al. 2021).

Consistent with other research in the region, elevations below 650 m and above 1050 m were used more than mid-range elevations (Thorne et al. 2017, Eng and Jachowski 2019). Lower elevations typically are associated with cove hardwood forests which are biologically and structurally diverse (Ford et al. 2002, Turner et al. 2003). Alternatively, high elevation old-growth evergreen cover or emergent rocky outcrops also provide ample escape cover from predation (Lesmeister et al. 2008, Thorne et al. 2017, Sprayberry and Edelman 2018, Eng and Jachowski 2019). Conservation and restoration of both forest types would benefit additional sensitive wildlife species, notably cerulean warblers (*Setophaga cerulea*) and northern flying squirrels (*Glaucomys sabrinus*) (Ford et al. 2002, Nareff et al. 2019). Many of the mid-elevation forests in our study region are mid-rotational forest without the complexity associated with early successional or older-growth forests ages (Yarnell 1998).

As we observed no use of non-forested areas and restricted den home range size and increased den home range overlap at sites with smaller core forest areas, we surmise forest patch size limits spotted skunk movement. Legacy reduction in core forest areas may impede spotted skunk extra-home range movement, dispersal among populations, and recolonization of unoccupied areas. Consequences of movement barriers, such as vulnerability to demographic stochasticity, loss of genetic variation, and disease outbreak have been observed in recent studies of eastern spotted skunks (Thorne 2020, Butler et al. 2021, Harris et al. 2021). The persistence of spotted skunks may depend on both habitat conservation and restoration through actions such as prescribed fire or forest harvesting. Additionally, assessments of spotted skunk population dynamics and genetic diversity could better inform current baselines, monitor future trends, and assist management planning that could increase connectivity among occupied and available forest patches.

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Southern Fox Squirrel and Eastern Gray Squirrel Interactions in a Fire-maintained Ecosystem

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Abstract: Southern fox squirrels (*Sciurus niger niger*) have been declining due to habitat fragmentation, cover type conversion, and fire suppression in the Southeast. A decrease in growing season burns has led to hardwood encroachment and forest mesophication that benefit the competing eastern gray squirrels (*S. carolinensis*). In the southern Coastal Plain and Piedmont of Virginia, these pattern raises the question of whether gray squirrels are competitively excluding southern fox squirrels in these altered landscapes. From October 2019 to October 2020, we conducted continual camera trapping for southern fox squirrels and gray squirrels on the Big Woods/Piney Grove Complex (BWPGC) and at Fort Barfoot (FB) in the Coastal Plain and lower Piedmont of Virginia, respectively. Both sites are among the few areas that still contain large, intact pine savanna and mixed-pine hardwood forests in southeastern Virginia. We used two-species occupancy modeling to investigate occupancy estimates of southern fox squirrels and possible competition with gray squirrels, based on detection histories collected from camera traps on BWPGC and FB. We then conducted informed single-species occupancy modeling to estimate the necessary level-of-effort (LOE) required to determine the probable absence of southern fox squirrels at sampling sites in the region. No fox squirrels were observed at FB. Our top, two-species occupancy model showed that gray squirrel occupancy increased with increasing time since last burn. However, southern fox squirrel occupancy, in the absence of gray squirrels, decreased with increasing time since last burn. Gray squirrels typically inhabited hardwood-dominant closed canopy areas whereas southern fox squirrels did so at BWPGC only in the absence of gray squirrels. This suggests that southern fox squirrels are selecting areas on BWPGC based on resource needs and possibly competition with gray squirrels. A single-season occupancy model confirmed that southern fox squirrel occupancy decreased with time since the last burn. Our LOE analysis indicated that seven consecutive days of camera trapping without a detection would provide 90% confidence of the subspecies' absence in areas burned two or more years prior to sampling. Southern fox squirrels may benefit from increased short-rotation burns to maintain or enhance pine-hardwood savannas and pine-hardwood savanna ecotones in southeastern Virginia.

Keywords: camera trapping, detection, occupancy, *Sciurus niger niger*

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The Coastal Plain of the southeastern U.S. has gone through major changes due to landscape conversions to agricultural or working forests for timber production (Weigl et al. 1989, Edwards et al. 2003, Edwards and Laerm 2007). Where pine savannas remain, natural disturbance regimes (i.e., frequent growing-season fire) have been replaced by fire suppression or at best, infrequent dormant season burning. Reduction of reoccurring, growing season fires often result in woody encroachment, and therefore changes in species composition, including open savanna specialists being replaced by generalists (Moorman et al. 2000).

