Box-nesting Wood Ducks and Black-bellied Whistling Ducks in Coastal South Carolina

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Abstract: Installation and maintenance of artificial nesting structures are established practices for increasing production of secondary cavity nesting waterfowl, especially wood ducks (*Aix sponsa*). In South Carolina, tens of thousands of nest boxes have been erected on public and private lands. Additionally, since the early 2000s, black-bellied whistling ducks (*Dendrocygna autumnalis*) have expanded their range into South Carolina and now are nesting sympatric with wood ducks in boxes. We conducted a survey of 364 and 354 nest boxes in 2016 and 2017, respectively, across the Ashepoo, Combahee, and Edisto river (ACE) and the Santee Rivers Delta and Winyah Bay (SRDW) basins in coastal South Carolina. We did not detect a difference in frequency of nest box use between basins by wood ducks (~61%) or black-bellied whistling ducks (~15%). We believe low use of nest boxes by black-bellied whistling ducks was due to their recent colonization of South Carolina. Nest success (i.e., ≥1 egg hatched) across both years was 65% for wood ducks and 51% for black-bellied whistling ducks. Based on presence of egg-shell membranes or ducklings counted in boxes, we estimated an average of 10.2 wood duck (SE = 0.3) and 9.5 black-bellied whistling duck (SE = 0.8) ducklings exited successful nests. We used our reproductive data and a published recruitment rate for yearling female wood ducks returning to nest boxes in South Carolina (6.8%) to cost-evaluate wood duck recruitment from boxes. Assuming 2.8 female recruits produced per box over a 20-year box life, cost per female recruit per box was only ~1/3 the lifetime cost of a box and its maintenance. Our study rationalized the need for regional and cross-flyway investigations of recruitment by wood ducks and other ducks nesting in artificial structures and natural cavities.

Key words: Aix sponsa, *Dendrocygna autumnalis*, nest box, reproduction

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Installation and regular maintenance of artificial nest structures are established practices for increasing production of secondary cavity nesting ducks (Kaminski and Weller 1992, Bellrose and Holm 1994). Most efforts in North America have focused on wood ducks, and extensive literature exists on the species' use of and production in boxes (Fredrickson et al. 1990, Prevost et al. 1990, Bellrose and Holm 1994, Baldassarre 2014). Artificial nest boxes have been reported to increase wood duck recruitment into fall populations, especially when boxes were seasonally maintained and located near brood cover (Utsey and Hepp 1997, Heusmann 2000, Davis et al. 2007, 2015). For example, an estimated 300,000 wood duck ducklings were produced in 100,000 boxes annually in the early 1980s in North America, with an assumed 50% duckling recruitment into fall populations (Bellrose and Holm 1994).

Wood ducks recently were the most harvested duck species in South Carolina (43%; Raftovich et al. 2019). They also were one of the most harvested ducks in the Atlantic and Mississippi flyways and therefore an economically important avian resource (Grado et al. 2011, Raftovich et al. 2019). To promote production of wood ducks in South Carolina, tens of thousands of nest boxes have been erected on public and private lands by the South Carolina Department of Natural Resources, South Carolina Waterfowl Association, and other partners (Otis and Dukes 1995). Additionally, secondary cavity nesting black-bellied whistling ducks and hooded mergansers (*Mergus cucculatus*) use artificial nest boxes in South Carolina (Croft et al. 2020). However, until the early 2000s, only wood ducks and hooded mergansers were known to nest in boxes in the state, although black-bellied whistling ducks subsequently expanded their breeding range in the south Atlantic region (Balkcom et al. 2013, Cohen et al. 2019), and all three species currently are sympatric nesters in boxes in South Carolina (Harrigal and Cely 2004, Croft et al. 2020).

Although researchers have conducted surveys of box-nesting wood ducks in South Carolina (Luckett 1977, Hepp et al. 1989, 2020,

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Utsey and Hepp 1997, Croft et al. 2020), contemporary, regional estimates are lacking for sympatric wood duck and black-bellied whistling duck nest-box use and duckling production. These data are important for understanding and managing box-nesting populations of these species in southeastern United States. Hence, we conducted a survey of over 350 nest boxes distributed across the Ashepoo, Combahee, and Edisto river (ACE) and the Santee Rivers Delta and Winyah Bay (SRDW) basins in South Carolina, a coastal plain ecosystem of international importance to North American waterfowl and other waterbirds (Gordon et al. 1998, North American Waterfowl Management Plan 2018, Masto et al. 2021). Our objectives were to: 1) estimate percent use of nest boxes, percent nest success, and average number of ducklings per successful nest that exited boxes for both species of ducks and compare estimates between the ACE and SRDW basins, 2) compare our results with relevant similar studies conducted elsewhere, and 3) calculate cost-benefit of nest boxes in our study region relative to wood duck recruitment using our wood duck reproductive data and a published estimate of recruitment rate for wood ducks in South Carolina (Hepp et al. 1989, 2020). Recruitment rate data for black-bellied whistling ducks did not exist at the time of our study, hence our concentration on wood ducks for the cost-benefit portion.

