Aquatic Invertebrate Biomass in Coastal South Carolina Impoundments Managed for Waterfowl

Beau A. Bauer[1], *Nemours Wildlife Foundation, 161 Nemours Plantation Road, Yemassee, SC 29945*

Richard M. Kaminski[2], *James C. Kennedy Waterfowl and Wetlands Conservation Center, Belle W. Baruch Institute of Coastal Ecology and Forest Science, Clemson University, P.O. Box 596, Georgetown, SC 29442*

Patrick D. Gerard, *School of Mathematical and Statistical Science, Clemson University, Clemson, SC 29634*

Ernie P. Wiggers[2], *Nemours Wildlife Foundation, 161 Nemours Plantation Road, Yemassee, SC 29945*

J. Drew Lanham, *Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC 29634*

Abstract: Production of submersed aquatic vegetation (SAV) is promoted for waterfowl forage through hydrological management in brackish tidal impoundments along the south Atlantic coast, USA. This management also promotes production of aquatic invertebrates as food resources for many bird species. We conducted a field experiment to compare effects of traditional complete drawdown to fissure substrates versus a novel partial drawdown (i.e., mudflat to 10 cm depth) on aquatic invertebrate biomass in impounded and non-impounded tidal wetlands in the Ashepoo, Combahee, and Edisto Rivers (ACE) Basin, South Carolina. We sampled 20 randomly selected impoundments (complete drawdown, $n = 8$; partial drawdown, $n = 12$) and adjacent non-impounded tidal marsh across three properties in August 2016, November 2016, January 2017, and April 2017. Partially drawn-down impoundments contained 4–13 times greater benthic invertebrate biomasses than complete drawdown impoundments in August 2016, November 2016, and April 2017. Benthic invertebrate biomass in complete and partial drawdown impoundments was five times greater than in non-impounded tidal marshes in January 2017. Total invertebrate biomass was 3–15 times greater in partial than complete drawdown impoundments in August 2016, November 2016, and April 2017. We also detected a significant positive association of total invertebrate biomass with SAV biomass across all sampling periods. Dabbling duck energetic use-days (EUDs), based on combined SAV and total invertebrate biomasses, were three times greater in partial than complete drawdown impoundments across sampling periods. We suggest annual partial drawdowns to increase invertebrate and SAV biomasses in brackish impoundments for ducks and other waterbirds but acknowledge need for periodic complete drawdowns to consolidate substrates.

Key words: drawdown, submersed aquatic vegetation, tidal marsh, waterfowl foraging

Journal of the Southeastern Association of Fish and Wildlife Agencies 10:85–91

Waterfowl and other waterbirds obtain energy, protein, amino acids, and minerals by consuming aquatic invertebrates, which enables these birds to fulfill requisites of molting, muscle development, and egg production (Baldassarre and Bolen 2006, Colwell 2010). In the coastal southeastern United States, waterfowl select impoundments managed for submersed aquatic vegetation (SAV), using these impoundments more than non-impounded tidal-marshes because of increased availability of energy- and protein-rich foods and reduced daily tidal fluctuations in the impoundments (Epstein and Joyner 1988, Gordon et al. 1989, Weber and Haig 1996, Gordon et al. 1998, Hagy et al. 2017, Masto et al. 2021). Additionally, non-game waterbirds, particularly shorebirds and wading birds, also use managed impoundments more than non-impounded tidal marsh (Epstein and Joyner 1988, Marsh and Wilkinson 1991, Weber and Haig 1996, Masto et al. 2021). Shorebird time budgets from impoundments indicate foraging is a primary behavior, likely reflecting presence of invertebrates (Goss-Custard et al. 1977, Weber and Haig 1996).

South Carolina coastal wetlands are important migration and wintering areas for North American waterfowl and other waterbirds and therefore are considered important for habitat conservation by the Atlantic Coast Joint Venture (ACJV) of the North American Waterfowl Management Plan (NAWMP; Epstein and Joyner 1988, Gordon et al. 1989, USFWS and CWS 2018). Most impoundments originally were swamps converted to diked rice fields during the 17th–19th centuries, when South Carolina was a global leader in rice production (Beach 2014). Following the rice era in the early 20th century, these impoundments have been managed primarily for waterfowl use and hunting (Gordon et al. 1989).

