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Breeding Ecology of Mottled Ducks in Southwestern Louisiana

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BREEDING ECOLOGY OF MOTTLED DUCKS IN SOUTHWESTERN LOUISIANA

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Abstract

Mottled ducks are a resident species found in the southern United States that rely on coastal marsh and associated habitat to fulfill the needs of the entirety of their annual cycle. Population monitoring has revealed declines in western Gulf Coast (WGC) mottled ducks since 2008. Mottled duck populations are influenced by survival and recruitment, and changes in these factors may contribute to population declines. The overarching goal of this project was to identify the mechanisms potentially limiting WGC mottled ducks.

I captured adult female mottled ducks during molt on Rockefeller Wildlife Refuge and adjacent lands in southwestern Louisiana from 2017–2019. I marked 148 individuals with a backpack solar-powered GPS-GSM transmitter and monitored them throughout the year for mortality and nest attempts. I used a Known Fate model in Program MARK to determine annual and seasonal survival and how survival varied temporally and spatially. Mottled duck survival was best explained by maximum partitioning of the year by the hunted periods and biological seasons and the proportion of GPS locations in agricultural land. Annual survival in this study was 0.60–0.64, one of the highest estimates for WGC mottled ducks.

I identified 29 nest attempts during the breeding seasons 2018–2020. I used the nest survival model accessed through RMark to obtain daily survival rates of nests and evaluate the effect of local and landscape-level characteristics on survival. Nest survival varied positively with vegetation density. Lastly, I matched used nest sites with random locations within the home range of the female to examine nest site selection. Nest site selection varied by habitat type and vegetation density. Old fields were most likely to be selected, while emergent marsh was least likely to be selected. Probability of use also varied positively with vegetation density. During this study, survival estimates were similar to that of waterfowl species not experiencing declines and

nest success and renesting propensity were relatively high. Nesting propensity was very low and future research should further investigate cues mottled ducks use to initiate nesting.

Chapter 1. Breeding Ecology of Mottled Ducks: A Review

1.1. Introduction

Mottled ducks (*Anas fulvigula*) are endemic to the Gulf Coast of North America and are non-migratory throughout their range. Accordingly, most mottled ducks rely on locally available habitat to completely fulfill their needs throughout the annual cycle (Stutzenbaker 1988), and as southern residents, they face threats to survival and reproduction that most migratory ducks avoid. These include predation from growing populations of American alligators (*Alligator mississippiensis*) and Burmese pythons (*Python molurus bivittatus*), wetland loss and degradation, lead toxicity, extreme heat and humidity, and increasingly powerful tropical storms that can inundate large swaths of breeding and molting habitat and alter salinity levels overnight (Wilson 2007). There are 2 genetically (McCracken et al. 2001, Peters et al. 2016, Lavretsky et al. 2014) and behaviorally (Varner et al. 2013) distinct populations that are associated with the Gulf Coast states: the Florida population, which inhabits the central and southern portion of the state, and the western Gulf Coast (WGC) population, which occupies the coast from Alabama stretching west to the Laguna Madre of Mexico (Baldassarre 2014; Figure 1.1). As evidenced by the lack of band recoveries from reciprocal areas, there is little to no exchange between these 2 populations (Wilson 2007). From 1975–1982, land managers translocated >1,200 mottled ducks derived from both source populations (the majority were from the WGC population) to establish the species in the Santee River Delta and the Ashepoo, Combahee, and Edisto River Basin of South Carolina for hunting opportunity. Currently, these introduced birds breed in coastal areas near Savannah, South Carolina and the Altamaha Wildlife Management Area in Georgia (Weng

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2006), but reliable estimates of population abundance are lacking, and hybridization with game-farmed mallards (*Anas platyrhynchos*) is rampant (Williams et al. 2005). In Florida, mottled ducks also readily hybridize with feral mallards (Williams et al. 2005), so although there have been historical surveys of breeding mottled ducks in Florida, these data are now considered unreliable and as future surveys are conducted, a correction factor will be applied to account for the proportion of feral mallards and hybrids in the population (Florida Fish and Wildlife Conservation Commission 2011). Along the western Gulf Coast, breeding mottled ducks have lower rates of hybridization (Ford et al. 2017) and have been surveyed annually since 2008. Mottled duck populations in Louisiana and Texas have declined since the survey began, and the mottled duck population in Louisiana is now estimated to be less than half of what it was a decade ago (Figure 1.2).

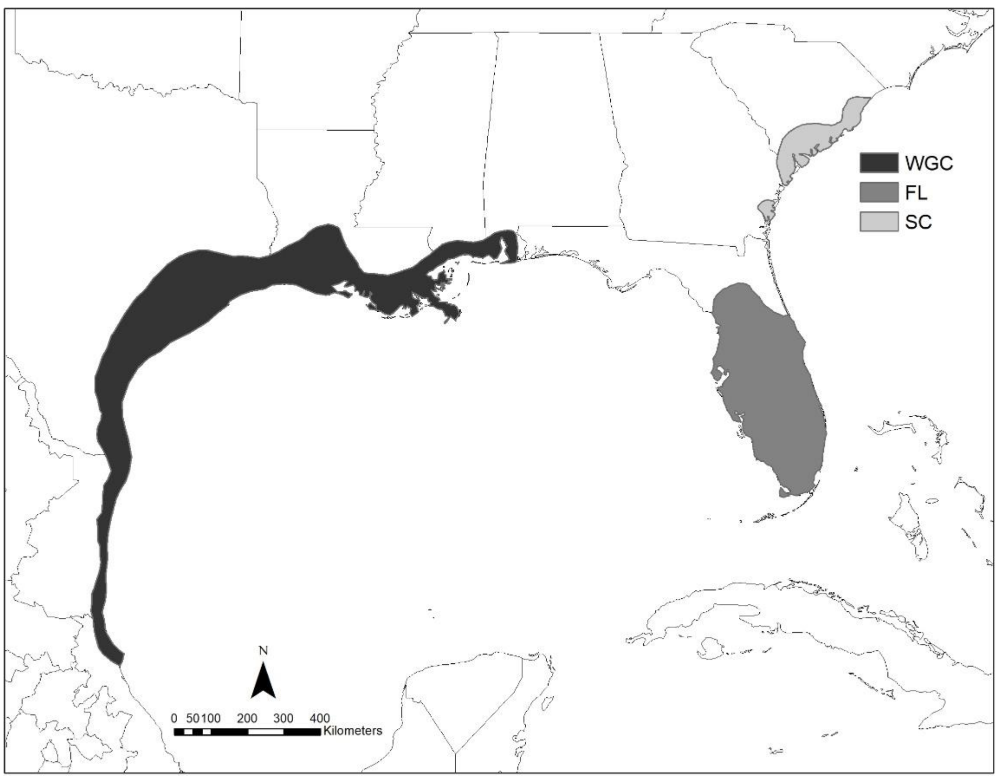

Figure 1.1. Mottled duck range in 2021, parsed by western Gulf Coast (WGC), Florida (FL), and south Atlantic (SC) populations.

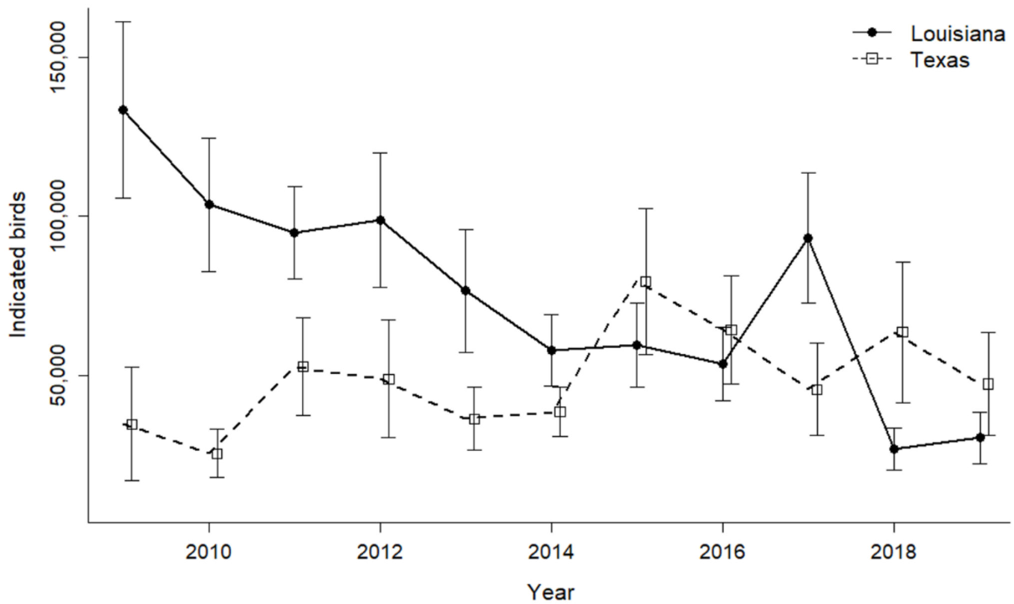

Figure 1.2. Western Gulf Coast mottled duck population estimates during the breeding population survey, 2009–2019 (excludes the Laguna Madre region of TX; U.S. Fish and Wildlife Service 2019).

Using band recovery data and age ratios for birds harvested in Louisiana and Texas 1994–2006, Johnson (2009) reported that the mottled duck population was in decline (population growth rate [λ] = 0.82) and annual survival accounted for >60% of the variation in population growth rate but was unable to evaluate the influence of individual vital rates, such as nesting propensity, nest success, re-nesting effort, and brood survival, on population growth rate. Rigby and Haukos (2014) directly incorporated reproduction vital rates with survival estimates and their elasticity analysis identified fertility as having the largest effect (r^2 = 0.675) on population growth, where nesting propensity (r^2 = 0.322) and nest success (r^2 = 0.200) were the most important components. Recruitment of mottled ducks is low compared to other dabbling duck species (Johnson 2009) and does not meet the recruitment level of 0.91 necessary to maintain a stable population (Rigby 2008), which indicates that changes in recruitment may be the primary reason for the recent decline in mottled duck populations. Researchers of nearly 50 publications attempted to address various aspects of mottled duck breeding season ecology and population dynamics since the 1970s.

I reviewed the literature on mottled duck breeding ecology. My goals were to translate results from disparate studies into common metrics to help parse geographic variation in vital rates; where possible, synthesize information across studies to develop generalizations about mottled duck ecology and facilitate comparisons with other dabbling ducks; and identify important knowledge gaps for future research endeavors.

1.2. Study area

The range of the mottled duck is restricted to the southern United States. The Florida mottled duck population inhabits the central and southern portion of the state, and the WGC population occupies the coast from Alabama stretching west to the Laguna Madre of Mexico (Baldassarre 2014; Fig. 1). Additionally, there is a small breeding population located in the Santee River Delta and the Ashepoo, Combahee, and Edisto River Basin of South Carolina and the Altamaha Wildlife Management Area in Georgia (Weng 2006).

1.3. Methods

I conducted my literature review using Google Scholar by searching a combination of key terms including mottled duck, breeding incidence, breeding season survival, nest success, habitat use, brood, and nesting ecology. I followed citation trees in those papers both forward and backward to identify other relevant research, and also sought advice from colleagues knowledgeable about historical studies of mottled ducks.

1.4. Breeding habitat use

Second-order habitat selection (i.e., home range; Johnson 1980, Eichholz and Elmberg 2014) for breeding dabbling ducks is shaped by habitat availability and territoriality (Lokemoen et al.

1984, Eichholz and Elmberg 2014). Thus, habitat selection may be constrained for species in some geographies, forcing pairs into sub-optimal territories (Seymour 1992). Mottled ducks are the only ground-nesting dabbling duck to breed in abundance along the Gulf Coast (Baldassarre 2014), and the vast stretches of wetlands and grasslands available imply that choice of a breeding home range is less constrained than ducks breeding at northern latitudes in North America. Moreover, because mottled ducks are non-migratory but locally nomadic (Davis 2012, Moon et al. 2015), they should be knowledgeable about breeding habitat, relative to migratory ducks returning to the breeding grounds after a year-long absence.

On the western Gulf Coast, breeding mottled ducks are most common in the coastal marshes of Louisiana and Texas (Stutzenbaker 1988). In the Chenier Plain region of Texas and Louisiana, pre-breeding mottled ducks selected coastal marsh, freshwater ponds, and pasture. A combination of salinity, vegetation, and land management, such as ranching, water manipulation, and prescribed burns, influenced this selection (Moon 2014), with shifts in habitat use as the breeding season progressed. Davis (2012) characterized salinity gradients by plant communities and reported that in Louisiana, pair densities were highest in freshwater marsh, but the use of intermediate marsh relative to its availability was highest, followed by brackish and freshwater marsh. Similarly, in Texas mottled ducks showed preference for estuarine and palustrine marsh, as opposed to cropland (Davis 2012), but in the Texas Chenier Plain, Haukos et al. (2010) reported that mottled duck pairs selected freshwater ponds. Pairs used freshwater ponds 13.1% of the time although they composed 1.1% of the ponds available on the landscape and used ponds of other salinity levels in proportion to their availability. Mottled ducks also selected for ponds with short surrounding vegetation (<0.6 m) often associated with grazing and avoided ponds with medium to tall vegetation. The common finding of these studies is that mottled ducks used wetlands with a lower salinity during the breeding season compared to other times of the year (Haukos et al. 2010, Davis 2012, Moon 2014). Inland pasture, particularly the stock ponds and potholes within pasture, may be important in times of drought and after tropical disturbances when storm surge increases the salinity of coastal marsh (Wehland 2012, Moon 2014). Late in the breeding season, mottled ducks increasingly use agricultural land, such as rice, where water conditions may be more stable (Stutzenbaker 1988, Davis 2012).