Gray squirrels (*Sciurus carolinensis*) and southern fox squirrels (*S. niger niger*) are sympatric tree squirrels that co-exist across much of the southeastern U.S. despite having overlapping habitat needs for ecological traits such as foraging and nesting (Edwards et al. 2003, McRobie et al. 2019). Both species utilize mast from oak (*Quercus* spp.), black walnut (*Juglans nigra*), hickory (*Carya* spp.), pine (*Pinus* spp.), and American beech (*Fagus grandifolia*; Koprowski 1994a, Koprowski 1995b, Edwards et al. 2003, Wilson et al. 2020, Moncrief et al. 2012). Both species also use mature hardwood trees for drey nests or cavities as denning substrate (Koprowski 1994a, Koprowski 1995b, Edwards et al. 2003, Moncrief et al. 2012). However, across much of the southeastern U.S., fire suppression and forest mesophication have shifted forest structure and composition towards conditions that favor gray squirrels,

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which have a broader usable niche space compared to southern fox squirrels (Whitaker and Hamilton 1998, Nowacki and Abrams 2008, Sovie et al. 2020, Sovie et al. 2021).

Gray and fox squirrels appear to niche partition to minimize interspecific competition. Gray squirrels largely occupy deciduous forests (Steele and Koprowski 2011, Parker and Nilon 2008, Benson 2013, Sovie et al. 2021), whereas southern fox squirrels are more likely to occupy open pine savanna woodlands and pine-hardwood mixed forests (Steele and Koprowski 2011, Sovie et al. 2021). Gray squirrels and southern fox squirrels have also been known to show temporal partitioning across leaf-on and leaf-off seasons to minimize competition (Sovie et al 2019). Even with somewhat different habitat niches, competition among the two species is evident, particularly in hardwood areas (Sovie et al. 2020, Sovie et al. 2021).

We used two-species, single-season occupancy models to assess the effect of forest condition (e.g., basal area, canopy height), prescribed burn treatment (i.e., number of burns since 2017, time since last burn), and cover type classifications on occupancy of southern fox squirrels given selection and potential competition with gray squirrels. We also estimated camera-trapping level-of-effort (LOE) for detecting southern fox squirrels in southeastern Virginia using a single-species occupancy model assessing time since last burn (yr) informed by two-species occupancy modeling. Further, we assessed how environmental variables including time of year, daily precipitation, and daily average temperature affect southern fox squirrel detection probabilities. We predicted that southern fox squirrel occupancy probability would be greatest in recently burned areas of pine-hardwood mixed savanna in the absence of gray squirrels. We also predicted that fox squirrel detection would be negatively influenced by greater amounts of daily precipitation and extreme daily temperatures (high heat or freezing temperatures), as has been documented previously (Weigl et al. 1989).

Study Area

We conducted our study at the Virginia Army National Guard's Maneuver Training Center Fort Barfoot and the Big Woods Wildlife Management Area and Piney Grove Preserve Complex (BWPGC) managed by the Virginia Department of Wildlife Resources and the Nature Conservancy, respectively (Figure 1). Fort Barfoot (FB) is a 16,500-ha Virginia Army National Guard installation located in Nottoway, Dinwiddie, and Brunswick counties in the lower Piedmont province. The installation consists of a mixture of deciduous, pine, mixed pine-hardwood, and bottomland hardwood forests with open shrub and grassland areas throughout. Additionally, FB has a long history of fire-maintained disturbance (i.e., fire return intervals of 1–5 yr) over the past three decades that has helped maintain cover and structure approximating past natural conditions that are rare in the region (Kalen et al. 2014, Emrick et al. 2018). The BWPGC is in Sussex County in the upper Atlantic Coastal Plain and covers ~2100 ha. The cover types of this area are characterized by mixed loblolly pine (*P. taeda*) and shortleaf pine (*P. echinata*) stands, loblolly pine savannas, young longleaf (*P. palustris*) plantings, upland hardwoods, and bottomland hardwoods. Most of the complex, exclusive of the bottomland hardwoods, is managed with frequent fire (i.e., 2–3-yr fire return interval) to support populations of red-cockaded woodpecker (*Dryobates borealis*), northern bobwhite (*Colinus virginianus*), and eastern wild turkey (*Meleagris gallopavo silvestris*; Watts and Harding 2007). Since the early 2000s, burning has been used to manage red-cockaded woodpecker habitat. The BWPGC is one of the last remaining large, fire-maintained, mature pine savannas in southeastern Virginia (Bradshaw and Watts 2003).

