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PRODUCTIVITY OF WOOD DUCKS, BLACK-BELLIED WHISTLING-DUCKS, AND HOODED MERGANSERS USING NEST BOXES IN LOUISIANA

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PRODUCTIVITY OF WOOD DUCKS, BLACK-BELLIED WHISTLING-DUCKS, AND HOODED MERGANSERS USING NEST BOXES IN LOUISIANA

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The School of Renewable Natural Resources

by
Dylan Lee Bakner
B.S., Pennsylvania State University, 2016
December 2023

I dedicate this dissertation to my late 9lb 8oz Chihuahua, Effy Bakner. Despite her small frame, Effy had the strength of a big dog. Her favorite thing to do was run along the Mississippi River Levee with her larger-dog friends. Effy was a constant reminder that, even in moments when I felt despondent, I held within me the capacity to conquer the grand challenges that lay before me.

Acknowledgments

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I am appreciative of the dedicated technicians who worked on this project, even in the challenging Louisiana climate to collect data. Your willingness to accommodate my last-minute, 9 o'clock at night requests did not go unnoticed or unappreciated. From the Renewable Natural Resources Building (RNR) at LSU, I want to thank my lab mates: L. Bonczek, J. Bushaw, A. Dopkin, T. Drake, Z. Loken, K. Miranda, G. Rhodes, and C. Terry for their support and making life outside work a blast. In addition to these individuals, there are many other graduate students from RNR, too many to name here, that supported me not only in a work setting, but also outside work. If all else fails, many of you are well-suited to be therapist according to my ratings; thanks for hearing me out about the troubles of life.

Thank you to my family and friends who have supported me along the way. I know the career path I chose has put physical distance between us but thankfully we have facetime and I'll always be just a call away, and willing to answer at the most inappropriate times. Although many of you have selfishly wanted me closer, you have done nothing but encourage me to keep pursuing the things that I care about. I thank my mom, dad, and brother who have always supported me in anything I wanted to do. I am grateful for my upbringing where we always worked as a team to achieve our goals and I am so glad we have continued to work together even at a great distance. I cannot put into words how much you all mean to me. I love you guys and I am so happy we all have each other.

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Abstract

Resident female wood ducks (*Aix sponsa*) in the southeastern United States are managed through nest box programs, with the goal of enhancing local hunting opportunities. Historically, hooded mergansers (*Lophodytes cucullatus*) were the only other cavity-nesting waterfowl species in the southeastern United States known to use these nest boxes. However, the recent northward range expansion of black-bellied whistling-ducks (*Dendrocygna autumnalis*) has extended into the range of wood ducks and mergansers. All three species are brood parasites, potentially using one another as hosts for their parasitic eggs and impacting their reproductive output. My research evaluated the nest box program administered by the Louisiana Department of Wildlife and Fisheries, focusing on the breeding ecology of cavity-nesting ducks and interspecific brood parasitism. Additionally, I analyzed a 14-year dataset for females banded from nest boxes to assess the impact of increasing the daily bag limit from 2 to 3 on wood duck survival and harvest rates. I monitored around 300 nest boxes weekly in Louisiana from 2020–2023, collecting data from February 1–July 31. I monitored individual eggs and nests, assigned fates, captured and banded incubating females, and marked ducklings. Trail cameras were placed inside a subset of nest boxes to collect videos. Among 261 black-bellied whistling-duck nests, I found nesting from late-March through late-July. About 7% of their nests were parasitized, primarily by wood ducks, with hooded mergansers as infrequent parasites. Black-bellied whistling-ducks hatched large clutches with varying compositions. I also monitored 1,206 wood duck nests; hooded mergansers and black-bellied whistling-ducks parasitized ~20% of nests. Parasitism by hooded mergansers reduced wood duck nest survival, but interspecific brood parasitism did not affect duckling recruitment. Wood duck egg survival decreased when in a clutch with hooded merganser eggs. Hooded mergansers had a more pronounced negative influence on wood duck productivity than black-bellied whistling-ducks. Red-bellied woodpeckers (*Melanerpes carolinus*) partially depredated wood duck clutches, reducing the number of wood duck eggs hatching at some sites. An analysis outside the breeding season revealed that increasing the daily bag limit did not affect the survival or harvest rates of box-nesting wood ducks. Future research should monitor black-bellied whistling-duck nesting chronology, as early-initiated wood duck nests are the most productive.

Chapter 1. Introduction

The wood duck (*Aix sponsa*) is a widely distributed waterfowl species, with most of its range falling in the eastern portion of North America (Bellrose and Holms 1994). Wood ducks are an obligate cavity-nesting species that will also use artificial nesting structures (hereafter, nest boxes). At northern latitudes, wood ducks will nest from late March through mid-June and migrate south annually (Baldassarre 2014). At southern latitudes, females begin nesting as early as mid-January and continue to nest through the end of June, and females in this region are year-round residents. Range-wide, both migratory and resident wood duck populations are currently stable; however, this was not always the case.

Wood ducks were nearly extirpated across their range during the early 1900s, due to unregulated harvests and the clearing of forests that provided nest cavities (Bellrose and Holms 1994). The Migratory Bird Treaty Act (hereafter, MBTA) of 1918 and the establishment of nest box programs both played a critical role in saving wood ducks from extinction. The MBTA made it illegal to harvest wood ducks and provided this species protection at the federal level. To compensate for the loss of nest cavities, managers developed nest box designs that were suitable for wood ducks and established them across their range. These actions revived wood duck populations to a level that allowed for legal, regulated harvest again in 1941.

Today many state wildlife agencies, nonprofit organizations, and private individuals still use nest boxes as a management tool for wood ducks. For example, the Louisiana Department of Wildlife and Fisheries (hereafter, LDWF) maintains roughly 2,000 nest boxes across their state (L. Reynolds, LDWF, personal communication). The goal of their program is to bolster local wood duck populations in wildlife management areas to increase hunter harvest opportunity.

In many programs, nest boxes are clustered and highly visible, which increases rates of brood parasitism. Parasitism can lead to the excessive clutch sizes and an increase the risk of nest abandonment or reduce egg hatch rates. Brood parasitism is a concern in box-nesting wood duck populations, both conspecific brood parasitism (hereafter, CBP; Yom-Tov 1980, Lyon and Eadie 2008), where a wood duck parasitizes the nest of another wood duck, and interspecific brood parasitism (hereafter, IBP; Davies 2010), where a different species lays parasitically in the nest of a wood duck. CBP is common in nest box populations, and over 95% of nests can be conspecifically parasitized in some populations (Semel and Sherman 1986, Bellrose and Holm 1994).

While CBP has been studied extensively in wood ducks, less attention has been given to IBP. The hooded merganser (*Lophodytes cucullatus*) is the most common interspecific brood parasite of wood duck nests range-wide (Mallory et al. 2002, Mallory and Weatherhead 2003). However, the black-bellied whistling-duck (*Dendrocygna autumnalis*; hereafter, whistling-duck) has recently expanded its breeding distribution into the southeastern United States, where it could be a new parasite of wood duck nests (Cohen et al. 2019, Croft et al. 2020). While whistling-ducks are known to use nest boxes erected for wood duck use (Bolen and Cain 1968, Croft et al. 2020), little is known about their breeding ecology in Louisiana. Understanding the breeding ecology of whistling-ducks in Louisiana is crucial, and the potential for whistling-ducks to use wood ducks as hosts for parasitic eggs hinges on their nesting chronology.

I monitored approximately 300 nest boxes in Louisiana and collected nest data from February 1–July 31, spanning the years 2020–2023. In chapter 2 I explore the nesting chronology of whistling-ducks, quantify rates of brood parasitism, and investigate the outcomes of parasitized clutches. In the subsequent chapters, I further examine various aspects of wood duck nesting ecology, including the unexpected phenomenon of red-bellied woodpeckers (*Melanerpes carolinus*) partially depredating clutches (Chapter 3), the costs to interspecific parasites via differential egg survival (Chapter 4), the impact of IBP on wood duck nest survival and duckling recruitment (Chapter 5), and the assessment of a recent change in the daily wood duck harvest limit by estimating survival and harvest rates for box-nesting females (Chapter 6). By unraveling the complexities of these dynamics, this study contributes valuable insights into the ecology and conservation of wood ducks, shedding light on the delicate balance between these remarkable waterfowl and the challenges they face in their nesting habitats.

Chapter 2. Louisiana black-bellied whistling-duck clutch characteristics in the presence of conspecific and interspecific brood parasitism

2.1. Introduction

The black-bellied whistling-duck (*Dendrocygna autumnalis*; hereafter, whistling-duck) is primarily a neotropical waterfowl species historically distributed from northern South America to southern Texas (James and Thompson 2020). However, their range began expanding northward in the middle part of the 20th century, with individuals commonly sighted in Arizona, Louisiana, and Florida by the 1960s (Baldassarre 2014). By the early 2000s, breeding populations had also been established in Arkansas, Oklahoma, Tennessee, and South Carolina (Bergstrom 1999, Baldassarre 2014, Cohen et al. 2019, Croft et al. 2020), and since then whistling-ducks have been documented breeding as far north as Wisconsin and Nebraska, and pioneering individuals observed as far north as central Quebec (ebird.org, accessed 2 Feb 2022).

Whistling-ducks are generalists and can flourish in a wide variety of habitats including wetlands, agricultural fields, stockyards, and urban areas (Bourne 1981, Matta et al. 2014, Cohen et al. 2019), which has undoubtedly contributed to their northward range expansion. Similarly, whistling-ducks will use a variety of nesting strategies and can nest in natural cavities, artificial nest structures (hereafter, nest boxes), or on the ground (Bolen et al. 1964, McCamant and Bolen 1979, Markum and Baldassarre 1989, Edmonds and Stolley 2008). Thus, as facultative cavity-nesters, whistling-ducks have

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the potential to interact and compete for nest sites with other cavity nesting species, such as the wood duck (*Aix sponsa*). Croft et al. (2020) identified substantial niche overlap in both nest box preferences and timing of nesting in South Carolina, where wood ducks nested January–July and whistling-ducks nested May–September. Given the temporal overlap in nest box use (Croft et al. 2020) and that both species are conspecific brood parasites (McCamant and Bolen 1979, James 2000, Semel et al. 1988), there is potential for IBP to occur. A single instance of whistling-ducks parasitizing wood duck nests has been documented in the literature based on two mixed clutches that were incubated by wood ducks (Bolen and Cain 1968); there are no publications that document wood ducks laying parasitic eggs in whistling-duck nests. Additionally, IBP between whistling-ducks and hooded mergansers (*Lophodytes cucullatus*) is possible as the latter can initiate nests as late as April (Baldassarre 2014).

While the frequency and fitness implications of IBP between whistling-ducks and other species are unknown, CBP has been described through nest box studies (Delnicki 1973, McCamant and Bolen 1979). In whistling-ducks, the prevalence of CBP varies by study, because eggs have not been genetically vetted, and researchers have selected different clutch size thresholds to demarcate eggs laid by a single female (Delnicki 1973, James 2000). However, parasitism generally results in larger clutch sizes, which increases the odds of nest abandonment and decreases the portion of eggs that hatch (hereafter, hatchability; Delnicki 1973, McCamant and Bolen 1979). For example, McCamant and Bolen (1979) observed CBP in 70% of whistling-duck nests and found the hatchability of 21,982 eggs was only 20% due to high rates of nest abandonment.

The paucity of research on whistling-duck breeding ecology is noteworthy, given their rapid expansion and potential competitive and parasitic interactions with wood ducks. Insufficient information exists regarding whistling-duck ecology to predict how their range expansion and parasitic behavior may affect native waterfowl species and thereby prompt management actions. Here, my objectives were to monitor whistling-duck nests to 1) describe nesting chronology as it overlaps with sympatric nesting duck species, 2) estimate rates of CBP and IBP, 3) estimate clutch size for nests with CBP and IBP, and 4) estimate hatchability for clutches of different sizes and types (i.e., parasitized and non-parasitized clutches).

2.2. Study area

I monitored nest boxes erected by the Louisiana Department of Wildlife and Fisheries (hereafter, LDWF) for wood duck use. My study areas were Sherburne Wildlife Management Area (hereafter, Sherburne), Thistlethwaite Wildlife Management Area (hereafter, Thistlethwaite), Indian Creek Reservoir, Lake Rodemacher, and Oden Lake (Figure 2.1). Sherburne is in Iberville, Pointe Coupee, and St. Martin Parishes, 17,652 ha in size, and owned by LDWF (4,775 ha), U.S. Fish and Wildlife Service (6,159 ha) and U.S. Army Corps of Engineers (6,725 ha). Adjacent to the Atchafalaya River, Sherburne is primarily a bottomland hardwood forest with several backswamps and bayous. Two eastern portions of Sherburne known as “North Farm” and “South Farm” are managed as moist soil impoundments for waterfowl, shorebirds, and wading birds. Thistlethwaite is 4,492-ha privately-owned bottomland hardwood forest within St. Landry parish that is managed by LDWF. As part of the Thistlethwaite study area, I oversaw nest boxes at the St. Landry Parish Solid Waste Disposal District (hereafter, disposal district). Located ~1.5 km northeast of Thistlethwaite, the disposal district constructed a pond and installed nest boxes for wood ducks as part of a mitigation project. Indian Creek is a 1,052-ha reservoir located in Rapides parish. Alexander State Forest Wildlife Management Area surrounds the reservoir. Patches of loblolly (*Pinus taeda*) and longleaf pine (*Pinus palustris*) stands can be found scattered throughout hardwood stands that line creek drainages. Oden Lake (Rapides parish) is privately owned and located ~6.5 km northeast of Indian Creek, partially surrounded by residential housing. As part of the Oden Lake study site, I monitored nest boxes located in a cypress swamp directly north of the lake and west of Highway 165. Lake Rodemacher is 1,189 ha in size and located in Rapides parish and ~3 km west of Boyce, Louisiana. The Brame Energy Center is located on the northwest side of the lake and uses its water as a cooling resource when generating power. Nest boxes were located over open water at sites accessed by boats and off the side of levees in areas that could be navigated by all-terrain vehicles and on foot.

During 2020, I monitored 285 nest boxes, consisting of 236 duplexes (two boxes mounted on either side of a pole) and 49 single units. To increase sample size in 2021, I converted 10 single units to duplexes at both North and South Farm and started overseeing 10 duplexes at Lake Rodemacher. Considering these additions, I increased my nest box sample size to 325, consisting of 296 that were arranged in duplexes and 29 single units. All nest boxes had conical sheet metal predator guards.

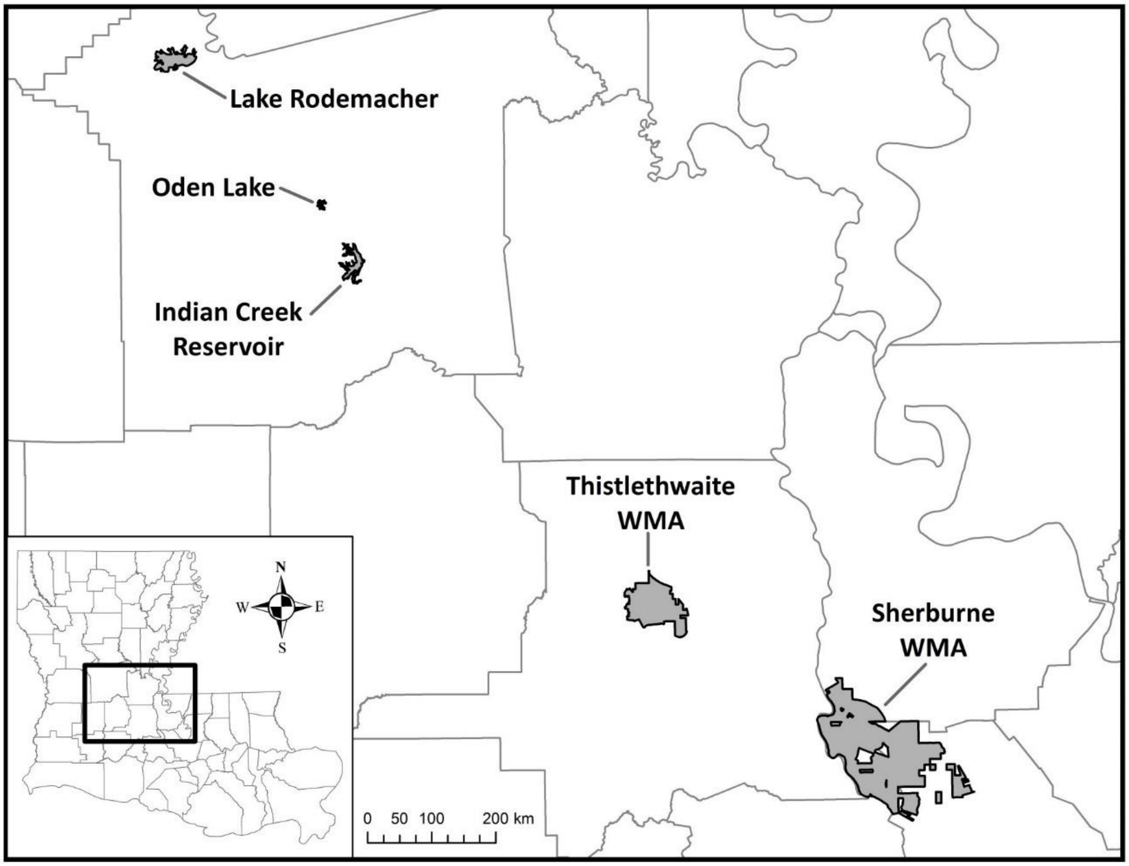

Figure 2.1. Map of Louisiana with study areas outlined in gray. Lake Rodemacher, Oden Lake, and Indian Creek Reservoir are located in Rapides Parish, whereas Thistlethwaite Wildlife Management Area is located in St. Landry Parish. Sherburne Wildlife Management Area is located within Iberville, St. Martin, and Point Coupee Parishes.

2.3. Methods

I visited nest boxes at approximately 7-day intervals in 2020 and 2021. I determined nest initiation dates by back-calculating to the day when the first egg was laid, assuming a laying rate of one egg per day with no partial clutch losses (Delnicki 1973, Emery et al. 2005). During weekly visits, I determined whether nests were active or terminated. I considered nests to be active if new eggs were added since the prior visit, egg incubation progressed (Weller 1956), or by observing a bird incubating the clutch. I classified terminated nests as being abandoned, depredated, or successful. I considered a nest abandoned if I observed egg laying or incubation discontinue without sign of clutch loss between two consecutive visits. Otherwise, I classified nests as depredated when eggs went missing or were destroyed and egg laying or incubation ceased. I considered a nest successful if it survived to hatch ≥1 egg; I counted unhatched eggs and counted egg membranes to determine the number of eggs that hatched.

I assigned all eggs from each nest a numeric identifier written with a permanent marker as they appeared in the nest (Semel et al. 1988). I determined the species of each egg and measured the length, width, and mass. I measured egg length and width to the nearest 0.1 mm using a dial caliper and mass to the nearest 0.1 g using a digital pocket scale. Due to logistical restraints, I was unable to collect egg morphology data at Sherburne and the disposal district. There is no published literature to aid in distinguishing whistling-duck from wood duck eggs. Therefore, I developed my own protocols to differentiate between the two species using egg candling techniques (Weller 1956). When viewed through a candling device, wood duck eggshells were transparent, while whistling-duck eggs showed a distinct blotchy pattern (Figure 2.2). The blotchy pattern persisted throughout the incubation period but was more difficult to view during later stages; however, I began monitoring most nests during laying or early incubation facilitating species identification. I used egg morphology and color to distinguish hooded merganser eggs (they are very round and white) from wood ducks and whistling-ducks (Mallory and Weatherhead 1990, Baldassarre 2014).

Figure 2. 2. (A) Comparison of black-bellied whistling-duck (*Dendrocygna autumnalis*; [whistling-duck]; left) and wood duck (*Aix sponsa*; right) eggshell transparency. Note the distinct mottled pattern of the whistling-duck egg, which becomes less visible as incubation progresses. (B) Comparison of whistling-duck (left) and wood duck (right) eggs as they appear in the nest box. Note that whistling-duck eggs are bright white and nests do not typically have down feathers present.