Mottled ducks captured in the rural Everglades Agricultural Area in southeast Florida used agricultural landscapes, mainly drainage ditches in sugarcane fields, but also citrus and other row crops, and freshwater, non-forested glades marsh at the onset of the breeding season. In the Upper St. Johns River Basin, mottled duck use of ponds and canals equaled that of marsh during the reproductive period, perhaps because pond and canal patches are smaller and easier to defend from intruding pairs compared to marshes (Bielefeld 2002). Mottled ducks avoided artificial impoundments, reservoirs, forested wetlands, and uplands during the breeding season (Johnson et al. 1991, Varner 2013). Mottled ducks in Florida also used urban habitat, such as residential areas, golf courses, and roadsides and those mottled ducks captured in urban areas did not disperse to agricultural areas but instead remained in urban areas for the duration of the breeding season. Mottled ducks in rural areas typically did not move into urban areas (Varner 2013); however, similar to the WGC population, during times of drought, mottled ducks may shift habitat use. Mottled ducks in rural areas may move to urban-suburban wetlands to take advantage of stable wetland availability (Bielefeld and Cox 2006) or use a wider variety of land cover types (e.g., ponds, canals, flooded pasture, marsh; Bielefeld 2002).

In contrast to WGC and Florida populations, mottled ducks in South Carolina and Georgia selected for managed impoundments during the breeding season (Pollander et al. 2019), specifically those in brackish salinity zones as opposed to fresh or saline impoundments (Shipes et al. 2015). Impoundments used by breeding mottled ducks were characterized by brackish salinity, stable water levels, and hemi-marsh vegetation structure composed of dwarf spikerush (*Eleocharis parvula*) and wigeongrass (*Ruppia maritima*; Shipes 2014, Pollander et al. 2019). Mottled duck preference for brackish water over freshwater in South Carolina stands in stark contrast to WGC and Florida populations, and a better understanding of habitat quality (food, cover, water stability) in impoundments of varying salinity may shed further light on this discrepancy.

Scientists have a basic understanding of mottled duck breeding habitat preferences throughout their range. Additional longitudinal work is necessary to understand how preferences may shift during years of poor habitat quality, such as drought; will mottled ducks shift geographies to locate fresher water, or accept higher salinities in preferred breeding areas? This is especially relevant in the face of climate change and associated sea-level rise. There also seems to be geographical variation in mottled duck tolerance for various types of disturbance (e.g., agricultural and urban disturbance in Florida), but this has not been rigorously quantified. Disturbance has not been a research focus for the WGC population of mottled ducks because many nesting areas have a low human population density; nevertheless, roads, oil and gas activity, and human development (Skaggs et al. 2020) have the potential to influence breeding mottled ducks.

1.5. Nesting ecology

1.5.1. Nesting propensity

Measured at a population level, nesting propensity is the proportion of females that attempt to nest in a breeding season. The decision to nest or forgo breeding in any given year can be a strategy to optimize lifetime reproductive success (Devries et al. 2008). That decision may be influenced by environmental conditions on the breeding grounds, such as habitat suitability, weather, and food availability, because females must accumulate the resources necessary for egg production and successful incubation (Sedinger and Alisauskas 2014). For example, mallards in relatively poor body condition were less likely to breed than those in better body condition and initiated nests later in the season (Devries et al. 2008, Dugger et al. 2016). Body condition in turn is influenced by environmental conditions that affect food availability. Thus, in areas of little water and poor habitat quality, nesting propensity may be lower (Warren et al. 2014).

Mottled duck researchers report large variation in nesting propensity across years and geographies that is tied to the interaction between environmental conditions and resultant female body condition. In drier years, both mottled duck female mass at capture and nesting propensity were lowest, at 867 g and 22–27% respectively, compared to 893–898 g and 30–56% in other years (Dugger et al. 2010). In southwest Louisiana in a drought year, females did not lay eggs until farmers flooded the nearby rice fields; prior to flooding, there were few suitable wetlands available, which likely reduced perceived suitability of brood habitat or foraging areas where breeding females could acquire the nutrients necessary for the nesting period (Durham and Afton 2006). In a 3-year study conducted on the upper Gulf Coast of Texas, nesting propensity ranged from 15%, the lowest recorded estimate for this parameter, to 63%, the second highest recorded estimate (Rigby and Haukos 2012). The highest nesting propensity estimates, 77% in the mid Gulf Coast, and 63% in the upper Gulf Coast of Texas both occurred when drought indices indicated average environmental moisture (abnormally wet years did not occur during these studies; Finger et al. 2003, Rigby and Haukos 2012). Nesting propensity estimates for mottled ducks in Florida are similar to birds in the WGC population, ranging from 22–56% (Dugger et al.

2010, Varner et al. 2013). Over all studies, mottled duck nesting propensity ranged from 15–77%, typically falling below the 95–100% observed in mallards when conditions are favorable (Hoekman et al. 2002, 2006). For mallards nesting in the prairie parklands, even birds in poor body condition had a nesting propensity range of 60–80% (Devries et al. 2008). An improved understanding of how nesting propensity varies with environmental conditions is needed so that managers may be able to target the cues and improve habitat to increase nesting propensity (Rigby and Haukos 2012).

1.5.2. Nest-site selection

Predation is the primary cause of nest failure in ducks (Greenwood et al. 1995), so it is important for waterfowl species to select nest sites that minimize exposure to predators, often through lateral vegetative concealment (Borgo and Conover 2016). Early studies documented that mottled ducks in coastal Texas and Louisiana nested in dry cordgrass (*Spartina* spp.) meadows (Baker 1983, Stutzenbaker 1988); however, in areas of flooding mottled ducks may elevate their nests within vegetation or on plant litter (Finger et al. 2003). In 1 study, mottled ducks also nested over water in flooded wetlands, specifically in marsh dominated by giant cutgrass (*Zizaniopsis milliaceae*), and built their nests up using residual vegetation (Bonczek and Ringelman 2019). Along the Mississippi River Delta and Atchafalaya River Delta, mottled ducks nested more than expected on islands, canal banks, pastures, and river levees in mixed grassland and shrub landscapes (Holbrook et al. 2000, Walters et al. 2001), which might take the place of the cordgrass meadows most frequently used in Texas (Stutzenbaker 1988) and southwest Louisiana (Baker 1983). Mottled ducks nesting on the deltas avoided shrub-sparse land cover composed of bare ground and minimal vegetation, which likely lacked adequate cover for nesting females (Holbrook et al. 2000). Mottled ducks that nested farther from the coast where agricultural land was common, selected idle fields that had been untilled for >3 years and pastures with knolls managed for grass forage (Durham and Afton 2003). Mottled ducks have been observed nesting on marsh terraces, a marsh restoration technique designed to reduce wave action, fetch, and turbidity and slow marsh erosion (Brasher et al. 2007); however, few quantitative data exist for mottled duck nest density or success on marsh terraces.

In contrast to mottled ducks in the WGC population, mottled ducks in Florida frequently nested in human-dominated areas such as neighborhoods, golf courses, parks, and commercial properties, selecting sites in small patches of native or ornamental vegetation (Varner et al. 2013). Mottled ducks in rural Florida nested in marsh, hayfields, native prairie, cattle pastures, and other agricultural areas including sugarcane and citrus groves (Varner et al. 2013). In South Carolina, all nests were located in unflooded managed impoundments, islets of emergent vegetation within flooded impoundments, or on impoundment levees; this area of the breeding range lacks the grassland prairie equivalent found along the Gulf Coast (Shipes 2014, Kneece 2016).

Across geographies, mottled ducks selected nest sites with greater percent vegetation, vegetation height, and vegetation density compared with the surrounding area (Varner et al. 2013, Kneece 2016). A greater diversity of plant species may add vertical and horizontal heterogeneity and therefore, offer greater concealment (Durham and Afton 2003). In addition to microhabitat nest-site characteristics, nest-site selection is also likely influenced by community-level factors such as invertebrate abundance, local predator populations, and competition with other locally nesting mottled ducks (Shipes 2014), which are more difficult to measure. Mottled ducks in Florida seem to have adapted to the loss of traditional nesting habitat by using urban areas (Varner et al. 2013), whereas mottled ducks in the WGC population are uncommon in urban areas. Pasture along the coast and farther inland are likely to be valuable nesting habitat for mottled ducks in the WGC population, so it would be beneficial for mottled ducks if cattle-stocking and grazing were managed to promote tall, dense stands of perennial grasses and forbs (Durham and Afton 2003). The majority of nest-site selection studies included marked individuals, so my understanding of nest-site preference may be biased based on capture location (e.g., Florida ducks captured in agricultural areas used agricultural areas). Unfortunately, it is difficult to systematically search for mottled duck nests in different landscapes and achieve sufficient sample sizes, so there are no easy solutions to this capture location bias. Studies following marked individuals have the potential to document adaptive shifts in nest-site selection over multiple attempts or multiple seasons (Ringelman et al. 2017). As land use continues to change, understanding mottled duck nest-site fidelity could lend insight into how good quality nesting habitat could shift into an ecological trap.

1.5.3. Nesting span

Mottled ducks have a protracted nesting season because they do not migrate, and nest in the mild climate of the Gulf Coast states. Across the range of mottled ducks, nesting begins as early as the end of January (Dugger et al. 2010), lasting through the beginning of August (Walters 2000); however, the latest hatch was observed in late December (Stutzenbaker 1988), effectively making this species a potential year-round breeder. Peak nest initiation typically occurs in March, April, and May (Varner et al. 2013). Nest initiation varies by year; Johnson et al. (2002) reported mean nest initiation to differ by 16 days between years (30 Apr 1994 vs. 14 Apr in 1995), whereas Grand (1992) reported a much greater difference of >60 days, resulting in no overlap of initiation dates (median initiation date of 7 May in 1986 vs. 28 Feb in 1987). This difference may be due to rainfall, which influences wetland availability. In Texas, females nested latest in the year with the lowest autumn and winter rainfall (Grand 1992). Similarly, in Florida, mottled ducks nested earlier in a wet year compared to a dry year, with mean initiation dates of 31 March and 20 May, respectively (Dugger et al. 2010). Rainfall may influence nesting chronology because the amount of water on the landscape affects the condition and availability of wetlands for pre-breeding nutrient acquisition (Johnson et al. 2002).

1.5.4. Egg laying

Clutch size averages 7.5–10.5 eggs (Durham 2001, Johnson et al. 2002, Varner 2013), with a maximum of 13 eggs (Stutzenbaker 1988). The first case of intraspecific nest parasitism (the addition of eggs to the nest of another female) was documented on a dredge spoil island of the Atchafalaya River Delta (Johnson et al. 1996). Holbrook (1997) further documented nest parasitism in the Atchafalaya, finding nests containing up to 23 eggs, and Walters (2000) also observed nest parasitism in the Mississippi River Delta. Rates of nest parasitism were marginally higher in the Mississippi Delta (4.4–8.9%; Walters 2000) than the Atchafalaya Delta (3.0%, Johnson et al. 1996; 3.5%, Holbrook 1997), which likely coincides with greater nest density on islands in the Atchafalaya. Many of the parasitized nests were located after mean nest initiation, suggesting that parasitism may be a strategy used by renesting females unable to produce a second full clutch (Walters 2000). Mottled duck eggs were found in laughing gull (*Leucophaeus atricilla*) nests in the Mississippi Delta on an island supporting large numbers of both mottled duck and laughing gull nests; however, there is no estimate for occurrence of interspecific parasitism because not all other nests were checked for the presence of duck eggs (Walters 2000). Because of the mismatch of incubation stage between parasitic eggs and nonparasitic eggs, egg hatchability of parasitized nests (68.8%) was lower than for unparasitized nests (92.3%; Walters 2000). Across all studies, egg hatchability ranged from 83.5% on the

Atchafalaya Delta (Holbrook 1997) to 96.2% in Texas (Singleton 1953).

1.5.5. Nest success

Mayfield nest success for mottled ducks ranges from 5.0% (Baker 1983) to 57.0% (Stieglitz and Wilson 1968; Table 1.1). The highest estimates of nest success occurred among the river deltas of Louisiana (Holbrook 1997, Walters 2000) and in coastal Florida (Stieglitz and Wilson 1968) where islands make up the primary nesting habitat and birds benefit from lower predator abundance because of the increased difficulty of access. In South Carolina, island size was the most influential variable on nest success. Islands with successful nests were on average over twice as large as those with unsuccessful nests, measuring 18.73 m^2 and 8.24 m^2, respectively (Shipes 2014). As sea levels rise and islands subside, mottled duck nests are also more prone to inundation. Caillouet (2015) conducted work on the Atchafalaya River Delta 17 years after Holbrook (1997), and reported that although nest predation remained low, nest flooding was common and was the primary source of nest mortality. As exemplified by these islands, certain habitats may become ecological traps for nesting females in the current era of human-induced environmental change. In interior Florida, mottled ducks nested in hayfields associated with dairy farms. Although females typically have enough time to successfully nest between mowing intervals, if nesting begins later in the interval, they may be destroyed by mowing (about 36% nests destroyed). Nests that were initiated later as vegetation approached a mean height of 69 cm were most vulnerable to destruction because of mowing (Dugger et al. 2010). Similarly, in the Mississippi River Delta, the greatest number of nests were found in cow pastures, but high stocking rates may cause the trampling of vegetation necessary for nest concealment, and disturbance by cattle and people may increase the abandonment of nests (Walters et al. 2001). In Florida, the majority of mottled ducks may nest in urban and suburban areas (Bielefeld 2008) and survival of urban nests did not differ compared to those located in other areas, despite high levels of human disturbance (Varner et al. 2013). Range-wide, many estimates of nest success (Table 1.1) fall below the 15% success deemed necessary to maintain populations of mid-continent mallards (Cowardin et al. 1985) and the 20% estimated to sustain dabbling duck populations with lower renesting rates (Klett et al. 1988). With nest success <15–20%, breeding pairs must immigrate into the population from other regions to sustain current numbers (Klett et al. 1988), which may not be possible given the limited movement patterns (Varner et al. 2014*b*) and distribution of mottled ducks.