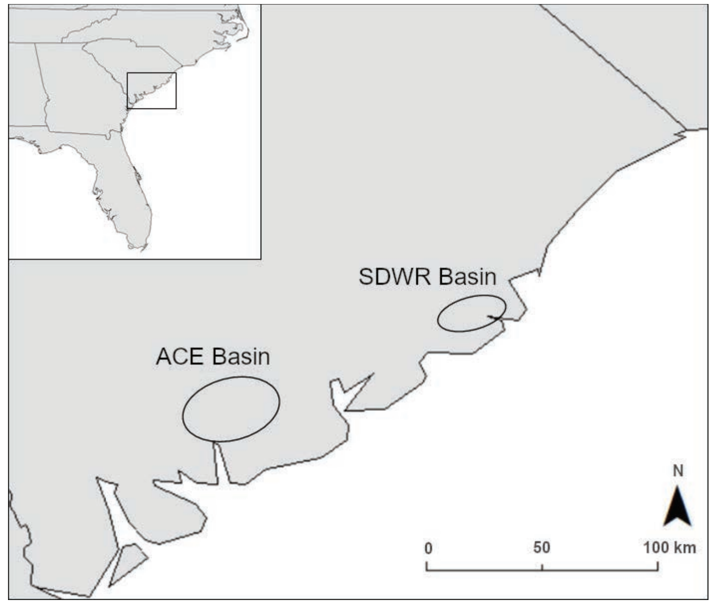

Figure 1. Approximate locations of study areas with monitored nest boxes in the Ashepoo, Combahee, and Edisto rivers (ACE) and the Santee Rivers Delta and Winyah Bay (SDRW) basins in coastal South Carolina in 2016–2017.

Study Area

We conducted our study across the Coastal Plain of South Carolina, contiguous with the Atlantic Ocean in Beaufort, Charleston, Colleton, and Georgetown counties. Our study area extended approximately from Beaufort, South Carolina (32.4316° N, 80.6698° W) to Georgetown, South Carolina (33.3768° N, 79.2945° W), a distance of more than 200 km across the ACE and SRDW Basins (Figure 1). These basins contained lowland forested wetlands, fresh, brackish, and saline tidal emergent marshes, managed and non-managed impounded wetlands (i.e., historic rice fields; Beach 2014, Folk et al. 2016), beaches and dunes, pine (*Pinus* spp.) and other conifers, and softwood and hardwood deciduous trees (NOAA 2018a, b, Croft 2018).

In the ACE basin, our study sites were Clarendon Farms (Beaufort), South Carolina Department of Natural Resources (SCDNR) Donnelley Wildlife Management Area (Green Pond), Halls Island (Sheldon), Nemours Wildlife Foundation (Yemassee), and Rosehill Plantation (Yemassee). In the SRDW basin, our study sites were Annandale Plantation (Georgetown), DeBordieu Colony (Georgetown), Hobcaw Barony (Georgetown), Kinloch Plantation (Georgetown), and SCDNR Santee Coastal Reserve Wildlife Management Area (McClellanville). We did not randomly select study sites but instead chose sites with active nest-box management programs which we assumed were representative of public and private-land nest-box sites in coastal South Carolina. Within sites, nest boxes were distributed among emergent fresh and brackish wetlands, managed impoundments, ponds, drainage ditches and creeks, scrub-shrub wetlands, and forested bottomlands. Dominant macro-vegetation in wetlands and associated sites included duckweed (*Lemna minor*), cattail (*Typha* spp.), sturdy bulrush (*Bolboschoenus robustus*), giant cutgrass (*Zizaniopsis miliacea*), smooth cordgrass (*Spartina alterniflora*), dwarf palmetto (*Sabal minor*), buttonbush (*Cephalanthus occidentalis*), bald cypress (*Taxodium distichum*), red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), tupelo gum (*Nyssa* spp.), water, willow, and live oaks (*Quercus nigra*, *Q. phellos*, *Q. virginia*, respectively), and willows (*Salix* spp.). Long-term temperature and precipitation in the region during our January–July study period averaged 23 °C (range = 6–31 °C) and 9 cm (range = 7–13 cm), respectively (National Oceanic and Atmospheric Administration [NOAA] 2018a,b).