I categorized clutches based on the presence or absence of CBP and IBP.

whistling-duck nests with CBP present (hereafter, CBP clutches) received >1 whistling-duck egg per day during the laying stage (MacWhirter 1989) and/or additional eggs following day 4 of incubation, as whistling-ducks begin incubation ~3 days prior to laying the last egg (Delnicki 1973). Whistling-duck nests with IBP via wood ducks or hooded mergansers were termed “mixed clutches.” I found CBP was also present in some mixed clutches; I assigned these as mixed clutches. Nests not assigned to the CBP or mixed clutch types were termed “normal clutches.” I compared clutch sizes for different clutch types using t-tests and all measures reported are means ± standard deviation unless otherwise specified.

Due to the potential for CBP to go undetected in clutches designated "normal" based on the previous criteria, I evaluated egg morphology in an effort to verify that normal clutches were produced by a single female. I conducted a one-way analysis of variance (hereafter, ANOVA) for each egg measurement to compare within- and between-clutch variability for normal and CBP clutches. I performed ANOVA tests in R version 4.1.3 using the aov() function (R Core Team 2021). I expected between-clutch variability to be greater than within-clutch variability because individual ducks lay eggs that are consistent in shape and size (Pöysä et al. 2009, Eadie et al. 2010, Lemons et al. 2011). To verify that greater variability between clutches was due to individuals laying morphologically consistent eggs, I estimated repeatability (Lessells and Boag 1987). I considered egg measurements to be characteristic of individual female whistling-ducks if repeatability estimates were moderate (0.4 – 0.7; Harper 1994), while estimates < 0.4 suggest CBP was present. When analyzing egg measurements, I excluded clutches containing < 3 eggs, following James (2000) who used egg morphology to quantify CBP in whistling-duck nests.

I calculated hatchability for different clutch sizes and types by taking the total number of eggs laid in a given nest-species cohort and dividing by the total number that hatched (Semel et al. 1988). I considered incubated and non-incubated clutches when estimating hatchability. To achieve appropriate sample sizes for hatchability estimates, I binned clutches in five-egg increments (e.g., the first bin contained clutches ranging from 1 to 5 eggs, the second ranged from 6 to 10 eggs; McCamant and Bolen 1979). Because hatchability can vary seasonally with increasing temperatures (Hepp et al. 2006, DuRant et al. 2010), I produced monthly estimates of hatchability for different clutch types by grouping nests based on the month they were initiated. I conducted my work under U.S. Fish and Wildlife Service banding permit #06669 and Special Use Permit 43614-20-04; Louisiana Department of Wildlife and Fisheries state collecting permits WDP-20-037 and WDP-21-060, and Wildlife Management Area Permit WL-Research-2020-03; Louisiana State University Institutional Animal Care and Use Protocol A2019-27.

2.4. Results

I monitored nest boxes from February 1 until July 28 in 2020 and 2021. Whistling-ducks began initiating nests in early spring (March 21 and April 11 in 2020 and 2021) and continued through the end of July, when financial limitations forced us to cease monitoring boxes. Across both years, I observed new nests initiated over a span of 117.5 ± 14.8 days. There was no strong peak in nest initiation date; however, most nest initiation occurred during June (Figure 2.3; Table 2.1). I monitored a total of 261 whistling-duck nests (126 and 135 nests in 2020 and 2021, respectively) that contained 4,569 eggs. Of those nests, I determined the clutch type for 231 (88.5%). I observed 105 (45.5%) normal clutches, 73 (31.6%) CBP clutches, 51 (22.1%) mixed clutches parasitized by wood ducks and 2 (0.9%) by hooded mergansers. Additionally, I observed CBP in 27 clutches assigned to the mixed clutch category. Considering these nests, I observed CBP in 99 (42.9%) clutches.

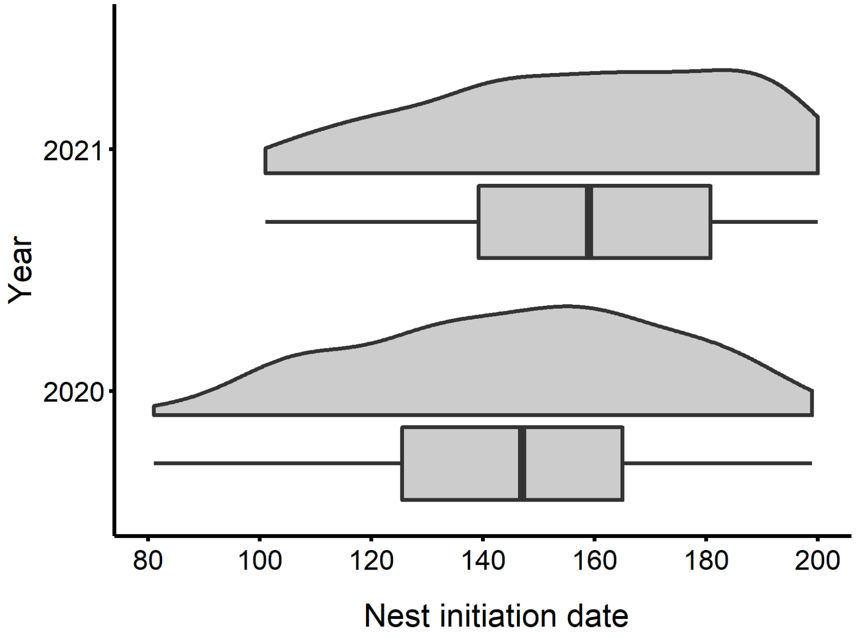

Figure 2.3. Julian dates for initiated black-bellied whistling-duck (*Dendrocygna autumnalis*) nests in Louisiana (n = 126 and 135 nests in 2020 and 2021, respectively). The distributions above each boxplot are density plots drawn from the observed data points.

I measured 1,858 (41.4%) whistling-duck eggs from 97 individual nests. Before analyzing egg measurements, I excluded 496 eggs from 23 mixed clutches and 13 eggs from 9 normal clutches containing < 3 eggs; therefore, I considered 1,349 eggs from 65 nests. CBP was present in 44 (67.7%) nests containing 1,108 (82.1%) eggs and was absent in 21 (32.3%) nests containing 241 (17.9%) eggs. For all eggs considered, the mean length was 52.2 ± 2.0 mm, width was 38.6 ± 1.2 mm, and mass was 43.0 ± 3.6 g. My ANOVA results showed more variation in egg morphology between clutches compared to within (all pairwise $P < 0.0001$; Table 2.2). Repeatability estimates were lower for nests with CBP and higher for normal clutches. However, repeatability never exceeded 0.40, which suggests that whistling-duck nests do not contain eggs consistent in size and shape; therefore, CBP was likely present in some clutches classified as normal.

Table 2.1. Monthly sample sizes and summary statistics of black-bellied whistling-duck (*Dendrocygna autumnalis*; whistling-duck) clutches in Louisiana during 2020 and 2021. Normal clutches contained only whistling-duck eggs, conspecific brood parasitism (CBP) clutches received > 1 egg per day during the laying stage or additional eggs following day four of incubation, and mixed clutches contained ≥ 1 wood duck (*Aix sponsa*) or hooded merganser (*Lophodytes cucullatus*) egg.

			Incubated clutches (n)			Clutch size ($\bar{x}$ ± SD)		
Month	Initiated	Incubated†	Normal	CBP	Mixed	Normal	CBP	Mixed
March	2	0	0	0	0			
April	38	17	2	8	7	21.5 ± 14.8	34.6 ± 11.4	20.3 ± 7.2
May	79	29	5	13	11	18.2 ± 3.5	24.5 ± 7.3	23.9 ± 4.3
June	87	45	19	21	5	14.1 ± 3.6	23.6 ± 6.3	24.9 ± 5.8
July	55	14†	12	2	0	15.2 ± 2.45	28.5 ± 14.8	
Total	261	105	38	44	23			

† Does not include nests with incubation starting after July

Table 2.2. Mean square variation among (MSA) and within clutches (MSW), F-statistics, p-values, and repeatability (r) estimates for black-bellied whistling-duck (*Dendrocygna autumnalis*) eggs measured from nests where conspecific brood parasitism (CBP) was present and absent. The coefficient value related to sample size per group (n_0) was used to calculate repeatability (Lessells and Boag 1987).

Measurement	MSA	MSW	F-statistic	p-value	r
CBP clutches (n = 44 nests, 1,108 eggs, n_0 = 25.66)					
Egg length	20.65	3.54	5.83	<0.0001	0.16
Egg width	8.04	1.12	7.17	<0.0001	0.19
Egg mass	77.67	10.90	7.13	<0.0001	0.19
Normal clutches (n = 21 nests, 241 eggs, n_0 = 11.81)					
Egg length	15.39	2.61	5.91	<0.0001	0.29
Egg width	4.75	0.80	5.91	<0.0001	0.29
Egg mass	57.12	8.01	7.13	<0.0001	0.34

A total of 126 nests were incubated, and I determined the clutch type for 105; these were used to describe clutch sizes throughout the nesting season (Table 2.1). The average clutch size of all incubated nests was 21.4 ± 8.2 and decreased throughout the nesting season (Figure 2.4). Normal clutches averaged 15.4 ± 4.4 eggs ($n = 38$ nests). When compared to the mean clutch size of all incubated nests, normal clutches were significantly smaller ($t = -5.561$, $df = 120.470$, $P < 0.0001$). CBP clutches averaged 26.1 ± 8.8 eggs ($n = 44$ nests) which was significantly larger than normal clutches ($t = -7.116$, $df = 65.347$, $P < 0.0001$). Mixed clutches averaged 22.2 ± 5.3 eggs ($n = 23$ nests), which is also significantly larger than normal clutches ($t = -5.162$, $df = 40.152$, $P < 0.0001$).

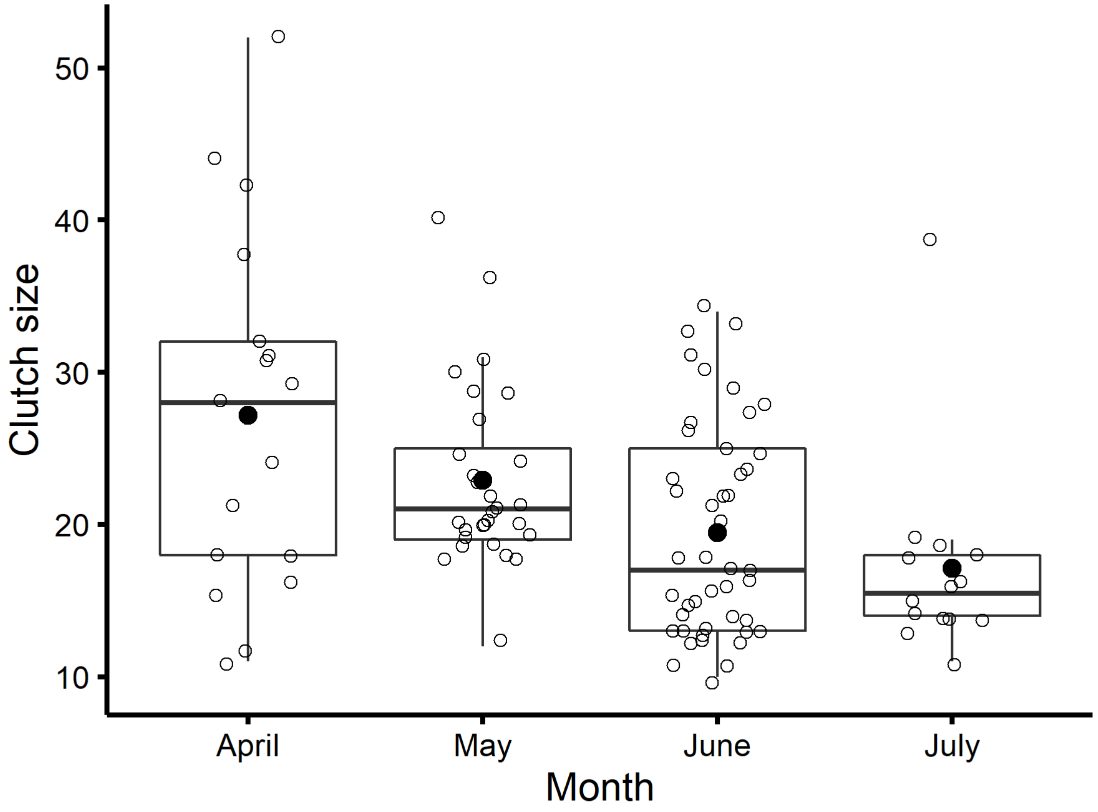

Figure 2.4. Clutch size of black-bellied whistling-duck (*Dendrocygna autumnalis*) nests in Louisiana by month with the means dotted in black and the center line of each boxplot representing medians.

I used 180 nests with determined fates to estimate hatchability. For the nests with determined fates, 66 (36.7%) were successful, 49 (27.2%) were abandoned, 64 (35.6%) were depredated, and 1 (0.6%) was nonviable. Hatchability averaged 29.8% across both years and was higher in 2020 (37.4%) compared to 2021 (22.2%). Hatchability was greatest (45.5%) for clutch sizes ranging from 31-35 and least (0.0%) for clutches ranging from 1-5 and 6-10 (Table 3). I found no clear relationship between clutch size and hatchability. Considering only successful nests, hatchability was greatest (81.6%) for clutch sizes ranging from 11-15 and least (24.3%) for clutches ranging from 51-55. Successful clutches smaller than the mean size of all incubated nests ($\bar{x}$ = 21.4 ± 8.2, n = 105) had higher hatchability than those exceeding the mean. Of the nests with determined fates, I assigned a clutch type to 164 which I used to produce monthly hatchability estimates for each clutch type (Table 4). The overall hatchability of CBP clutches was 34.1% which exceeded estimates for normal (26.7%) and mixed clutches (25.5%). I did not derive monthly estimates for clutches initiated in July, as they were projected to hatch following the conclusion of my field season. Hatchability was highest in April for normal (33.8%) and CBP clutches (43.2%), and June for mixed clutches (59.9%; Table 4).

A total of 1,038 eggs successfully hatched; 973 (93.7%) were whistling-ducks, 63 (6.1%) were wood ducks, and 2 (0.2%) were hooded mergansers. Normal clutches hatched 135 (13.0%) whistling-ducks, CBP clutches hatched 588 (56.6%), and mixed clutches hatched 190 (18.3%). The remaining 125 (12.0%) eggs hatched from either a normal or CBP clutch (I was unable to determine the clutch type). I observed 15 successful mixed clutches, with each containing an average of 3.9 ± 2.9 wood duck ducklings and 11.9 ± 7.3 whistling-duck ducklings. Normal clutches hatched an average of 12.2 ± 5.5 ducklings (n = 11 nests) and CBP clutches averaged 16.3 ± 7.0 ducklings per nest (n = 36 nests).

Table 2.3. Total number of Louisiana black-bellied whistling-duck (*Dendrocygna autumnalis*) nests and hatchability of eggs across clutch size bins.

				Hatchability	
Clutch size	Nests	Eggs Laid	Eggs hatched	All nests	Successful nests
1-5	29	67	0	0.0%	
6-10	8	68	0	0.0%	
11-15	27	357	112	31.4%	81.6%
16-20	37	663	228	34.4%	73.3%
21-25	33	754	209	27.7%	60.0%
26-30	20	555	165	29.7%	65.2%
31-35	13	422	192	45.5%	66.9%
36-40	3	114	49	43.0%	62.8%
41-45	7	298	58	19.5%	67.4%
46-50	0				
51-55	3	158	25	15.8%	24.3%
Total	180	3,456	1,038	30.0%	64.7%

Table 2.4. Total number of Louisiana black-bellied whistling-duck (*Dendrocygna autumnalis*; whistling-duck) nests and hatchability of eggs by month from 2020–2021. Normal clutches contained only whistling-duck eggs, conspecific brood parasitism (CBP) clutches received greater than one egg per day during the laying stage or additional eggs following day four of incubation, and mixed clutches contained greater than one wood duck (*Aix sponsa*) or hooded merganser (*Lophodytes cucullatus*) egg.

Clutch Type	March	April	May	June	Total†
Normal					
Nests	0	7	19	34	60
Eggs laid	0	77	211	271	559
Eggs Hatched	0	26	37	86	149
Hatchability	NA	33.8%	17.5%	31.7%	26.7%
CBP					
Nests	0	13	25	20	58
Eggs laid	0	440	595	453	1,488
Eggs Hatched	0	190	154	163	507
Hatchability	NA	43.2%	25.9%	36.0%	34.1%
Mixed					
Nests	2	10	28	6	46
Eggs laid	32	214	688	157	1,091
Eggs Hatched	0	46	138	94	278
Hatchability	0.00%	21.5%	20.1%	59.9%	25.5%

† Excludes nests and eggs with unknown clutch type

2.5. Discussion

This is the largest evaluation of whistling-duck nesting ecology to date, and the first to document whistling-ducks incubating and successfully hatching mixed clutches of wood ducks and hooded mergansers. Whistling-ducks initiated nests earlier in Louisiana when compared to other breeding populations in the southeastern U.S (Bolen 1967, Croft et al. 2020), and sympatric nesting with wood ducks occurred for > 3 months, with IBP found ~20% of nests. The majority of hatched eggs were whistling-duck, with < 7% being a wood duck or hooded merganser. On one occasion, I observed a whistling-duck pair incubating a nest containing whistling-duck, wood duck, and hooded merganser eggs. While the wood duck eggs were lost during incubation due to a suspected partial depredation or removal by the pair, two hooded merganser eggs were successfully hatched along with 16 whistling-duck ducklings. IBP did not lower hatchability, as mixed and normal clutches hatched similar percentages of eggs. My results suggest IBP via wood duck and hooded merganser likely does not limit whistling-duck productivity; however, the implications of CBP are less clear.

I found CBP present in ~43% of the clutches I observed, while previous studies have estimated CBP in 70−100% of whistling-duck nests (Delnicki 1973, McCamant and Bolen 1979, James 2000). However, my analysis of egg morphology showed low estimates of repeatability, suggesting that CBP was likely present in some normal and mixed clutches. Thus, classifying CBP clutches using the techniques described in my methods likely underestimates the number of nests with CBP present. As a result, the true prevalence of CBP in whistling-ducks remains somewhat unclear, and future research should consider using genetic techniques to unequivocally quantify rates of parasitism (Pöysä et al. 2009, Eadie et al. 2010, Lemons et al. 2011).

CBP and mixed clutches were generally larger than normal clutches. The number of eggs in mixed clutches closely resembled CBP clutches, except in April when they were smaller. Many wood ducks are still incubating their first nest attempts in April, potentially limiting IBP opportunity, whereas later in the season, renesting wood ducks and whistling-ducks attempting their first nests will simultaneously lay eggs in vacant nest boxes, thus facilitating mixed clutches. While I had expected parasitism to reduce hatchability, both CPB and mixed clutches had higher hatchability than normal clutches. Thus, whistling-ducks may actually benefit from parasitism, and ~75% of whistling-duck ducklings hatched from parasitized nests (Sorenson 1991, Péron and Koons 2012).

In general, I found the percentage of nests incubated (48.3%), and the hatchability of both successful (64.7%) and all nests (30.0%) were comparable to previous studies (Bolen 1967, McCamant and Bolen 1979, O'Kelley 1987). While other studies have documented that large whistling-duck and wood duck clutches have lower hatchability (O’Kelley 1987, Semel et al. 1988), I found no such pattern. Considering only those nests that hatched at least one egg, hatchability was reliably > 60% for all clutch sizes 11–45 eggs. Whistling-ducks incubating large clutches routinely hatched 20-30 eggs, which further suggests that the costs of parasitism are relatively low in this system.

The baseline breeding ecology data provided here is an important step in filling the gaps in the knowledge about this under-studied species. While nest box programs could be facilitating whistling-duck range expansion, further research to quantify productivity of other nesting strategies (e.g., natural cavity and ground nests) is needed. Additionally, my observations in the field often left us with more questions than answers.

For example, upon arrival in spring, whistling-ducks appeared to remain in family groups; it is unknown whether the high rates of CBP I observed in this study are instances of kin laying in the same box (Andersson et al. 2019), which combined with astonishingly high rates of hatchability for large clutches could dramatically increase inclusive fitness. Additionally, while I documented many instances of mixed broods hatched by whistling-ducks, I (anecdotally) never observed mixed broods of ducklings led by whistling-ducks in the field (D. L. Bakner and K. M. Ringelman, Louisiana State University, personal observation). It is unclear whether species re-assort post-hatch, or whether wood duck ducklings are driven off, killed, or otherwise suffer differential mortality. However, in 2021 I recaptured 2 nesting wood duck hens that hatched in 2020 as part of a single mixed clutch incubated by whistling-ducks (D. L. Bakner and K. M. Ringelman, unpublished data). Clearly, there are bountiful opportunities for further investigation of whistling-duck ecology, and how they compete with (or facilitate) species like wood ducks and hooded mergansers remains an important research priority as whistling-ducks continue to expand their range northward.