Predation was the most prevalent cause of nest failure across mottled duck nest survival studies, although nest abandonment (Walters 2000) and flooding (Caillouet 2015) are important sources of mortality in some contexts. Although no studies to date have directly examined the effect of individual predator species on mottled duck nest survival, researchers attribute most nest predation to mammalian predators. Raccoons (*Procyon lotor*) are believed to be the most common predator of mottled duck nests (Stutzenbaker 1988, Holbrook 1997, Walters 2000, Dugger et al. 2010, Shipes 2014, Kneece 2016). Other mammalian predators include coyote (*Canis latrans*), striped skunk (*Mephitis mephitis*; Durham and Afton 2003), and armadillo (*Dasypus novemcinctus*; Stieglitz and Wilson 1968). Evidence of avian depredation was present in some studies and may be attributed to crows (*Corvus* spp.), grackles (*Quiscalus* spp.; Kneece 2016), or gulls (Laridae; Stieglitz and Wilson 1968). Snakes may account for partial clutch loss (Baker 1983, Finger et al. 2003), and alligators may also depredate mottled duck nests. Mottled duck eggs have been recovered in the stomach of alligators collected from Marsh Island State Wildlife Refuge, Louisiana, but because of the asynchrony of alligator diet studies and the timing

Table 1.1. Comparison of nest success estimates of mottled ducks across its range (adapted from Holbrook 1997, Durham and Afton 2003, and Kneece 2016).

Geography	Years	*n*	Nest success (%) Mayfield	Apparent	Reference
Merritt Island, Florida	1965–1967	90	57.0[a]	76.7	Stieglitz and Wilson (1968)
Interior Florida	1997–1999	25	9.5	16.0	Dugger et al. (2010)
Upper St. Johns River Basin, Florida	2000–2002	25	40.0	40.0	Bielefeld (2002)
ACE Basin, South Carolina	2011–2014	67	11.9	26.8	Kneece (2016)
Southeast Texas	1948–1949	51	11.0[a]	27.5	Engeling (1950)
Mid-coast, Texas	2000–2002	59		32.2	Finger et al. (2003)
Texas and Louisiana	1970s and 1980s	146	9.0[a]	24.7	Stutzenbaker (1988)
Cameron Parish, Louisiana	1981–1982	30	5.0[a]	16.6	Baker (1983)
Southwest Louisiana	1999–2000	66	6.0	21.0	Durham and Afton (2003)
Atchafalaya River Delta, Louisiana	1995–1996	265	30.6	47.5	Holbrook (1997)
Atchafalaya River Delta, Louisiana	2012–2013	>90		50.4	Caillouet (2015)
Mississippi River Delta, Louisiana	1998–1999	279	20.0	40.0	Walters (2000)

[a] Based on conversion as described by Green (1989).

of mottled duck nesting, there is little other evidence to evaluate the rates of nest depredation by alligators (K. N. Sloan, Louisiana Department of Wildlife and Fisheries, unpublished report). Assessing predator dynamics such as which predator species cause nest failure and how habitat components may influence nest success can help identify which areas are most productive for mottled ducks and guide conservation initiatives.

1.5.6. Renesting intensity

Renesting following the loss of a clutch is common in dabbling ducks, and a high rate of renesting is an important component of annual recruitment (Arnold et al. 2010). The decision of an individual to renest and how quickly after nest failure is primarily dictated by the age of the nest at the time of loss, habitat conditions, food availability (Grand and Flint 1996), and initiation date (Arnold et al. 2010). Relative to most other duck species, mottled ducks have a longer breeding window in which to renest, and may not be as constrained by limiting resources or changes in environmental conditions. Mottled ducks in the WGC regularly renest at least once, and although likely rare, have been observed renesting up to 5 times (Engeling 1950, Stutzenbaker 1988). In Texas, the interval between subsequent attempts averaged 16 days, with a range of 0–36 days (Finger et al. 2003). Although observed in other waterfowl species (Olsen et al. 2003, James et al. 2012), mottled ducks have not been documented renesting upon successfully hatching a clutch or rearing a brood (Finger et al. 2003). Observations of renesting attempts have been made throughout the mottled duck range (Finger et al. 2003, Dugger et al. 2010, Varner 2013); however, more investigation is needed to determine how the extent of renesting, one of the most poorly understood reproductive parameters in birds (Arnold et al. 2010), affects mottled duck populations, and how this may be influenced by environmental conditions.

1.6. Brood ecology

1.6.1. Brood and duckling survival

Survival of hatched offspring is affected by food availability, predation, and weather (Pietz et al. 2003). Most brood mortality in dabbling ducks occurs during the first 2 weeks (Reed 1975, Baker 1983), whereas survival after day 18 is high and most ducklings survive to fledge (Orthmeyer and Ball 1990, Rotella and Ratti 1992). As with other reproductive parameters, mottled duck brood survival varies by year and geography. Brood survival on the Texas mid-coast ranged from 0–0.69 and duckling survival ranged from 0–0.41 (Finger et al. 2003), and on the upper Texas coast, duckling survival averaged 0.57 (Rigby and Haukos 2015). Brood survival in South Carolina was estimated to be 0.50 (Kneece 2016). These estimates of survival are relatively high compared to other closely related dabbling ducks; American black duck (*Anas rubripes*) duckling survival was estimated at 0.42 (Ringelman and Longcore 1982) and mallard duckling survival ranged from 0.16–0.36 (Krapu et al. 2006, Amundson and Arnold 2011), except where predator removal likely influenced duckling survival (Pearse and Ratti 2004). In the Prairie Pothole Region, broods that moved farther had lower survival; therefore, broods in areas of lower wetland density may experience higher mortality rates (Rotella and Ratti 1992). Large expanses of coastal marsh may benefit mottled duck broods because of ease of accessing suitable habitat compared to the increasingly fragmented grassland and ponds of the Prairie Pothole Region (Rigby and Haukos 2015). Similarly, along the Gulf Coast, duckling survival estimates may be lower in the more fragmented habitat of the inland rice fields and crawfish (*Procambarus* spp.) ponds; however, there are no studies that have focused on this area. Additionally, exposure to colder temperatures on prairie breeding grounds also caused duckling mortality (Pietz et al. 2003), whereas temperatures along the Gulf Coast are milder and more favorable for duckling survival throughout the year. Broods often have lower survival in dry years (Rotella and Ratti 1992), which appeared to be true in Texas, although survival could not accurately be measured because of small sample size of successful nests (Finger et al. 2003).

It is unclear whether water salinity levels are a limiting factor for mottled duck broods. In Texas, broods were observed in areas with salinities ranging from freshwater up to 35 parts per thousand (ppt) with no preference between low and high salinity marsh (Stutzenbaker 1988, Rigby and Haukos 2015). This may be the case because some studies have used vegetation community composition as a proxy for salinity, which may be misleading because marsh salinity changes with environmental conditions (e.g., precipitation) on a shorter time scale than vegetation. Broods may use wetlands classified as saline by vegetation community only when salinity is adequately low (Rigby and Haukos 2015). Similarly, in South Carolina breeding mottled ducks used wetlands with high salinity (Shipes 2014), and Kneece (2016) reported that broods were observed during extreme drought on those wetlands with salinity levels >15 ppt. This contradicts a study of salinity tolerance in captive mottled duck ducklings, which found that all ducklings died at salinity levels exceeding 18 ppt, mortality increased and growth rates were reduced at 12 ppt, and ducklings suffered eye fatigue and lack of appetite at 9 ppt (Moorman et al. 1991). The discrepancy suggests that wild mottled duck broods can tolerate periods of high salinity but need access to fresher water to survive and may be something to be examined further. Currently, there are few estimates of mottled duck brood and duckling survival, especially during the first week of life when ducklings are most vulnerable to mortality (Rigby and Haukos 2015).

1.6.2. Brood habitat use

Prior to hatch, females were observed frequenting the area they subsequently choose for brood rearing (Baker 1983). After initial overland movements to brood habitat, environmental conditions are likely to dictate subsequent movement and habitat use. Increased inter-wetland movement may be due to drought or the search for better quality habitat (Baker 1983), whereas in wet years increased intra-wetland movement may be due to ease of movement within patches and increased connectivity (Rigby 2008). Barriers such as levees and roads may discourage broods from making inter-wetlands moves, except when conditions require it (i.e., a brood rearing area dries up; Rigby 2008). Across all geographies, broods used areas with open water interspersed with submerged and emergent vegetation, which offers escape cover and provides habitat for invertebrates to flourish. Managed impoundments met these needs best in South Carolina (Kneece 2016), perhaps because they provide a stable water level. Managers can maintain water at a level that affords ducklings the best opportunity for reaching quality food sources and escaping predators. Poor environmental conditions, such as drought, can result in higher water salinity, and the lower water levels put broods at a greater distance from escape cover and concentrates predators such as alligators. In Texas, broods selected areas with more open water and closer to emergent vegetation, and avoided fresh marsh dominated by cattail (*Typha* spp.) and phragmites (*Phragmites australis*), which may obstruct brood movement. Moreover, alligators prefer freshwater marsh, so broods may avoid this type of land cover for safety (Rigby and Haukos 2015). As broods get older, they favor more open (Johnson 1974) and deeper water (Esters 1988). Most researchers have focused on coastal habitat; however, because mottled ducks move inland to agricultural areas during the breeding season (Davis 2012), investigating brood habitat use in other areas in addition to coastal marsh is warranted. With so few studies on mottled duck broods, brood survival and habitat selection are core research needs, and brood movements, especially, may vary by geography. By continuing to refine my knowledge of what constitutes suitable brood habitat and which land cover types are avoided, scientists and managers can improve their understanding of which wetlands should be prioritized for conservation.

1.7. Adult breeding season survival

Adult survival during the breeding season is one of the most predictive parameters in determining population growth of mallards (Hoekman et al. 2002). The breeding season is a dangerous biological period for females because incubation and brood rearing place females at a higher risk of predation, typically resulting in lower survival compared to other times of the year (Cowardin et al. 1985). Habitat quality, predator community, environmental conditions, and cross-seasonal effects all influence breeding season survival. Mottled duck breeding season survival appears to be similar to or higher than survival rates in other dabbling duck species (Finger et al. 2003, Bielefeld and Cox 2006, Rigby and Haukos 2012). Breeding season survival for mallards in the Canadian Prairie Pothole Region ranged from 0.62–0.84 (Devries et al. 2003, Brasher et al. 2006) and for those breeding in the Great Lakes states was 0.74 (Coluccy et al. 2008). Breeding season survival for Florida mottled ducks, defined as early-March until mid-June to late-July, ranged from 0.58–0.90, with many years and cohorts of birds experiencing survival estimates >0.85 (Bielefeld and Cox 2006, Dugger et al. 2010, Varner 2013). Florida mottled ducks had higher breeding season survival in urban areas (0.82) than those in rural areas (0.61; Varner 2013). Food availability, such as supplemental corn and bird seed, lower predator abundance, reduced movements, and stability of urban water levels, especially in periods of drought, likely lead to this difference in breeding season survival (Varner et al. 2014*a*). Breeding season survival for WGC mottled ducks is somewhat lower (Table 1.2), ranging from 0.71–0.88 (Finger et al. 2003, Rigby and Haukos 2012, Wehland 2012). Researchers in the Chenier Plain of

Texas reported that hunt periods are most influential in temporal variation in mottled duck survival, and models that contained biological periods were not competitive (Moon et al. 2017). Survival during the breeding and hunting season was lower for WGC mottled ducks than during the post-breeding season (Wehland 2012), whereas in Florida, breeding season survival was higher than the post-breeding and hunting season (Bielefeld and Cox 2006). These differences may be a result of variation in habitat conditions, hunting pressure, and predation and may be evidence that these 2 populations are operating under different constraints (Wehland 2012).

In mottled ducks, there is evidence for a tradeoff between breeding season survival and nesting propensity (Bielefeld and Cox 2006). This may be especially pronounced in times of poor habitat conditions (e.g., drought; Dufour and Clark 2002, Wehland 2012). Females in Texas with a greater body mass had higher survival likely because nesting females experience a decrease in body mass as egg production and nest incubation draws from nutrient reserves (Rigby and Haukos 2012). Additionally, age may play a role in this tradeoff—older, more experienced individuals were more likely to nest compared to younger individuals (Coluccy et al. 2008), which by forgoing nesting may experience higher survival rates (Reynolds et al. 1995, Dufour and Clark 2002). By forgoing breeding, females are less vulnerable to the predation risks associated with nesting, which is likely to increase seasonal survival (Rigby and Haukos 2012, Wehland 2012). Breeding season survival has been relatively well-studied; however, similar to nest survival, determining the exact sources of mortality, identifying the effect of key predators (including hunters), and assessing how survival is further linked with environmental conditions could provide a better understanding of the quantitative values scientists assign to breeding season survival rates.

Table 1.2. Comparison of mottled duck breeding season survival estimates from across its range (adapted from Rigby and Haukos 2012).

		Breeding season			
Geography	Years	Length	Monthly survival	Survival	Reference
Interior Florida	1998	26 Feb–10 June	0.97	0.90	Dugger et al. 2010
	1999		0.96	0.88	
East-central Florida	1999–2002	1 March–31 July	0.97	0.86	Bielefeld and Cox 2006
South Florida- rural	2009	1 March–31 July	0.92	0.64	Varner 2013
Urban	2009		0.97	0.84	
Rural	2010		0.90	0.58	
Urban	2010		0.96	0.80	
Rural	2011		0.91	0.61	
Urban	2011		0.96	0.82	
Mid coast, Texas	2000	3 Feb–July 20	0.95	0.77	Finger at al. 2003
	2001		0.94	0.72	
	2002		0.98	0.87	
Upper coast, Texas	2006–2008	1 Feb–30 June	0.94	0.76	Rigby and Haukos 2012

1.8. Discussion

In summary, mottled ducks use brackish and intermediate coastal marsh, including managed impoundments, and use agricultural land during the breeding season throughout their range (Davis 2012, Wehland 2012, Moon 2014, Pollander et al. 2019). Their nests can be found in pastures, levees, dry cordgrass marsh, cutgrass marsh, spoil banks, and small islands (Stutzenbaker 1988, Bielefeld and Cox 2006, Varner 2013, Shipes et al. 2015). Florida mottled ducks are unique because they also use urban areas during the breeding season compared to mottled ducks in the WGC population (Bielefeld and Cox 2006, Varner et al. 2013). Nesting propensity and nest success estimates are often lower than other waterfowl species that are characterized by stable or increasing populations. Although mottled duck brood survival can be as high as 0.69, many researchers investigating brood and duckling survival start to monitor broods when they are older and less vulnerable to mortality, potentially inflating these estimates. Broods use wetlands composed of a mix of open water with submerged and emergent vegetation. Breeding season survival is higher for mottled ducks in Florida than mottled ducks in the WGC population, but adult survival in both geographies is comparable to (or higher than) that of other dabbling duck species (Devries et al. 2003, Bielefeld and Cox 2006, Brasher et al. 2006, Dugger et al. 2010, Varner et al. 2014*a*). All aspects of recruitment appear linked with seasonal environmental conditions, especially during years of drought. Drought alters the availability of food and water on the landscape, which directly affects nesting females and their broods as they try to acquire resources and likely concentrates predators.