Hydrology drives wetland systems (Bataille and Baldassarre

1. E-mail: bbauer@nemourswildlife.org
2. Retired.

1993, Batzer 2013, Mitsch and Gosselink 2015). Hydroperiods influence aquatic invertebrate community composition, colonization, growth, development, and persistence in impoundments and other wetlands (Anderson and Smith 2000, Stocks and Grassle 2003, Wrubleski 2005). The primary objective of impoundment management in South Carolina is to produce native forage for migrating and wintering waterfowl via cross-seasonal hydrological management, intended to promote growth of brackish-adapted widgeongrass (*Ruppia maritima*), other SAV (e.g., dwarf spikerush [*Eleocharis parvula*], pondweeds [*Potamogeton* spp.], muskgrass [*Chara* spp.]), and certain emergent vegetation (e.g., saltmarsh bulrush [*Bolboschoenus maritimus*]; Gordon et al. 1989, Williams et al. 2018). Hydrological techniques vary depending on managers, impoundments, and objectives, but generally involve winter flooding, gradual early spring drawdown, several days or weeks of drawdown to expose sediments in late spring to early summer, and gradual reflooding in mid-summer through fall before major influxes of migratory ducks (Gordon et al. 1989, Williams et al. 2018, Bauer et al. 2020). More specifically, late spring–early summer drawdowns involve two alternative strategies in coastal South Carolina (Prevost 1987, Bauer et al. 2020): 1) complete drawdown that fissures substrates and decomposes organics over a period of 2–4 wk, and 2) partial drawdown which maintains saturated substrate or shallow water (≤10 cm). However, there is a lack of information about comparative effects of these strategies. Invertebrate studies in freshwater systems (e.g., Anderson and Smith 2000, Murkin and Ross 2000, Schummer et al. 2021) are not generalizable to impounded brackish wetlands managed for SAV and aquatic invertebrates. Further study of widgeongrass and SAV management as it relates to invertebrate biomass and communities in managed brackish impoundments will inform wetland managers of ecological relationships and support estimation of fall-winter carrying capacity in these impoundments for waterfowl and other waterbirds along the south Atlantic coast (Hunter et al. 2000, USFWS and CWS 2018).

To address this need, we conducted an experiment in coastal South Carolina during 2016–2017 to compare aquatic invertebrate biomasses among three wetland management categories: impoundments managed with complete late spring–early summer drawdown, impoundments managed with partial late spring–early summer drawdown, and non-impounded tidal marshes. We predicted invertebrate biomass would be greater in partial than complete drawdown impoundments and that invertebrate biomass would be positively associated with SAV biomass (Krull 1970, Batzer and Wissinger 1996, Anderson and Smith 2000). Additionally, using combined mean invertebrate and SAV biomass estimates for complete and partial drawdown treatments, we calculated energetic use days (EUDs) per ha for dabbling duck species (Anatini) that typically use South Carolina coastal impoundments. We excluded non-impounded tidal marsh from EUD estimation because dabbling ducks use these wetlands little compared to managed impoundments (Gordon et al. 1998, Masto et al. 2021).

Study Area

Our study was conducted across three properties within the coastal plain of South Carolina: Nemours Wildlife Foundation property (N 32.640, W 80.680 [797 impounded ha]), Cheeha Combahee Plantation (N 32.606, W 80.542 [543 impounded ha]), and Bear Island Wildlife Management Area (WMA) managed by the South Carolina Department of Natural Resources (N 32.593, W 80.463 [1,960 impounded ha]). Study sites contained impoundments having complete and partial drawdown management, with salinity gradients ranging from intermediate (1–5 ppt) to brackish (5–20 ppt). We selected non-impounded tidal marsh adjacent to each property for comparison. Other study-area details are described in Bauer et al. (2020).

Methods

Experimental Design and Invertebrate Collection and Processing

We employed a complete block design to account for possible spatial variability in invertebrate and SAV communities and other possible environmental influences among our study areas. We randomly selected 20 of 60 available impoundments for the study (Bear Island WMA, $n = 8$; Cheeha Combahee Plantation, $n = 8$; Nemours Wildlife Foundation, $n = 4$). Impoundments were managed with either complete or partial drawdown, with each manipulation involving drawdown for 2–4 weeks during May–June 2016. We balanced treatments at each site except Bear Island WMA, which included six partial and two complete drawdown impoundments due to a change from complete to partial drawdown management by WMA staff immediately preceding our study. We sampled adjoining non-impounded tidal marsh at each site ($n = 3$ total).