Methods

Nest Boxes and Inspections

Initially, we selected 324 existing nest boxes that were erected prior to our study. In January 2016, we installed additional boxes at Santee Coastal Reserve Wildlife Management Area (SDRW, $n = 20$), Rosehill Plantation (ACE, $n = 10$), and Halls Island (ACE, $n = 10$), replacing other existing dilapidated structures. In total, we monitored 364 boxes in 2016 and 354 boxes in 2017 (because 10 boxes were destroyed between years by Hurricane Matthew in October 2016).

For all boxes, annually in December–January we refurbished structures, removed nest remains, and added wood shavings. During the breeding season across the ACE and SRDW Basins, we inspected most boxes twice monthly (309 in 2016, 299 in 2017). At DeBordieu Colony in the SDRW we inspected 55 boxes only in May and September each year because we lacked field staff at that site during spring-summer.

During each inspection, we recorded: 1) duck species by presence of hen and/or eggs, 2) number of eggs by species, 3) number of ducklings or egg-shell membranes by species—the latter to index number of ducklings that had already exited boxes (Davis et al. 1998), 4) number of unhatched eggs, 5) number of live and dead ducklings, and 6) number of depredated eggs and predator if determinable (Bellrose and Holm 1994). Following determination of fate of first nests, we removed egg-shell membranes, unhatched eggs, and down feathers but not wood shavings; we removed shavings and replaced them anew in early May 2016 and 2017 to promote subsequent nest box use and duckling production (Utsey and Hepp 1997, Davis et al. 2015).

Statistical Analyses

Our sampling units for all statistical analyses ($\alpha = 0.05$) were individual boxes and nests. We neither had records of age nor previous years' use of boxes by nesting hens; thus, we could not include these covariates in analyses. We calculated the proportion of boxes used by each species by year and basin. We tested for differences in numbers of boxes used and not used by wood duck and black-bellied whistling duck between basins, using logistic regression (PROC GLIMMIX; SAS Institute Inc. 2018). We accounted for repeated monitoring of boxes and nests within and between years by using a correlated error model specifying an auto-regressive covariance structure (Ackerman et al. 2009, Lancaster et al. 2015). We used PROC FREQ (SAS Institute Inc. 2018) to calculate proportions of clutches depredated by rat snakes (*Pantherophis obsolete*) or woodpeckers (Picidae). We calculated average nest success per box by dividing the number of clutches with ≥1 hatched egg by total nests initiated in a box per year. For these analyses of depredation and nest success, we used only the subset of boxes inspected twice monthly each breeding season. Using all monitored boxes, we compared numbers of wood duck and black-bellied whistling duck ducklings produced per box between basins for each year, using maximum likelihood count regression models with the COUNTREG procedure (Erdman et al. 2008, SAS Institute 2018). We analyzed these data by year, because not all the same boxes were monitored each year, and we were not able to explain any significant year effects or interactions that may have been influenced by exogenous (e.g., weather, hydrology, social, etc.) or female endogenous effects (e.g., age, body condition). To account for zero hatched ducklings in clutches and observed or indexed numbers of ducklings from egg-shell membranes, we fitted Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial distributions to the data and determined best model fit (Erdman et al. 2008, Morris 2008). We selected a distribution and model based on Akaike's information criteria (AIC; Akaike 1974). We calculated the deviation in a model's AIC score from the top model with lowest AIC value (ΔAIC), considering distributions and models competitive with ΔAIC values ≤2 (Burnham and Anderson 2002).

For wood ducks, we performed a nest-box cost-benefit analysis, including reproductive metrics from our study, a published index of yearling female recruitment rate (i.e., 6.8%; Hepp et al. 1989, 2020), contemporary costs to fabricate and annually maintain boxes (i.e., Barry 1992, costs inflated to 2021 U.S. currency values per Croft 2018), and an assumed longevity of 20 years for an annually maintained bald-cypress (*Taxodium distichum*) or another durable wooden box. We conducted a cost-benefit analysis for wood ducks only, because no recruitment estimate was available for black-bellied whistling ducks.

Results

Wood Ducks

We did not detect a difference in the number of boxes used between basins ($F = 1.46$, df = 1, 353; $P = 0.23$). Box use was 69.8% and 52.5% in 2016 and 2017, respectively, and overall, 61.2% (SE = 8.6%, $n = 718$ boxes surveyed in both years). Wood ducks used 66 boxes twice (9.2%) and 9 boxes three times (1.3%) per year.