Chapter 3. A simple trail camera modification reveals red-bellied woodpeckers as important egg predators of box-nesting wood ducks

3.1. Introduction

Artificial nesting structures have been used to aid the recovery and maintenance of certain avian populations (Bellrose 1994, Liboiset et al. 2012, Gowaty and Plissner 2015). For example, wood duck (*Aix sponsa*) populations declined during the early 1900s partially due to the loss of tree cavities used for nesting (Bellrose 1994); nest box programs helped them recover by providing additional nest sites on the landscape. Today, wood duck populations are stable or increasing (Baldassarre 2014, United States Fish and Wildlife Service 2023) and nest box programs are still maintained throughout the species' range to bolster local abundance.

The success of nest boxes for wood ducks relies on excluding common nest predators (Bailey and Bonter 2017) such as raccoons (*Procyon lotor*) and rat snakes (*Pantherophis spp.*) using various types of predator guards (Bellrose 1994). While these efforts have proven to be effective, some avian nest predators such as woodpeckers cannot be excluded. For example, red-bellied woodpeckers (*Melanerpes carolinus*) are foraging generalists (Hazler et al. 2004) and have been documented opportunistically preying on wood duck eggs (Semel and Sherman1986, 1988, Yetter et al. 1999). Semel and Sherman (1986) anecdotally observed red-bellied woodpeckers foraging on wood duck eggs (n = 12 nests) when the boxes were vacant and found the nest host removed

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damaged eggs (n = 5 egg removals). However, beyond these anecdotes, the pervasiveness and intensity of woodpecker predation remains unclear. In fact, identifying any individual predator or predation event, quantifying the extent of egg depredation, documenting the removal of egg remains, and determining the timing of each event is difficult to accomplish through traditional nest box monitoring.

Here, I custom-modified Bushnell Nature View trail cameras to document activity inside wood duck nest boxes.

3.2. Methods

I deployed trail cameras in 9 nest boxes located at Sherburne Wildlife Management Area, Louisiana (30.433262, -91.652588) from 17 April – 24 June 2021. To modify cameras, I replaced the threaded ring around the camera lens with one that accommodated an Alilusso 7.5mm iPhone fisheye lens (Figure 3.1), using J-B Weld Waterweld Epoxy Putty to attach it. Following these modifications, I drilled a hole in each nest box ~5 cm above the center of the entrance hole and used a threaded rod and wing nut to mount the camera inside the nest box, giving us a bird’s eye view inside (Figure 3.1). I programmed cameras to capture 10-second videos with a 1-second delay between recordings each time motion was detected.

I monitored boxes at weekly intervals and replaced camera batteries; occasionally batteries were drained before they could be replaced. After the conclusion of the monitoring period, I reviewed videos and recorded events related to predation. For red-bellied woodpeckers, I classified predation events as when I observed ≥ 1 egg pecked open, foraging instances where individuals returned to feed on previously depredated eggs, and all other woodpecker activity was assigned as prospecting events. For wood ducks, I identified removal events when depredated eggs were removed from the nest box; all other activity was assigned as occupancy. I considered a >5-minute gap between video clips to represent different events. I determined if each event occurred during the laying or incubation period using data collected at the nest.

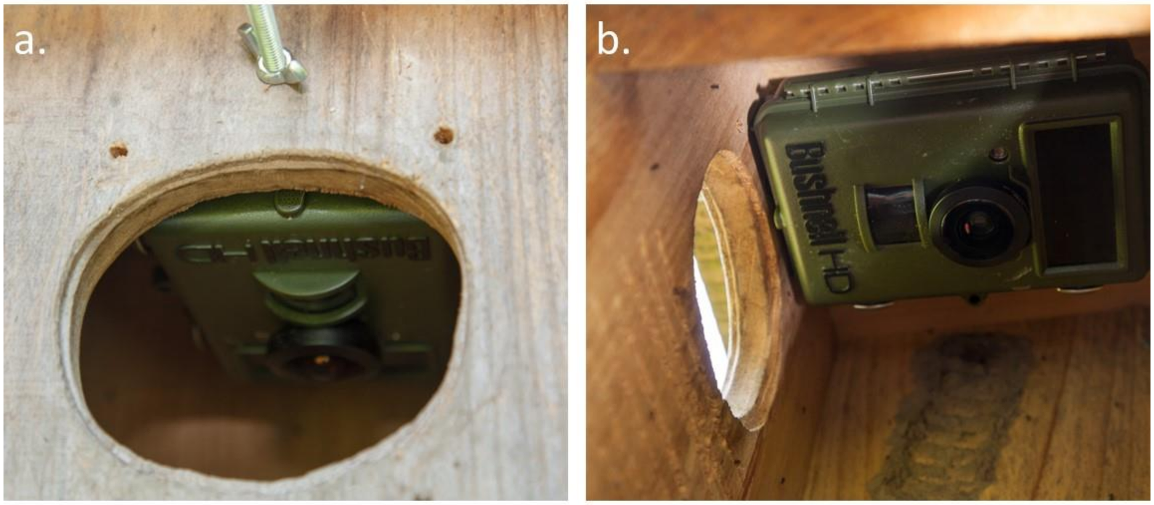

Figure 3.1. Modified Bushnell Nature View trail camera equipped with an Alilusso 7.5 mm iPhone fisheye lens used to monitor nest boxes for wood ducks (*Aix sponsa*). Cameras were mounted inside nest boxes using a threaded rod and wing nut (a) providing a top-down view inside (b).

I compared the number of visits made by red-bellied woodpeckers during the laying and incubation period using t-tests in R version 4.2.1 (R Core Team 2022). All other measures are reported as means ± standard deviation. I conducted my work under U.S. Fish and Wildlife Service banding permit #06669 and Special Use Permit 43614-20-04; Louisiana Department of Wildlife and Fisheries state collecting permits WDP-20-037 and WDP-21-060, and Wildlife Management Area Permit WL-Research-2020-03; Louisiana State University Institutional Animal Care and Use Protocol A2019-27.

3.3. Results

I captured 35,686 videos and documented 1,173 different events. Trail cameras captured 608 (51.8%) videos of woodpeckers composed of 119 (19.6%) depredation events, 374 (61.5%) foraging events, and 115 (18.9%) prospecting events. I observed wood ducks in 565 (48.2%) videos, and I recorded 499 (88.3%) box occupancy events and 66 (11.7%) egg removals. For wood duck videos, I determined 262 (46.4%) were captured during the laying period, 44 (7.8%) during the incubation period, and 259 (45.8%) videos were unassigned. I monitored a total of 11 nests with trail cameras, consisting of 6 (54.5%) that failed during the laying period, 3 (27.7%) that failed during the incubation period, and 2 (18.2%) that were successful. During the laying period, an average of 5.2 ± 5.0 eggs were depredated from each nest and 60.5% were removed. During the incubation period, an average of 3.2 ± 2.9 eggs were depredated from each nest and 92.9% were removed.

I found no difference in the daily number of times red-bellied woodpeckers visited boxes with nests at the laying stage ($\bar{x}$ = 3.49, SD = 3.18) compared to nests that were being incubated ($\bar{x}$ = 4.50, SD = 2.92, t = -0.967, df = 14.699, P = 0.349). During the laying period, the timing of egg depredations ranged from 06:00 – 17:10 ($\bar{x}$ = 11:20, SD = 2.83 hours, n = 38) with egg removals occurring from 05:12 – 17:15 ($\bar{x}$ = 08:11, SD = 3.58 hours, n = 23; Figure 3.2). During the incubation period, the timing of egg depredations ranged from 05:57 – 15:32 ($\bar{x}$ = 09:39, SD = 3.36 hours, n = 14) with egg removals occurring from 07:21 – 18:37 ($\bar{x}$ = 12:51, SD = 3.89 hours, n = 13; Figure 3.2).

Considering all observations (including those unassigned to the laying or incubation period), red-bellied woodpeckers on average depredated 1.0 ± 0.2 eggs during each event, and 124 eggs were lost across all events. Red-bellied woodpeckers returned to boxes to forage on previously depredated eggs 5.3 ± 4.4 times each day spending 2.1 ± 1.1 minutes during each return. Red-bellied woodpeckers only used nest boxes when they were vacant, and I observed no physical interaction between red-bellied woodpeckers and wood ducks.

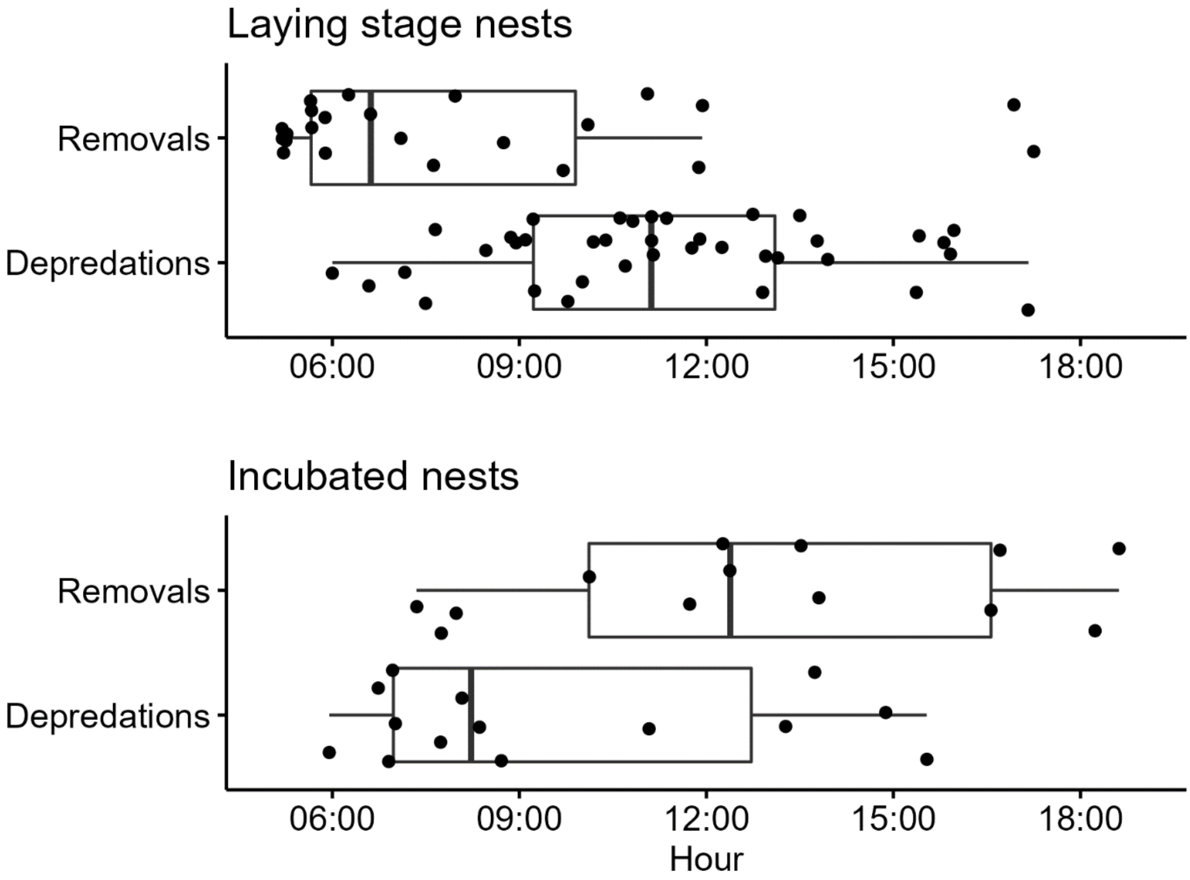

Figure 3.2. Time of wood duck (*Aix sponsa*) egg depredations by red-bellied woodpeckers (*Melanerpes carolinus*) and removal of damaged eggs by the nest host during the laying and incubation periods. Observations were made in Louisiana from 17 April – 24 June 2021.

3.4. Discussion

The simple modification of a commonly available trail camera allowed us to quantify wood duck egg depredations via red-bellied woodpeckers. The standard lenses that come with the Bushnell Nature View trail camera can be used to monitor nest boxes; however, modification to the nest box itself may be necessary to achieve the correct focal distance (Surmacki and Podkowa 2022). Documentation of individual egg predation and foraging events would not have been possible through conventional nest monitoring and observation, and although the review of video footage is laborious, the modified trail cameras I used here provided new insights into the importance of red-bellied woodpeckers as wood duck nest predators.

My results extend and emphasize the observations made by Semel and Sherman (1986), as I found that red-bellied woodpeckers were the most common and damaging predator at my sites in Louisiana, destroying 124 eggs. Wood ducks lay one egg in the morning each day during the laying period, and nest boxes remain vacant for the remainder of the day. Red-bellied woodpeckers took advantage of unprotected nests by depredating eggs (generally ~1 egg per box each day) and returning multiple times throughout the day to forage on them. Egg-laying wood ducks that returned the following morning first removed any depredated eggs before laying the next egg in the clutch (Figure 3.3). Red-bellied woodpeckers continued to depredate eggs during the incubation period when the wood duck female was absent during morning and afternoon incubation recesses. In such cases, depredated eggs were also removed by the nest host before incubation resumed.

Figure 3.3. The sequence of events showing the depredation of a wood duck (*Aix sponsa*) egg by a red-bellied woodpecker (*Melanerpes carolinus*) and the removal of the damaged egg during the laying period in Louisiana in 2021. Following egg-laying which occurs at dawn, red-bellied woodpeckers forage on eggs (a) which are then removed by the nest host the next morning (b), reducing the clutch size (c).

I found predation rates were similar for all nests during the laying stage with 6 clutches transitioning into the incubation period. We determined predation rates were also similar among nests being incubated. Here I report coarse estimates of egg depredations occurring at two discrete stages of the nesting cycle; however, to better understand egg-loss scenarios that result in nest failure, future research should determine the frequency with which egg depredations occur at finer temporal scales. I hypothesized overall nest survival (i.e., the decision to abandon a clutch) would be lower for nests repeatedly losing eggs during conservative days compared with those that only occasionally lose eggs to predators. It is possible that red-bellied woodpeckers were unusually abundant at my study site; however, I have observed them using nest boxes in a wide range of habitats around Louisiana.

My methods have a wider application beyond assessing predator-prey relationships, as they can also be used to study interspecific interactions at nest boxes. During my monitoring of 11 nests, I found 2 nests containing eggs of parasitic black-bellied whistling-ducks (*Dendrocygna autumnalis*; hereafter, whistling-duck). After reviewing trail camera videos from these nests, I anecdotally observed woodpeckers selecting wood duck eggs after attempting to peck open whistling-duck eggs, suggesting that they may have harder shells to penetrate. Although these observations were infrequent, if woodpeckers do prefer wood duck eggs, there would be a cost to wood ducks incubating clutches containing eggs of both species as egg mortality of their eggs would be higher than that of the parasitic eggs.

Here I documented egg depredations occurring in all 11 nests I monitored. Additionally, 52 (41.9%) egg depredations occurred in nests that were both initiated and terminated between weekly visits. That is, because of woodpecker predation, clutch initiation and egg-laying activity would have been undetectable without the use of nest box cameras. My results suggest that red-bellied woodpeckers have previously been under-recognized in the literature as predators of wood duck nests and future nest box programs should consider their impact on egg loss and nest survival.

Chapter 4. Reproductive costs of interspecific brood parasitism in wood ducks and hooded mergansers using nest boxes in Louisiana and Mississippi

4.1. Introduction

Brood parasitism is an alternate reproductive strategy that is more pervasive in waterfowl than in any other group of birds (Yom-Yov 1980, Lyon and Eadie 2008). Parasitic females lay their eggs in the nest of the same species (hereafter, conspecific brood parasitism) or a different one (hereafter, interspecific brood parasitism). Researchers contend that high rates of brood parasitism in waterfowl are associated with low costs of post-hatch care as the young are precocial (Rohwer and Freeman 1989).

While rearing parasitic young may be inexpensive to hosts, considerable costs may occur during laying and incubation stages, such as increased risk of nest abandonment or a decline in egg hatchability (i.e., proportion of eggs hatching; McCamant and Bolen 1979, Semel et al. 1988, Sorenson 1997). Many waterfowl species will incubate clutches that are supernormal (Rohwer 1985, McCamant and Bolen 1979, Bellrose and Holm 1994, Davis et al. 1999, Odell and Eadie 2010); however, excessive parasitism can cause hosts to abandon the clutch, thus forfeiting their investment in the nest (McCamant and Bolen 1979, Semel et al. 1988, Odell and Eadie 2010). When hosts incubate heavily parasitized nests, maladaptive incubation can result in reduced egg hatchability (McCamant and Bolen 1979, Semel et al. 1988). While some studies have documented negative consequences of brood parasitism to nest hosts (McCamant and Bolen 1979, Odell and Eadie 2010, Péron and Koons 2012). others found negligible effects (Nielsen et al. 2006, Hepp et al. 2020), and some suggest hosts may benefit from being parasitized because parasitic offspring dilute post-hatch predation risk (Eadie and Lumsden 1985, Robertson 1998).

Understanding costs of brood parasitism to hosts has received substantial scrutiny, but less attention has been given to the potential costs to parasites (Lyon and Eadie 2008). The costs and benefits of parasitic laying may be especially important when it is the only reproductive effort for a female in a breeding season (Eadie 1989, Sorenson 1991). Sorenson (1991) developed a widely accepted decision model where reproductive effort invested by individuals was predicted to vary with annual environmental and social conditions. One component of the model suggests when nest hosts are abundant in the population, more individuals should choose to lay parasitically. Because nest hosts may be easier for parasites to find, the occurrence of brood parasitism is more common in populations with high local nesting densities (Lokemoen 1991, Robertson 1998, Thompson et al. 2023), those nesting over water (Weller 1959, Nielsen 2006, Péron and Koons 2012), or in fixed locations such as cavities or boxes (McCamant and Bolen 1979, Haramis and Thompson 1985, Eadie 1989). While nest hosts may be easy to find in some populations (i.e., the cost of searching is low), eggs are still energetically expensive for waterfowl to produce; hence, parasites should choose to lay eggs in nests that maximize odds of eggs hatching. This choice may be based on the number of eggs already present, stage of laying (pre-incubation; Robertson 1998, Odell and Eadie 2010), or choosing to parasitize different species of nest hosts (Eadie 1989, Lokemoen 1991, Péron and Koons 2012, Bakner et al. 2022).

Here, I evaluate the success of wood ducks (*Aix sponsa*) and hooded mergansers (*Lophodytes cucullatus*) parasitizing each other's nests in Louisiana and Mississippi. My study spans 7 separate study areas and 7 total years across different decades. Both species are facultative conspecific and interspecific brood parasites that nest in tree cavities and artificial nest structures (Griscom 1949, Bellrose and Holms 1994, Heusmann et al. 2000). Although interspecific brood parasitism between these two species is common (Doty et al. 1984, Semel and Sherman 1986, Kennamer et al. 1988, Zicus 1990, Mallory 1991, Heusmann et al. 2000, Mallory et al. 2002, Mallory 2003), the cost to parasites laying eggs interspecifically is poorly understood. In this study, I modeled the survival of eggs laid in interspecifically parasitized clutches in nest boxes to provide insights into potential costs incurred by parasites. I hypothesized that costs for parasites would depend on maximum realized clutch size, as hosts may be more likely to abandon the nest and incubation becomes suboptimal at very large clutch sizes.