At each experimental unit (i.e., impoundment or tidal marsh), we sampled in August 2016, November 2016, January 2017, and April 2017 (late summer, fall-winter, and spring, respectively) to collect benthos and epifauna. At each of 10 randomly selected coordinates per unit, we used a 5-cm diameter beveled schedule 40 PVC core sampler to collect invertebrates from the upper 5 cm of substrate of impoundments and non-impoundment marsh (Swanson 1983, Cramer et al. 2012). We sampled to a depth of 5 cm as this encompassed approximate bill lengths of dabbling ducks and the substrate wherein most benthos existed (Murkin et al. 1996, Sherfy et al. 2000). We acknowledge this core sampler may have collected nekton (Swanson 1978); however, we assumed these samples primarily contained benthos because non-impounded marsh samples were collected during low tide and because relatively shallow water existed across impoundments and sampling periods ($\bar{x}=29.4$ [SE = 2.4] cm, $n=80$; Bauer 2018). We also collected SAV and attached epifaunal invertebrates at a random-azimuth point within 1 m of the core sample using a circular unit sampler within a ~1 m^2 area. However, this collection largely occurred in impoundments because of general absence of SAV in the non-impounded tidal marshes (Bauer et al. 2020, Masto et al. 2020). We extracted SAV and attached epifauna from within the unit sampler with a modified rake (Bauer 2018, Masto et al. 2020). We placed SAV samples in plastic bags and transported them on ice to the laboratory where samples were stored in a freezer until processed.

We allowed samples to thaw at room temperature prior to washing them through a series of sieves 12.7 mm to 500 µm to remove organics and debris while retaining invertebrates (Foth et al. 2012). We dried washed SAV samples to a constant mass (g) at 70 C for 48–72 h and weighed dried samples with a 0.1 mg digital balance (Bauer et al. 2020). We transferred invertebrate samples to white plastic photo developing trays to identify them to order or family (Merritt et al. 2008, Thorp and Covich 2010, Bauer 2018). We preserved invertebrate samples in 90% ethanol until we dried them to constant mass (g) at 60 C for 18–24 h. We weighed dried invertebrate samples with a 0.1 mg digital balance. We aggregated invertebrate taxa from impoundments to derive mean total invertebrate biomass (g[dry] m^{-2}) per impoundment and sampling period.

Energetic Use-Days

Energetic use-days are the number of days a specified area may sustain waterfowl given average energy requirements of focal birds for the fall-winter period (Reinecke et al. 1989, Stafford et al. 2011). We focused on dabbling ducks because they are the dominant waterfowl tribe using managed impoundments (Masto et al. 2021). We calculated EUD ha^{-1} for SAV (Bauer et al. 2020) and total invertebrate biomasses combined using the following equation:

$$EUD_i = (FD \times TME)/DER$$

wherein i is food type (SAV or invertebrates), FD is food density (i biomass of SAV or invertebrates converted to g[dry] ha^{-1}), TME is true metabolizable energy of food i (kcal g[dry]$^{-1}$; Miller and Reinecke 1984), and DER is daily energy requirement of focal duck species. We used widgeongrass and Chironomidae larvae as representative SAV and invertebrate forages, respectively, because of their importance as waterfowl foods (Landers et al. 1976, Krapu and Reinecke 1992), availability of TME data for these taxa (Sherfy 1999, Gross 2018), and major occurrences in our samples (~73% widgeongrass [$n=284$; Bauer et al. 2020] and ~27% Chironomidae [$n=96{,}526$; Bauer 2018]). We used a mean TME value for widgeongrass (0.84 kcal[dry] g^{-1}, Gross 2018) and chironomids (0.27 kcal g^{-1}, Sherfy 1999). We used a DER value of 241.83 kcal day^{-1}, calculated from resting metabolic rates × 3, for Nearctic dabbling duck species commonly using South Carolina waterfowl impoundments (i.e., American black duck [*Anas rubripes*], northern pintail [*A. acuta*], gadwall [*Mareca strepera*], and northern shoveler [*Spatula clypeata*]) or Palearctic species when data for Nearctic species were lacking (i.e., Eurasian teal [*A. crecca*], Eurasian wigeon [*M. penelope*], and Garganey teal [*S. querquedula*]; Miller and Eadie 2006, Bauer 2018). We considered the latter three species as Nearctic ecological equivalent species for green-winged teal (*A. carolinensis*), American wigeon (*M. americana*), and blue-winged teal (*S. discors*), respectively, because they have similar body sizes to their Nearctic congeners.