Average size of incubated clutches across years was 13.1 eggs (SE = 0.3, $n = 443$ nests). Nest success (≥1 egg hatched) across years for 608 boxes monitored twice monthly was 65% (268 successful of 412 nests). Determinable nest failures for twice-monthly monitored boxes resulted from woodpeckers (13.1%, $n = 54$ nests) and rat snakes (6.6%, $n = 27$ nests).

The number of ducklings or egg-shell membranes observed in boxes was best modeled with a zero-inflated negative binomial (ZINB) distribution (Table 1). We did not detect any difference in the zero-duckling portion of the model between basins in 2016 ($t = -0.56$; $P = 0.58$) and 2017 ($t = 0.61$; $P = 0.54$) or in the duckling count portion of the model in 2016 ($t = 1.04$; $P = 0.30$) and 2017 ($t = 1.81$; $P = 0.07$). For 718 total boxes surveyed in both years, an average of 4.7 (SE = 0.28) wood duck ducklings exited boxes. For 332 successful nests in both years, an average of 10.2 (SE = 0.3) ducklings exited boxes.

Table 1. Scaled Akaike information criterion (ΔAIC) values for fitted models of wood duck and black-bellied whistling duck ducklings exiting nest boxes in coastal South Carolina in 2016 and 2017.

	Wood duck		Black-bellied whistling duck	
Model	**2016**	**2017**	**2016**	**2017**
Zero-inflated negative binomial	0	0	0.0	0.0
Zero-inflated Poisson	220	64	26.2	8.4
Negative binomial	180	185	39.6	17.2
Poisson	3198	2817	1570.5	918.9

Cost-Benefit Analysis

Estimated cost of a nest structure plus its installation and annual maintenance over 20 years was US$158.15. We calculated 0.14 yearling female wood duck recruit/box/year (i.e., 61.2% box use × 65% nest success × 10.2 ducklings per successful nest × 50% females [1:1 assumed sex ratio, Hepp et al. 2020] × 6.8% yearling female wood duck recruitment rate per year [Hepp et al. 2020]). Therefore, calculated cost per yearling female wood duck recruit over 20 years was US$56.48 (US$158.15 per box / [0.14 recruit/box/year × 20 years = 2.8 total recruits/box]).

Black-bellied Whistling Ducks

We did not detect a difference in the number of boxes used by black-bellied whistling ducks between basins ($F = 1.48$, df = 1, 353; $P = 0.23$). Box use was 15.4% and 14.1% in 2016 and 2017, respectively, and 14.8% overall across both years. Black-bellied whistling ducks used 11 boxes twice (1.5%) and none three times per year.

Average clutch size of all incubated clutches across years was 11.1 eggs (SE = 0.9, $n = 110$). Nest success across both years for 608 boxes monitored twice monthly was 50.9% (56 successful of 110 nests). Across years, known nest failures were from woodpecker depredation of eggs (13.6%, $n = 15$ nests).

Model evaluation revealed that number of ducklings produced in boxes was best modeled with a ZINB distribution (Table 1). We did not detect any difference in the zero-duckling portion of the model in 2016 ($t = 0.81$; $P = 0.42$) and 2017 ($t = 0.45$; $P = 0.65$). In the duckling count portion of the model, we detected a basin effect in 2016 ($t = 3.77$; $P \leq 0.01$) but not in 2017 ($t = -0.88$; $P = 0.38$). For 718 boxes surveyed in both years, an average of 0.7 (SE = 0.12) black-bellied whistling duck ducklings exited boxes. For 56 successful nests, an average of 9.5 (SE = 0.8) ducklings exited boxes.

Discussion

We believe our study was the first cross-riverine basin, coastal South Carolina investigation of reproductive performance by sympatric box-nesting wood ducks and black-bellied whistling ducks. Wood ducks were the dominant species nesting in boxes in this region (90%), followed by black-bellied whistling ducks — a recent immigrant to South Carolina (Harrigal and Cely 2004, Cohen et al. 2019). In three of the four species by year comparisons, we did not detect a difference in box use or duckling production between basins. Consequently, our results may be applicable to all coastal South Carolina and possibly similar environs along the south Atlantic coast.