4.2. Study area

I monitored existing nest boxes maintained by the Louisiana Department of Wildlife and Fisheries (hereafter, LDWF) at Sherburne Wildlife Management Area (hereafter, WMA), Thistlethwaite WMA, Indian Creek Reservoir, Lake Rodemacher, and Oden Lake in Louisiana 2020–2022. Sherburne WMA is in Iberville, Pointe Coupee, and St. Martin Parishes. The WMA is a bottomland hardwood forest with many backswamps and bayous and is located within the Atchafalaya floodplain. "North Farm" and "South Farm" are managed as moist soil impoundments on the eastern side of Sherburne WMA. Thistlethwaite is a bottomland hardwood forest in St. Landry parish that is privately owned but managed by LDWF. Indian Creek is located in Rapides Parish and surrounded by Alexander State Forest WMA. The WMA contains loblolly (*Pinus taeda*) and longleaf pine (*Pinus palustris*) stands and hardwoods that border creek drainages. Lake Rodemacher is in Rapides Parish and used by the Brame Energy Center as a cooling resource when generating power. Oden Lake is in Rapides Parish, is privately owned, and surrounded by a mixture of residential housing and cypress swamps. Most nest boxes I monitored were duplex-style, with two boxes mounted on either side of a pole (190, 287, and 245 in 2020, 2021, and 2022 respectively) and some were single units (76, 44, and 31 in 2020, 2021, and 2022 respectively).

In Mississippi, data was collected at the Sam D. Hamilton Noxubee and Yazoo National Wildlife Refuges (hereafter, Noxubee and Yazoo) in the Interior Flatwoods and the Mississippi Alluvial Valley (i.e., Delta; Pettry 1977), by Davis (2001). Nest boxes in Loakfoma Lake, Doyle Arm, and Bluff Lake at Noxubee were monitored during summer 1993 (Stephens et al. 1998). Dominant shoreline vegetation in Loakfoma Lake (243 ha) was willow (*Salix spp.*), scrub-shrub (e.g., buttonbush; *Cephalanthus occidentalis*), and emergent vegetation (e.g., *Polygonum hydropiperoides*). Doyle Arm was a 16-ha wetland with scattered smartweed (*Polygonum spp.*) and other herbaceous vegetation along its shoreline. Wood duck boxes in Bluff Lake (405 ha) were situated within a needle-leaved, deciduous forest dominated by bald cypress (*Taxodium distichum*) and emergent vegetation as in Loakfoma Lake. At Yazoo NWR, boxes were erected in Deer Lake and Alligator Pond. Deer Lake (48 ha) was dominated by giant cut grass (*Zizaniopsis miliacea*) and giant water lily (*Nelumbo lutea*). Alligator Pond (28 ha) contained buttonbush, lotus (*Nelumbo nucifera*), and dead trees.

Single-unit nest boxes at Noxubee and Yazoo. All nest boxes were wooden and representative of dimensions of natural cavities used by these species (Stephens et al. 1998, Davis et al. 1999, Denton et al. 2012). The number of nest boxes monitored each year varied slightly with deterioration, windstorms, or flooding, and additional boxes were added in some years. Overall, Davis (2001) monitored ~115 nest boxes annually at Noxubee from 1996–1999 and ~70 nest boxes at Yazoo from 1994–1997 (Davis et al. 1999). Stephens et al. (1998) and Davis (1999) provided further descriptions of the study areas.

4.3. Methods

In Louisiana, I visited nest boxes at approximately 7-day intervals to monitor egg and nest fates; in Mississippi, boxes were checked at one-month intervals to meet specific research questions (Davis et al. 1999, 2007, 2009). I considered nests to be active if new eggs were added since the prior visit, egg incubation progressed (Weller 1956), or by observing a bird incubating the clutch. I concluded nests failed due to abandonment if I observed egg laying or incubation discontinue without sign of clutch loss between two consecutive visits. I determined nests failed due to a predation event when ≥1 egg went missing or was found depredated inside the nest box, causing egg laying or incubation to cease between two consecutive visits. I considered a clutch successful if it survived to hatch ≥1 egg.

In Louisiana, I assigned all eggs from each nest a numeric identifier written with a permanent marker and documented the species of each egg (Semel et al. 1988). I recorded eggs present or missing during weekly visits to nests. I determined the clutch size of each nest as the maximum number of eggs we observed in the clutch across all visits to the nest. Following the termination of nests, I counted the number of eggs that failed or hatched. Eggs that were missing, unhatched, and non-viable were declared failed; egg membranes were used to enumerate hatched eggs (Davis et al. 1998). One limitation of data that I analyzed is that eggs were not marked in Mississippi, thus I did not have detailed information regarding egg failures. As a result, while I could distinguish between hatched and failed eggs, we could not diagnose specific causes of failure.

I determined the host of each nest by observing the female incubating the clutch. In cases where I did not observe a female incubating, I determined the host species as being the one with the higher number of eggs in the clutch. I categorized clutches as being normal or mixed. Normal clutches were nests containing eggs belonging to a single species that corresponded to the nest host. Mixed clutches were nests that were interspecifically parasitized, and I categorized eggs as being host or parasitic. Host eggs were defined as those that matched the species incubating the clutch; others were classified as parasitic eggs. I determined eggs were laid by a wood duck if they were elliptically shaped and a creamy white color (Baldassarre 2014); hooded merganser eggs were spherical and white (Mallory and Weatherhead 1990). Given the prevalence of parasitism in both wood duck and hooded merganser populations, I recognize that conspecific brood parasitism was likely present in some normal clutches. However, limitations in the historical data prevented me from determining which nests were parasitized by conspecifics and the number of host eggs in each clutch.

I conducted two-sample t-tests to compare normal and mixed clutches. Specifically, I compared the clutch size, the number of parasitic eggs, as well as the number of hatched parasitic eggs. I analyzed mixed clutches to predict egg survival (i.e., the probability an egg hatches) for host and parasitic eggs as a binomial outcome:

$$yi,j \sim Binomial(ni,j,\ \Phi i,j),$$

$$logit(\Phi i,j) \sim \beta_0 + \beta_1 * host_{i,j} + \beta_2 * clutch\ size_{i,j} + \beta_3 * (host_{i,j} * clutch\ size_{i,j}) + \varepsilon_{i,j},$$

$$\varepsilon_{i,j} \sim Normal(0,\ \sigma 2),$$

where y is egg survival for nest i and egg type j (i.e., host or parasitic). For each nest i and egg type j, I considered the total number of eggs as the number of trials (n), with the success probability (Φ) as the number of eggs that hatched. I considered nest host and clutch size as fixed effects in my models. I also considered the interaction of these covariates. Each model contained nest identity (ID) as a random effect. Given the limited number of parameters considered, my model set contained all possible combinations of fixed effects.

I fit my models within a Bayesian framework in Program R version 4.2.2 (R Core Team 2023) using package brms (Bürkner 2017). I ran 4 Markov Chain Monte Carlo (after, MCMC) chains of 5,000 iterations, discarding 2,500 samples during the warm-up period, and used the default uninformative prior distributions. I ensured MCMC chains converged by examining trace plots and by using the Gelman-Rubin statistic ($\hat{R}$ value < 1.05; Gelman and Rubin 1992). I used k-fold cross-validation (using default brms settings; hereafter, K-CV; Bürkner 2017, Vehtari et al. 2017) and Bayesian R^2 values to assess model fit (Gelman et al. 2019). Models with low K-CV scores and high R^2 values were deemed to have a better fit. I used the expected log pointwise predictive density (hereafter, ELPD) differences to compare the fit of ranked models. Specifically, I determined the fit of models was significantly different when the absolute value of each ELPD was greater than its standard error. All my models were compared against a random-effects-only null model. 95% credible intervals (hereafter, CI) of fixed effects that did not overlap zero indicated significant effects. I calculated the percentage of variation explained by the fixed effects in my top model using Grosbois et al. (2008) seventh equation:

$$\frac{\hat{\sigma}^2(\textit{random-effects-only model}) - \hat{\sigma}^2(\textit{fixed effects model})}{\hat{\sigma}^2(\textit{random-effects-only model})}$$

To model the cost to parasites choosing to lay in nests with varying numbers of host eggs, I predicted the number of host and parasitic eggs hatching from different clutch compositions (i.e., number of host and parasitic eggs in the clutch), using the model coefficients from my top model. In the first illustrative scenario, I held the number of host eggs constant at 10 while varying the number of parasitic eggs (after, constant mixed clutch scenario). In the second scenario, the number of host and parasitic eggs was proportional, while the overall clutch size varied (after, proportional mixed clutch scenario).

Research at the Louisiana study sites was conducted under U.S. Fish and Wildlife Service banding permit #06669 and Special Use Permit 43614-20-04; Louisiana Department of Wildlife and Fisheries state collecting permits WDP-20-037 and WDP-21-060, and Wildlife Management Area Permit WL-Research-2020-03; Louisiana State University Institutional Animal Care and Use Protocol (after, IACUC) A2019-27. Research activities in Mississippi were approved by Mississippi State University IACUC Protocol No. 96-018

4.4. Results

I studied 1,622 nests that were hosted by 1,356 wood ducks and 266 mergansers (Table 4.1). A total of 180 (13.3%) wood duck and 57 (21.4%) merganser nests contained mixed clutches. A total of 21,902 wood duck and 4,314 merganser eggs were monitored. A total of 10,792 (49.3%) wood duck and 2,624 (60.8%) merganser eggs hatched. For wood ducks, 9,330 eggs (86.5%) hatched from 872 normal clutches, and 1,397 wood duck (12.9%) and 342 merganser eggs (13.0%) hatched from 131 mixed clutches. For mergansers, 1,920 eggs (73.2%) hatched from 164 normal clutches, and 362 (13.8%) merganser and 65 (0.06%) wood duck eggs hatched from 41 mixed clutches.

I considered 2,612 host and 580 parasitic eggs from 172 successful mixed clutches in my analyses. I found mixed wood duck clutches were larger ($\bar{x}$ = 19.9) than mixed merganser clutches ($\bar{x}$ = 14.8; p <0.001; Figure 4.1). The mean number of parasitic eggs in mixed clutches was similar for nest hosts (wood duck $\bar{x}$ = 3.5, merganser $\bar{x}$ = 3.3, p-value = 0.728), but wood ducks hatched 1.5 times more parasitic ducklings ($\bar{x}$ = 2.6 vs. $\bar{x}$ = 1.7, p = 0.021).

Table 4.1. Number of wood duck (*Aix sponsa*) and hooded merganser (*Lophodytes cucullatus*) nests monitored and successful (%) in Louisiana (2020–2022) and Mississippi (1996–1999) by clutch type. Normal clutches were nests containing eggs belonging to a single species that corresponded to the nest host. Mixed clutches were nests that were interspecifically parasitized.

	Louisiana				Mississippi			
	Wood duck		Hooded Merganser		Wood duck		Hooded Merganser	
Nests	Normal	Mixed	Normal	Mixed	Normal	Mixed	Normal	Mixed
Total	758	73	93	35	418	107	116	22
Successful	480 (63%)	38 (52%)	61 (66%)	24 (69%)	392 (94%)	93 (87%)	104 (90%)	17 (77%)

All models of egg survival successfully converged and performed better than the random-effects-only model (Table 4.2). My best fitting model included an interaction between clutch size and nest host (K-CV = 1423.7, $R^2 = 0.914$; Table 4.2). There was no significant difference between the top and second ranked model that did not contain the interaction term (ELPD = -9.45 SE = 11.00); however, because mixed clutch sizes were different for each nest host, I based my subsequent evaluations on the model that included the interaction term.

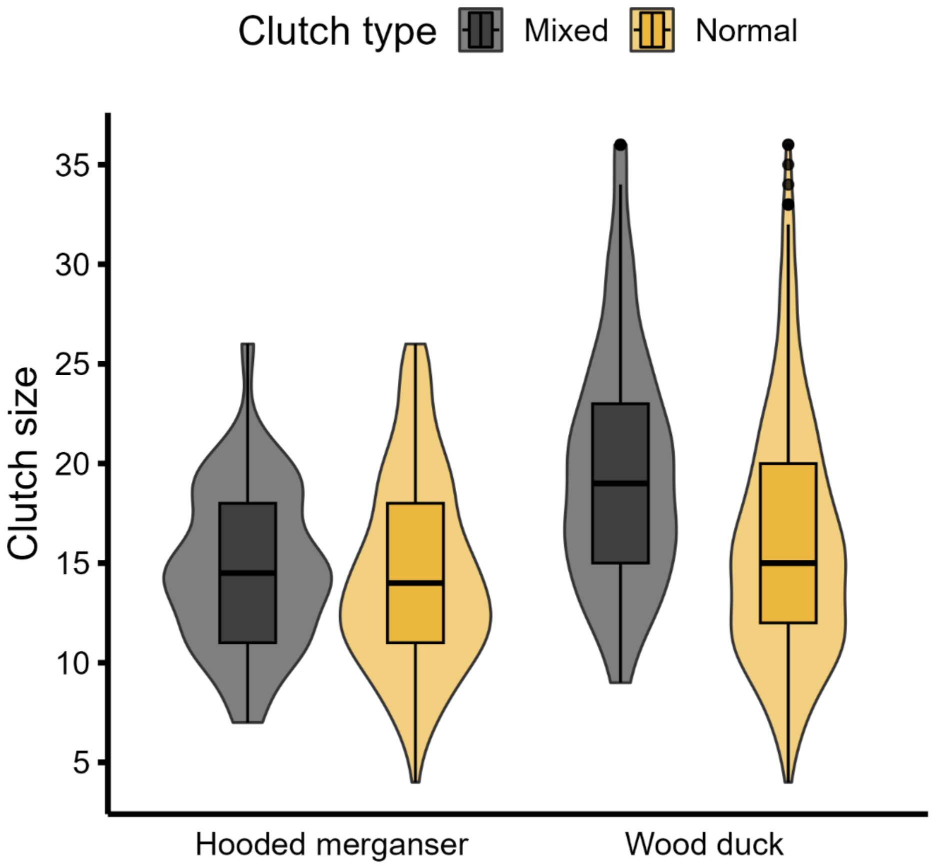

Figure 4.1. Violin plots of clutch size for hatched wood duck (*Aix sponsa*) and hooded merganser (*Lophdytes cucullatus*) nests. Mixed clutches were interspecifically parasitized and normal clutches contained only eggs that matched the host species. Nest were observed in Louisiana (2020– 2022) and Mississippi (1996– 1999).

Table 4.2. K-fold cross-validation scores (K-CV), expected log pointwise predictive density differences (ELPD), and Bayesian R^2 values used to select the best fitting egg survival model. Clutch size was the maximum number of eggs observed across all weekly visits to each nest. Nest host was a variable indicating either a wood duck (*Aix sponsa*) or host hooded merganser (*Lophdytes cucullatus*) incubated the nest. Nest ID was the random effect in each model.

Model	K-CV	ELPD ± SE	R^2
Clutch size * Nest host + Nest ID	1423.66	0.00 ± 0.00	0.914
Clutch size + Nest host + Nest ID	1442.55	-9.45 ± 11.00	0.910
Nest host + Nest ID	1462.71	-19.53 ± 11.14	0.911
Clutch size + Nest ID	1511.32	-43.83 ± 21.95	0.904
Nest ID	1535.98	-56.16 ± 21.82	0.906
Null	1675.25	-125.80 ± 44.71	0.750

Survival was the same for most egg types (host wood duck eggs: $\mu = 0.715$, CI = 0.672, 0.756; host hooded merganser eggs: $\mu = 0.808$, CI = 0.715, 0.878; parasitic hooded merganser eggs: $\mu = 0.780$, CI = 0.726, 0.828), except for parasitic wood duck eggs laid in hooded merganser nests, which had lower survival ($\mu = 0.281$, CI = 0.150, 0.460; Figure 4.2). Clutch size had a negative effect on egg survival ($\beta = -0.06$, CI = -0.09, -0.02). The interaction term had a negative effect on the survival of parasitic wood duck eggs ($\beta = -0.25$, CI = -0.43, -0.09) and a slight positive influence on parasitic hooded merganser eggs ($\beta = 0.08$, CI = 0.04, 0.13; Figure 4.3). Fixed effects explained only 2.7% of the variation in egg survival observed between nests.

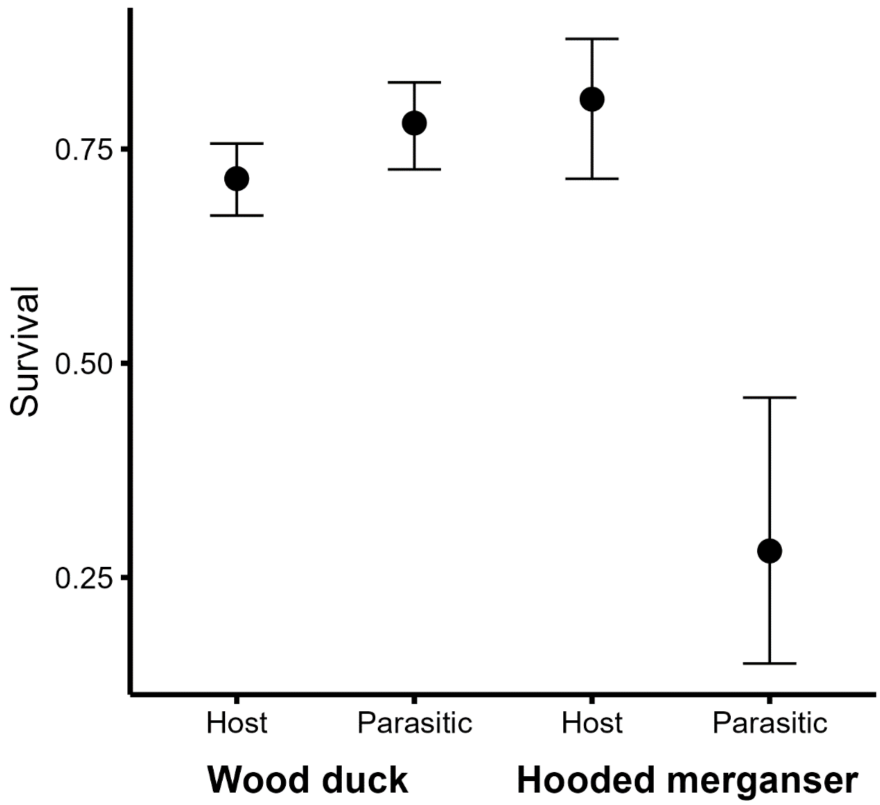

Figure 4.2. Model predictions of egg survival for nests hosted by wood ducks (*Aix sponsa*) and hooded mergansers (*Lophodytes cucullatus*). Host eggs were those that matched the species incubating the clutch, including eggs that were laid parasitically by conspecifics; all others were parasitic eggs.

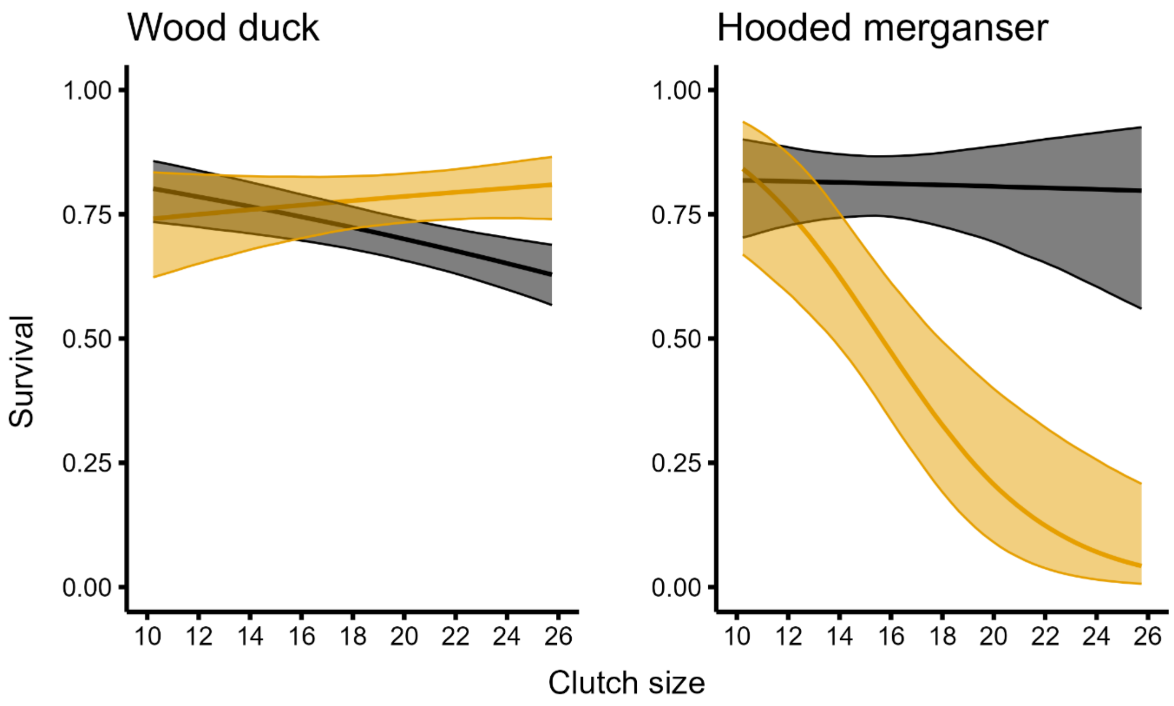

Figure 4.3. Model predictions (with 95% credible intervals; after, CI) of egg survival across different clutch sizes for wood ducks (*Aix sponsa*) and hooded mergansers (*Lophodytes cucullatus*). Host eggs (gray CIs) were those that matched the species incubating the clutch, including eggs that were laid parasitically by conspecifics; all others were parasitic eggs belonging to the other species (gold CIs).