An understanding of mottled duck population dynamics requires detailed inquiry into the components of annual recruitment (Hoekman et al. 2002). Furthermore, the effective management of mottled ducks requires a basic understanding of how the surrounding environment influences these demographic parameters. To date, data needed to elucidate this understanding and these relationships have been very difficult to obtain and several reproductive vital rates remain poorly quantified. Breeding habitat use, breeding season survival, and nest-site selection and success have been studied more than nesting propensity, renesting intensity, and post-hatch ecology. Given the geographical variation in breeding season demographic rates and differing population trajectories in Louisiana, Texas, and Florida, location-specific studies will be required to understand the dynamics of local mottled duck populations, which are likely functioning on smaller scales relative to other dabbling ducks. Perhaps the management of mottled ducks needs to be focused on the local scale, as opposed to the regional scale. For example, differing harvest pressure, land use, and habitat conditions in north and south Florida have resulted in different survival and harvest rates (Bielefeld et al. 2020), which is also likely the case for reproductive parameters.

Currently, telemetry is the most common way to quantify these breeding season vital rates. Solar-powered global positioning system-groupe spécial mobile (GPS-GSM) transmitters now allow researchers more frequent fix intervals and longer battery life for units. Nevertheless, estimation of many important breeding season vital rates assumes perfect discrimination of individual nesting attempts. There is potential for early nest failure before researchers can pinpoint a nesting attempt, which would bias vital rates such as nesting propensity and renesting effort low and nest success high, and overlook areas where there are high depredation rates early in nesting. Moreover, transmitter effects of (especially backpack harnesses) are well-known (Kesler et al. 2014) in other duck species, and have the potential to depress reproductive activity. Recently available implantable GPS-GSM units may have fewer effects on reproductive behavior than backpack transmitters (Pacquette et al. 1997), but their use in determining nesting activity has not been adequately tested. Where contiguous tracts of upland nesting habitat exist and are used by mottled ducks for nesting, longitudinal nesting studies using traditional chain-drag methods (Klett et al. 1986) may elucidate relationships between nesting ecology and environmental variation (Ringelman et al. 2018), but admittedly such areas are geographically restricted and not representative of the full range of mottled duck breeding habitats. Unmanned aerial vehicles equipped with visual and thermal imaging cameras are effective at locating nests at northern latitudes (Bushaw et al. 2020), but may be less effective at detecting nests in warm Gulf Coast states.

Nesting propensity remains difficult to evaluate because even when birds are tracked throughout the year, data may not be collected at a fine enough scale to identify all nesting attempts, especially if failure occurs in laying or early incubation. There are no estimates of mottled duck renesting intensity in current literature, and yet high rates of renesting can increase female success within a wide range of nest survival rates (Cowardin and Johnson 1979). Instead, mottled duck population models incorporate renesting intensity estimates from mallards into population models (Rigby and Haukos 2014), which may not accurately reflect the demographic rates of mottled ducks; the protracted mottled duck nesting season may afford even higher rates of renesting than mallards in the prairies. Light-level geolocators mounted on a leg band are less intrusive than radio-transmitters, and could provide potential insight into nesting parameters such as nesting propensity, renesting effort, and nest success by recording periods of darkness associated with incubation (Cook 2018). Similar to the limitations of transmitters, the ability to discriminate nesting attempts terminated during laying may be problematic.

Adult female mottled ducks with broods are often difficult to monitor, especially in the vast and nearly inaccessible coastal marshes of the Gulf Coast states. Ground-based surveys, especially those in which an airboat is involved, would likely encourage broods to seek refuge in nearby escape cover, therefore hindering the survey. Unmanned aerial vehicles have been used to survey broods across a variety of landscapes (Pöysä et al. 2018) and cause little disturbance to breeding birds (Barr et al. 2020). Additionally, unmanned aerial vehicles equipped with thermal-imaging cameras allow researchers to identify the presence of broods even when in dense vegetative cover. Although unmanned aerial vehicles may be a viable (even superior) option for brood surveys in northern landscapes (Bushaw et al. 2021), further investigation is warranted to determine how the thermal camera would perform in the hot and humid weather of the Gulf Coast and Florida.

Research on mottled duck breeding ecology guides the development of strategic conservation planning tools that can assist biologists in prioritizing management actions. For example, by incorporating what is known about the habitat requirements of mottled ducks during the nesting and breeding seasons, decision support tools can identify areas that should be prioritized for conservation, management, and restoration. At present, a decision support tool exists for WGC mottled ducks, which was validated using mottled duck survey data (Krainyk et al. 2019), and provides a basic framework for conservation prioritization. No such tool exists for researchers of mottled ducks in Florida.

Moreover, the landscape is changing rapidly, emphasizing a need for ongoing research to update conservation planning. For example, climate change threatens the sustainability of much of the habitat that mottled ducks rely on throughout their range, especially low-lying coastal areas that are forecast to be lost as a result of sea-level rise (Spencer et al. 2016, Borchert et al. 2018) exacerbated by subsidence in some geographies (DeLaune et al. 1994, Couvillion et al. 2011). Climate change may also lead to increases in the frequency of extreme El Niño events

(Cai et al. 2014), which is associated with cooler and wetter conditions in early spring. It is not clear how mottled ducks will adapt to a rapidly changing landscape, but there is likely to be geographic variation in responses. When overlaying mottled duck locations and predicted sea-level rise in the Texas Chenier Plain, Moon (2014) determined that the majority of individual locations were in irregularly flooded marsh, which was forecast to decline >50% and converted to saline or brackish open water and regularly flooded marsh. Hurricane season coincides with the nesting and brood rearing period, which make coastal nests and broods vulnerable to damage from tropical storms and hurricanes; this threat will escalate with increasingly severe storms and the frequency of severe storms attributed to climate change (Knutson et al. 2020). Additionally, hurricanes and storm surges cause lasting damage to coastal areas, and these carry-over effects on breeding mottled ducks are not well understood (Moon et al. 2017).

1.9. Management implications

Along the Gulf and the southern Atlantic coasts, the mottled duck breeding season overlaps with the presence of wintering waterfowl after the hunting season and managers must determine how to balance the needs of wintering waterfowl with those of breeding mottled ducks. Draining of managed wetlands typically begins at the end of the hunting season in late January, thereby reducing the amount of habitat available for mottled ducks to acquire adequate nutrient reserves or use as brood rearing habitat. Consequently, management for wintering waterfowl in itself may act as an ecological trap; a female that nests on a levee adjacent to a flooded moist soil unit that is drawn down will be forced to move her brood through the canal, exposing the ducklings to a number of predators. The tall, dense, vegetation in fields that are used for haying or cattle forage may attract nesting mottled ducks, only to be mowed over at a later date. Private working lands are often used for rice and crawfish farming, ranching, oil and gas extraction, and hunting clubs.

Landowners would benefit from understanding how their actions may affect mottled ducks throughout the annual cycle, and scientists and managers should work with them to deliver conservation programs and strategies that will attract and benefit breeding mottled ducks on their property. For example, habitat management practices commonly implemented in the Prairie Pothole Region, such as planting dense nesting cover in suitable areas, and delaying haying may both also benefit mottled ducks. Mottled duck populations are vulnerable to a number of threats across their range, so it is crucial to understand how vital rates may affect population growth and how these unique birds respond to environmental changes to sustain their populations.

Chapter 2. Temporal Variation and Landcover Influence Survival in Adult Female Mottled Ducks

2.1 Introduction

Effective management of wildlife populations requires an understanding of how demographic traits (e.g., fecundity, survival) affect population growth (Caughley 1994, Benton and Grant 1999, Sæther and Bakke 2000). Although components of fecundity often explain most of the variation in population growth for short-lived animals, for many waterfowl species, elasticity analyses have revealed the population growth rate will respond to changes in adult survival (Flint et al. 1998, Hoekman et al. 2002, Flint et al. 2006, Koons et al. 2006, Koons et al. 2014). Temporal and spatial variability in vital rates like survival can generate substantial variation in population growth rate. Across space, vegetation composition and structure, predator communities, food availability, competition, and disturbance affect survival (Royle and Dubovsky 2001, Devries et al. 2003, Zhao et al. 2018). On a temporal scale, certain time periods are associated with greater risk of mortality, such as hunting (Fleskes et al. 2007, Yetter et al. 2017) and breeding seasons (Kirby and Cowardin 1986, Arnold et al. 2012).

Mottled ducks (*Anas fulvigula*) are endemic to the southeastern United States and are year-round residents (Baldassarre 2014). There are 2 genetically (McCracken et al. 2001, Peters et al. 2016, Lavretsky et al. 2014) and behaviorally (Varner et al. 2013) distinct populations of mottled ducks: the western Gulf Coast (WGC) mottled duck (*A. f. maculosa*) resides along the Gulf Coast from coastal Alabama to the Laguna Madre of Mexico, and the Florida mottled duck (*A. f. fulvigula*) inhabits peninsular Florida (Baldassarre 2014). Louisiana Department of Wildlife

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and Fisheries (LDWF), Texas Parks and Wildlife, and the United States Fish and Wildlife Service began annually surveying WGC mottled ducks in 2008, and the population has declined by about 50% since the survey began (L. A. Reynolds, LDWF, unpublished data). Mottled duck populations are threatened by coastal wetland loss and degradation, changes in farming practices, predators such as the American alligator (*Alligator mississippiensis*), and year-round lead exposure (Wilson 2007). Between 1932 and 2016, Louisiana lost about 25% of its wetlands, primarily because of the combined effects of sea-level rise and subsidence (Couvillion et al. 2017). In addition to natural processes such as erosion (Valentine and Mariotti 2019) and increased flooding from multi-decadal water level changes (Hiatt et al. 2019), anthropogenic activities, including the construction of navigation canals and oil and gas extraction (Day et al. 2020), have altered sediment delivery (Blum and Roberts 2009), increased saltwater intrusion (White and Kaplan 2017), and exacerbated the effects of sea-level rise and subsidence (Turner 1997, White et al. 2019). Agricultural wetlands (i.e., rice) provide additional habitat for mottled ducks and have helped compensate for losses of native coastal and prairie wetlands throughout much of the twentieth century; however, since the 1980s rice production has declined because of low commodity prices, high production costs, and farm policy (Petrie et al. 2014, Marty et al. 2020).

Previous researchers provided evidence of low annual survival and productivity contributing to declines in the WGC mottled duck population (Wilson 2007). Johnson (2009) used band recovery analysis and age ratios of harvested mottled ducks and confirmed the WGC population of mottled ducks was in decline (population growth rate [λ] = 0.82) and annual survival explained a large portion of the variation in population growth. Their method did not parse how the vital rates comprising fertility affected population growth, so Rigby and Haukos

(2014) built a matrix population-model using estimates of vital rates for WGC mottled ducks (e.g., nesting propensity, nest success, duckling survival, renesting propensity, adult survival) to address the issue. Variation in fertility explained most of the variation in λ; however, variation in survival still contributed to almost 33% of the variation in λ, highlighting the importance of adult survival to mottled duck population dynamics (Rigby and Haukos 2014).

Several researchers investigated WGC mottled duck survival at various time scales. Annual survival of WGC mottled ducks derived from band recovery data ranged from 0.50–0.53 (Haukos 2015, McClinton et al. 2019), whereas estimates from telemetry data have ranged from 0.12–0.48 (Wehland 2012, Moon et al. 2017). In the Chenier Plain of Texas and Louisiana, mottled duck survival varied by temporal period (post-breeding, hunting, late winter, breeding), age, and the state in which the individual spent the most time (Wehland 2012). Weekly survival was lower during the hunting and breeding seasons compared to the post-breeding season. Similarly, in the Texas Chenier Plain, mottled duck survival varied among years and between hunting and non-hunting periods (Moon et al. 2017).

I initiated this study in response to recent declines in the WGC mottled duck population, a priority species for the Gulf Coast Joint Venture (Brasher et al. 2012), as an attempt to better understand survival rates and how they may be linked to mottled duck decline. Southwestern Louisiana is a stronghold of the Louisiana mottled duck population, but despite the historical importance of the region to the breeding population, it is generally underrepresented in the literature. My objectives were to examine temporal and spatial variation in weekly survival of adult female WGC mottled ducks in southwestern Louisiana. I expected survival to be lowest during time periods associated with risky activities (e.g., hunting, breeding seasons, during molt) and for survival to vary by the proportion of time spent in different landcover types.