Statistical Analyses

We used PROC MIXED in SAS (SAS Institute 2013) to compare dried benthic invertebrate biomass (g m^{-2}) among wetland types for each sampling period, with study site as a random block effect. We used PROC MIXED in a mixed model analysis of covariance (i.e., block was a random effect and SAV biomass was the covariate) to test effects of complete and partial drawdowns on total dried invertebrate biomass (i.e., benthos, epifauna, and possible nekton) within impoundment. Our response variable for analyses was mean biomass of total invertebrates from 10 randomly selected paired rake (where SAV was present) and core samples from within each impoundment or 10 core samples from non-impounded marsh sites. When SAV was absent at impoundment sample sites, this covariate was assigned a zero value. We conducted Tukey's post hoc tests to compare significant differences by sampling period. Distributions of residuals revealed non-normality; however, we relaxed this assumption due to robustness of analysis of variance for departures from normality, and because outcomes of tests were similar using transformed or raw data (Miller 1997). We set $\alpha=0.10$ *a priori* (Tacha et al. 1982).

Results

Benthic Invertebrate Biomass

We detected a treatment effect on benthic invertebrate biomass for all sampling periods (August 2016 [$F_{2,18}=3.24$, $P=0.063$], November 2016 [$F_{2,18}=4.72$, $P=0.022$], January 2017 [$F_{2,18}=2.93$, $P=0.079$], and April 2017 [$F_{2,18}=3.79$, $P=0.042$]; Table 1). Mean biomass in partial drawdown impoundments was 13, 11, and 4 times greater ($-2.88 \leq t_{18} \leq -2.38$, $0.026 \leq P \leq 0.07$) than in completely drawndown impoundments in August 2016, November 2016, and April 2017, respectively (Table 1). Benthic invertebrate

Table 1. Least-squares mean (SE) benthic and total (benthic + epifaunal) aquatic invertebrate biomass (g[dry] m^{-2} for unmanaged tidal marshes ($n=3$), complete drawdown managed impoundments ($n=8$), and partial drawdown managed impoundments ($n=12$) sampled August 2016–April 2017 in the Ashepoo, Combahee, and Edisto Rivers Basin, South Carolina. For unmanaged marshes, total invertebrate biomass is omitted due to absence of submersed aquatic vegetation and associated epifaunal invertebrates. Means within sampling periods followed by the same letters do not differ ($P > 0.10$).

Month	Benthic	Total
August 2016		
Unmanaged marsh	1.54 (4.77)^{ab}	n/a
Complete drawdown	0.73 (2.92)^{a}	0.88 (4.58)^{a}
Partial drawdown	9.72 (2.39)^{b}	13.63 (3.74)^{b}
November 2016		
Unmanaged marsh	1.22 (2.68)^{ab}	n/a
Complete drawdown	0.64 (1.64)^{a}	2.17 (1.50)^{a}
Partial drawdown	6.75 (1.34)^{b}	6.57 (1.22)^{b}
January 2017		
Unmanaged marsh	0.85 (1.26)^{a}	n/a
Complete drawdown	4.08 (0.80)^{b}	4.53 (0.83)^{a}
Partial drawdown	4.05 (0.67)^{b}	4.05 (0.68)^{a}
April 2017		
Unmanaged marsh	0.49 (1.41)^{ab}	n/a
Complete drawdown	0.88 (0.86)^{a}	1.09 (1.00)^{a}
Partial drawdown	3.57 (0.70)^{b}	3.64 (0.90)^{b}

Table 2. Mean (SE) energetic density (ED; kcal ha^{-1}) and energetic use-day (EUD; days ha^{-1}) estimates for widgeongrass and associated submersed aquatic vegetation (SAV [e.g., dwarf spikerush, muskgrass]) and midge larvae (Chironomidae) measured in completely or partially drawdown managed impoundments sampled August 2016–April 2017 in the Ashepoo, Combahee, and Edisto Rivers Basin, South Carolina.