In both the constant mixed clutch and proportional mixed clutch scenarios, there were minimal costs to hooded mergansers parasitizing wood duck nests. The number of hatched parasitic hooded merganser eggs continued to increase as more parasitic eggs were laid, even at large clutch sizes (Figure 4.4). In contrast, wood duck parasites gained little benefit from contributing more than 3 parasitic eggs to merganser nests, as hatching more than 3 parasitic eggs was unlikely (Figure 4.4). Wood ducks incurred little cost when parasitizing smaller hooded merganser clutches under the proportional mixed clutch scenario (Figure 4.5); however, when the clutch size exceeded twelve eggs (6 host and 6 parasitic), the proportion of parasitic eggs hatching decreased (Figure 4.5).

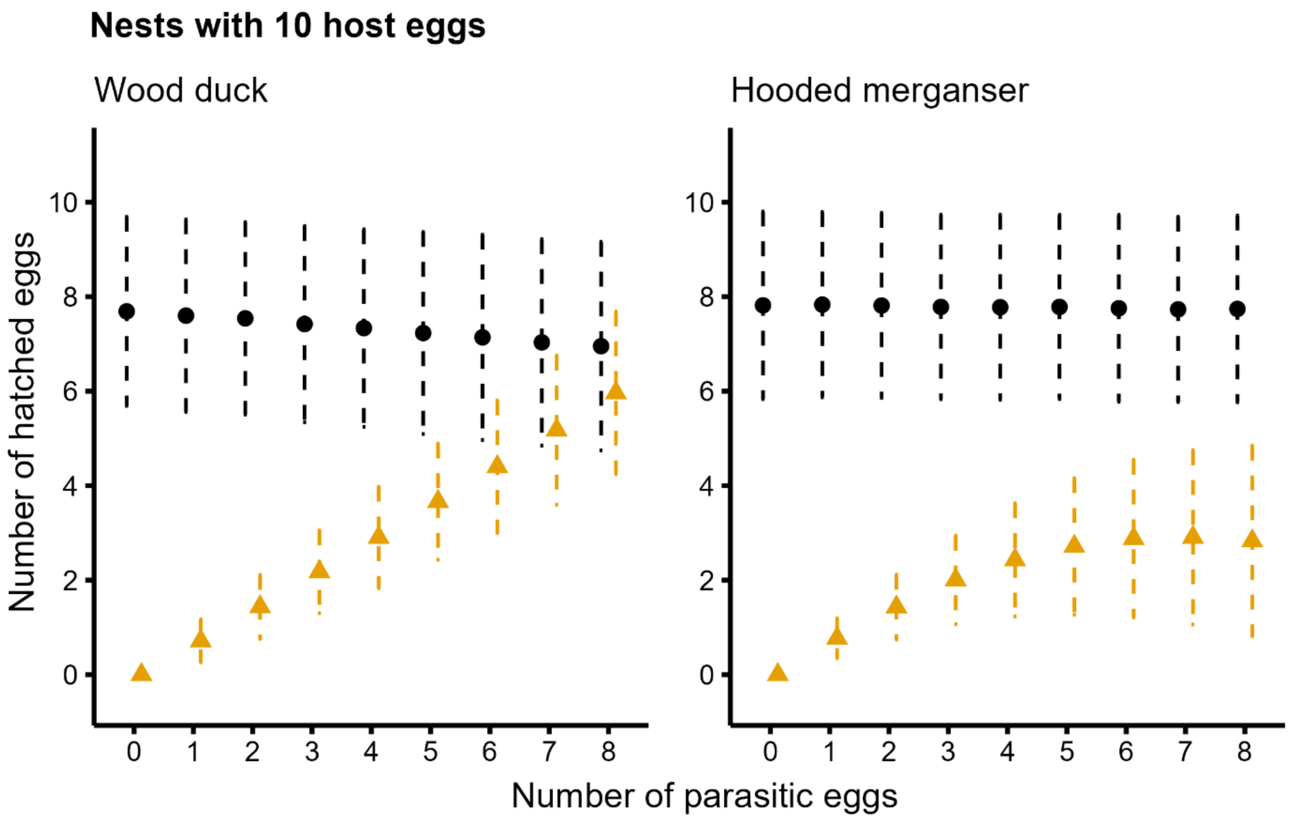

Figure 4.4. Model predictions (with 95% credible intervals; after, CI) showing the number of wood duck (*Aix sponsa*) and hooded merganser (*Lophodytes cucullatus*) eggs expected to hatch from mixed clutches (i.e., interspecifically parasitized). The number of host eggs is held constant at 10. Host eggs (black circles and CIs) were those that matched the species incubating the clutch, including eggs that were laid parasitically by conspecifics; all others were parasitic eggs belonging to the other species (gold triangles and CIs).

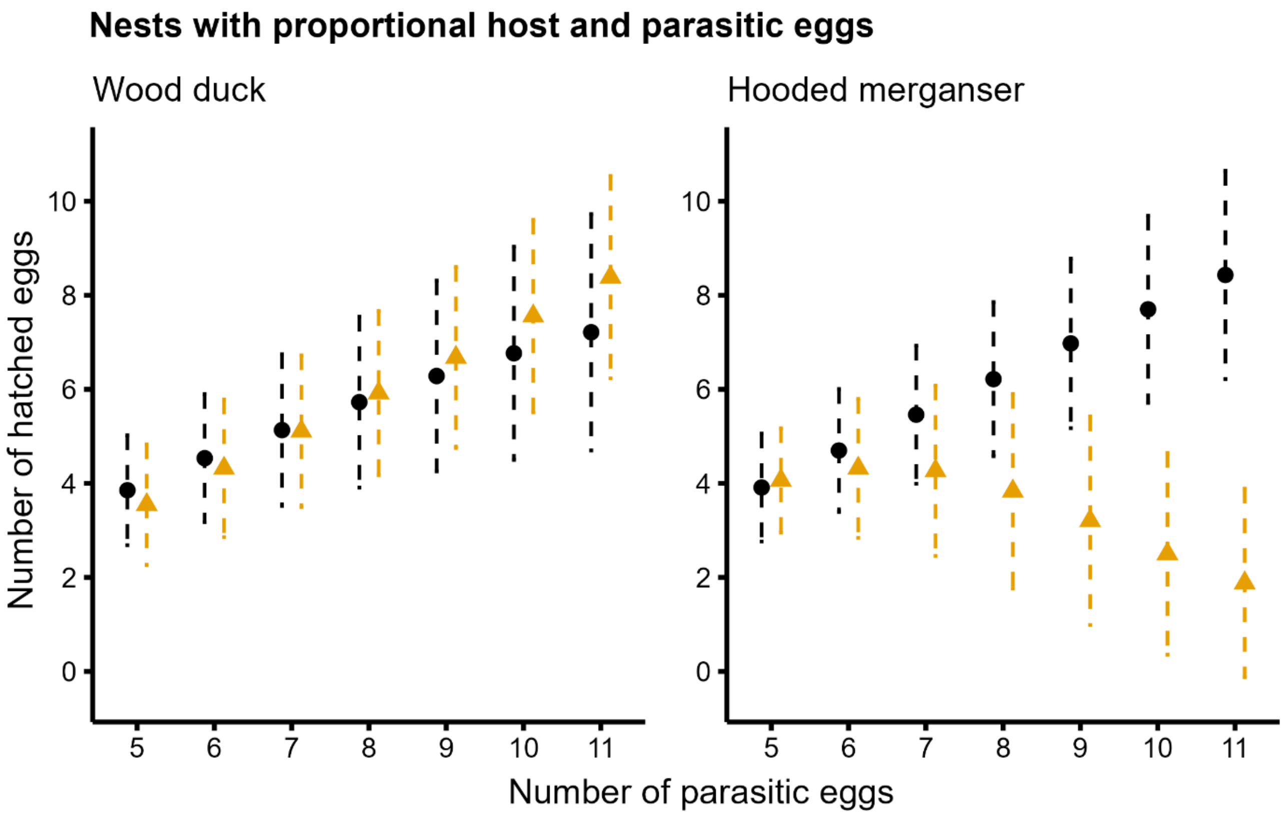

Figure 4.5. Model predictions (with 95% credible intervals; after, CI) showing the number of wood duck (*Aix sponsa*) and hooded merganser (*Lophodytes cucullatus*) eggs expected to hatch from mixed clutches (i.e., interspecifically parasitized). The number of host eggs is proportional to the number of parasitic eggs. Host eggs (black circles and CIs) were those that matched the species incubating the clutch, including eggs that were laid parasitically by conspecifics; all others were parasitic eggs belonging to the other species (gold triangles and CIs).

4.5. Discussion

Mixed clutches of wood duck and hooded merganser eggs have been observed across a large geographic region (Doty et al. 1984, Semel and Sherman 1986, Kennamer et al. 1988, Zicus 1990, Mallory 1991, Heusmann et al. 2000, Mallory et al. 2002, Mallory 2003), and the proportion (~10%; Doty et al. 1984 and Mallory et al. 2002) and success (~66%) of mixed clutches reported in previous studies are comparable to my findings (Doty et al. 1984). In my study, 13.3% of wood duck nests and 21.4% of hooded merganser nests contained mixed clutches, with successful hatches for 72.8% of wood duck nests and 71.9% of hooded merganser nests. Overall, I observed low costs to hooded mergansers parasitizing wood duck nests as the survival of their parasitic eggs remained high across all clutch sizes. Furthermore, clutch composition had little influence on the fate of parasitic hooded merganser eggs. Conversely, there were greater costs to wood ducks that laid $\geq$3 parasitic eggs in hooded merganser nests, where egg survival seemed especially influenced by clutch size and composition.

Parasitic wood duck eggs survived at lower rates when compared to parasitic hooded merganser eggs, which may have several explanations. The most likely explanation is that shells of wood duck eggs are thinner and structurally weaker than those of hooded mergansers (Gibson 2022). Accordingly, wood duck eggs may be more likely to crack in hooded merganser nests, and the damaged eggs are subsequently removed by the host (Dugger et al. 1999, Bakner and Ringelman 2023). Dugger et al. (1999) conducted experiments using urethane to coat a subset of wood duck eggs to enhance durability. Urethane-treated wood duck eggs were less likely to be removed from the nest box than untreated eggs. These results were consistent with Eadie's

(1989) hypothesis that egg removal is a response to broken eggs in a nest and not an antiparasitic behavior exhibited by a host. Eggs may crack in the nest for various reasons, and at my Louisiana study sites the frequency of cracked eggs was unusually high because of frequent partial clutch depredation by red-bellied woodpeckers (*Melanerpes carolinus*; Bakner and Ringelman 2023). My observations of trail camera videos recorded inside nest boxes show that woodpeckers often fail to peck and fracture black-bellied whistling-duck (*Dendrocygna atumnailis*) eggs (Bakner et al. personal observations), whose eggshell strength is intermediate to wood ducks and mergansers (Gibson 2022). Thus, I speculate that wood duck eggs, with their thinner and weaker eggshells, may be depredated at greater rates compared to hooded merganser eggs.

Stronger eggshells likely benefit hooded merganser eggs but this may not be the sole factor explaining their high survival when laid parasitically in wood duck nests. I advocate that the timing of egg-laying is also important. My field observations from Louisiana study sites indicate that most mixed wood duck clutches receive parasitic hooded merganser eggs prior to incubation. Odell and Eadie (2010) found that wood ducks selected smaller clutches to host their parasitic eggs, potentially perceiving them as in the laying stage. Likewise, hooded mergansers could potentially use host nest clutch sizes as a cue for gauging the nesting stage before laying parasitically. This behavior could boost their egg survival by avoiding nests already being incubated (Morse and Wight 1969, Sorenson 1993).

My results and observations herein are supported by a previous study in Missouri, where nesting efficiency for merganser eggs incubated by wood ducks was

0.56 and 0.46 for wood duck eggs incubated by hooded mergansers (Lemons 2004). Hooded mergansers laid 444 eggs in wood duck nests and 251 (57%) parasitic ducklings exited nest boxes which accounted for ~14% of all hooded merganser production observed during the three-year study. During the same study, wood ducks laid 91 eggs in hooded merganser nests with only 15 (16%) parasitic ducklings exiting nest boxes. Hooded mergansers may have constraints in effectively incubating large clutches, or actively rearrange nest contents to prioritize effective incubation of their own eggs. Future experiments may be able to better diagnose behavioral responses to parasitic cues: for example, manipulation of egg numbers might offer valuable insight into the preferred wood duck clutch sizes targeted by parasitic hooded mergansers (Dugger et al. 1994, Odell and Eadie 2010). Furthermore, laboratory- or aviary-based studies could explore the relative tolerance of wood duck and merganser eggs to imperfect incubation conditions (DuRant et al. 2010). It should also be noted that physical characteristics of the box can affect rates of parasitism: Stephens et al. (1998) found lower rates of parasitism in half-volume small boxes, but more ducklings ultimately left standard boxes which accommodated larger clutches.

My findings provide baseline information on the costs and benefits of laying parasitically, which may have important ramifications for nest box programs. I also recommend consideration of the effects of conspecific parasitism, which would provide a more comprehensive view of the costs of parasitism. Achieving this would require using genetic techniques to better assign eggs to nest hosts and parasites (Pöysä et al. 2009, Eadie et al. 2010, Lemons et al. 2011). To understand the lower survival of parasitic wood duck eggs in hooded merganser nests, it will be important for future studies to conduct weekly nest box visits and keep detailed records of egg losses, such as through the use of trail cameras, to confirm some of my speculations. One important conclusion from my study is that hooded mergansers incur low costs when laying eggs parasitically in wood duck nests, while wood ducks experience greater costs when laying parasitically in hooded merganser nests. Future research should assess the combined effects of conspecific and interspecific brood parasitism to achieve a full understanding of the cost to both nest hosts and parasites.

Chapter 5. Nest survival and duckling recruitment for wood duck clutches parasitized by hooded mergansers and black-bellied whistling-ducks

5.1. Introduction

Avian brood parasitism is a reproductive strategy wherein individuals lay their eggs in the nests of others, enabling them to reduce the costs associated with reproduction (Yom-Tov 1980, Lyon and Eadie 2008, Davies 2010). Brood parasitism comes in two forms: conspecific brood parasitism (hereafter, CBP) where eggs are laid in the nests of the same species (Yom-Tov 1980, Lyon and Eadie 2008), and interspecific brood parasitism (hereafter, IBP) where eggs are laid in the nests of a different species (Davies 2010). The costs incurred by the parasitized nest host depend on the developmental mode of the young involved. Species with altricial young, which need to be fed, impose higher costs on the host compared to species with precocial young, which are self-feeding (Rohwer and Freeman 1989). Consequently, defense mechanisms to avoid or mitigate brood parasitism are more common in species with altricial young, while those with precocial young exhibit fewer defensive adaptations (Rohwer and Freeman 1989).

The offspring of waterfowl species are precocial and facultative brood parasitism is commonly observed across these taxa (Rohwer and Freeman 1989, Lyon and Eadie 1991). Brood parasitism has been studied extensively in waterfowl that nest in high densities (Lokemoen 1991, Robertson 1998, Thompson et al. 2023), over water (Weller 1959, Péron and Koons 2012), or in nest cavities (McCamant and Bolen 1979, Haramis and Thompson 1985, Eadie 1989), as parasites can easily find host nests in these environments (Rohwer and Freeman 1989). Brood parasitism commonly increases the clutch size of nests in the population, resulting in increased nest abandonment and a reduction in hatch rate (i.e., number of eggs hatching; McCamant and Bolen 1979, Semel et al. 1988, Péron and Koons 2012). Moreover, brood parasitism can alter the composition (i.e., the number of host and parasitic young) of the broods (Péron and Koons 2012, Bakner et al. 2022), which can directly influence duckling survival (Pietz et al. 2003, Péron and Koons 2012, Dyson et al. 2018). The implications of brood parasitism are complex but the pervasiveness of this reproductive strategy makes it an important consideration for the management of waterfowl populations.

Wood ducks (*Aix sponsa*) are a cavity-nesting species and nest box programs are managed by state and federal agencies, nonprofit organizations, and the general public (Bellrose and Holm 1994, Baldassarre 2014). The shared goal of these programs is to provide safe nest sites for wood ducks to bolster populations; however, these programs often inadvertently increase rates of brood parasitism when nest boxes are highly visible and established at high densities (Semel et al. 1988). CBP is particularly prevalent in nest box populations (Eadie et al. 1998, Baldassarre 2014), and over 95% of nests are parasitized in some areas (Semel and Sherman 1986, Bellrose and Holm 1994). CBP has been studied extensively in wood ducks, and recent research indicates that it has a minimal impact on population growth rate (Hepp et al. 2020); however, little attention has been given to the potential effects of interspecific brood parasitism.

Range-wide, the most common interspecific brood parasite of wood duck nests is the hooded merganser (*Lophodytes cucullatus*; Mallory et al. 2002, Mallory and Weatherhead 2003) whose range overlaps substantially with wood ducks (Baldassare 2014). Hooded merganser eggshells, which are nearly three times stronger than wood duck eggs (Gibson 2022), frequently cause wood duck eggs to break when the hen repositions eggs, resulting in reduced hatch rates (Dugger et al. 1999). Nevertheless, evaluations aimed at understanding the broader consequences to wood ducks being parasitized by hooded mergansers are lacking. Such research is needed, especially because black-bellied whistling-ducks (*Dendrocygna atumnalis*; hereafter whistling-duck) are rapidly expanding their breeding distribution into the southeastern united states (Cohen et al. 2019, Croft et al. 2020, Bakner et al. 2022) and are a potential new parasite of southern wood duck nests (Bolen and Cain 1968).

Currently, there is one documented observation of whistling-ducks parasitizing a wood duck nest in south Texas (Bolen and Cain 1968). More recent studies have documented whistling-ducks nesting in South Carolina (Croft et al. 2020) and Louisiana (Bakner et al. 2022), where the timing of nesting overlaps with wood ducks and hooded mergansers. Wood ducks and hooded mergansers both parasitize whistling-duck nests (Bakner et al., 2022); therefore, it is likely that wood duck nests are routinely parasitized by whistling-ducks. Such potential has raised concern among managers of wood ducks because whistling-ducks exhibit extraordinary rates of CBP, resulting in some of the largest clutch sizes ever documented in waterfowl. For example, observations in south Texas show CBP was present 100% of nests in one population (James 2000) and clutch sizes regularly exceeding 50 eggs (the largest containing 101 eggs; McCamant and Bolen 1979). While CBP is a common aspect of the life history of wood ducks and whistling-ducks, the impact whistling-ducks have on breeding wood duck populations in the southeastern United States is unknown.

Given the presence of hooded mergansers throughout much of the breeding distribution of wood ducks, as well as the expanding range of whistling-ducks throughout the southeastern United States, it is vital to evaluate IBP in wood duck nests and its broader consequences to wood duck populations. Such an assessment requires consideration of the most important vital rates: recently, Hepp et al. (2020) found nest survival and duckling recruitment accounted for 11.4% and 57.7% of the variation in wood duck population growth rate. Here, I report on wood duck nests that were parasitized by hooded mergansers and whistling-ducks in central Louisiana to quantify the prevalence of IBP in wood duck nests and evaluate the influence of IBP on nest survival and duckling recruitment.