2.2. Study area

I conducted the study primarily in southwestern Louisiana, which includes Cameron, Vermilion, Jefferson Davis, Calcasieu, and Acadia parishes (Figure 2.1) from 2017–2020. The capture site was at and around Rockefeller Wildlife Refuge (RWR), a property just under 29,000 ha managed by LDWF. Rockefeller Wildlife Refuge is located at the southern end of the Mermentau River Basin near Grand Chenier in Cameron and Vermilion parishes, which borders the Gulf of Mexico and extends inland about 10 km. The refuge contains managed and unmanaged wetland impoundments of varying salinity from fresh to saline, and moist soil management units (Selman et al. 2011). For perspective on the area I studied, individuals traveled as far east as Phoenix, Louisiana, as far west as McFaddin National Wildlife Refuge, Texas, and as far north as Larto, Louisiana, which encompasses an area >5.5 million ha. The core study area was about 750,000 ha and was bordered by Calcasieu Lake to the west, I-10 to the north, Louisiana Highway 35 to the east, and the Gulf of Mexico to the south. Southwestern Louisiana is characterized by flat, low-lying wetlands and agricultural land <10 m in elevation. The coastal wetlands are classified into 4 types: saline marsh, in which the salinity averages 18 parts per thousand (ppt) and dominant plant species include smooth cordgrass (*Spartina alterniflora*), seashore saltgrass (*Distichlis spicata*), and needlegrass rush (*Juncus roemerianus*); brackish marsh, in which the salinity averages 8.2 ppt and dominant plant species include saltmeadow cordgrass (*Spartina patens*), seashore saltgrass, Olney bulrush (*Schoenoplectus americanus*), and widgeongrass (*Ruppia maritima*); intermediate marsh, in which the salinity averages 3.3 ppt and dominant plant species include saltmeadow cordgrass, common reed (*Phragmites australis*), arrowhead (*Sagittaria* spp.), and coastal waterhyssop (*Bacopa monnieri*); and freshwater marsh, in which salinity averages 1.0 ppt and dominant plant species include maidencane (*Panicum hemitomon*), spikerush (*Eleocharis* spp.), arrowhead, and alligator weed (*Alternanthera philoxeroides*; Esslinger and Wilson 2001). Historically, inland areas were dominated by tallgrass prairie; however, much of that area today has been converted to agriculture (Esslinger and Wilson 2001). The American alligator is commonly found in the wetlands of Louisiana and is a known predator of mottled ducks (Elsey et al. 2004). Agriculture in the region is mostly made up of rice, crawfish (*Procambarus* spp.), and cattle pasture, with some soybean and sugarcane production. The region also contains forested wetlands, stock ponds, recreational ponds, lakes, rivers, and bayous. Common throughout the region, a variety of mesocarnivores are predators of mottled ducks and their eggs including raccoons (*Procyon lotor*; Stutzenbaker 1988), coyotes (*Canis latrans*), and striped skunks (*Mephitis mephitis*; Durham and Afton 2003). Waterbirds such as great egret (*Ardea alba*), snowy egret *(Egretta thula*), little blue heron (*Egretta caerulea*), tricolored heron (*Egretta tricolor*), great blue heron (*Ardea herodias*), rails (*Rallus* spp.), yellow rail (*Coturnicops noveboracensis*), black rail (*Laterallus jamaicensis*), common gallinule (*Gallinula galeata*), and purple gallinule (*Porphyrio martinica*) are often found using similar habitat to mottled ducks. The study area was composed of 36.1% agricultural land and 37.5% wetlands. The climate of Louisiana is subtropical, marked by hot, humid summers, and mild winters. The growing season ranges from 220–320 days. The average temperature from 2017–2020 in southwestern Louisiana was 20.8°C and average monthly precipitation was 13.1 cm (National Oceanic and Atmospheric Administration [NOAA] 2021*a*).

Mottled ducks pair October–January and breed February–July; peak nesting occurs March–May and broods fledge 45–60 days after hatch. Mottled ducks molt June–September, and females generally molt later than males (Stutzenbaker 1988). Mottled ducks are also a legal gamebird in Louisiana and can be hunted during the general waterfowl season. The Louisiana

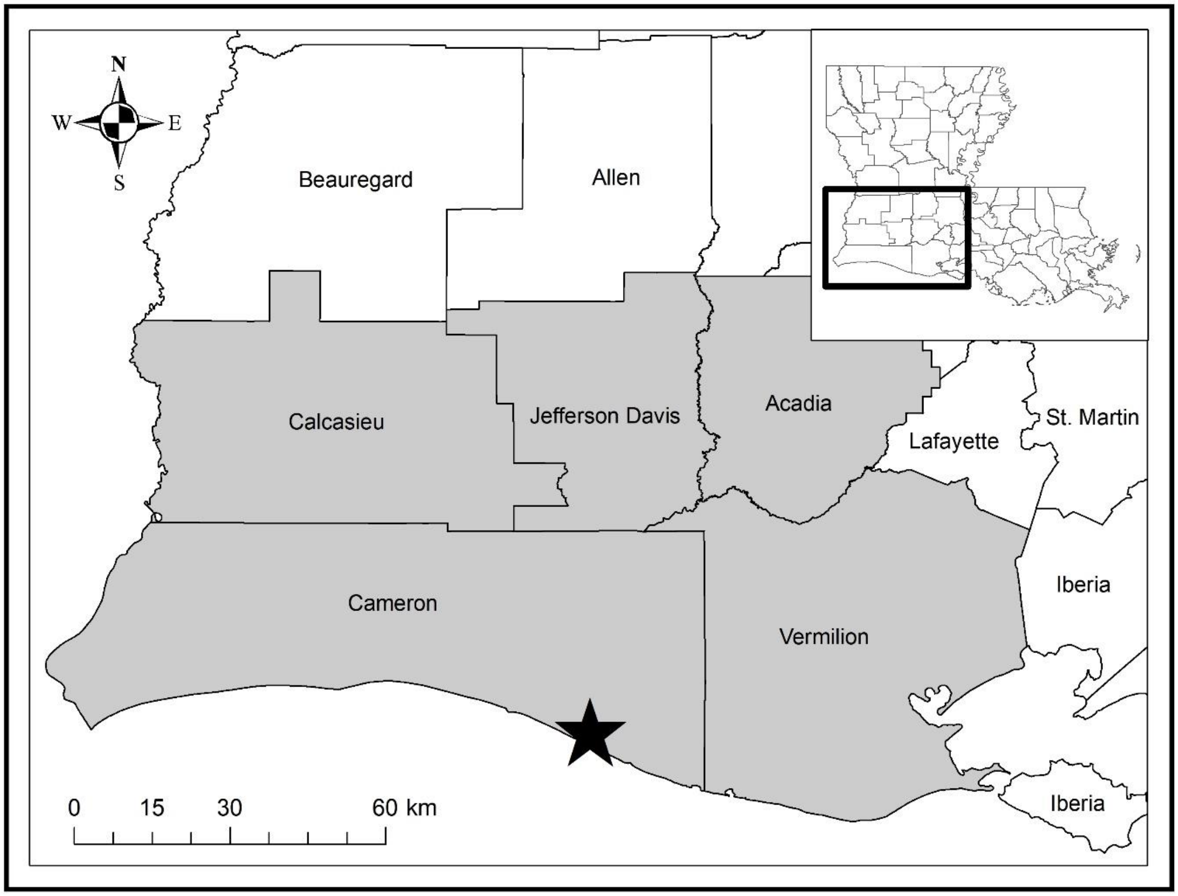

Figure 2.1. The core study area was southwestern Louisiana, USA, highlighted by the shaded area. The star denotes where I captured mottled ducks around Rockefeller Wildlife Refuge in 2017–2019.

general waterfowl season is divided into 2 hunting periods called splits, that are separated by a 12-day break during which no hunting is allowed. The first split is generally from mid-November through early December and the second split is generally mid-December through late January. Additionally, there is a 16-day teal season in which hunters may harvest American green-winged teal (*Anas crecca*), blue-winged teal, (*Spatula discors*), and cinnamon teal (*S. cyanoptera*), but it is not legal to harvest mottled ducks. Teal season is generally mid to late September.

2.3. Methods

I captured adult female mottled ducks on RWR and adjacent unmanaged privately owned land in conjunction with LDWF annual banding operations during summers 2017–2019 from airboats at night by hand when the birds were molting and unable to fly (Cummings and Hewitt 1964). Captures occurred July–September. Captured individuals received a United States Geological Survey aluminum or incoloy leg band, and some individuals received 21-g solar-powered Saker-L global positioning system-groupe spécial mobile (GPS-GSM) transmitters (Ecotone Telemetry, Gdynia, Poland), which use a cellular network to transmit locations. The body mass of birds I selected was ≥690 g, to ensure transmitters were ≤3% of body mass. I prioritized transmitter deployment on mottled ducks that completed molt and were flight capable, or individuals that were furthest along in molt because they would be less vulnerable to predation and less energetically stressed as they grew accustomed to the transmitter. I assumed that the stage of molt on the day of capture was not associated with the ability of the female to complete molt in a proficient manner and, excluding 2017 when time constraints forced us to deploy transmitters over a 2-day period, I captured females from mid-July through mid-September, likely resulting in a sample of females of varying breeding status (e.g., non-breeders, failed breeders, successful breeders). Furthermore, Wehland (2012) examined survival in the first 6 months following transmitter deployment and concluded molt stage, or the percent of regrowth of the primaries, had little to no effect on survival. I attached the transmitters in a modified Dwyer style configuration (Dwyer 1972) with 2 separate loops for the body and neck, which were secured with a knot and epoxied. I used Conrad-Jarvis 6-mm black nylon automotive elastic with neoprene elastomer (Casazza et al. 2020) and tightened until the tip of the thumb fit under the unit. I released marked birds within 12 hours at the location of capture. Transmitters logged GPS coordinates every 2 hours during daylight to balance frequency of data collection with battery life and were monitored throughout the year. I recorded individuals as mortalities when transmitters recorded little or no activity. I confirmed and recovered all mortalities in the field when possible.

I investigated the influence of season and landcover on weekly survival using the known fate model in Program MARK (White and Burnham 1999). Individuals that died or lost signal within the first 2 weeks following deployment were not included in analysis (Gilmer et al. 1974). I built encounter histories in weekly increments using a live-dead format. To evaluate temporal trends in survival, I parsed the year by hunt period, biological seasons, or a combination of both. Models containing hunt period components were categorized into the non-hunting period and 3 hunting periods: teal season (15–30 Sep 2017 and 2018, 14–29 Sep 2020), the first split (11 Nov–3 Dec 2017, 10 Nov–2 Dec 2018, 9 Nov–8 Dec 2020), and second split (16 Dec 2017–21 Jan 2018, 15 Dec 2018–20 Jan 2019, 21 Dec 2019–19 Jan 2020). I used the dates of the Louisiana coastal zone to define hunting periods because most marked birds were located within this hunt zone (LDWF 2017, 2018, 2019). If any portion of the week was open for hunting, I labeled the week as a hunt period (Table 2.1). I defined the biological periods using field observations combined with what has been established in the literature. The biological seasons used in survival modeling were molt (15 Jul–14 Sep), pairing (15 Sep–31 Jan), and breeding (1 Feb–14 Jul; Stutzenbaker 1988, Moon et al. 2017). I labeled the non-hunted and biological periods according to which period comprised the majority of the week (Tables 2.1, 2.2). I observed considerable temporal overlap of nesting and brood rearing, so I combined these time periods into the breeding season.

Table 2.1. Season dates as labeled in the models used to estimate weekly survival of mottled ducks in southwestern Louisiana, USA, 2017–2020, including the number of ducks with active transmitters monitored over the course of each season. In cases of overlap between hunted periods and biological seasons, if hunting occurred in any portion of the week, it was labeled as a hunted period.

Season	2017–2018		2018–2019		2019–2020		2020–2021	
	Dates	Number of active units	Dates	Number of active units	Dates	Number of active units	Dates	Number of active units
Teal	11 Sep –1 Oct	58	10–30 Sep	63	9–29 Sep	41		
First split	6 Nov–3 Dec	43	5 Nov–2 Dec	52	4 Nov–8 Dec	29		
Second split	11 Dec–21 Jan	38	10 Dec–20 Jan	44	16 Dec–19 Jan	26		
Molt	21 Aug–17 Sep	56	16 Jul–16 Sep	73	15 Jul–15 Sep	45	13 Jul–23 Aug	19
Pairing	18 Sep–28 Jan	57	17 Sep–3 Feb	60	16 Sep–2 Feb	41		
Breeding	29 Jan–15 Jul	39	4 Feb–14 Jul	43	3 Feb–12 Jul	28		

Table 2.2. Non-hunted period dates, as labeled in the models used to estimate weekly survival of mottled ducks in southwestern Louisiana, USA, 2017–2020. Models contain a combination of the molt period (molt), non-hunted period (non-hunted), teal season (teal), first split of the general waterfowl season (hunt 1), second split of the general waterfowl season (hunt 2), and breeding season (breeding).

Model	Year	Non-hunted time periods		
Non-hunted + hunted	2017	21 Aug–5 Nov		4 Dec–10 Dec
	2018	22 Jan–4 Nov		3 Dec–9 Dec
	2019	21 Jan–3 Nov		9 Dec–15 Dec
	2020	20 Jan–23 Aug		
Non-hunted + hunt 1 + hunt 2	2017	21 Aug–5 Nov		4 Dec–10 Dec
	2018	22 Jan–4 Nov		3 Dec–9 Dec
	2019	21 Jan–3 Nov		9 Dec–15 Dec
	2020	20 Jan–23 Aug		
Non-hunted + teal + hunt 2 + hunt 2	2017	21 Aug–10 Sep	2 Oct–5 Nov	4 Dec–10 Dec
	2018	22 Jan–9 Sep	1 Oct–4 Nov	3 Dec–9 Dec
	2019	21 Jan–8 Sep	30 Sep–3 Nov	9 Dec–15 Dec
	2020	20 Jan–23 Aug		
Molt + non-hunted + hunt 1 + hunt 2 + breeding	2017		11 Sep–5 Nov	4 Dec–10 Dec
	2018	22 Jan–28 Jan	10 Sep–4 Nov	3 Dec–9 Dec
	2019	21 Jan–3 Feb	9 Sep–3 Nov	9 Dec–15 Dec
	2020	20 Jan–2 Feb		
Molt + teal + non-hunted + hunt 1 + hunt 2 + breeding	2017		2 Oct–5 Nov	4 Dec–10 Dec
	2018	22 Jan–28 Jan	1 Oct–4 Nov	3 Dec–9 Dec
	2019	21 Jan–3 Feb	30 Sep–3 Nov	9 Dec–15 Dec
	2020	20 Jan–2 Feb		

I used the United States Geological Survey National Land Cover Database 2016 to define landcover (U.S. Geological Survey 2016, Homer et al. 2020) and assign each individual the proportion of GPS locations logged in specific landcover types over the course of the lifespan of the transmitter. These included open water, marsh (woody wetlands and herbaceous emergent wetlands), agriculture (pasture or hay and cultivated crops), and developed areas (developed open space, developed low intensity, and developed high intensity). The proportions acted as a proxy for the amount of time spent in each landcover type because the length of the encounter history of each individual varied and it was impossible to know the exact amount of time spent at a location with locations collected every 2 hours. The proportion of locations in the marsh was inversely correlated with the proportion of locations in agriculture ($r = -0.96$); I retained agriculture in my modeling because survival in agricultural lands is of management interest. I also investigated models that included the latitude of last known location (essentially the location at the time of mortality), which I used as a proxy for gradation of landscape characteristics like anthropogenic disturbance and fragmentation, both of which increase with latitude in southwestern Louisiana. I developed my first set of *a priori* candidate models using combinations of the hunting and biological periods while avoiding confounding variables (e.g., teal season overlaps with pairing, so these periods were not included in a model together). I also explored hunting and biological periods in combination with year (as a factor variable), a constant survival model, and a time-dependent (weekly) survival model. I used corrected Akaike's Information Criterion (AIC_c) to rank resulting models (Burnham and Anderson 2002, Arnold 2010). I then used competitive temporal models $\leq 2\ \Delta AIC_c$, plus my strictly biological model, to explore the influence of spatial covariates. I used ΔAIC_c to rank the remaining models and deemed models $\leq 2\ \Delta AIC_c$ to be competitive. All means are reported with standard deviation unless otherwise specified.