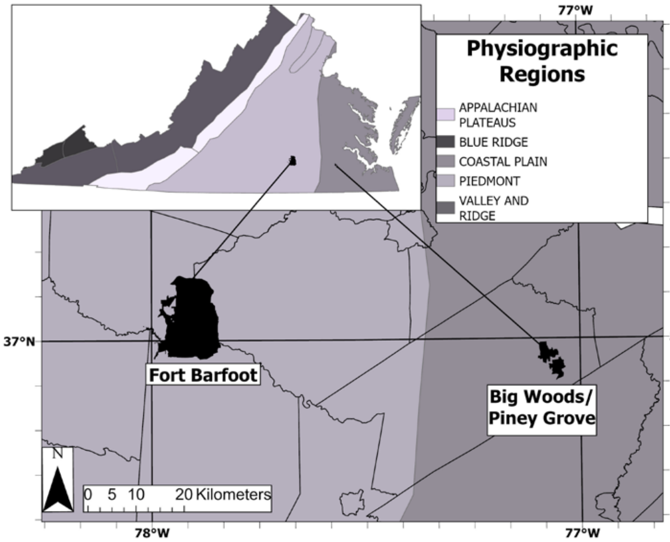

Figure 1. Southern fox squirrel (*Sciurus niger niger*) field sites, 2019–2022: Military Training Center Fort Barfoot, Nottoway County, Virginia (left) in the Piedmont region and the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County (right) in the Coastal Plain region.

Methods

Camera Surveys

We established trail camera survey points at FB and BWPGC to assess the presence of southern fox squirrels and gray squirrels following the methods of Tye et al. (2015), Greene et al. (2016), and Greene and McCleery (2017). Camera point selection was based on taking the boundary of the study areas, overlaying a systematic point grid, and then selecting random points that were evenly distributed among the main landcover types in ArcMap 10.8 (ERSI

Inc., Redlands, California). We stratified points using land cover as delineated by the National Land Cover Database, 2019 release (Dewitz and USGS 2022). Prior to final selection, we confirmed the presence of potential fox squirrel habitat through visual inspection against U.S. Department of Agriculture National Agriculture Imagery Program (NAIP) aerial imagery (2015, USDAFSA-APFO Aerial Photography Field Office, Salt Lake City, Utah) coupled with on-the-ground inspection, whereby points in unsuitable conditions such as water and buildings were avoided. We considered potential habitat as landcover important to southern fox squirrels elsewhere in the Southeast such as pine savannas, upland mixed pine-hardwood stands, and upland hardwood/hardwood bottomlands (Edwards et al. 1989, Edwards et al. 2003, Prince et al. 2014, Prince et al. 2016). Finally, we selected nine transect locations consisting of five cameras each based on the random points distributed in the potential southern fox squirrel habitat. We deployed trail cameras (Bushnell Trophy HD cameras, Bushnell Outdoor Products, Overland, Kansas) within the transects at approximately 250-m intervals to ensure independence of sample locations, as well as independence between camera survey transects (Tye et al. 2015).

Camera-trapping efforts at BWPGC were focused site's primary cover types: mature upland loblolly pine savannas, loblolly pine/hardwood forests, and bottomland hardwood-dominant riparian areas. At FB, we deployed camera transects in upland mixed loblolly pine/hardwood forests and upland loblolly pine forests to survey for potential presence of southern fox squirrels and in mature upland hardwood forests and bottomland hardwood forests that possibly could be occupied by eastern fox squirrels (*S. n. vulpinus;* Edwards et al. 1989, Edwards et al. 2003, Perkins and Conner 2004, Prince et al. 2014, Prince et al. 2016). We differentiated Sciurid species or subspecies based on pelage and size (Edwards et al. 2003, Edwards and Laerm 2007), although we note that the genetic foundation of fox squirrel sub-species categorization is questionable (Moncrief et al. 2010).