5.2. Study area

I oversaw nest boxes established by Louisiana Department of Wildlife and Fisheries (LDWF) in Iberville, Pointe Coupee, Rapides, St. Landry, and St. Martin Parishes (Figure 5.1). My study sites were located in Sherburne Wildlife Management Area (hereafter, Sherburne), Thistlethwaite Wildlife Management Area (hereafter, Thistlethwaite), Indian Creek Reservoir, Lake Rodemacher, and Oden Lake. Sherburne is 17,652 ha in size, and owned by LDWF, U.S. Fish and Wildlife Service, and U.S. Army Corps of Engineers. Sherburne is located along the Atchafalaya River and is primarily bottomland hardwood forest with backswamps and bayous. Sherburne has two moist soil units located on the eastern side of the property known as “North Farm” and “South Farm,” which are managed for migratory waterbirds. Thistlethwaite is 4,492 ha of bottomland hardwood forest and is leased to LDWF by a private individual. Indian Creek is a 1,052 ha reservoir surrounded by Alexander State Forest Wildlife Management

Area, which is a mix of loblolly (*Pinus taeda*) and longleaf pine (*Pinus palustris*) and hardwood stands. Oden Lake is a smaller private lake ~6.5 km northeast of Indian Creek, and the perimeter of the lake is lined with residential housing. As part of the Oden Lake study site, I also monitored nest boxes located in a cypress swamp directly north of the lake and west of highway 165. Lake Rodemacher is 1,189 ha in size and ~3 km west of Boyce, Louisiana; the lake is used as a cooling resource when generating power for The Brame Energy Center that is located on the northwest side of the lake. Across all sites, I monitored ~300 nest boxes annually, and most of the nest box populations I oversaw were ~30 years old. Nest boxes were located over open water and accessed by boats, or off the side of levees and navigated to by all-terrain vehicles or on foot.

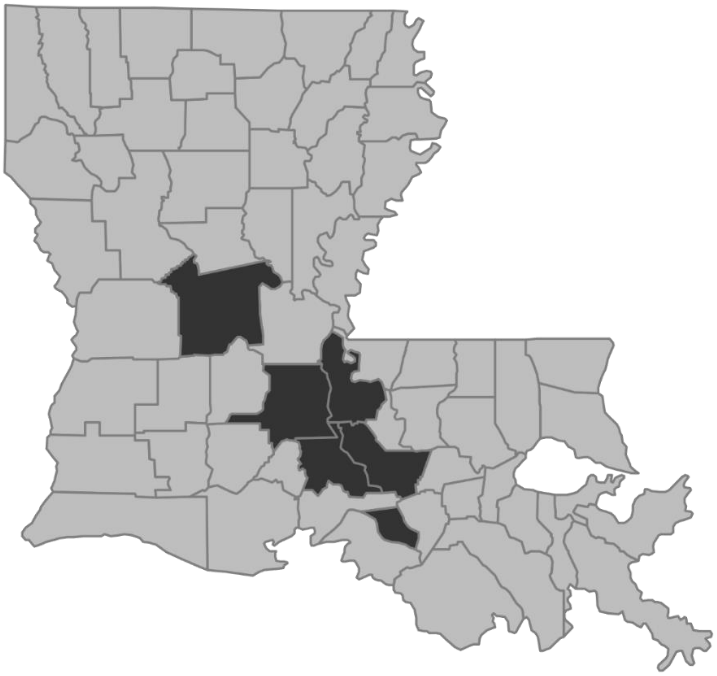

Figure 5.1. Study sites were located in central Louisiana within Iberville, Pointe Coupee, Rapides, St. Landry, and St. Martin Parishes.

5.3. Methods

I visited nest boxes from February 1–July 31, at approximately 7-day intervals, during 2020–2023. I monitored the progression of wood duck nests throughout the laying and incubation stages to assign a vital status during each visit. I considered a nest to be alive during the laying stage when I observed an increase in clutch size from the prior visit, otherwise I considered it failed due to nest abandonment. I considered a nest to be alive during the incubation stage when I observed the incubation of the clutch progress from the prior visit, as determined by egg candling (Weller 1956), else I considered it to be abandoned. In addition to nest abandonment, any predation event, severe weather, or observer damage that caused laying or incubation progression to cease resulted in a nest failure. I considered a nest successful if it survived to hatch ≥1 egg.

I assigned all eggs from each wood duck nest a numeric ID written with a permanent marker, and I documented the species of each egg (Semel et al. 1988, Sorenson 1997). I determined an egg belonged to a wood duck if it was elliptically shaped and a creamy white color (Baldassarre 2014); hooded merganser when spherical and white (Mallory and Weatherhead 1900); and whistling-duck if the egg was elliptically shaped, white in color, and showed a blotchy eggshell pattern when viewed through a candling device (Weller 1956, Bakner et al. 2022). I recorded which eggs were present or missing at each visit to nests. Following the termination of a nest, I counted the number of eggs that failed or hatched. I counted eggs that went missing, remained unhatched, or were non-viable as failing; egg membranes were used to get a count of hatched eggs. I used egg data when the clutch was found to determine nest initiation dates by back-calculating to the day when the first egg was laid, assuming a laying rate of one egg per day with no partial clutch losses (Emery et al. 2005). I determined the clutch size of each nest as being the maximum number of eggs observed in it across all visits, considering all egg species.

I visited wood duck nests daily once they were within three days from their expected hatch date to capture broods from nest boxes. I randomly divided wood duck ducklings in each brood into two groups and fit the first group with web tags (Hepp et al. 1989) and the other with passive integrated transponders tags (hereafter, PIT tag; Bridge et al. 2019). Web tags were placed near the tarsometatarsus end of the phalanges (Alliston 1975) and located on the inner webbing of the right foot. I inserted 2x12 mm PIT tags (www.cyntag.com) under the skin, between the scapula using 12-gauge injector needles (Bridge et al. 2019; www.biomark.com). Once PIT tags were inserted under the skin, I used 3M Vetbond Tissue Adhesive to suture the injection point. I used both web tags and PIT tags as part of a separate project testing the differences in survival and recapture rates using these two common marking techniques. For the project duration reported here, I recaptured similar proportions of web and PIT tagged individuals; therefore, I assumed the two marking techniques did not influence my results. I returned all ducklings to nest boxes once they were marked. In addition to marking ducklings, I captured adult female wood ducks from the nest boxes during incubation (Hepp et al. 1989). Once captured I fitted each female with a United States Geological Survey aluminum leg band. Waterfowl species exhibit female-based philopatry, which allowed us to recapture marked female ducklings and adults from nest boxes in subsequent breeding seasons (Rohwer and Anderson 1988, Hepp et al. 1989). I checked all unbanded adults for web tags and used a handheld radio frequency identification device (www.biomark.com) to check for PIT tags.

I used my egg data to bin nests into clutch types based on the presence of IBP and nest initiation date. I termed wood duck nests containing ≥1 hooded merganser egg “mixed merganser clutches” and those with ≥1 whistling-duck egg “mixed whistling-duck clutches”; all other nests were “normal clutches,” which may have contained parasitic eggs from conspecifics. To facilitate the comparison of parameter estimates between mixed clutches and normal clutches, I divided the normal clutches into two distinct periods that aligned with the temporal periods in which I observed mixed merganser and mixed whistling-duck clutches. I labeled nests initiated before April 1 "early clutches," as parasitic merganser eggs were most likely to be observed in wood duck nests initiated prior to that date at my study sites. Conversely, nests initiated following April 1 were referred to as "late clutches," when parasitic whistling-duck eggs begin to appear in wood duck nests at my study sites. I confirmed April 1 was a satisfactory cutoff date for assigning early and late clutches by examining the variation in nest initiation dates for mixed clutches through visual plots. I then compared the clutch sizes and number of hatched eggs using two sample t-tests, where I reported measures as means ± standard deviations. Specifically, I compared early clutches to mixed merganser clutches, and late clutches to mixed whistling-duck clutches. I used Cohen’s D statistic to measure the effect size (hereafter, ES) of any significant p-values from t-tests.

I estimated daily nest survival rate (hereafter, DSR) and overall nest success (i.e., hatched ≥1 egg) within a Bayesian framework (Schmidt et al. 2010). To do so, I constructed daily encounter histories for each nest as described by (Schmidt et al.

2010). My encounter histories represented a chronological record of live-dead observations, starting with a 1 on the first day the nest was observed alive. For successful nests, the encounter history contained a continuous series of 1's for each day I observed it. In the case of failed nests, the encounter history included 1's for the days I observed the nest alive, followed by NA values for the days between the last observed alive state and the subsequent visit confirming the nest failed. The use of NA values specified my uncertainty of which day nest failures occurred (Mayfield 1975, Dinsmore et al. 2002). The encounter history of failed nests ended with a 0, representing the day field observers first detected the nest failed. I estimated DSR as a series of Bernoulli trials:

$$y_{i,t} \sim Bernoulli(y_{i,t-1} * DSR_i),$$

where $y_{i,t}$ is the assigned vital status of nest i at time and $y_{i,t-1}$ is the assigned vital status of nest i at time t-1. I used a logit link function to evaluate the relationship between covariates and DSR as:

$$logit(DSR_i) = \beta_0 + \beta_1 * clutch\ type_i + \beta_2 * clutch\ size_i + \beta_3 * clutch\ size_i^2 + \varepsilon_i,$$

$$\varepsilon_i \sim Normal(0, \sigma^2),$$

where β_0 is DSR on the logit scale and overall nest survival is DSR exponentiated to the forty-first power assuming the laying and incubation stages take 11 and 30 days to complete (Bellrose and Holm 1994, Baldassarre 2014). My linear predictor included clutch type and clutch size along with its quadratic form as fixed effects and study site as a random effect (ε). I included the quadratic term for clutch size as I predicted the effects of excessive brood parasitism could be non-linear, wherein wood ducks may abandon nests at some clutch size threshold (Semel et al. 1988). I tested this by comparing the variation in clutch size between abandoned and successful nests. This comparison was done using a Welch’s t-test, where I reported means ± standard deviations, and accompanied estimates with Cohen’s D statistic adjusted for unequal variances. I used Uniform (0, 1) priors for modeling DSR, Normal (0, 0.01) priors for fixed effect coefficients, and Uniform (0, 5) priors to estimate study site variance (σ^2).

I used my duckling and adult capture-mark-recapture data to estimate a single duckling recruitment probability (hereafter, recruitment probability). I assumed half the marked ducklings from each brood were females and excluded male ducklings from my analysis. I used a Bayesian multistate model to derive mean estimates of apparent survival (Φ) and capture probability (φ; Lebreton et al. 2002, Kéry and Schaub 2012). I built individual encounter histories where individuals were in one of the following three states: duckling, adult, and dead. To execute the model, I first constructed a state-transition matrix to describe the state of individuals at time t + 1 given their state at time t:

$$\begin{array}{ccc} & & \textit{state}_{t+1} \\ & & \begin{array}{ccc} \textit{duckling} & \textit{adult} & \textit{dead} \end{array} \\ \textit{state}_{t} & \begin{array}{r} \textit{duckling} \\ \textit{adult} \\ \textit{dead} \end{array} & \begin{bmatrix} 0 & \Phi_d & 1 - \Phi_d \\ 0 & \Phi_a & 1 - \Phi_a \\ 0 & 0 & 1 \end{bmatrix}, \end{array}$$

where the matrix defines the true states and specifies that once duckling i advances to the adult state, it remains there until mortality occurs. I then built an observation matrix to link the true states to what we observed in the field:

$$\begin{array}{cc} & \textit{observation}_t \\ \textit{state}_t & \begin{array}{r|ccc|} & \textit{seen as duckling} & \textit{seen as adult} & \textit{not seen} \\ \textit{duckling} & 1 & 0 & 0 \\ \textit{adult} & 0 & \varphi_a & 1 - \varphi_a \\ \textit{dead} & 0 & 0 & 1 \end{array} \end{array},$$

where the matrix describes the observations on individual i at time t, given the latent state at time t. I detected all individuals observed in the duckling state; therefore, I fixed this parameter at 1. φ was only estimated for the adult state because ducklings were not observable beyond their hatch dates. I used Uniform (0, 1) priors for estimates of Φ and φ. While the multistate model provides estimates of Φ_a and φ_a we do not report them here as they are not needed for my evaluation. I defined recruitment probability as the probability female duckling i marked at time t survives to its breeding age (1 year old) and returns to the study area at time t + 1 to be captured as a breeding adult, which is analogous to Φ_d.

I built a separate Bayesian multilevel model to evaluate the effects brood-level variables had on the recruitment probability (Bürkner 2017). I employed a zero-inflated binomial distribution to fit my data:

$$x_i \sim Zero\text{-}Inflated\ Binomial(n_i,\ p_i,\ \pi_i),$$

$$logit(p_i) = \beta_0 + \beta_1 * nest\ initiation\ date_i + \beta_2 * brood\ size_i + \gamma_i,$$

$$\gamma_i \sim Normal(0,\ \sigma^2),$$

where I treated the quantity of female wood duck ducklings in brood i as the number of trials (n) and the number later observed in the adult state as successes (p). I considered nest initiation date and brood size as fixed effects and brood identity (hereafter, ID) as the random effect (γ) in my model. Small sample sizes precluded us from including brood composition (i.e., number of merganser or whistling-duck ducklings in each wood duck brood). Therefore, I used nest initiation date as a replacement variable to represent the temporal variation in brood composition.

Prior to running my models, I standardized all my variables to have a mean of 0 and standard deviation of 1. I calculated the percentage of variation explained by my fixed effects to evaluate their contribution to my models (Grosbois et al. 2008). This involved constructing an additional nest survival and multilevel recruitment model containing only the random effects terms. I used the variance estimates ($\hat{\sigma}^2$) obtained from my fixed effects and random-effects-only models, to execute my calculation using Grosbois et al.'s (2008) seventh equation:

$$\frac{\hat{\sigma}^2(random\ effects\ only\ model) - \hat{\sigma}^2(fixed\ effects\ model)}{\hat{\sigma}^2(random\ effects\ only\ model)}$$

I fit my DSR and multistate models in JAGS 4.3.1 (Plummer 2003) using the R2jags 0.7-1 package (Su and Yajima 2021) in Program R 4.2.2 (R Core Team 2023). I employed the brms 2.19.0 package (Bürkner 2017) to fit my multilevel recruitment model, leveraging its interface with Stan (Stan Development Team 2023). For my multilevel recruitment model, I used default prior and link function settings. For all JAGS models we ran 4 chains of 50,000 iterations, considered 20,000 as burn-in, and saved every twentieth iteration. I confirmed my models converged via inspection of trace plots and by using the Gelman-Rubin statistic, where a $\widehat{R}$ value < 1.05 indicated convergence (Gelman and Rubin 1992). For my Bayesian analyses, I report coefficient values (β), where credible intervals (hereafter, CI) that did not overlap zero indicated significance effects from regression coefficients at the 0.05 alpha level.

5.4. Results

I monitored a total of 1,206 wood duck nests from 2020–2023. I observed mixed merganser clutches initiated from January 26–April 29 and mixed whistling-duck clutches in those initiated from March 16–June 15. We determined April 1 was a satisfactory cutoff date for assigning early and late clutches (Figure 5.2). Of the nests I monitored, 98 (8.1%) were mixed merganser clutches, 582 (48.1%) were early clutches, 134 (11.1%) were mixed whistling-duck clutches, and 392 (32.4%) were late clutches. Additionally, I observed 3 wood duck nests that contained both parasitic merganser and whistling-duck eggs, which were excluded from my analyses. A total of 39 (39.8%) mixed merganser, 287 (49.3%) early clutches, 74 (55.2%) mixed merganser and 180 (45.9%) late clutches were successful. From these nests, 5,905 wood duck eggs hatched. A total of 339 (5.7%) hatched from mixed merganser clutches, 3,378 (57.2%)

from early clutches, 525 (8.9%) from mixed whistling-duck clutches, and 1,663 (28.2%) from late clutches. Additionally, wood duck nests hatched 140 mergansers and 185 whistling ducks.

The clutch size of mixed merganser clutches ($\bar{x} = 17.4 \pm 6.2$) was larger than early clutches ($\bar{x} = 14.3 \pm 7.5$; $t = -4.37$, df = 149.72, $P < 0.0001$, ES = 0.42). Mixed merganser clutches contained an average of 4.5 ± 3.4 merganser eggs and 12.9 ± 6.0 wood duck eggs. Considering successful nests, an average of 3.6 ± 2.2 merganser and 8.7 ± 3.9 wood duck eggs hatched from mixed merganser clutches; more wood duck eggs hatched from early clutches ($\bar{x} = 11.8 \pm 8.7$, $t = 4.51$, df = 51.28, $P < 0.0001$, ES = 0.54). The clutch size of mixed whistling-duck clutches ($\bar{x} = 15.3 \pm 5.8$) was larger than late clutches ($\bar{x} = 11.3 \pm 6.6$; $t = -6.57$, df = 258.32, $P < 0.0001$, ES = 0.62). Mixed whistling-duck clutches contained an average of 4.5 ± 4.8 whistling-duck eggs and 10.7 ± 5.1 wood duck eggs. Considering successful nests, an average of 2.5 ± 3.5 whistling-duck and 7.1 ± 3.8 wood duck eggs hatched from mixed whistling-duck clutches; more wood duck eggs hatched from late clutches ($\bar{x} = 9.2 \pm 3.7$, $t = 4.12$, df = 135.39, $P < 0.0001$, ES = 0.50).

My DSR models successfully converged according to trace plot inspections and $\widehat{R}$ values. The DSR estimate from my fixed effects model was 0.977 (CI = 0.965, 0.984) which yielded a nest success estimate of 0.385 (CI = 0.232, 0.516). The variance estimate for the fixed effects model was 0.603 (CI = 0.594, 0.716) and 0.624 (CI = 0.563, 0.745) for the random-effects-only model; therefore, model covariates explained only 0.3% of the variation in DSR across study sites. Clutch size ($\beta = 2.25$, CI = 2.01, 2.50) and the quadratic term (β = -1.42, CI = -1.64, -1.20; Figure 5.3) had a positive and negative influence of DSR that were both significant.

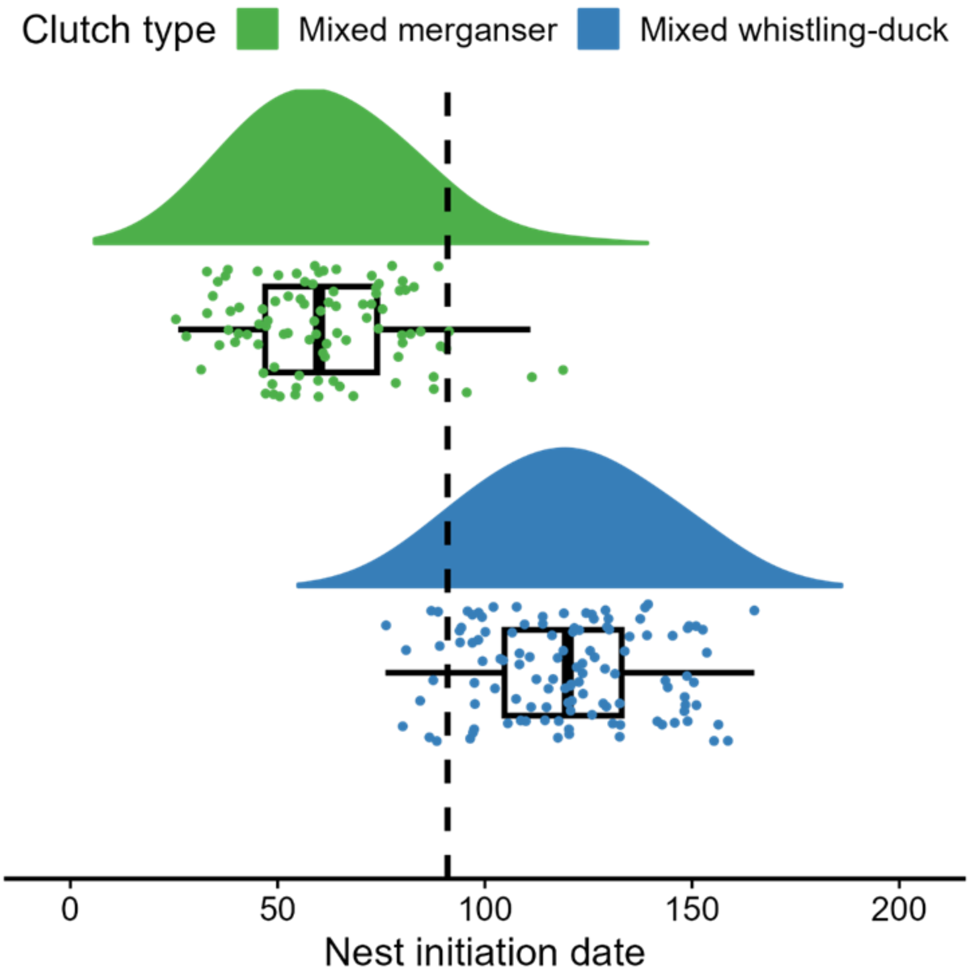

Figure 5.2. Boxplots showing nest initiation dates for wood duck (*Aix sponsa*) nests that contained parasitic hooded merganser (*Lophodytes cucullatus*; mixed merganser clutch) and black-bellied whistling-duck (*Dendrocygna autumnalis*) eggs. The density plots above box plot were drawn from the observed data points. The vertical dashed line is at April 1 and used as the cutoff date for early and late wood duck nests.