Because it is difficult to ascertain mortality status of individuals when a transmission signal is lost, I conducted an additional analysis when those individuals were not censored from the data. I included known mortalities and those individuals whose signal transmissions ceased abruptly (e.g., full battery, areas of known cell service). Therefore, this analysis represents a worst-case scenario survival estimate. I used the same *a priori* model structures in the worst-case scenario survival analysis, used ΔAIC_c scores to rank models in all analyses, and deemed models ≤ 2 ΔAIC_c to be competitive (Burnham and Anderson 2002, Arnold 2010).

2.4. Results

I deployed transmitters on 69, 58, and 21 adult female mottled ducks in 2017, 2018, and 2019, respectively. Of all marked birds, 29 transmitters were redeployed on 33 individuals. Captured individuals weighed 690–1,020 g, averaging 849 ± 74 g. I censored 23 individuals from my analysis that died or ceased transmitting within the first 2 weeks following deployment. The lifespan of transmission (until mortality occurred or the unit was censored) ranged from 15–1,197 days, averaging 344 ± 291 days. I documented 51 mortalities, 21 of which were recovered. For transmitters that I recovered, it was impossible to identify the cause of mortality because most carcasses had been scavenged. At least 3 mortalities appeared to be caused by avian predators based on carcass movement and recovery location (i.e., below a telephone pole). Hunters harvested 8 mottled ducks: 3 were shot during the 2017–2018 hunting season, 4 during the 2018–2019 season, and 1 during the 2019–2020 season. The proportion of GPS locations by individuals averaged 0.097 ± 0.065 in open water, 0.707 ± 0.244 in marsh, 0.185 ± 0.244 in agricultural lands, and 0.008 ± 0.013 in developed areas.

Models containing the proportion of locations in developed lands or open water, or the latitude of last known location were not competitive. My results suggested 3 competitive models ($\Delta AIC_c < 2$), all of which included temporal delineations of the first hunting split, second hunting split, and non-hunted period, plus the proportion of locations in agricultural lands (Table 2.3). The top model supported maximum temporal partitions of survival, where weekly survival varied among biological periods and hunted periods including molt ($\beta = 0.1641 \pm 0.5342$), teal season ($\beta = -1.4023 \pm 0.4214$), first split ($\beta = -1.2766 \pm 0.4315$), second split ($\beta = 0.5391 \pm 0.7654$), non-hunted period ($\beta = -0.8147 \pm 0.4105$), and breeding period (factor variable fixed at zero) in addition to the proportion of locations in agricultural lands ($\beta = 1.5023 \pm 0.6601$). Similarly, the second-ranked model included the same time periods and the proportion of locations in agricultural lands, but without the teal season. My third-ranked model included only the non-hunted period, teal season, first split, second split, and the proportion of locations in agriculture. The period of lowest weekly survival was the teal season and highest weekly survival was the second hunting split (Figure 2.2) and survival increased as proportion of GPS locations in agricultural lands increased (Figure 2.3; effects for other seasons were similar). Annual mottled duck survival did not vary among years and was 0.604 ± 0.068 (SE) in 2017–2018, 0.643 ± 0.066 in 2018–2019, and 0.623 ± 0.082 in 2019–2020.

In the worst-case scenario survival analysis, which included ducks whose transmitters stopped abruptly, I documented 88 suspected mortalities. The top models of this analysis were similar to those based on confirmed mortalities (Table 2.4), including the periods of lowest survival (Figure 2.4). The top-ranked model included the non-hunted period, teal season, first split, second split, and proportion of locations in agricultural lands. The second-ranked model included the same seasons and proportion of locations logged in agricultural lands in addition to the molt and breeding season. Annual survival rates were lower in the worst-case scenario and ranged from 0.413 ± 0.061 (SE) to 0.482 ± 0.065 among years.

Table 2.3. Model results from known-fate analyses in Program MARK that best explained spatial and temporal variation in survival of female mottled ducks in southwestern Louisiana, USA, 2017–2020. I used corrected Akaike's Information Criterion (AIC_c), ΔAIC_c, AIC_c weights, and number of parameters (K) to rank models. I present models with ΔAIC_c <2 and the null model for comparison. Models contain a combination of the molt period (molt), non-hunted period (non-hunted), teal season (teal), first split of the general waterfowl season (hunt 1), second split of the general waterfowl season (hunt 2), breeding season (breeding), and proportion of locations in agricultural lands (ag).

Model	AIC_c	ΔAIC_c	AIC_c weights	K
Molt + non-hunted + teal + hunt 1 + hunt 2 + breeding + ag	573.70	0.00	0.27	7
Molt + non-hunted + hunt 1 + hunt 2 + breeding + ag	574.30	0.58	0.20	6
Non-hunted + teal + hunt 1 + hunt 2 + ag	574.60	0.93	0.17	5
Null	589.84	16.15	0.00	1

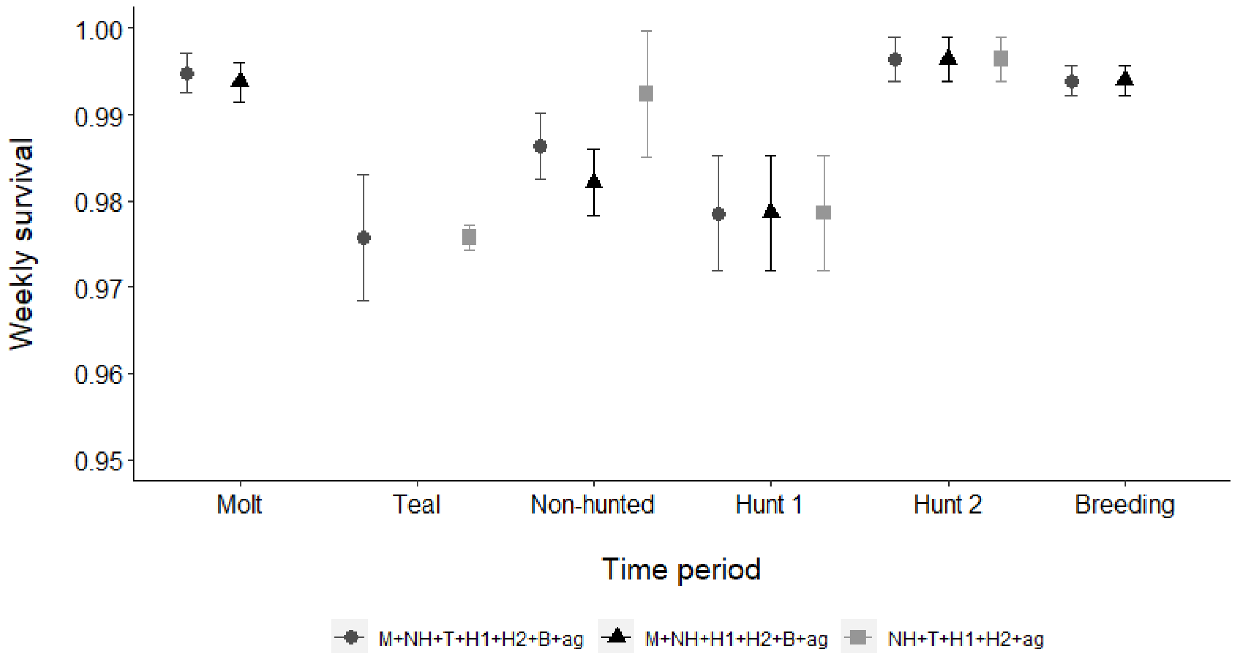

Figure 2.2. Estimated weekly survival rates, with standard error, of female mottled ducks in southwestern Louisiana, USA, 2017–2020, from supported models, which included combinations of molt (M), teal season (T), non-hunted period (NH), first split of the general waterfowl season (H1), second split of the general waterfowl season (H2), breeding season (B), and proportion of locations on agricultural lands (ag).

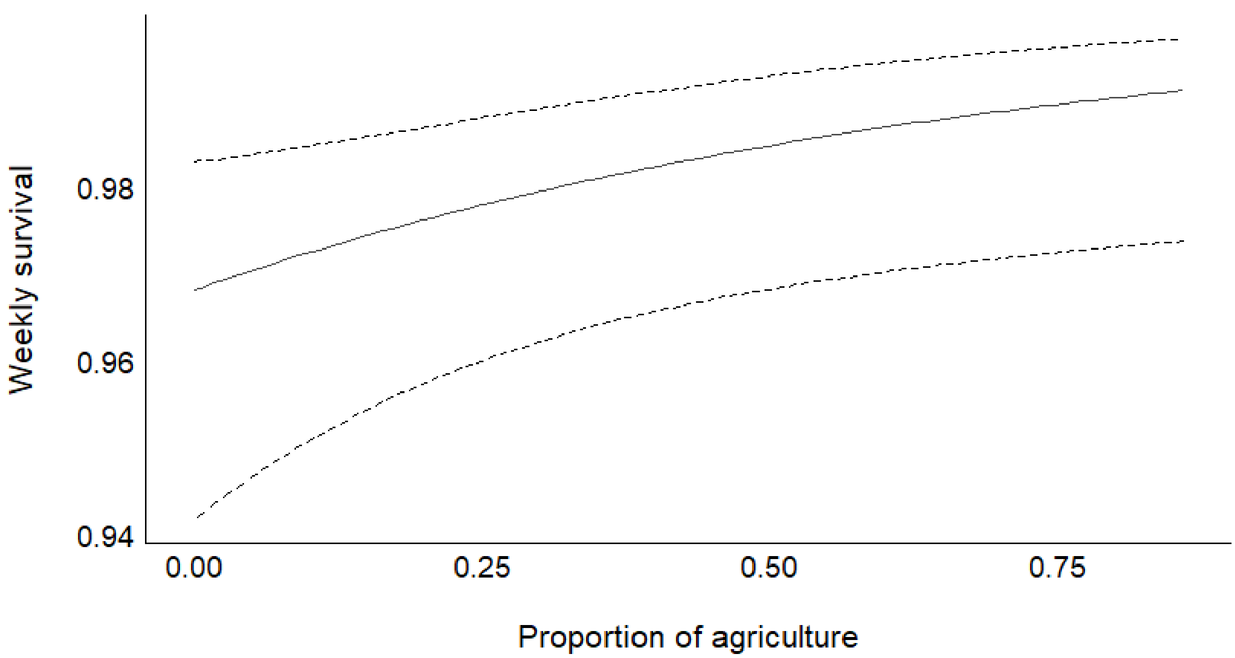

Figure 2.3. The relationship between the proportion of locations in agricultural lands and weekly survival during the teal season for mottled ducks in southwestern Louisiana, USA, 2017–2020. The dashed lines represent the 95% confidence intervals.

Table 2.4. Model results from known-fate analyses in Program MARK that best explained spatial and temporal variation in survival of female mottled ducks in southwestern Louisiana, USA, 2017–2020 using worst-case scenario data, in which I labeled those individuals that lost signal as mortalities. I used corrected Akaike's Information Criterion (AIC_c), ΔAIC_c, AIC_c weights, and number of parameters (K) to rank models. I present models with ΔAIC_c <2 and the null model for comparison. Models contain a combination of the molt period (molt), non-hunted period (non-hunted), teal season (teal), first split of the general waterfowl season (hunt 1), second split of the general waterfowl season (hunt 2), breeding season (breeding), and proportion of locations in agricultural lands (ag).