We deployed cameras from October 2019 to October 2020 on both BWPGC and FB. Due to equipment restraints, we deployed only three transects at a time for approximately 28 consecutive days. At the end of each 28-day rotation, we moved cameras to another grouping of three randomly chosen transect sites. We used three different rotations around the landscape for a total of nine randomly chosen transect locations. At each survey location, we placed a camera on the nearest tree to the assigned point 50–70 cm above the ground and pointed them at bait stations consisting of a nut and berry suet mixture. We used suet cakes as bait to increase capture potential (Curtis and Sullivan 2001, Edwards et al. 2003), placing bait stations no more than 10 m from the camera and 30–70 cm from the ground attached to a tree (Boone et al. 2017). We then used DeerLab (2013, DeerLab, Inc. Jacksonville, Florida) to identify all observed mammals to species.

Predictor Variables

We considered six habitat covariates for two-species occupancy modeling (below): canopy cover, basal area, number of burns since 2017, time since last burn, canopy height, and general cover type (savanna vs. other). We considered these six variables as they would be directly related to forest stratification and vegetation structure useful for further predictive efforts across the larger landscape (Hayes et al. 1981, Deuser et al. 1988). Time since last burn and number of burns is important as prescribed fire has been deemed an important management tool for fox squirrel habitat in other parts of their range (Conner et al. 1999). These data were collected from land management records at both sites. Basal area and canopy cover (%) were collected in the field with a 10 basal area factor prism and concave spherical densiometer (Model-C, Forestry Suppliers, Jackson, MS) (Lemmon 1957). Both variables were used to capture fine scale differences between hardwood dominant areas and pine dominant areas that might affect fox squirrel and gray squirrel site selection (Greene and McCleery 2017). Average canopy height was calculated using USGS 2014 LiDAR point clouds (VGIN 2016) and the package lidR (Roussel et al. 2020) in R (R Core Team 2022), as canopy height is positively correlated with fox squirrel presence (Conner and Godbois 2003). We then used a 50-m circular moving window analysis to find the focal mean of percent canopy height for all pixels across the landscape. The presence of savanna, also an important cover type for fox squirrels (Edwards et al. 2003), was considered as a covariate as BWPGC is mainly covered by loblolly pine woodland savannas. We reclassified landcover to savanna or not savanna by creating a supervised classification ensemble model from known areas of savanna on the landscape using a vegetation height layer (LANDFIRE 2022) and percent evergreen forest derived from the National Land Cover Database, 2019 release (Dewitz and USGS, 2022). We then cut predictions based on a threshold that maximized sensitivity and specificity in relation to the training point classifications.

Data Analysis

We assessed the presence/absence of southern fox squirrels and eastern gray squirrels using occupancy analysis for both field sites. The sample interval reflected time between camera deployments (i.e., 28 days), with each day treated as a survey occasion. Our occupancy model sets included combinations of a forest cover model (canopy cover + basal area) as well as canopy cover and basal area separately, two fire frequency models (number of burns since 2017, time since last burn), a canopy height model, and a general cover type model (1 as savanna; 0 as other cover types). To account for collinearity among our covariates, we used the package usdm (Naimi 2017) in R, where any variables with $r > 0.7$ were compared and the covariate with the least support was not included in our final analysis (Amspacher et al. 2019). We standardized all continuous variables (MacKenzie et al. 2006, Fiske and Chandler 2011) and created dummy variables for categorical variables prior to analysis. We used single-season, two-species occupancy to specifically assess the associations and possible competition of southern fox squirrels and gray squirrels. We then modeled survey effort using single-species occupancy and detection models informed by informative occupancy variables derived from two-species top modeling results.

We used the wiqid package in R (Meredith 2022) to assess interactions of gray squirrels and fox squirrels utilizing single-season, two-species occupancy modeling. Two-species occupancy models estimate the probability of a subordinate species at a site, conditional on the presence or absence of a dominant species. As our focus was on southern fox squirrel occupancy, and because gray squirrels have been documented to outcompete fox squirrels in closed canopy hardwood stands (Sovie et al 2020, 2021), we considered gray squirrels to be dominant and fox squirrels to be the subordinate species.

We focused on parameterization that assessed 1) ψCa: the probability of fox squirrel occupancy in absence of gray squirrels; 2) ψCA: the probability of fox squirrel occupancy in the presence of gray squirrels, and 3) ψA: the probability of gray squirrel occupancy. We concurrently assessed *a priori* models regarding the interactions of gray squirrels and southern fox squirrels when gray squirrels were absent (ψA:ψCa), and the interactions of gray squirrels and southern fox squirrels when gray squirrels are present (ψA:ψCA) for a total of 16 model interactions. Detection probably was modeled as constant (p[.]) for two-species occupancy modeling. Using Akaike's Information Criteria for small sample sizes (AIC_c), we considered models within 2 AIC_c units of the top models to be competing models (Burnham and Anderson 2002). Of the covariates in the top models, we considered covariates with 95% CI not crossing zero to be significant predictors of occupancy (Shake et al. 2011, Bowling et al. 2014).