Mixed merganser clutches had a negative effect on DSR but was significant (β = -0.664, CI = -1.00, -0.296), yielding a DSR estimate of 0.955 (CI = 0.931, 0.972). DSR was the similar for all other clutch types and ranged from 0.974− 0.981. I found little evidence of larger clutches being abandoned by wood ducks, as abandoned clutches ($\bar{x}$ = 12.5 ± 7.9) were significantly smaller than successful ones ($\bar{x}$ = 16.3 ± 5.6; t = -5.55, df = 194.38, $P < 0.0001$, ES = 0.55; Figure 5.4).

I considered the capture histories of 2,124 female ducklings marked from 433 successful nests and 541 adult females captured from nest boxes. Assuming an equal sex ratio for the ducklings we marked, I tagged 187 (8.8%) female wood duck ducklings from 40 mixed merganser clutches, 1,095 (51.6%) from 193 early clutches, 202 (9.5%) from 57 mixed whistling-duck clutches, and 639 (30.1%) from 143 late clutches. I recaptured 49 (2.3%) ducklings as breeding adults with 6 (12.2%) returning from mixed merganser clutches, 29 (59.2%) from early clutches, 1 (2.0%) from a mixed whistling-duck clutch, and 13 (26.5%) from late clutches.

The mean recruitment probability was 0.038 (CI = 0.028, 0.049) across the entire study period. My multilevel recruitment model showed nest initiation had a negative effect ($\beta = -0.625$, CI = -1.020, -0.249; Figure 5.5) on duckling recruitment probability, while brood size had no effect ($\beta = -0.150$, CI = -0.484, 0.175). The across-brood variance estimate was 0.682 (CI = 0.034, 1.636) for the model containing fixed effects and 0.795 (CI = 0.043, 1.796) for the random-effects-only model, suggesting fixed effects explained 26.4% of the across-brood variation in recruitment probability.

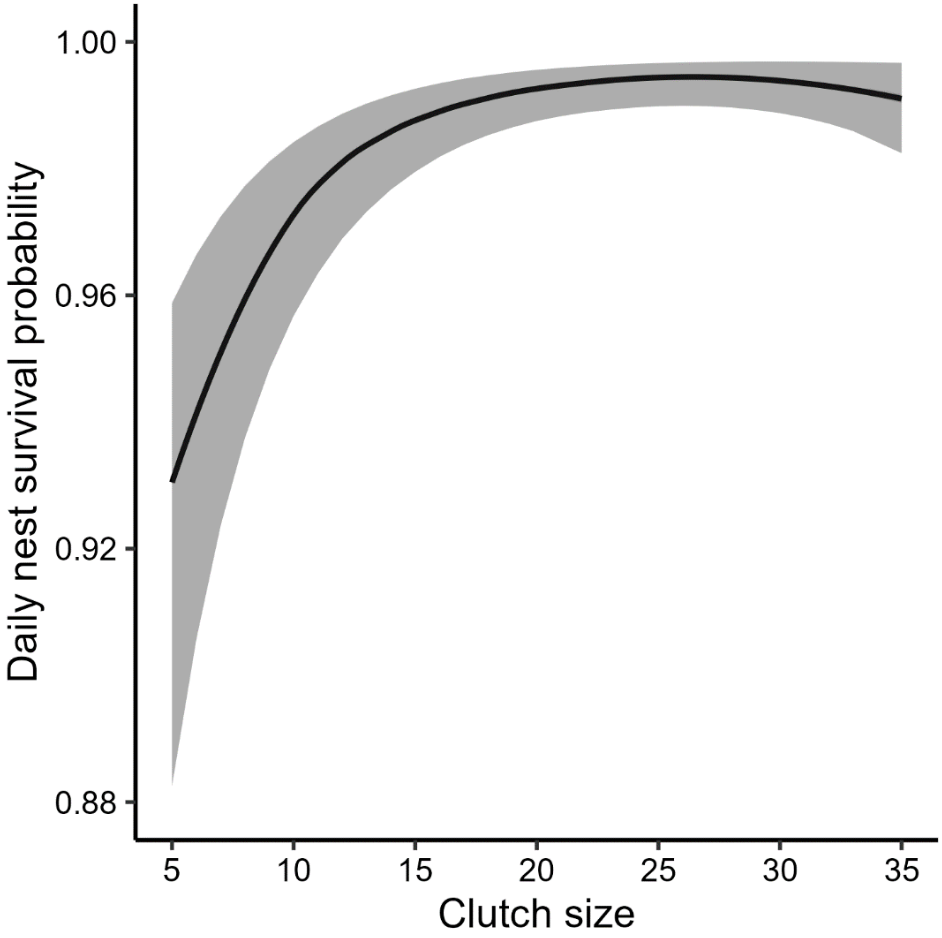

Figure 5.3. Daily nest survival rate of wood duck (*Aix sponsa*) nests across different clutch sizes. Clutch size was the maximum number of eggs we observed in each nest across all visits. This plot was produced excluding effects from clutch type.

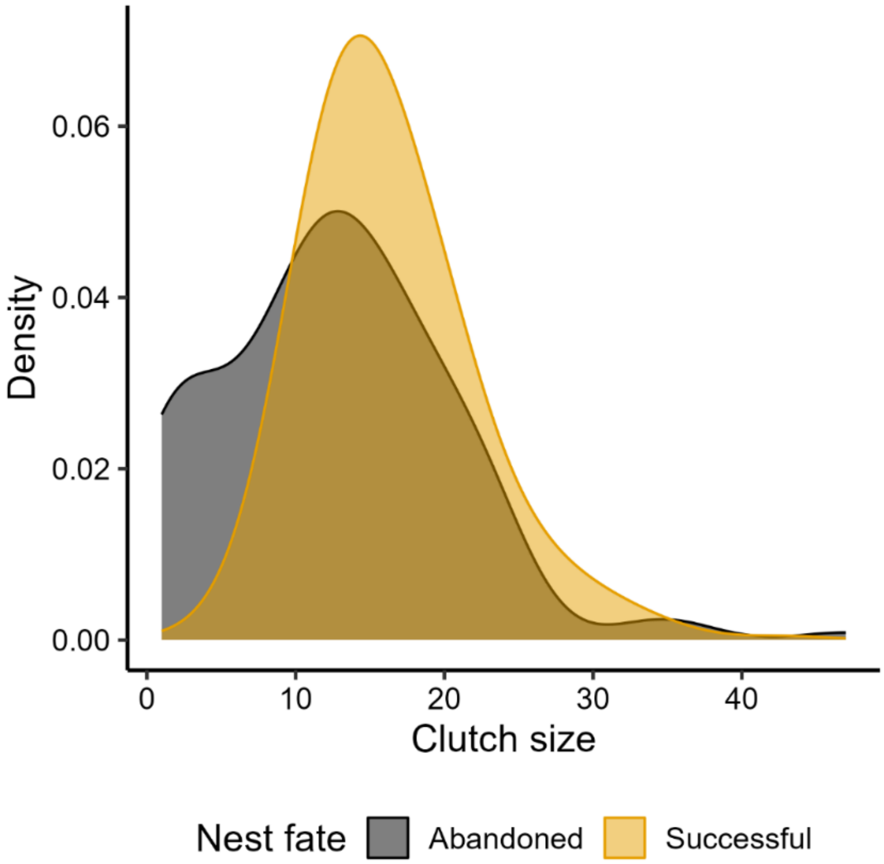

Figure 5.4. Density plots of clutch size for wood duck (*Aix sponsa*) nests that hatched ≥1 egg (successful) and that were abandoned. Clutch size was the maximum number of eggs we observed in each nest across all visits to it. Abandoned nests were never incubated and were not associated with any predation events.

5.5. Discussion

I found mergansers and whistling-ducks each parasitized wood duck nests for ~3 months during the breeding season, and wood duck nests were simultaneously parasitized by both species for a period of ~1.5 months (Figure 5.2). Approximately 20% of the wood duck nests we observed were interspecifically parasitized. These mixed clutches were larger, and my DSR model predicted higher survival for larger clutches, so it was surprising that mixed merganser clutches were not important in predicting survival. I suspect that mixed merganser clutches decoupled this relationship because DSR tended to be lower for this clutch type, whereas DSR for mixed whistling-duck clutches was commensurate to early and late normal clutches. Explaining the lower DSR observed in mixed merganser clutches presents a challenge, but it is potentially linked to a high abundance of early-season wood ducks and hooded mergansers that are strictly brood parasites and do not incubate. These brood parasites often produce "dump nests" that are never incubated (Semel et al., 1988), which appear in my data as failed (i.e., abandoned) nests.

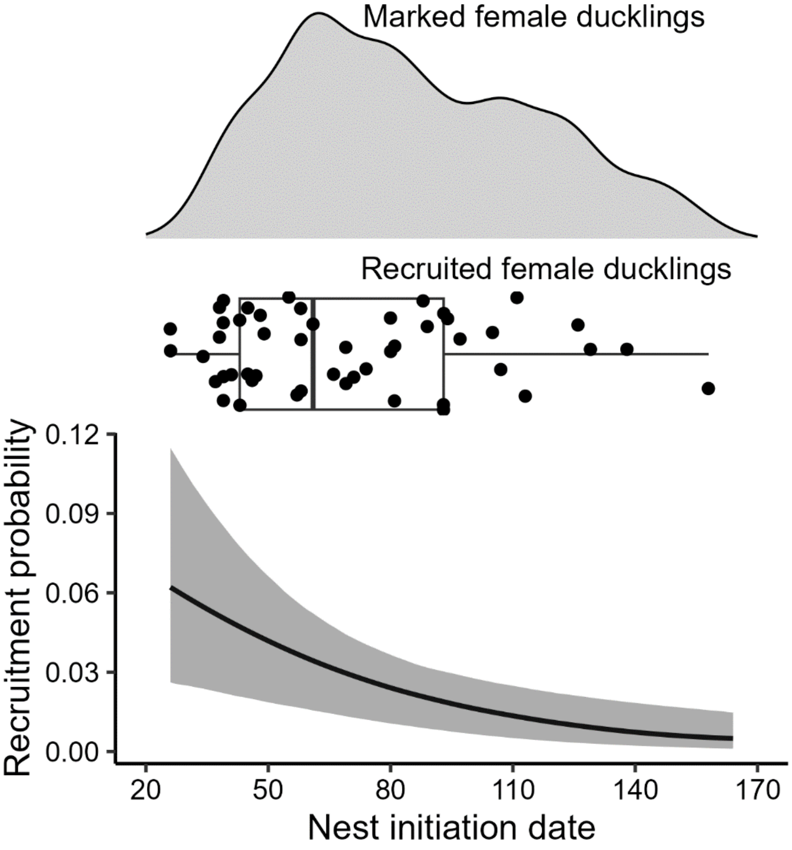

Figure 5.5. Recruitment probability for wood duck (*Aix sponsa*) ducklings across nest initiation dates. The box plot shows the variation in nest initiation dates for ducklings recaptured as breeding adults. The density plot shows the distribution of female ducklings marked during 2020–2023 in Louisiana.

I found IBP had no detrimental effect on the DSR of wood duck nests when considering clutch size and type. On the contrary, IBP contributed to larger clutch sizes which were associated with higher DSR, and there was no evidence that even excessive clutch sizes diminished survival. The relationship between larger clutch sizes and higher DSR may be driven by partial clutch predation by red-bellied woodpeckers (*Melanerpes carolinus*), which occurred when nest boxes were vacated by wood ducks during laying and incubation recesses (Bakner and Ringelman 2023). I hypothesize that parasitic egg laying and large clutch sizes act as a protective mechanism against nest abandonment. Without the addition of eggs from parasitic individuals, wood duck clutches would be depleted by partial predation, particularly during the laying period, which would increase the probability of nest abandonment. In addition, my nest boxes are ~30 years old, and previous research has demonstrated that as a nest box population ages, the breeding density increases, leading to higher levels of brood parasitism (Haramis and Thompson 1985, Bellrose and Holm 1994). It is possible that the wood ducks nesting in my study sites may have adapted to accept larger clutches when excessive brood parasitism saturates the box population year after year.

The mean recruitment probability from my study is comparable to estimates from wood duck populations in South Carolina, which ranged from 2.24– 6.84% (Hepp et al. 1989). Surprisingly, ducklings hatched from mixed merganser clutches had the highest apparent return rate (0.7%); however, most of these recaptures were from a single study site, where the other factors such as brooding habitat may have been favorable. Nest initiation date was the only important predictor of recruitment probability and strongly suggests that earlier-hatched female ducklings have a greater chance of entering the nest box population as breeding adults. Hepp et al. (1989) analyzed 6 years of data for wood duck ducklings web-tagged in South Carolina and found no relationship between duckling recruitment and hatch date. Similarly, studies estimating 30-day duckling survival found hatch date had little influence on survival (Davis et al. 2007, Dyson et al. 2018). In my analysis, I found that nearly 75% of the recruited ducklings hatched from nests initiated prior to mid-April. I believe the lower recruitment probability for ducklings hatched in the late spring and summer is a result of diminished brood habitat, where water levels are lower at many of my study sites either due to drier weather conditions or have been intentionally drawn-down for management purposes (e.g., moist soil and invasive aquatic vegetation management).

Overall, my findings indicate that IBP in wood duck nests has minimal effects on DSR and duckling recruitment probability; however, it is worth exploring potential reductions in individual fecundity as a result of mixed clutches. To evaluate these costs, future research could use modern genetic techniques to measure the reduction in hatched host eggs in mixed clutches, which includes determining the number of eggs belonging to conspecific parasites (Eadie et al. 2010, Lavretsky et al. 2023). Furthermore, it would be valuable to investigate other vital rates during the breeding season, such as breeding propensity and 30-day brood survival, particularly in relation to breeding densities of whistling-ducks. Personnel from Louisiana Department of Wildlife and Fisheries and Louisiana State University Agricultural Center report whistling-ducks displaying aggressive behavior, potentially discouraging wood ducks from accessing nest boxes and even attempting to drown wood duck broods. These observations present promising avenues for future research studies.

Chapter 6. An increase in daily bag limit did not change survival or harvest rates for box-nesting wood ducks in Louisiana

6.1. Introduction

In the early 1900s, wood duck (*Aix sponsa*) populations experienced a significant decline, largely due to unregulated hunting and the destruction of breeding habitat (Bellrose and Holms 1994). During this era, wood ducks were highly sought after by hunters, especially during spring hunts, and their meat was considered a culinary delicacy. Additionally, the extensive clearing of old-growth forests led to the loss of vital nesting sites as they are obligate cavity nesters. A pivotal moment for wood ducks occurred in 1918 with the establishment of the Migratory Bird Treaty Act, which made it illegal to hunt wood ducks and provided them with federal protection. This action, combined with the implementation of nest box programs aimed at supplementing nest sites across their range, played a vital role in facilitating population recovery. By 1941, wood duck populations had rebounded to the extent that controlled harvesting became feasible, and nest box programs were celebrated.

Today, numerous state wildlife agencies, including the Louisiana Department of Wildlife and Fisheries (hereafter, LDWF), actively manage wood duck populations through nest box programs (L. Reynolds, LDWF, personal communication). For example, since 1990, they have overseen approximately 2,000 nest boxes across the state to bolster local breeding populations and enhance hunting opportunities. Within these programs, nest boxes are equipped with predator guards, serving a dual purpose: safeguarding eggs from nest predators and reducing female mortality. Recognizing the critical role of reproduction in wood duck population dynamics (Hepp et al. 2020), ensuring the survival of females is critical for these programs to achieve their intended goals. However, it is important to emphasize that wood ducks are a game species, where there is a need to balance conservation efforts and harvest regulations.

When wood duck hunting reopened, states initially allowed the harvest of 1 bird daily during the open hunting season, a regulation that persisted until 1961. In 1962, hunters were allowed to harvest 2 birds daily (Bellrose and Holms 1994, Garrettson 2007). In 2007, an assessment of Atlantic and Mississippi flyway wood ducks indicated that these populations could tolerate an increase in the bag limit (Garrettson 2007). Consequently, since the 2008 hunting season, hunters have been permitted to harvest 3 wood ducks daily (Balkcom et al. 2010). This increase in bag limit was projected to increase the harvest rate of adult male wood ducks by 7.1%; however, research regarding adult females is lacking. Such research is essential, as the increased harvest could potentially impact female survival, potentially jeopardizing the success of nest box programs. Here, I assess the most recent increase in the bag limit by comparing survival and harvest rates before and after the change to gain insights into its potential impacts on box-nesting wood ducks in Louisiana.

6.2. Methods

Nest boxes were routinely inspected at least twice a year: first in January at the onset of the breeding season and again in April when females began renesting (L. Reynolds, LDWF, personal communication). In addition to these scheduled checks, nest boxes were also opportunistically examined between January and July. During checks, damaged nest boxes and predator guards were either repaired or replaced. Females were captured and banded with aluminum United States Geological Survey leg bands. Personnel from LWDF recorded the band number for any individuals that were recaptured from nest boxes during subsequent breeding seasons. Females were aged as being a second-year breeder (i.e., first breeding season alive as an adult), a after second-year breeder (i.e., ≥ 2 breeding seasons alive as an adult), or after hatch year (i.e., ≥ 1 year old). I acquired data from the Bird Banding Laboratory (hereafter, BBL) for individuals that were marked and recaptured from nest boxes during 2001−2014. Additionally, I obtained information regarding individuals that were harvested by hunters from the BBL. The BBL possessed few records of females that were recaptured from nest boxes; therefore, I obtained paper copies of such records from LDWF and entered these data manually.

I analyzed these data using a Bayesian live-dead model (hereafter, LD model; Burnham 1993, Lebreton et al. 1999, Kéry and Schaub 2012). The LD model provides estimates of survival (S), fidelity (F), recapture (p), and reported mortality (r; Kéry and Schaub 2012). S is the true survival probability because it accounts for emigration outside the sampling area. F is probability that an individual remains faithful to the banding area. p is the probability that an individual will be recaptured from a nest box given it is alive and in the study area. r is the probability that a dead individual is found and reported. Estimates from LD models lack biases when p and r are ≥0.20 and ≥0.10 (Weegman et al. 2020).

I executed the LD model using a multi-state framework, where female i took on one of the following four states: alive in study area, alive outside study area, recently dead, and dead (Figure 6.1; Kéry and Schaub 2012). These comprised the state transition matrix (Ω):

$$z_{i,t+1}|z_{i,t} \sim categorical(\Omega_{zi,t,1\ldots s,i,t}),$$

where the true state of individual i at time t was $z_{i,t}$. I used the categorical distribution to predict the probability that individual i was in state s at time t + 1 ($z_{i,t+1}$) given its current state ($z_{i,t}$). I linked the state transition matrix to my field observations, where individual i was able to be detected in one of the following observational states (o): seen alive, recovered dead, not seen or recovered (Figure 6.1). These states made up the observation matrix (θ):

$$y_{i,t}|z_{i,t} \sim categorical(\theta_{z_{i,t},1\ldots o,i,t}),$$

where the observed state of individual i at time t was $y_{i,t}$, given its current true state ($z_{i,t}$). I used my observation matrix to estimate p using the categorical distribution. I did not include r in θ matrix but did include it Ω, as this was a workaround to handle an issue during model updating (Kéry and Schaub 2012). Important to the framework I used is that only recently dead individuals can be recovered as dead. I pooled all my data into a single age class and did not separately estimate survival for second year and after second year breeders.