	Complete drawdown ($n=8$)				Partial drawdown ($n=12$)			
Month	ED		EUD		ED		EUD	
August 2016								
SAV	79,957	(20,260)	331	(84)	302,235	(63,623)	1,250	(263)
Invertebrate	2,375	(511)	10	(2)	36,791	(12,909)	152	(53)
Total	82,332	(20,395)	340	(84)	339,026	(69,309)	1,402	(287)
November 2016								
SAV	33,619	(27,361)	139	(113)	99,144	(32,101)	410	(133)
Invertebrate	1,975	(595)	8	(2)	20,384	(5,388)	84	(22)
Total	35,593	(27,776)	147	(115)	119,529	(36,325)	494	(150)
January 2017								
SAV	11,326	(3,357)	47	(14)	47,548	(25,147)	197	(104)
Invertebrate	11,380	(2,637)	47	(11)	11,502	(1,742)	48	(7)
Total	22,706	(3,796)	94	(16)	59,050	(26,208)	244	(108)
April 2017								
SAV	53,261	(32,132)	220	(133)	65,773	(50,293)	272	(208)
Invertebrate	2,486	(646)	10	(3)	10,652	(3,055)	44	(13)
Total	55,747	(32,030)	231	(132)	76,426	(52,564)	316	(217)

biomass for partially and completely drawn-down impoundments was five times greater ($-2.31 \le t_{18} \le 2.23$, $0.08 \le P \le 0.094$) than in non-impounded tidal marsh in January 2017 (Table 1).

Total Invertebrate Biomass and Energetic Use-Days

We detected a treatment effect on total invertebrate biomass ($F_{1, 16} = 4.65$, $P = 0.047$) for August 2016 (Table 1). We could not control for SAV biomass due to a treatment effect on SAV biomass for August 2016 (Bauer et al. 2020). We also detected a treatment effect on total invertebrate biomass for November 2016 ($F_{1, 15} = 4.99$, $P = 0.041$) and April 2017 ($F_{1, 15} = 5.78$, $P = 0.030$) while controlling for SAV biomass (Table 1). Mean total invertebrate biomass in partially drawn-down impoundments was 15, 3, and 3 times greater than in complete drawdown impoundments for August 2016 ($t_{16} = -2.16$, $P = 0.047$), November 2016 ($t_{15} = -2.23$, $P = 0.041$), and April 2017 ($t_{15} = -2.41$, $P = 0.030$), respectively (Table 1). We also detected a positive effect of SAV biomass on total invertebrate biomass for November 2016 ($F_{1, 15} = 14.67$, $\beta = 0.31$, $P = 0.002$), January 2017 ($F_{1, 15} = 3.31$, $\beta = 0.12$, $P = 0.089$), and April 2017 ($F_{1, 15} = 14.71$, $\beta = 0.13$, $P = 0.002$). Because EUDs were derived using combined SAV and total invertebrate biomass estimates, EUDs patterned variation of biomass estimates. Across sampling periods, EUDs for partial drawdown impoundments averaged ~3 times greater than those for complete drawdown impoundments (Table 2).

Discussion

Our results indicated that complete drawdowns and partial drawdowns differentially influenced aquatic macroinvertebrate biomass before, during, and after the arrival of migratory waterfowl and shorebirds to coastal South Carolina. Our results also showed that invertebrate biomass varied with SAV biomass and was consistent with previous studies (Krull 1970, Stoner 1980, Wrubleski and Rosenberg 1990, Strayer and Malcom 2007). This positive relationship may be related to increased foliar surface provided by SAV and associated invertebrate forage (i.e., epiphytic algae; Murkin and Ross 2000, Batzer 2013). Additionally, increased benthic and total invertebrate biomasses in partial drawdown impoundments may have been due to softer substrate and prolonged hydroperiods that sustained invertebrate communities and food resources (i.e., periphyton, epipelon) during summer droughts (Batzer and Wissinger 1996, Murkin and Ross 2000, Bolduc and Afton 2005). These impoundments also contained greater SAV biomass than complete drawdown impoundments in August 2016, before Hurricane Matthew occurred in October 2016 (Bauer et al. 2020). The additive effects of a sustained summer hydroperiod and resulting increased SAV and invertebrate biomasses in partial drawdown impoundments may have carried over winter to result in greater invertebrate biomass in partial drawdown impoundments in April 2017.