We performed single-species modeling using the package wiqid in R (Meredith 2022) to test single-season, single-species occupancy (ψ) and detection (p) for southern fox squirrels. To further inform land managers of southern fox squirrel survey efforts, we used results from occupancy modeling regarding time since last burn (yr) to examine LOE relationships. We used the formula provided by Wintle et al. (2012),

$$n = \frac{log(\frac{\alpha}{1-\alpha}) - log(\frac{\psi}{1-\psi})}{log(1-p)}$$

where α is a desired confidence level, or range of theoretical probabilities, ψ is occupancy, and p is detection probability, to estimate the total number of sequential non-detections (n) required to determine probable absence of southern fox squirrels. Detection covariates utilized in single-species occupancy models were maximum daily temperature (C), daily precipitation (mm), and Julian day standardized by year. Maximum daily temperature and daily precipitation were included in models because previous research has shown that fox squirrel activity is negatively correlated with these variables (Weigl et al. 1989, Ditgen et al. 2007). Weather data were retrieved from the National Oceanic and Atmospheric Administration National Weather Station located in Wakefield, Virginia. Julian day was utilized on a 1–365 scale whereas (January 1–December 31). The inclusion of Julian day as a covariate can provide insight into differing activity periods of fox squirrels, as activity peaks at different times of the year due to nesting, foraging, and caching activities (Edwards and Laerm 2007).

Results

From our efforts on October 2019 to October 2020, we recorded 370 trap days per camera point for a total effort of 16,650 trap days across all cameras in each transect for a total of 45 camera points at both BWPGC and FB. Within our entire survey period, we identified fox squirrels at 13 (29%) of the 45 camera points at BWPGC. Based on pelage and live captures from a concurrent radio-tracking study, along with the forest condition and composition, all fox squirrels at BWPGC were presumably the southern subspecies. Gray squirrels were identified at 17 (38%) of the 45 camera sites at BWPGC. Both southern fox squirrels and gray squirrels were detected on all landcover types on BWPGC (pine savanna, hardwood bottomland, young, managed pine, and hardwood-pine mixes). However, southern fox squirrels were typically detected at points located in pine savannas and gray squirrels were identified at points located in hardwood bottomlands. Southern fox and gray squirrels overlapped at only 2 (4%) of the 45 camera sites at BWPGC. At Fort Barfoot, we identified gray squirrels at 41 (91%) of the 45 camera sites. We did not detect either eastern or southern fox squirrels at FB over the study, therefore we limited occupancy and detection analyses for both species to BWPGC.

In assessing interactions among single-season, two-species occupancy modeling, our top model explaining the interaction of southern fox squirrels and gray squirrels was the influence of time since the last burn (ψA:ψCa; Table 1). Gray squirrel occupancy probability (ψA) increased the longer time persisted between burns (ψA $\beta_{\text{time since last burn}} = 0.75$, SE = 2.12). Moreover, in the absence of gray squirrels, southern fox squirrel occupancy probability (ψCa) decreased the longer time persisted between burns (ψCa $\beta_{\text{time since last burn}} = -1.44$, SE= 0.72; Figure 2).

We utilized the time since last burn covariate from our top, two-species occupancy model to inform LOE in surveying southern fox squirrels. For southern fox squirrels, our null for detection (constant p) had the most support (p[intercept] $\beta = -3.61$, $SE = 0.18$; Table 2). Our informed single-season occupancy model revealed that southern fox squirrel occupancy decreased with more years since last burn (ψ[Time since last burn] $\beta = -1.44$, $SE = 0.72$; Table 2). Furthermore, we estimated that the necessary LOE for sequential non-detections of southern fox squirrels would be 42 days for 1 yr since last burn, and 7 days for ≥2 yr since the last burn (Figure 3).

Table 1. Southern fox squirrel (*Sciurus niger niger*) two-species occupancy (ψA:Cψ) models on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020. Models considered as having strong empirical support at ΔAIC < 2.0 from the top model.