Bellrose and Holm (1994) reported data on use of nest boxes by wood ducks at the national, flyway (Atlantic, Mississippi, and Pacific), and flyway regional levels (northern, central, and southern) for 1939–1990. Nest box use averaged 42% at the national level and 42%, 40%, and 50% for the Atlantic, Mississippi, and Pacific flyways, respectively. Within the Atlantic Flyway, nest box use averaged 36%, 42%, and 49% in the northern, central, and southern regions (Bellrose and Holm 1994). Our coastal South Carolina estimate of 61% was appreciably greater than the those estimates but less than that (89%) reported by Utsey and Hepp (1997), who studied box-nesting wood ducks in Colleton County in the ACE Basin. We speculate that greater use of boxes in coastal South Carolina than elsewhere may be influenced by the extensive availability and maintenance of nest boxes in this region and statewide (Otis and Dukes 1995) in the 5 million hectares of forestland in South Carolina (Conner and Hartsell 2002), the extended nesting season for wood ducks in this region (Croft et al. 2020), and other possible population and environmental factors. Considering extensive forest land in South Carolina, we encourage researchers to use remotely sensed data or other means to determine availability of suitable natural cavities for wood ducks juxtaposed with wetlands (Lowney and Hill 1989, Zlonis et al. 2021).

Mean clutch size of 13 eggs (SE = 0.3) was consistent with prior records of wood duck egg production (Bellrose and Holm 1994). Vrtiska (1995) studied reproductive biology of captive, wild-strain wood ducks hatched in an incubator from eggs collected from nest boxes at Sam D. Hamilton-Noxubee National Wildlife and Yazoo National Wildlife Refuges in east-central and western Mississippi, respectively. These birds were maintained in an outdoor aviary with ad libitum access to a nutritious commercial ration and fresh water at Mississippi State University (MSU) (Vrtiska 1995, Demarest et al. 1997). Latitude near the center of our study area (Charleston, South Carolina, 32.7° N) was similar to that at the MSU site (33.4504° N; Vrtiska 1995, Demarest et al. 1997); thus, hours of daylight would be similar. Vrtiska's (1995) captive pairs of wood duck were maintained separately from other conspecific pairs and thus not subjected to intraspecific nest parasitism. Vrtiska (1995) reported mean clutch size for first and second nests of the captive females was 10 eggs (95% CI: ±1 egg; $n = 9–26$ clutches). Vrtiska's

(1995) estimate of clutch size in the absence of nest parasitism suggested our and other published estimates of wood duck clutch size were inflated by intraspecific nest parasitism from free-ranging wood ducks (Bellrose and Holm 1994). Thus, true mean clutch size by wood duck females, without intraspecific nest parasitism, may range from about 9–11 eggs, which is similar to many other duck species (Rohwer 1988). We hypothesize that this mean and limited range in clutch size may be a consequence of selection for an optimal number of eggs and ducklings that physically can be incubated, hatched, and brooded by females. Increased length of the incubation period associated with larger clutches may represent a physiological and reproductive cost of enlarged clutches from intraspecific nest parasitism (Hepp et al. 1990). Davis et al. (2007) presented daily survival data for wood duck ducklings that could be used to test this hypothesis.

Our estimate of nest success (65%) was similar to rates reported for wood ducks nesting in experimental small (59%) and conventional large nest boxes in Mississippi (66%, Stephens et al. 1998). In contrast, Utsey and Hepp (1997) reported an average nest success of 88% for wood ducks nesting in boxes in coastal South Carolina. One possible explanation for these disparate estimates is differences in population demographics and resource availabilities among the years of these two studies in coastal South Carolina.

Our estimates of wood duck duckling production from nest boxes were comparable to previous studies in South Carolina. Luckett (1977) monitored nest boxes in the Piedmont of northern South Carolina during 1974–1975 and reported an average of three wood duck ducklings per box across sites and years. We recorded a mean of about five wood duck ducklings (SE = 0.3) among all boxes during our study. Our estimate of mean number ducklings per box was within the range of means reported by Utsey and Hepp (1997; $\bar{x} = 4–5$ [SE ≤ 0.9]) for their coastal South Carolina study. We also found that egg hatching success (49%) from all nests and mean number of ducklings that exited boxes from successful nests (10.2 birds, SE = 0.3) were similar to values reported by Utsey and Hepp (1997; 39%–42%, 12–13 ducklings [SE ≤ 0.9]).

Black-bellied Whistling Ducks

In Texas, black-bellied whistling ducks used 81% of available boxes during a 12-year study between 1964 and 1975 (McCamant and Bolen 1979). In coastal South Carolina, black-bellied whistling ducks used only 15% of available boxes during 2016 and 2017. Black-bellied whistling ducks are recent immigrants to South Carolina, where nesting was first confirmed in 2003 (Harrigal and Cely 2004). Therefore, the South Carolina population likely is smaller than the long-established population in Texas, but size of the South Carolina breeding population has not been estimated.