Model	AIC_c	ΔAIC_c	AIC_c weights	K
Non-hunted + teal + hunt 1 + hunt 2 + ag	883.60	0.00	0.63	5
Molt + non-hunted + teal + hunt 1 + hunt 2 + breeding + ag	885.50	1.95	0.24	7
Null	903.89	20.34	0.00	1

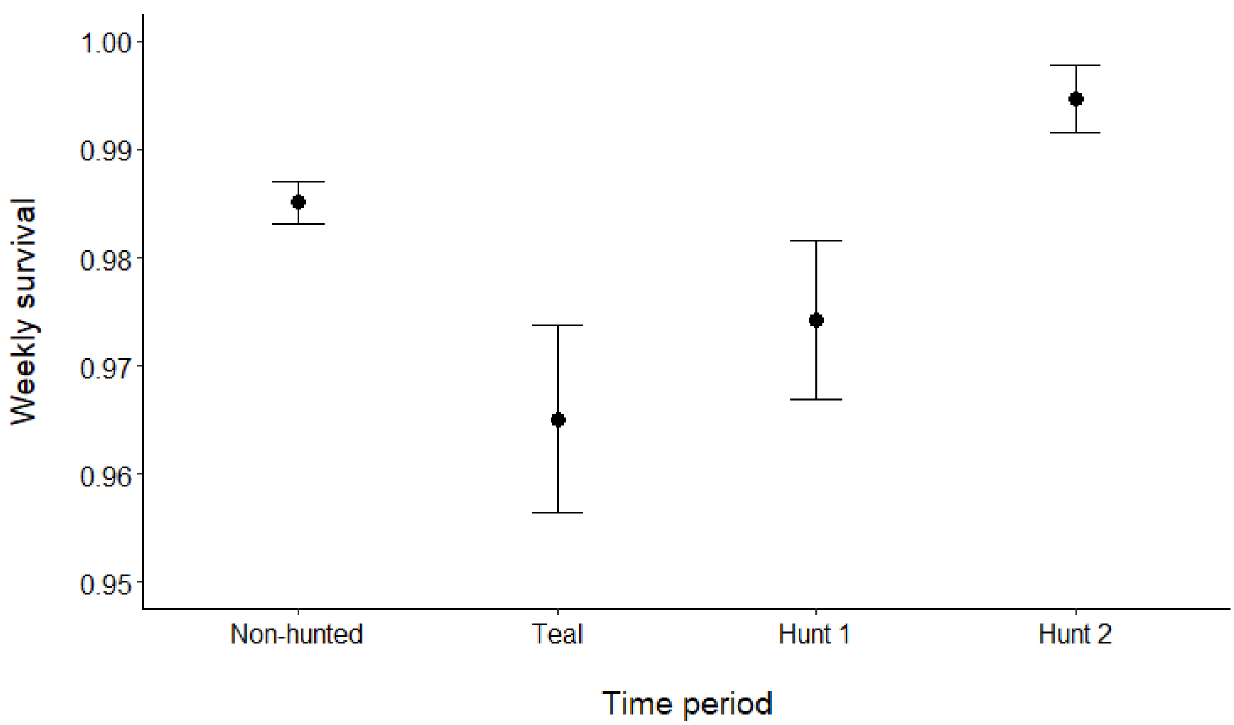

Figure 2.4. Estimated weekly survival rates, with standard error, of female mottled ducks in southwestern Louisiana, USA, 2017–2020, from my top model representing a worst-case scenario, containing the non-hunted period, teal season, first split of the general waterfowl season (Hunt 1), and second split of the general waterfowl season (Hunt 2).

2.5. Discussion

I documented little annual variation in mottled duck survival rates, but substantial variation within a year based on biological seasons and hunting periods. All top models included a combination of hunt periods, an indication that harvest period was important in explaining temporal variation in survival. These results are similar to those reported in other studies for mottled ducks in the Texas and Louisiana Chenier Plain, where survival models with hunt periods accounted for almost 100% of model weight (Wehland 2012, Moon et al. 2017). The period of lowest weekly survival for mottled ducks in southwestern Louisiana was during the teal season, despite mottled ducks not being legal to harvest at this time. Moon et al. (2017) documented the illegal harvest of mottled ducks during the teal season; however, I observed no hunter harvest of mottled ducks during teal season in Louisiana. Four of the 11 mortalities that occurred during teal season were located on RWR, where hunting is prohibited, and hunting-related disturbance is likely minimal. Furthermore, just under 5 of the 11 individuals that experienced mortality during the teal season spent the entirety of this time on the refuge, whereas the remaining individuals were located on private land. All but 1 individual remained on a single parcel of land for the duration of teal season. This suggests that factors other than direct harvest affect the survival of mottled ducks during late summer. Most mortalities during the teal season (8 of 11) occurred the same year as telemetry deployment, near the original release location (Figure 2.5), with mortality averaging 38 ± 10.8 days after deployment. Thus, these mortalities could signify deleterious effects of transmitter attachment, poor body condition following molt, or an interaction between them. Although I attempted to minimize this effect by using an elastic harness material, transmitter harnesses can become too loose or too tight, especially as body mass fluctuates throughout the year (Lameris and Kleyheeg 2017). Without direct observation, it was impossible to determine whether a mortality was a direct result of the transmitter, a result of an alteration of behavior (Pietz et al. 1993, Kesler et al. 2014) that made the individual more vulnerable to predation during acclimation, or an unrelated predation event.

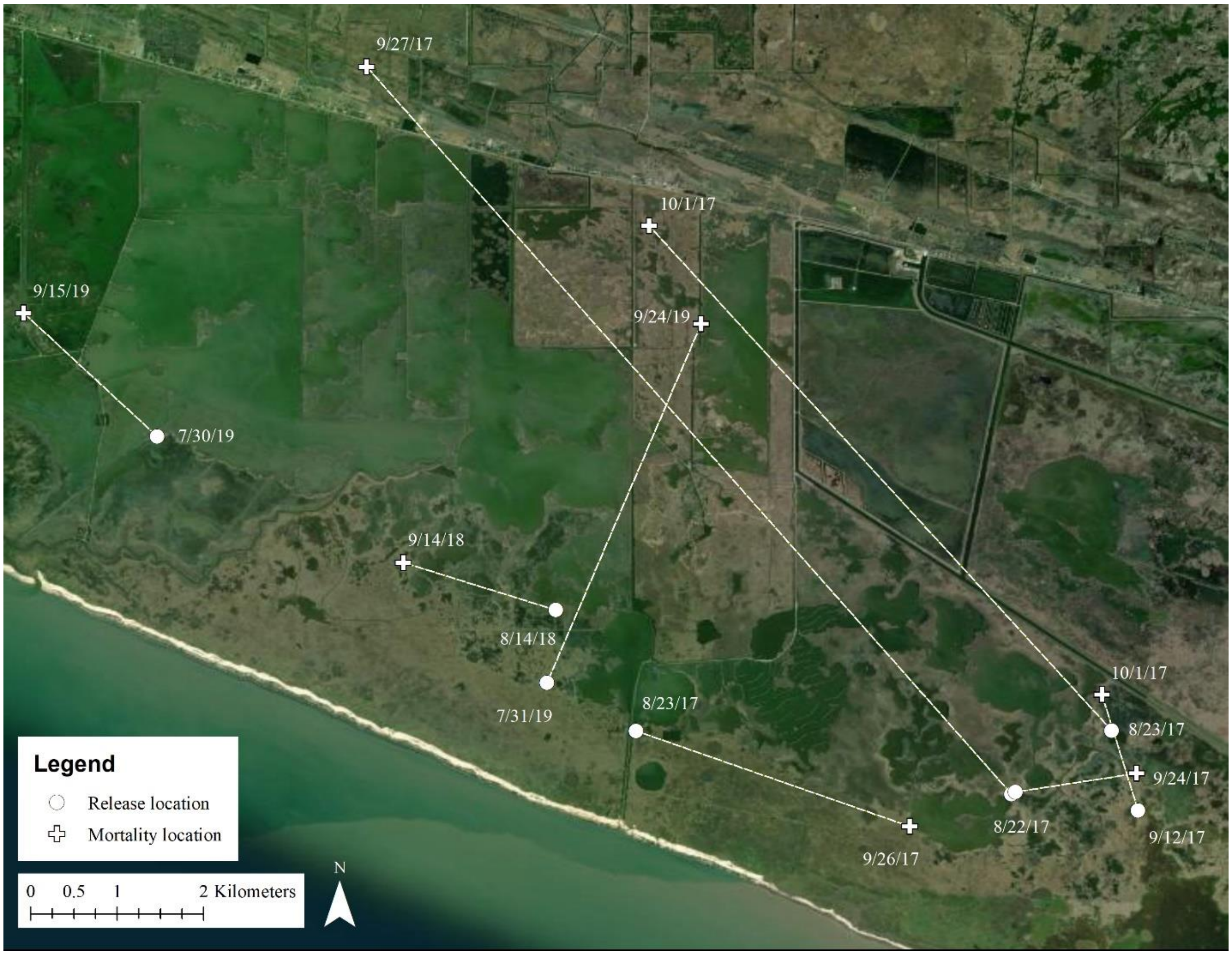

Figure 2.5. Mottled duck release and recovery locations for those individuals that died during teal season in the same year they were banded, around Rockefeller Wildlife Refuge in southwestern Louisiana, USA, 2017–2020.

The second lowest period of survival was the first split of the general waterfowl hunting season, while the highest period of survival was during the second split. Mottled duck harvest documented in this study occurred almost exclusively during the first split, and only 1 individual was harvested in the second split (during the 2019–2020 hunting season). Hunting regulations in Texas prohibit harvest of mottled ducks during the first 5 days of the general waterfowl season when birds are expected to be especially vulnerable to harvest, and my survival results from Louisiana provide corroborating evidence of this assumption.

Weekly survival of mottled ducks in southwestern Louisiana during breeding and molt was higher than at other times of the year, despite the increased risk of predation expected to be associated with these events (Cowardin et al. 1985, Bielefeld and Cox 2006, Varner et al. 2014*a*), corroborating results from a previous study on WGC mottled ducks (Wehland 2012). Environmental conditions, such as drought or direct and carry-over effects of tropical storms and hurricanes (Ringelman et al. 2021), are likely to influence survival. In Florida, drought conditions caused mottled ducks and American alligators to concentrate in the same available wetlands during the flightless period, resulting in lower survival during this period (Bielefeld and Cox 2006). In southwestern Louisiana, however, RWR is a hotspot for molting mottled ducks and the ability to manage water levels among units in the complex might lessen such effects during drought. Mottled ducks in southwestern Louisiana exhibited nesting propensity ranging from 17.6–25.0% (E. S. Bonczek, Louisiana State University, unpublished data), which was similar to the low nesting propensity and high breeding season survival reported in previous studies (Finger et al. 2003, Bielefeld and Cox 2006, Wehland 2012, Varner et al. 2014*a*). These findings suggest a tradeoff between breeding season demographic rates and survival, which may also be occurring in mottled ducks in southwestern Louisiana. Given large variation in the timing of nesting and molting, it was difficult to capture the effects of these specific activities on survival and incorporating the timing of specific breeding-season activities on an individual basis may improve the understanding of biological seasonal survival. For example, with females initiating nests as late as mid-July (E. S. Bonczek, unpublished data), there is potential for nesting, brood rearing, and molting to all occur simultaneously for different individuals.

The top-ranked survival model also indicated that individuals that logged a greater proportion of locations in agricultural lands had higher weekly survival. Agricultural lands in southwestern Louisiana consist primarily of rice fields, including first crops, which are harvested around August, and second crops (i.e., ratoon) from the same field (Ziska et al. 2018), which are typically harvested in November before winter flooding. Agricultural lands may provide more abundant or better-quality foods, resulting in reduced foraging time and increased rates of fat deposition compared to natural forage found in wetlands, as observed in geese (Anatidae; Fox and Abraham 2017). Dabbling ducks in the Central Valley of California, USA, exhibited increased body mass in 2006–2008 compared to 1982–1984, which coincided with an increase in managed wetlands and agricultural lands. Ducks had the largest increase in body mass in regions that flooded agricultural fields (e.g., rice and other crops) after harvest (Fleskes et al. 2016). There is more fragmentation in agricultural landscapes compared to remote wetlands because of the presence of human infrastructure. The mottled duck predator community has not been well studied in either cover type so there may be differences in predator communities between the 2 landscapes (such as lower densities of alligators in agricultural land) that could lead to different rates of mortality (Fleury and Sherry 1995). Further research is needed to identify aspects of the agricultural landscape that contribute to increased survival so that these types of landscapes can be conserved, and conversely, what aspects of wetlands may contribute to decreased survival.

Annual survival estimates (including the results of the worst-case scenario analysis) of 0.41–0.64 were similar to survival rates reported from studies using band recovery analysis across the mottled duck range (Table 2.5; Haukos 2015, McClinton et al. 2019, Bielefeld et al. 2020, Kneece et al. 2020). The lowest annual survival estimate in the Texas Chenier Plain occurred during extreme drought (Moon et al. 2017), whereas most periods during this study were characterized by average to moderate moisture, except for a brief period in May–August 2018 that was of moderate drought (NOAA 2021*b*). Southwestern Louisiana is composed of a wide range of land cover types, including wetlands of varying salinities that are managed and unmanaged, agricultural land, pastures, lakes, rivers, and bayous, within a relatively small area. As conditions change on the landscape, mottled ducks can easily travel to new habitat patches that meet their needs (Wehland 2012). It is not known whether decline in the WGC mottled duck population is related to survival; however, survival of female mottled ducks is similar to survival estimates of other female dabbling ducks garnered from banding analyses. For example, annual survival was in the range 0.47–0.64 for mallards (*Anas platyrhynchos*; Arnold and Clark 1996, Dufour and Clark 2002), gadwall (*Mareca strepera*), northern shovelers (*Spatula clypeata*), and blue-winged teal (Arnold and Clark 1996). Similarly, survival of mid-continent mallards was 0.565 (Smith and Reynolds 1992) and Gulf Coast American green-winged teal (*Anas crecca*) was 0.532 (Chu et al. 1995). Instead of survival, vital rates during the reproductive period (i.e., nest success, nesting propensity, brood survival) are likely factors influencing mottled duck population dynamics. My data generally support the data of others such that hunting influences survival and birds are vulnerable to harvest (Moon et al. 2017) and backpack transmitters attached with a harness may affect bird behavior (Garrettson et al. 2000, Kesler et al. 2014) and subsequently survival. Further research should be conducted to improve my understanding of reproductive parameters, factors that influence them, and how they drive population dynamics.

Table 2.5. Annual survival estimates of adult female mottled ducks across their range, USA. Point estimates shown are means.

Location	Survival	Method	Years	Reference
FL	0.44	Band analysis	2000–2013	Bielefeld et al. (2020)
SC	0.57	Band analysis	2008–2018	Kneece et al. (2020)
TX and LA	0.53	Band analysis	1997–2013	Haukos (2015)
Upper TX coast	0.50	Band analysis	2004–2015	McClinton et al. (2019)
TX and LA	0.48	Telemetry	2006–2010	Wehland (2012)
TX	0.12–0.38	Telemetry	2009–2011	Moon et al. (2017)
LA	0.60–0.64 (0.41–0.48)	Telemetry	2017–2020	This study (worst-case scenario)

2.6. Management implications

Survival rates in southwestern Louisiana are not likely the primary driver in the decline of the western Gulf Coast population of mottled ducks. Nevertheless, by understanding how seasonal survival varies across time and space, and identifying periods of higher mortality, scientists and managers can act to potentially increase survival during these periods. For example, the beginning of the general waterfowl season is a time of relatively high mortality for mottled ducks in Louisiana and adopting harvest restrictions on mottled ducks during that time may reduce mortality. Targeted efforts to increase adult survival has the potential to improve the population growth rate for WGC mottled ducks and may be especially important if such management actions are easier to undertake than working to improve elements of fecundity. Future research should investigate the relative importance of various mottled duck productivity metrics (i.e., nesting propensity, nest survival, renesting intensity, and brood survival) in driving mottled duck population dynamics.