Model[a]	AIC_c	ΔAIC_c	Model Likelihood	w_i
ψA:ψCa (Time since last burn)	964.63	0.00	1.000	0.777
ψA:ψCA (Time since last burn)	968.07	3.44	0.179	0.139
ψA:ψCa (.)	971.56	6.93	0.031	0.024
ψA:ψCa (Forest Condition)	972.44	7.81	0.020	0.016
ψA:ψCa (Savanna + Canopy Height)	972.90	8.27	0.016	0.012
ψA:ψCA (Forest Condition)	972.92	8.29	0.016	0.012
ψA:ψCA (.)	973.75	9.12	0.010	0.008
ψA:ψCa (Forest Condition + Savanna)	973.98	9.35	0.009	0.007
ψA:ψCA (Canopy Cover + Canopy Height)	974.48	9.85	0.007	0.006
ψA:ψCA (Forest Condition + Savanna)	975.23	10.61	0.005	0.004
ψA:ψCa (Canopy Cover + Canopy Height)	975.59	10.96	0.004	0.003
ψA:ψCa (Canopy Height)	975.69	11.06	0.004	0.003
ψA:ψCA (Savanna + Canopy Height)	976.12	11.49	0.003	0.002
ψA:ψCA (Canopy Height)	976.21	11.58	0.003	0.002
ψA:ψCa (Basal Area + Canopy Height)	977.77	13.14	0.001	0.001
ψA:ψCA (Basal Area + Canopy Height)	979.26	14.63	0.001	0.001

a. Detection modeled as p(.) in each model.

Table 2. Southern fox squirrel (*Sciurus niger niger*) single-species occupancy (ψ) and detection (p) models on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020. Models considered as having strong empirical support at ΔAIC < 2.0 from the top model. Significant variables denoted by *.

Model	AIC_c	ΔAIC_c	LogLik	w_i
ψ (Time since last burn)*, p (.)	395.6	0.00	−194.5	0.48
ψ (Time since last burn)*, p (Julian day)	396.2	0.63	−193.6	0.35
ψ (Time since last burn)*, p (Precipitation)	397.8	2.16	−194.4	0.16
ψ (Time since last burn), p (Julian day + Precipitation)	422.7	27.11	−205.6	0.00
ψ (Time since last burn), p (Temperature + Precipitation + Julian day)	422.7	27.13	−204.2	0.00
ψ (Time since last burn), p (Julian day + Temperature)	428.0	32.38	−208.2	0.00
ψ (Time since last burn), p (Precipitation + Temperature)	428.9	33.34	−208.7	0.00
ψ (Time since last burn), p (Temperature)	453.2	57.60	−222.1	0.00

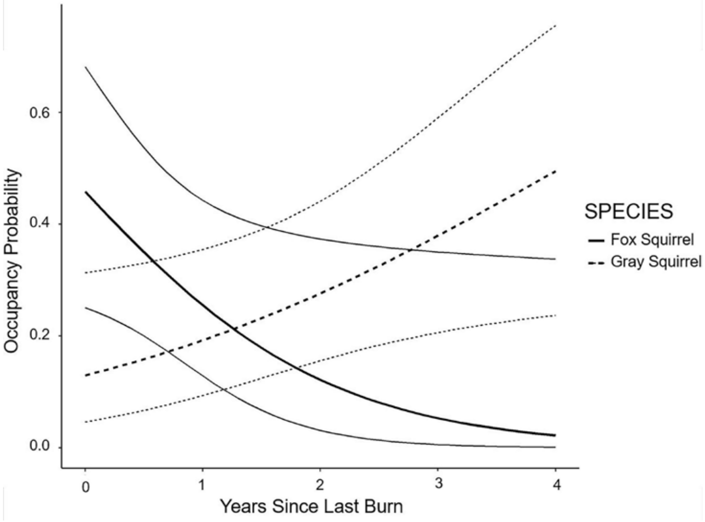

Figure 2. Effect of time since last burn (yr) for eastern gray squirrel (*Sciurus carolinensis*) occupancy (ψA) and southern fox squirrel (*Sciurus niger niger*) occupancy when gray squirrels are absent (ψCa) at remote trail camera locations on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020. Relationship between time since burn, gray squirrel occupancy, and southern fox squirrel occupancy when gray squirrels are absent from model ψA:ψCa (Time Since Burn), p(.). Dashed lines and solid black lines represent 95% confidence intervals for gray squirrels and fox squirrels, respectively.