Our recorded mean clutch size of 11 eggs for black-bellied whistling ducks was similar to that reported by Bolen (1967) for this species nesting in coastal Texas ($\bar{x} = 13$ eggs). Additionally, 77% of those nests produced at least one duckling (Bolen 1967). However, McCamant and Bolen (1979) reported only 28% of nests initiated by black-bellied whistling ducks in boxes in coastal Texas were successful, and egg hatching success was 20%. In comparison, nest success for black-bellied whistling ducks using boxes in coastal South Carolina during 2016–2017 was 50.9%, and egg hatching success was 43.4% and was decreased primarily by woodpeckers puncturing eggs. Bolen (1967) reported an average of six black-bellied whistling duck ducklings were produced in nest boxes in coastal Texas. In South Carolina, we recorded approximately one duckling produced and exiting across all boxes in 2016 and 2017. When black-bellied whistling duck nests were successful, hens of both species departed boxes with about 10 ducklings.

Management and Research Implications

Although indexes of wood duck nesting efficiencies have been published for box-nesting populations, they have been based on number of ducklings exiting boxes (e.g., Haramis and Thompson 1985, Stephens et al. 1998, Davis et al. 1999). We presented a method to cost-evaluate recruitment of yearling female wood ducks produced in nest boxes, using data from our study and a published estimate of yearling female recruitment rate for box-nesting wood ducks in South Carolina (Hepp et al. 1989, 2020). We suggest that wood duck nesting in and relative recruitment to boxes in our study area were cost-effective, given the cost per female recruit (US$56.48) was only ~1/3 the cost of the box and its maintenance over 20 years (US$158.15). Additionally, if yearling and older banded or web-tagged females encountered in boxes are considered breeding cohorts in local populations, cost per returning and nesting female would decrease appreciably. We suggest managers consider inclusion of return and nesting rates of marked yearling and older female cohorts in future cost assessments of wood duck box programs. Hepp et al. (2020) advocated that future researchers examine how emigration and immigration interact with survival and reproduction to influence local population dynamics of wood ducks. This information, coupled with the influence of nest parasitism on recruitment, will be important in determining the value of nest-box programs for wood ducks and other cavity nesters.

We also encourage a cross-flyway study involving marked nesting hens and ducklings to determine survival, recruitment, immigration, emigration, and cost-efficiency of artificial nest structures for wood ducks and other waterfowl (e.g., mallard [*Anas platyrhynchos*], Chouinard et al. 2005). Such a study for wood ducks was initiated in 2020 across eight states in the southeastern United States with public- and private-sector partners in the Atlantic Flyway (Maryland, Delaware, North Carolina, South Carolina, Georgia, and Florida) and Mississippi Flyway (Louisiana and Mississippi) (Wiggers et al. 2019, Bauer 2021). Over 1300 nest boxes were monitored (Bauer 2021). This and a simultaneous study of availability of suitable natural cavities and wood duck use of and recruitment from cavities will be important in further determining the value of nest-box programs across the breeding range of the species.

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Literature Cited

Ackerman, J.T., J.D. Bluso-Demers, and J.Y. Takekawa. 2009. Postfledging Forster's tern movements, habitat selection, and colony attendance in San Francisco Bay. Condor 111:100–110.

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.

Baldassarre, G.A. 2014. Ducks, geese, and swans of North America. John Hopkins University Press, Baltimore, Maryland.

Balkcom, G.D., B.T. Bond, and T.M. Schneider. 2013. Current status and distribution of the black-bellied whistling duck (*Dendrocygna autumnalis*) in Georgia. Oriole 77:81–84.

Barry, S.C. 1992. Evaluation of a wood duck nest box program at Yazoo National Wildlife Refuge, Mississippi, 1987–1991. Master's Thesis, Mississippi State University, Mississippi State.

Bauer, B.A. 2021. Regional examination of the contribution of nest boxes to wood duck recruitment in the southeast and Mid-Atlantic states. Annual report, Nemours Wildlife Foundation, Yemassee, South Carolina.

Beach, V.C. 2014. Rice & ducks: The surprising convergence that saved the Carolina Lowcountry. Evening Post Books, Charleston, South Carolina.

Bellrose, F.C. and D.J. Holm. 1994. Ecology and management of the wood duck. Stackpole Books, Mechanicsburg, Pennsylvania.