Our monthly variation in invertebrate biomass may have been related to rapid invertebrate life-cycle turnover rates, waterbird and fish predation, and Hurricane Matthew (MacKay et al. 1990, Anderson and Smith 2000). Bauer et al. (2020) reported that SAV in our study area was devastated by Hurricane Matthew, as evidenced by massive windrows of widgeongrass and other SAV on dikes and shores of impoundments. Similarly, we observed an overall decrease in invertebrate biomass following the hurricane (i.e., November 2016), except for an increase in total invertebrate biomass within complete drawdown impoundments. This increase may have been due to increased substrate firmness that promoted retention of SAV and associated epifauna during the hurricane (Bauer 2018). Additionally, 75% of our complete drawdown impoundments were located inland from tidal rivers and marsh, which may have buffered wind and storm surge effects.

Benthic and total invertebrate biomasses were greater in partial drawdown than complete drawdown impoundments in August 2016 before the hurricane, mostly due to increased hydrobiid snail densities. These Caenogastropods are sensitive to substrate drying and may not persist post-drawdown within complete drawdown impoundments (Poznańska et al. 2015). However, their horizontal and vertical migrations in substrate may have influenced their distribution and resilience within impoundment substrates (Poznańska et al. 2015). The effect of partial drawdown on invertebrates was coupled with greater SAV biomass in August 2016, where increased periphyton as forage may have contributed to increased snail densities (Heard et al. 2002, Thorp and Covich 2010, Bauer et al. 2020). The presence of hydrobiids in partial drawdown impoundments also may have positively influenced SAV biomass in August 2016 due to their grazing on filamentous algae (*Cladophora* spp.) attached to SAV (Thorp and Covich 2010). For Chironomid larvae, we observed peak densities in January 2017, possibly due to a rapid turn-over response to decreased water depths within complete drawdown impoundments (Murkin and Kadlec 1986, Batzer et al. 1997). Property managers lowered water depths to encourage late-winter SAV growth to offset losses from Hurricane Matthew and from foraging by ducks and American coot (*Fulica americana*; Hartke et al. 2009).

Partial drawdown management led to increased EUD. For conservation planning, we suggest using August 2016 EUD estimates (i.e., 340 [complete drawdown] to 1402 [partial] EUDs ha^{-1}) due to confounding effects of SAV and invertebrate losses from Hurricane Matthew in October 2016, waterbird foraging during fall–winter, and seasonal SAV senescence (Hartke et al. 2009, Bauer et al. 2020). Our August 2016 energetic densities (82,332 [complete drawdown] to 339,026 [partial] kcal ha^{-1}) were comparable to those reported by Livolsi et al. (2021) for brackish impoundments in the mid-Atlantic states (169,665–357,160 kcal ha^{-1}), despite the latter supporting different invertebrates (e.g., salt marsh snails [*Melampus* spp.]). We did not include foraging thresholds in our EUD estimates as these data are lacking for invertebrates and other natural foods in Atlantic Flyway brackish impoundments (Livolsi et al. 2021). We also note that our study may have underestimated invertebrate biomass due to effects of freezing, sample processing, and preservation in ethanol (Howmiller 1972, Murkin et al. 1996).

In conclusion, we suggest annual partial drawdowns in impoundments to promote biomass of SAV and aquatic invertebrates. Additionally, we caution that prolonged inundation may result in flocculent sediments and increased turbidity detrimental to the propagation, rooting, and retention of SAV. We also suggest periodic complete drawdowns to consolidate substrates as needed (Kantrud 1991, Bauer et al. 2020). Finally, for determination of regional foraging carrying capacity, we recommend replication of our experiment along the mid- and south Atlantic coast to evaluate repeatability of our results. We also recommend determination of area of managed impoundments with complete and partial drawdowns, estimation of plant and invertebrate forage biomasses relative to forage use by waterfowl and other waterbirds, and determination of foraging thresholds for conservation planning (Williams et al. 2014).

Acknowledgments

We thank Nemours Wildlife Foundation (Yemassee, South Carolina) and Clemson University's James C. Kennedy Waterfowl and Wetlands Conservation Center for providing funding and logistical support. We thank the South Carolina Department of Natural Resources and private landowners and managers for allowing access to their properties. We acknowledge C. P. Marsh, J. W. Pike, and B. A. Powell for their technical input. This article was approved for publication as Technical Contribution No. 6989 of the Clemson University Experiment Station. We thank two anonymous reviewers, D. Greene, and R. Gitzen, who provided input that improved the quality of this manuscript.

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