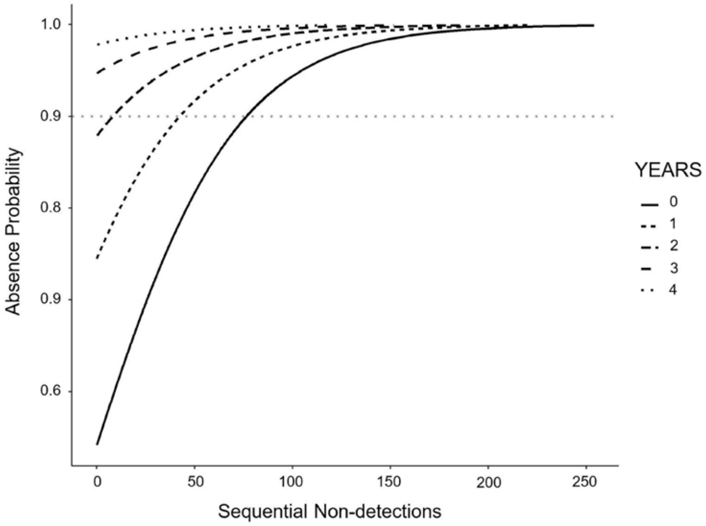

Figure 3. The total number of sequential non-detections required to determine the probable absence of southern fox squirrels (*Sciurus niger niger*) based on time since last burn (yr) and null detection, p(.) on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020.

Discussion

Our results documenting southern fox squirrel and gray squirrel occupancy interactions indicate that, like elsewhere in the Southeast, fox squirrel occupancy increases with shorter prescribed fire rotational periods, particularly in the absence of gray squirrels (Parker and Nilon 2008, Steele and Koprowski 2011, Benson 2013, Sovie et al. 2021). Burned areas at BWPGC included pine savannas/woodlands, pine/hardwood forests, and the edges of bottomland hardwood. Gray squirrels more often inhabit areas of closed canopies that are characterized by hardwood dominant areas, particularly bottomlands, whereas southern fox squirrels only did so in the absence of gray squirrels (Gilliam and Platt 1999, Sovie et al. 2021). However, our top, two-species occupancy model indicated that southern fox squirrels occurred in frequently burned areas regardless of cover type as well as areas without gray squirrels. Our cover type classification for occupancy analysis was a binary scale (pine savanna vs. other cover type), where other cover types included hardwood bottomlands and hardwood/pine mixed stands. This suggests that fox squirrels responded to fire-maintained forest structure but also to potential competition with gray squirrels.

Interactions between two species is likely partly due to Interference competition, as gray squirrels are more aggressive and tend to discourage fox squirrels from areas of use (Wauters and Gurnell 2002, Sovie et al. 2021). Additionally, there could be an element of exploitative competition. Hardwoods in the upland system at BWPGC were limited in extent, and gray squirrels readily utilized most of the available hardwood patches and bottomlands that would be available to southern fox squirrels. However, parsing out these mechanistic aspects of competition at our study areas would require additional research.

Our analysis of southern fox squirrel detectability revealed that neither Julian day, average daily temperature, nor precipitation influenced detection probability In other areas of the Southeast, Ditgen et al. (2007) documented low squirrel activity in the hottest times of the year, while Pynne et al. (2020) detected no significant changes in squirrel activity based on average daily temperatures or precipitation, as we observed. Geographically, temperature extremes vary and may drive the activity of the subspecies differently among regions (Brown and Yeager 1945, Bakken 1959), as well as the temporal partitioning between gray squirrels and southern fox squirrels (Sovie et al. 2019), and seasonal activity shifts (Weigl et al. 1989, Edwards et al. 2003). Therefore, depending on the objective, the activity of fox squirrels can be driven by environmental variables as well as variables related to the ecology of the squirrel itself. To counteract any potential, yet poorly known, effects of environmental variables on detection probabilities, managers should utilize multi-day surveys throughout multiple seasons to account for any possible variation (Pynne et al. 2020).