Bolen, E.G. 1967. The ecology of the black-bellied tree duck in southern Texas. Ph.D. Dissertation, Utah State University, Logan.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York, New York.

Chouinard, M.D., R.M. Kaminski, P.D. Gerard, and S.J. Dinsmore. 2005. Experimental evaluation of duck nesting structures in Prairie Parkland Canada. Wildlife Society Bulletin 33:1321–1329.

Cohen, B.S., S.E. Askin, G.D. Balkcom, J.R. Benedict, Jr., J.A. Rader, J.D. James, B.A. Collier, and M.J. Chamberlain. 2019. Survival and distribution of black-bellied whistling duck in the southeastern United States. Journal of the Southeastern Association of Fish and Wildlife Agencies 6:123–128.

Conner, R.C. and A.J. Hartsell. 2002. Forest area and conditions. Pages 357–402 *in* D.N. Wear and J.G. Greis, editors. Southern forest resource assessment. General Technical Report SRS-53. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina.

Croft, G.D. 2018. Reproduction and nest-box selection by wood ducks and black-bellied whistling ducks in coastal South Carolina. Master's Thesis, Clemson University, Clemson, South Carolina.

_____, R.M. Kaminski, E.P. Wiggers, P.D. Gerard, and G.Y. Yarrow. 2020. Nest-box use by wood ducks and black-bellied whistling ducks in coastal South Carolina. Wildlife Society Bulletin 44:662–669.

Davis J.B., R.R. Cox Jr., R.M. Kaminski, and B.D. Leopold. 2007. Survival of wood duck ducklings and broods in Mississippi and Alabama. Journal of Wildlife Management 71:507–517.

_____, R.M. Kaminski, and S.E. Stephens. 1998. Wood duck eggshell membranes predict duckling numbers. Wildlife Society Bulletin 26:299–301.

_____, S.E. Stephens, B.D. Leopold, R.M. Kaminski, and P.D. Gerard. 1999. Wood duck reproduction in small and large nest boxes in Mississippi: a continued experiment. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 53:257–269.

_____, J.N. Straub, G. Wang, R.M. Kaminski, and B.D. Leopold. 2015. Simulations of wood duck recruitment from nest boxes in Mississippi and Alabama. Journal of Wildlife Management 79:907–916.

Demarest, D.W., R.M. Kaminski, L.A. Brennan, and C.R. Boyle. 1997. Body-mass, survival, and pairing consequences of winter-diet restriction in wood ducks. Journal of Wildlife Management 61:822–832.

Erdman, D., L. Jackson, and A. Sinko. 2008. Zero-inflated Poisson and zero-inflated negative binomial models using the COUNTREG procedure. Paper 322 *in* Proceedings of SAS Global Forum 2008. SAS Institute, Inc., Cary, North Carolina.

Folk, T.H., E.P. Wiggers, D. Harrigal, and M. Purcell, editors. 2016. Rice fields for wildlife: History, management recommendations, and regulatory guidelines for South Carolina's managed tidal impoundments. Nemours Wildlife Foundation, Yemassee, South Carolina.

Fredrickson, L.H., G.V. Burger, S.P. Havera, D.A. Graber, R.E. Kirby, and T.S. Taylor, editors. 1990. Proceedings of the North American wood duck symposium. St. Louis, Missouri.

Gordon, D.H., B.T. Gray, and R.M. Kaminski. 1998. Dabbling duck habitat associations during winter in coastal South Carolina. Journal of Wildlife Management 62:569–580.

Grado, S.C., K.M. Hunt, C.P. Hutt, X.T. Santos, and R.M. Kaminski. 2011. Economic impacts of waterfowl hunting in Mississippi derived from a state-based mail survey. Human Dimensions of Wildlife 16:100–113.

Haramis, G.M. and D.Q. Thompson. 1985. Density-production of box-nesting wood ducks in a northern green-tree impoundment. Journal of Wildlife Management 49:429–439.

Harrigal, D. and J.E. Cely. 2004. Black-bellied whistling-ducks nest in South Carolina. The Chat 68:106–108.

Hepp, G.R., R.A. Kennamer, and W.F. Harvey, IV. 1989. Recruitment and natal philopatry of wood ducks. Ecology 70:897–903.

_____, R.A. Gitzen, and R.A. Kennamer. 2020. Relative importance of vital rates to population dynamics of wood ducks. Journal of Wildlife Management 84:320–330.

Heusmann, H.W. 2000. Production from wood duck nest boxes as a proportion of the harvest in Massachusetts. Wildlife Society Bulletin 28:1046–1049.