I fit the LD model in JAGS (Plummer 2003) using the R2jags (Su and Yajima 2021) package in Program R 4.2.2 (R Core Team 2023). I considered annual inconsistencies in sampling efforts by including year as a random effect in the model. I used uninformative uniform (0,1) priors for S, F, p, and r (Kéry and Schaub 2012, Hoobs and Hooten 2015). I used the normal distribution with a mean of 0 and variance (σ^2) to obtain estimates of annual variation. I ran 4 chains of 50,000 iterations, after considering 25,000 as burn-in, and saved every twentieth iteration. I confirmed my models converged via inspection of trace plots and by using the Gelman-Rubin statistic, where a $\widehat{R}$ value < 1.05 indicated convergence (Gelman and Rubin 1992). I report means (μ) and 95% credible intervals for the LD model. I used posterior means and standard deviations to calculate the coefficient of variation (hereafter, CV) for each parameter to provide measures of precision.

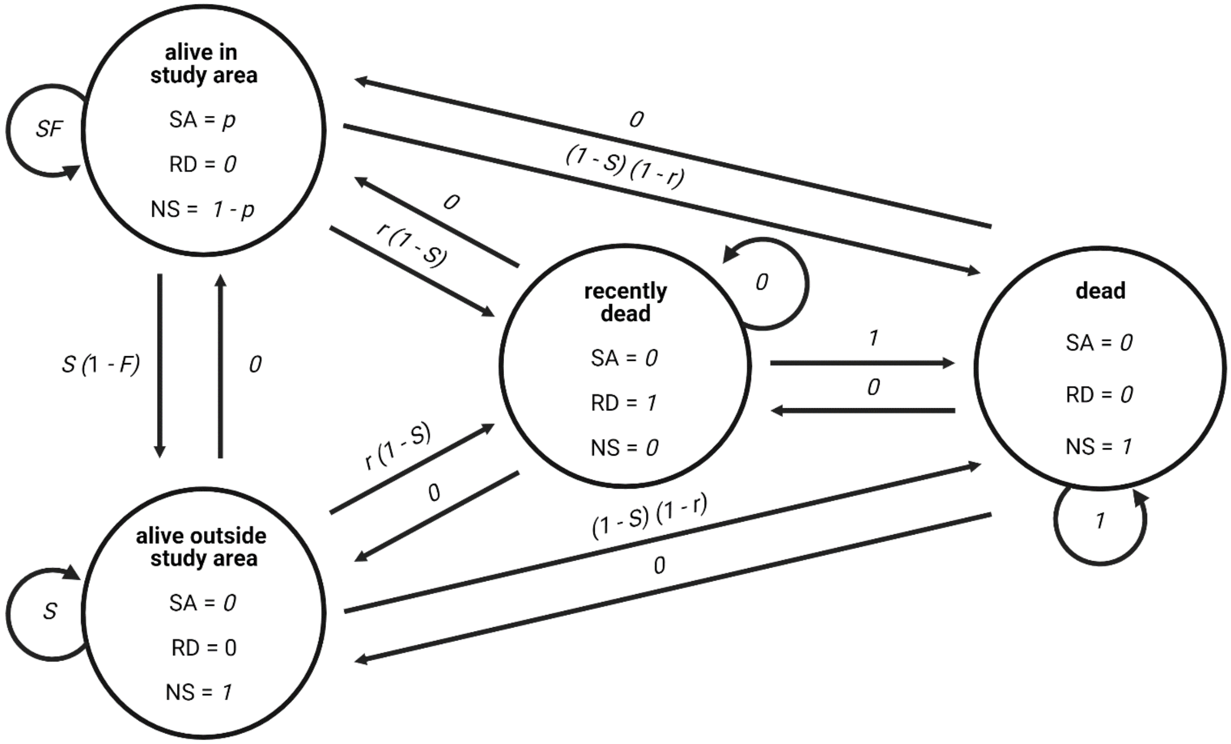

Figure 6.1. Conceptual diagram outlining the probabilities considered in state transition and observational matrices for a live-dead survival model of box-nesting wood ducks (*Aix sponsa*) in Louisiana. Alive in study area, alive outside study area, recently dead, and dead, were the states individuals could be in and made up the state transition matrix. The arrows represented the state transition probabilities where movement among states depended on survival (S), fidelity (F), and reported mortality (r) probabilities. The observational states were seen alive (SA), recovered dead (RD), and not seen or recovered (NS). The state individuals were observed in depended on recapture (p) probability (shown inside circles).

6.3. Results

From 2001–2014 a total of 6,182 female wood ducks were banded from nest boxes and 1,137 recaptures were made during subsequent breeding seasons (Figure 6.2). During the same years, 473 individuals were harvested by hunters and 147 were direct recoveries (Figure 6.2). My LD model successfully converged according to trace plots and $\widehat{R}$ values. For the entire study period, mean S was 0.684 (CI = 0.618, 0.951), mean F was 0.735 (CI = 0.488, 0.970), mean p was 0.281 (CI = 0.156, 0.415), and mean r was 0.101 (CI = 0.067, 0.379). The CV was 0.116 for S, 0.140 for F, 0.239 for p, and 0.845 for r. Estimates of all four parameters were similar following the increase in daily bag limit (Figure 6.3). The mean harvest rate was 0.032 (CI = 0.027, 0.038) during the study period and ranged from 0.012− 0.038. The average annual harvest rate prior to 2008 and was 0.033 (CI = 0.023, 0.043) and 0.031 (CI = 0.026, 0.036) after the bag limit increase (Figure 6.4).

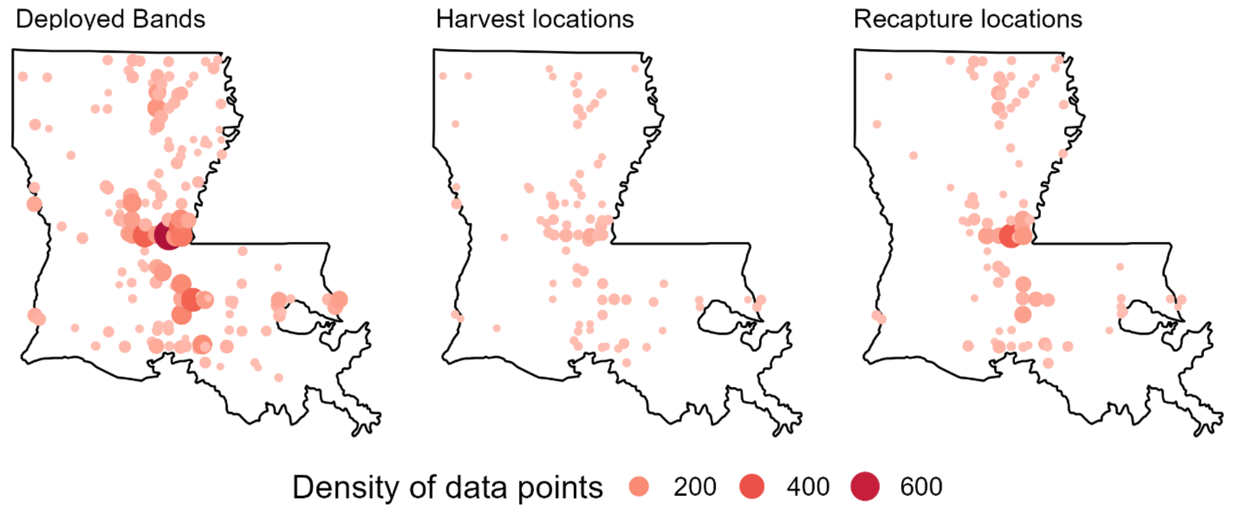

Figure 6.2. Louisiana maps showing the locations where adult female wood duck (*Aix sponsa)* bands were deployed, recovered by hunters, and recaptured by banders from 2001−2014.

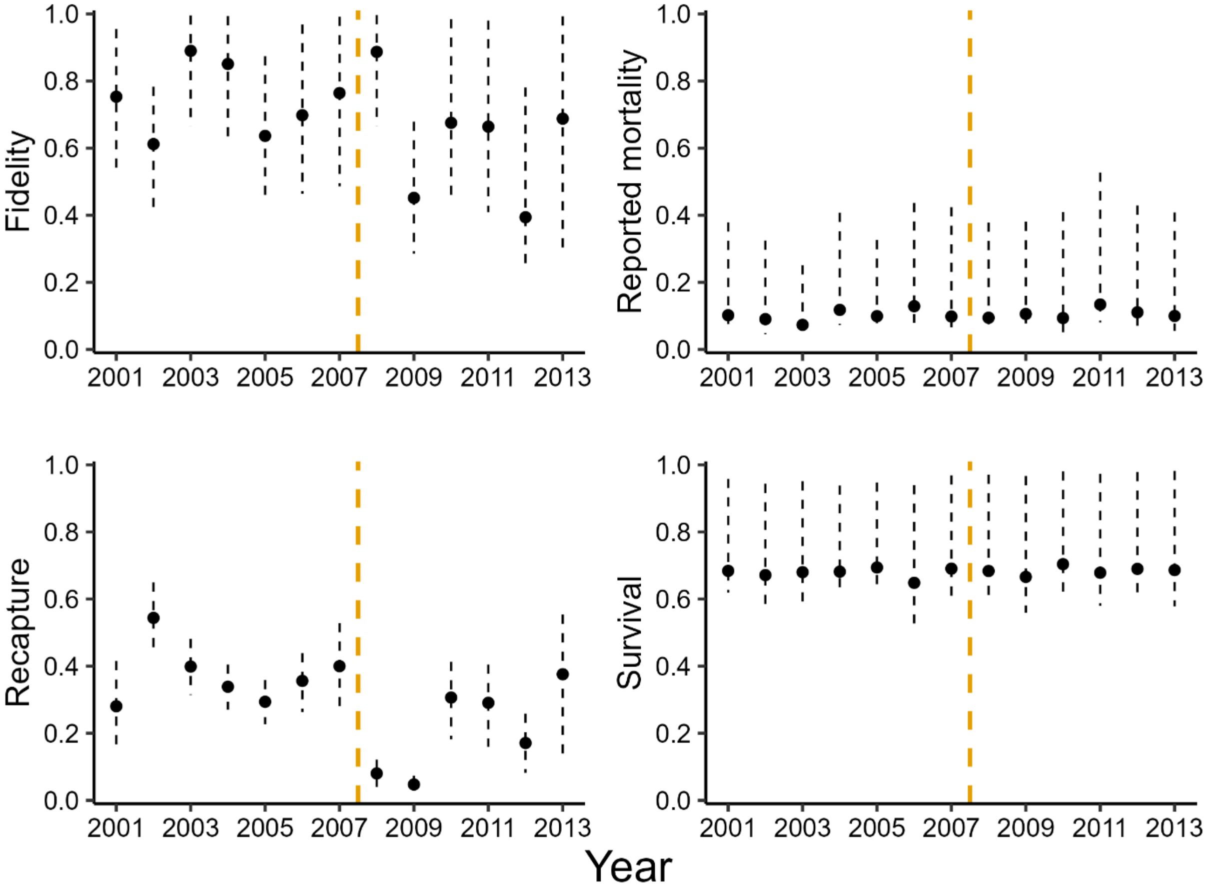

Figure 6.3. Probabilities of survival, fidelity, recapture, and reported mortality for female wood ducks (*Aix sponsa*) captured and banded from nest boxes in Louisiana from 2001− 2014. The black dots represent posterior means and dashed lines show 95% credible intervals from a Bayesian live-dead analysis.

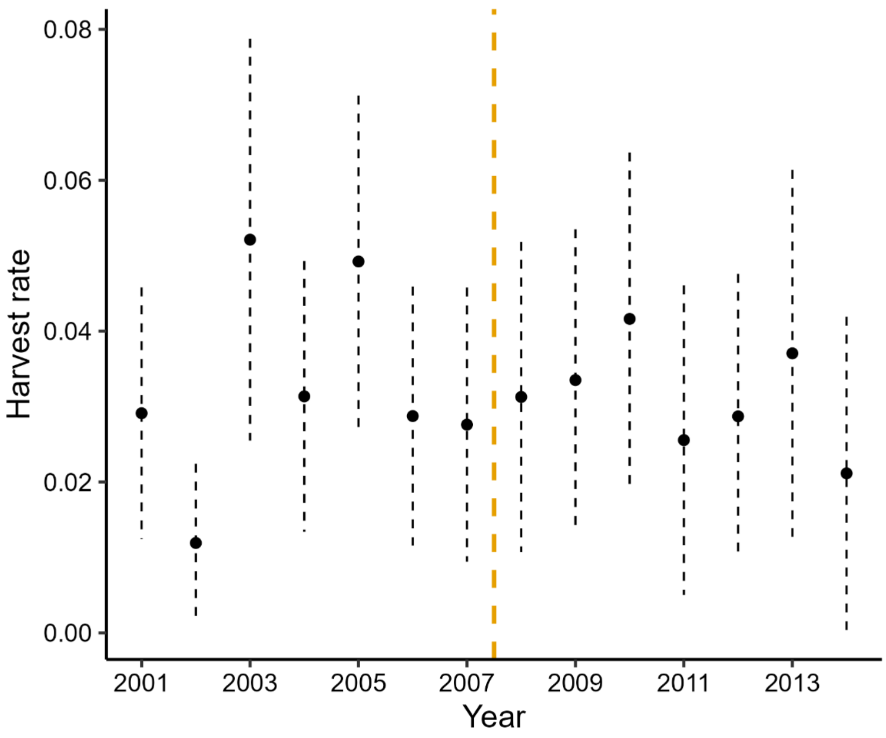

Figure 6.4. Harvest rate estimates for wood ducks (*Aix sponsa*) captured and banded from nest boxes in Louisiana from 2001− 2014. The back dots are means and the dashed lines show 95% confidence intervals.

6.4. Discussion

My results suggest that increasing the daily bag limit from 2 to 3 birds had a minimal effect on the survival of box-nesting wood ducks. Likewise, fidelity, recapture, and reported mortality probabilities were similar before and after the bag limit increase. Annual harvest rates were comparable before and after the bag limit increase, suggesting hunting related mortality for box-nesting females did not increase. Previous studies conducted in the southeastern United States have produced annual survival estimates for box-nesting wood ducks (Hepp et al. 1987, Dugger et al. 1999). Annual survival estimates are inclined to be biased low because they do not allow for emigration out of the study area. Despite this limitation, annual survival was 55% for box-nesting wood ducks in South Carolina (Hepp et al. 1987) and 63% in Missouri (Dugger et al. 1999), which closely resembled the mean annual survival rate of (68%) my study population. The resemblance between apparent and true survival estimates is likely due to the strong fidelity exhibited females to their nest box populations, were only a small portion of banded females leave their natal nest box populations. I observed high rates of fidelity which averaged 74%. These findings align with Hepp and Kennamer (1992), who reported that 80% of adult females remained faithful to their nest box population.

My results do not agree with one recent study from Ohio that found adult and juvenile female survival decreased by 8% and 4% following the increase in bag limit (Shirkey and Gates 2020). Likewise, my findings are not supported by Trost (1988) who found survival was lower during years when harvest rates were high in the southeastern United States. One major difference between my analysis and these studies aimed at evaluating survival in relation to harvest is the data used. I used data collected during the breeding season for wood ducks marked from nest boxes, while other studies have used preseason band data (Trost 1988, Garrettson 2007, Shirkey and Gates 2020). My results may have differed if I had utilized Louisiana preseason band data, as such a dataset encompasses individuals that nest in natural cavities, which might result in distinct survival rates during the breeding season when compared to nest boxes equipped with predator guards. Therefore, my results are only applicable to the box-nesting wood ducks.

Harvest rates remained consisted over the study period and were slightly lower than estimates for adult female wood ducks in Ohio (7%; Shirkey and Gates 2020) and the Atlantic flyway (7%; Zimmerman et al. 2017). The lower harvest rate estimates from my study can be explained by findings from several other studies. First, adult female wood ducks are less vulnerable to harvest compared to other sex-age cohorts (Garrettson 2007), which likely explain why survival and harvest rates were unaffected by the bag limit increase. Secondly, my study population consisted of resident females (Bellrose and Holms 1994, Baldassarre 2014), which allows them to inhabit areas they are familiar with year-round, thus avoiding being harvested by hunters (Bowers and Martin 1975). Next, Balkcom et al. (2010) suggested the greatest change in harvest rate would be observed when increasing the bag limit from 1 to 2 birds, which occurred in 1962, while increasing the limit to 3 birds daily would result in a lessor change in harvest rate. Lastly, in Fallon, Nevada harvest rates remained similar during experimental hunting seasons, when the daily bag limit was increased to 7 birds (Sedinger et al. 2019), providing further evidence that even when bag limits are increased, harvest rates do not always change.

Given Louisiana is a wintering area for northern latitude wood ducks, future research should determine the major natal regions of wood ducks harvested by hunters. It is likely that wood ducks born outside Louisiana are the primary source of birds harvested by hunters. Knowing such information would allow managers to allocate additional efforts to conserve these populations. For local breeding box-nesting wood ducks, my results suggest the increase in bag limit has provided additional harvest opportunities, without altering the survival of these populations.

Chapter 7. Conclusions

My research explored the breeding ecology of cavity-nesting ducks in Louisiana, which is particularly timely given the rapid range expansion of black-bellied whistling-ducks into the southeastern United States. I observed high rates of conspecific and interspecific brood parasitism where that latter was a result of sympatric nesting among wood ducks, hooded mergansers, and whistling-ducks that occurred for approximately 3 months of the breeding season. My research was the first to document whistling-ducks hatching mixed-species broods. I observed high hatchability rates across varying clutch sizes which demonstrates the high reproductive success of whistling-ducks, a factor that may be a contributing to their expanding range.

I demonstrated red-bellied woodpeckers were a previously under-recognized predator of wood duck eggs during the laying and incubation periods. Wood ducks were observed actively removing depredated eggs, showcasing their adaptability to this phenomenon. Our findings highlight the need for a more comprehensive understanding of woodpecker behavior and its impact on wood duck productivity. Moving forward, nest box programs should consider avoiding sites where woodpeckers are present.

I uncovered valuable insights into IBP occurring between wood ducks and hooded mergansers in Louisiana and Mississippi. I found parasitic wood duck eggs laid in hooded merganser nests experience lower survival rates compared to parasitic hooded merganser eggs in wood duck nests. I hypothesize this finding is attributed to differences in eggshell strength, where hooded merganser eggs are more resilient to accidental breakage or depredation by woodpeckers. This research highlights the species-specific, host-dependent, and contextual nature of waterfowl nest parasitism.

I monitored over a thousand wood duck nests and found that approximately 8% were parasitized by mergansers and 11% by whistling-ducks. Surprisingly, daily nest survival rate (hereafter, DSR) for nests parasitized by whistling-ducks was comparable to clutches containing only wood duck eggs, while clutches with parasitic hooded merganser eggs had lower DSR. I found IBP did not have a detrimental effect on duckling recruitment, with most recruits originating from nests initiated earlier in the season. These findings contribute to our understanding of the complex interplay between cavity-nesting waterfowl species and their reproductive strategies, highlighting the resilience of wood ducks in the face of interspecific brood parasitism.

I investigated the impact of increasing the daily bag limit from 2 to 3 birds on box-nesting wood ducks in Louisiana and found it had a minimal effect on the survival and harvest rates. The consistency in harvest rates suggest that hunting-related mortality for box-nesting females did not increase significantly. Overall, the increase in the bag limit appears to have provided additional harvest opportunities for wood duck populations in Louisiana without compromising their survival.

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Vita

Dylan L. Bakner grew up in Mont Alto, Pennsylvania. During his childhood, he spent each fall trapping furbearing species with his father, grandfather, and brother, where he developed a passion for wildlife. Dylan obtained a B.S. in Wildlife and Fisheries Science from Pennsylvania State University in 2016. Following his undergraduate education, he spent his summers working with waterfowl in the prairie pothole region, receiving employment through North Dakota Game and Fish Department and Delta Waterfowl Foundation. During the fall and winter months, he worked for Virginia Department of Wildlife Resources to band American black ducks. Dylan started his Ph.D. at Louisiana State University in 2019 examining breeding season productivity of cavity-nesting waterfowl using nest boxes. Dylan plans to receive his Ph.D. in December 2023 and hopes to continue working as an avian researcher in an academic workplace.