Camera trapping efforts confirmed that, despite the presence of putative habitat, the probability of occurrence for southern fox squirrels at BWPGC is low to moderate, and therefore likely low to moderate densities, similar to current observations across much of the Southeast (Weigl et al. 1989, Loeb and Moncrief 1993, Edwards and Laerm 2007). Also, no fox squirrel subspecies was observed at FB despite anecdotal accounts of presence. Because our camera-trapping sessions exceeded the necessary LOE duration at most cameras at BWPGC and FB, we have high confidence that there are no established populations of fox squirrels of both subspecies at FB presently, though we note much of this large installation has yet to be surveyed. Our results from BWPGC suggest at least 7 camera-trapping days are required to determine probable absence of southern fox squirrels in stands burned at least 2 yr prior. Unfortunately, necessary effort greatly increases on newly burned sites as conditions immediately post-fire might not be conducive to fox squirrel detection at BWPGC, or detection decreases due to increases in home range as newly burned sites provide more available areas of use. Deeley et al. (2021) noted that maximizing the number of survey points rather than survey duration is often most optimal, assuming some broad understanding of level of effort needed. Accordingly, in southeastern Virginia, managers probably could survey with confidence for less than our 28-day periods at any given site thereby allowing more sites to be surveyed.

Our lack of detections of fox squirrels at FB may suggest that the lower Piedmont of Virginia has not yet been colonized from the Blue Ridge Mountains to the east or from the Coastal Plain. Fox squirrels that appear to be a southeastern subspecies are present at BWPGC, but much of the surrounding landscape is likely of marginal quality (i.e., intensive agriculture, dense working pine forests), hence populations therein may be somewhat isolated. Additional surveys are warranted in the Coastal Plain of Virginia to better define the regional distribution of fox squirrels.

We also found that southern fox squirrels use hardwood-pine mixed ecotones in the absence of gray squirrels. Therefore, for managers attempting vegetative restoration to improve habitat quality for fox squirrels, habitat is best achieved with short fire return intervals (i.e., 1–2 yr) that create these open canopy conditions and decrease excessive hardwood encroachment (or practices that mimic these conditions). Additionally, increasing hardwood sources in dispersed, small patches within mature pine savannas coupled with fire might benefit fox squirrels without overly benefiting gray squirrels. For managers interested in efficiently documenting the presence of southern fox squirrels in southeastern

Virginia, we suggest prioritizing initial camera surveys in forests with short fire return intervals where our findings suggest detection probability is high and necessary LOE is lower.

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Journal Statement

The Southeastern Association of Fish and Wildlife Agencies is composed of governmental fish and wildlife agencies in the states of Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, Missouri, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, Virginia, West Virginia and the territories of Puerto Rico and the U.S. Virgin Islands. The Southeastern Association is one of four such regional fish and wildlife associations. While the regional associations are autonomous, they work very closely with the Association of Fish and Wildlife Agencies, of which all southeastern states are also members. Only state wildlife agencies in the 15 southeastern states and territories are members of the SEAFWA.

Its objectives are to protect the right of jurisdiction of the member states over their wildlife resources on public and private lands; to carefully scrutinize state and federal wildlife legislation and regulations and to offer support or opposition to legislative proposals or federal regulations in accordance with the best interests of the member states; to consult with and make recommendations to the federal wildlife and public land agencies in order that federal management programs and programs involving federal aid to member states shall be so conducted as to be in the best interests of the member states; and to serve as a clearinghouse for the exchange of ideas concerning wildlife and fisheries management, research techniques, wildlife law enforcement, hunting and outdoor safety, and information and educations programs.

The Association participates with the Association of Fish and Wildlife Agencies, other regional associations, other governmental agencies and citizens' organizations in pursuing mutual goals benefiting fish and wildlife resources; maintains a variety of committees consisting of fish and wildlife professionals who explore and analyze a wide range of issues and factors affecting fish and wildlife resources and makes recommendations as appropriate; sponsors cooperative fish and wildlife programs among member states and other entities to address issues of mutual interest and to benefit to fish and wildlife resources; provides effective, efficient and allied representation for member states regarding natural resource matters, particularly for issues which are beyond the capability of one agency to address or which may unduly tax the ability of individual states.

The Association's annual meeting and conference is held every year, usually in October. The annual meeting and conference are on a rotational basis with each state having its turn as host. Officers are elected at a spring meeting, usually held in May, with the host state normally being that of the incoming President. These meetings promote exchanges of ideas and philosophy between administrators and the professional fish and wildlife biologists, managers, enforcement, information and education, and technical workers in related fields.

Organized March 14, 1938, at a meeting of state officials at Jacksonville, Florida, the Association has played a major role in the evolution of state, regional and national conservation affairs. Its officers and member have included many of the nation's conservation leaders. The Clarence W. Watson Award is the most prestigious award given in the Southeast and is presented annually to the career individual who, in the opinion of the Award Committee, has made the greatest contribution to wildlife or fish conservation during the previous year or years.