Kaminski, R. M. and M. W. Weller. 1992. Breeding habitats of Nearctic waterfowl. Pages 568–589 *in* Batt, B. D. J., A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis.

Lancaster, J. D., B. J. Davis, R. M. Kaminski, A. D. Afton, and E. J. Penny. 2015. Mallard use of a managed public hunting area in Mississippi. Journal of the Southeastern Association of Fish and Wildlife Agencies 2:281–287.

Lowney, M. S. and E. P. Hill. 1989. Wood duck nest sites in bottomland hardwood forests of Mississippi. Journal of Wildlife Management 53:378–382.

Luckett, L. M. 1977. Ecology and management of the wood duck, *Aix sponsa*, in the Piedmont Region of South Carolina. Master's Thesis, Clemson University, Clemson, South Carolina.

Masto, N. M., R. M. Kaminski, P. D. Gerard, B. E. Ross, M. R. Kneece, and G. L. Wilkerson. 2021. Aerial strip-transect surveys: Indexing autumn-winter waterbird abundance and distribution in South Carolina. Journal of the Southeastern Association of Fish and Wildlife Agencies 8:89–100.

McCamant, R. E. and E. G. Bolen. 1979. A 12–year study of nest box utilization by black-bellied whistling ducks. Journal of Wildlife Management 43:936–943.

Morris, A. D. 2008. Use of forest edges by bats in a managed pine forest landscape in coastal North Carolina. Master's Thesis, University of North Carolina, Greensboro.

National Oceanic and Atmospheric Administration (NOAA). 2018a. National Estuarine Research Reserves internet services team. ACE Basin National Estuarine Research Reserve. <https://coast.noaa.gov/nerrs/reserves/ace-basin.html>. Accessed 17 January 2019.

_____. 2018b. National Estuarine Research Reserves internet services team. North Inlet-Winyah Bay National Estuarine Research Reserve. <https://coast.noaa.gov/nerrs/reserves/north-inlet-winyah-bay.html>. Accessed 17 January 2019.

North American Waterfowl Management Plan (NAWMP). 2018. North American Waterfowl Management Plan (NAWMP) 2018 update: connecting people, waterfowl and wetlands. U.S. Department of the Interior, Environment Canada, and Environment and Natural Resources Mexico, Washington, D.C.

Otis, D. L. and W. F. Dukes, Jr. 1995. Improving wood duck survival estimates in the Mid-Atlantic region by using nest box banding programs. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 49:618–628.

Prevost, M. B., T. H. Strange, and R. D. Perry. 1990. Management of a large-scale wood duck nesting project in South Carolina. Pages 297–302 *in* Fredrickson, L. H., G. V. Burger, S. P. Havera, D. A. Graber, R. E, Kirby, and T. S. Taylor, editors. 1990. Proceedings of the North American wood duck symposium. St. Louis, Missouri.

Raftovich, R. V., K. K. Fleming, S. C. Chandler, and C. M. Cain. 2019. Migratory bird hunting activity and harvest during the 2017–18 and 2018–19 hunting seasons. U.S. Fish and Wildlife Service, Laurel, Maryland.

Rohwer, F. C. 1988. Inter- and intraspecific relationships between egg size and clutch size in waterfowl. Auk 105:161–176.

SAS Institute. 2004. SAS user's guide: statistics, version 9.4 edition. SAS Institute, Inc., Cary, North Carolina.

Stephens, S. E., R. M. Kaminski, B. D. Leopold, and P. D. Gerard. 1998. Reproduction of wood ducks in small and large nest boxes. Wildlife Society Bulletin 26:159–167.

Utsey, F. M. and G. R. Hepp. 1997. Frequency of nest box maintenance: effects on wood duck nesting in South Carolina. Journal of Wildlife Management 61:801–807.

Vrtiska, M. P. 1995. Aspects of reproductive and remige molt biology in wood ducks. Ph.D. Dissertation, Mississippi State University, Mississippi State.

Wiggers, E. P., B. A. Bauer, P. Schmidt, R. M. Kaminski, and G. R. Hepp. 2019. Regional examination of the contribution of nest boxes to wood duck recruitment in the Southeast and Mid-Atlantic United States. Nemours Wildlife Foundation, Yemassee, South Carolina.

Zlonis, E. J., R. Deo, and J. B. Berdeen. 2021. LiDAR and multispectral imagery predict the occurrence of tree cavities suitable for a cavity-nesting duck. Remote Sensing in Ecology and Conservation. doi: 10.1002/rse2.236