Chapter 3. Nesting Ecology of Mottled Ducks

3.1. Introduction

Recruitment is an essential element of waterfowl population dynamics. A number of demographic rates comprise recruitment, including nesting propensity, clutch size, egg hatchability, nest success, renesting propensity, and duckling survival; these components can vary spatially and temporally across landscapes and environmental conditions (Sheaffer 1998). Perturbation analyses have enabled researchers to explore how vital rates influence population growth rates. For many waterfowl species, modeled population growth rates respond quickly to changes in adult survival; however, reproductive vital rates (e.g., recruitment) that can be governed by fluctuating environmental conditions or management actions may contribute more to inter-annual variation in population size than vital rates with a higher elasticity (Koons et al. 2014). In mid-continent mallards (*Anas platyrhynchos*), nest success explained 43% of the variation in population growth rate (Hoekman et al. 2002). Similarly, nest success ranked second in explaining variation in population growth rate for box-nesting wood ducks (*Aix sponsa*) in the southeastern United States (Hepp et al. 2020). As such, when a stochastic environment presents favorable conditions for a given vital rate, the resulting success may lead to increased population growth rate (Koons et al. 2009).

Throughout the breeding season, landscape characteristics and inter-annual variation in precipitation and land use influence reproductive parameters. Nesting propensity, or the proportion of females that nest in a given year, is likely affected by age, previous experience, environmental conditions (Warren et al. 2014), and body condition (Devries et al. 2008), and is expected to be lower when environmental conditions are poor, such as in years of drought (Dugger et al. 2016). For example, drought directly affects food availability, which influences the ability of breeding ducks to obtain the nutrients necessary for reproduction (Alisauskas and Ankney 1992). Nest predation is the primary cause of failure for most nesting birds (Ricklefs 1969, Greenwood et al. 1995). Consequently, individuals should choose nest sites that decrease detection by predators (Borgo and Conover 2016) by taking advantage of landscape features that affect the way predators forage (Phillips et al. 2003), choosing sites where predator movement is affected on a larger scale (Elton 1939, Hines and Mitchell 1983), or assessing the local predator community and making behavioral decisions based on that knowledge (Eichholz et al. 2012, Eichholz and Elmberg 2014). Predators may be less successful when foraging in habitats with taller and thicker vegetation (Livezey 1981, Klett et al. 1988). Other landscape characteristics that may influence nest success are distance to edge (Andrén et al. 1985, Donovan et al. 1997, Winter et al. 2000, Howerter 2003, Racquel et al. 2015), level of anthropogenic disturbance, such that buildings may provide shelter for predators (Lariviere and Messier 1998, Lariviere et al. 1999) or nearby roads/trails may provide travel corridors (Ludlow and Davis 2018), and distance to nearest wetland and wetland density (Clark and Shutler 1999, Lariviere et al. 1999, Phillips 2001, Stephens et al. 2005).

Renesting rates may be able to partially compensate for low nest survival (Cowardin and Johnson 1979, Arnold et al. 2010). Variation in renesting propensity may be influenced by age or experience (Gregg et al. 2006, Devries et al. 2008, Arnold et al. 2010), parental investment in the previous clutch (Fondell et al. 2006), habitat conditions such as food availability and water levels (Krapu et al. 1983), and initiation date (Grand and Flint 1996, Arnold et al. 2010); however, renesting propensity is a poorly understood reproductive parameter in waterfowl species.

Mottled ducks are a unique species that occur in the southern United States and are non-migratory throughout their range (Baldassarre 2014). There are two populations of mottled ducks that are genetically (McCracken et al. 2001, Peters et al. 2016, Lavretsky et al. 2014) and behaviorally (Varner et al. 2013) distinct. The western Gulf Coast (WGC) population is found primarily along the coast from the Laguna Madre of Mexico to Alabama, and the Florida population can be found in peninsular Florida (Baldassarre 2014). The WGC mottled duck population has declined by about 50% since annual surveys began in 2008 (Bonczek and Ringelman 2021). Previous studies have identified poor recruitment as a limiting factor of mottled duck population growth; in fact, recruitment in mottled ducks was estimated to be 0.176 (Rigby and Haukos 2014), compared to >0.79 for mallards in eastern Canada (Hoekman et al. 2006). Variation in fecundity explains most of the variation in population growth rate of WGC mottled ducks and within fecundity, nesting propensity and nest success were most important (Rigby and Haukos 2014). As such, it is crucial to understand these components of recruitment, how they may affect population dynamics, and how they vary in response to habitat and environmental conditions.

Several previous studies have examined reproductive vital rates in mottled ducks. Nesting propensity ranged from 15–77% (Finger et al. 2003, Dugger et al. 2010, Rigby and Haukos 2012, Varner et al. 2013). In a drought year, mottled ducks in southwestern Louisiana did not lay eggs until rice farmers flooded the fields, indicating that the foraging areas required for nutrient acquisition may have been limiting (Durham and Afton 2006). The highest nesting propensity estimates occurred when environmental moisture was average; however, abnormally wet years did not occur during these studies (Finger et al. 2003, Rigby and Haukos 2012). Nest success ranged from 5–57% (Stieglitz and Wilson 1968, Baker 1983, Durham and Afton 2003, Finger et al. 2003, Dugger et al. 2010) and was highest where nesting habitat was composed of islands within the river deltas of Louisiana (Holbrook et al. 2000, Walters et al. 2001) and in coastal

Florida (Stieglitz and Wilson 1968). In southwestern Louisiana, mottled duck nest success was associated with higher plant species richness, a greater distance to water, and denser vegetation (Durham and Afton 2003). Estimates of renesting propensity in mottled ducks are lacking; thus, researchers used estimates from mallards as a substitute in mottled duck recruitment models (Rigby and Haukos 2014). Mottled ducks have been observed renesting in Florida (Dugger et al. 2010, Varner 2013) and Texas (Engeling 1950, Stutzenbaker 1988, Finger et al. 2003), so some qualitative data do exist. Mottled ducks have been described as "determined renesters" and have been documented nesting up to 5 times in a breeding season (Engeling 1950, Stutzenbaker 1988).

Effective mottled duck management requires an understanding of the potential mechanisms limiting mottled duck populations, which is lacking in southwestern Louisiana, despite that this geography supports a large proportion of the WGC population of mottled ducks. Of additional importance is understanding the linkage between landscape characteristics and conditions and vital rates, as this information is crucial for developing effective conservation strategies. I used GPS-GSM transmitters as a novel means of monitoring individuals and obtaining a more representative sample of nest locations across the landscape, as opposed to targeting specific habitats or searching a limited range. My goals were to quantify nesting propensity, estimate and model nest survival with respect to local and landscape-level characteristics, and quantify renesting propensity for mottled ducks in southwestern Louisiana.

3.2. Study area

The primary capture site was at Rockefeller Wildlife Refuge (hereafter Rockefeller) in southwestern Louisiana, a 29,000 ha property managed by the Louisiana Department of Wildlife and Fisheries. Rockefeller is located in both Cameron and Vermilion Parishes at the southern end of the Mermentau River Basin near Grand Chenier, Louisiana; Rockefeller borders the Gulf of

Mexico and extends inland about 10 km. Rockefeller contains both managed and unmanaged wetland impoundments of varying salinity from fresh to saline, as well as moist soil management units (Selman et al. 2011). For perspective on the area I studied, marked individuals traveled as far east as Phoenix, Louisiana, as far west as McFaddin National Wildlife Refuge, Texas, and as far north as Larto, Louisiana, The average temperature 2017–2020 in parishes in which nests were commonly found was 21.2°C in Cameron Parish, 21.0°C in Vermilion Parish, and 20.6°C in Jefferson Davis Parish and average monthly precipitation was 13.0 cm, 13.4 cm, and 12.7 cm respectively (National Oceanic and Atmospheric Administration, National Centers for Environmental Information [NOAA, NCEI] 2021*a*).

3.3. Methods

I captured adult female mottled ducks on Rockefeller and adjacent private land during the summers of 2017–2019 by hand from airboats at night when the birds were molting and unable to fly (Cummings and Hewitt 1964) in conjunction with annual waterfowl banding activities conducted by Louisiana Department of Wildlife and Fisheries. Captured individuals received a U. S. Geological Survey aluminum or incoloy leg band and some individuals received a 21 g solar-powered Saker-L GPS-GSM transmitter (Ecotone Telemetry, Gdynia, Poland), which use the cellular network to transmit locations. The body mass of birds I selected was ≥690 g, to ensure transmitters were ≤3% of body mass. I prioritized deploying transmitters on mottled ducks that had already completed molt and were flight capable, or individuals that were furthest along in molt, as I reasoned that these birds would be less vulnerable to predation and less energetically stressed as they grew accustomed to the transmitter. I attached the transmitters in a modified Dwyer style configuration (Dwyer 1972) with two separate loops— one around the body behind the wings and one around the neck which sat at the base of the furcula; these loops were secured with knots and epoxied. I used Conrad-Jarvis 6 mm black nylon automotive elastic with neoprene elastomer (Casazza et al. 2020) and tightened until the tip of the thumb fit under the unit. I released marked birds within 12 hours back to location of capture. Transmitters logged GPS coordinates every 2 hours during daylight and were accurate to 30 m. I obtained transmitted data from the manufacturer-designed web-based Ecotone data management panel. From this panel, I could obtain transmitter metrics, such as battery level, activity level, temperature, and date of most recent GPS location, and download individual kmz files with monthly GPS locations to be input into Google Earth or .csv files of bird locations for further analysis. My procedures were approved by Louisiana State University Institutional Animal Care and Use Committee under permit A2016-27 and federal bird banding permit 06669.

Monitoring began 1 Feb 2018–2020. I examined the locations and movements of each individual every 3 days using the Google Earth kmz file obtained from the web-based Ecotone data management panel. Once I identified an individual that logged locations in the same area consecutively (Figure 3.1), I waited 10 days from the inferred date of nest initiation, which was determined by the first date the female was observed at the presumed nest site, to ensure the female had begun incubating and visited the site on foot to confirm the presence of a nest. The use of a dog was extremely helpful in locating nests (Glover 1956, Keith 1961) when they were unable to be located by researchers alone, especially for nests where the female was not present or had already failed at the time of discovery. At the initial nest visit I collected clutch size and incubation stage by candling (Weller 1956). At the landscape scale, I recorded the habitat type, which I defined as pasture, old field (lightly grazed or ungrazed), emergent marsh, idle rice, or crawfish (*Procambarus* spp.) pond levee. At the scale of the nest site, I measured visual obstruction as an index of vegetation density using a Robel pole at a height of 1 m and a distance of 4 m from the nest bowl in each cardinal direction (Robel et al. 1970). I also recorded height of the tallest vegetation adjacent to the nest bowl and the top 3 dominant plant species and their percent cover within a 4 m radius around the nest bowl. I monitored active nests using the transmitted GPS locations of the nesting female, and once the female no longer logged locations at the nest site, I returned to the nest to check the fate and collected the same measurements I gathered at the time of discovery. For nests that were depredated when found, I estimated the initiation date as the first day that I observed the female at the nest site using the transmitted GPS locations. I determined the exact fate day by the last day that I observed the female at the nest site from the GPS locations. All means are reported with standard deviation and estimates with standard error unless otherwise specified.

Figure 3.1. Example of a series of coordinates for a presumed, and later confirmed, mottled duck nest location based on data collected from a GPS-GSM transmitter in southwestern Louisiana, USA, 1–4 April 2018 downloaded from the Ecotone data management panel. Transmitters are reported to have 30 m accuracy, and the line added to the map shows 15 m for scale.

3.3.1. Nesting propensity

I calculated nesting propensity by dividing the number of marked individuals that initiated nests by the total number monitored during the breeding season. Individuals that ceased transmissions before 15 April were not included in the total number of individuals monitored during the breeding season because their activities were unknown for over half of the peak nesting period. During the 2018 breeding season, two individuals temporarily ceased regular transmissions during the breeding season but downloaded data at a later date. These two individuals are suspected to have nested judging by the telemetry data, but nests were not confirmed on foot; thus, estimated nesting propensity is given as a range for 2018. I used linear regression to model the effects of year on nesting propensity as a proxy for annual variation in environmental conditions.

3.3.2. Nest survival

I used the nest survival module (Dinsmore et al. 2002) in Program MARK (White and Burnham 1999) modeled through RMark (Laake 2013, RStudio Team 2022) to estimate daily survival rate of mottled duck nests. I constructed univariate models using a combination of local covariates including average visual obstruction, dominant plant species, and nesting strategy (e.g., upland or overwater). Landscape-level covariates included land cover type, distance to road, distance to water, size of the patch, and presence of cows, and other environmental or biological covariates included year (as a proxy for environmental conditions as a whole) and initiation date. I constructed additional models including multiple covariates when I expected the combination of covariates to be biologically meaningful. I used visual obstruction readings collected at nest discovery given the inherent bias that the vegetation at hatched nests grows for longer, and therefore higher/denser, than at failed nests (Ringelman and Skaggs 2019). I also added the quadratic term for visual obstruction because previous research found that nesting ducks may select an intermediate level of vegetation height and density (Clark and Shutler 1999). I ranked the resulting models using AIC$_c$ score (Burnham and Anderson 2002) and considered models ≤2 ΔAIC$_c$ to be competitive.

3.3.3. Renesting propensity

I estimated renesting propensity as the proportion of females that were unsuccessful on their first nest attempt that subsequently initiated a second nesting attempt. I used linear regression to model the effects of initiation date of the first nest, incubation stage at failure of the first nest, and clutch size of the first nest and ranked the resulting models using AIC$_c$ scores (Burnham and Anderson 2002). I calculated the renesting interval as the time between the failure of the first nest and initiation of the second nest and reported the average interval with standard deviation. I was not able to model differences among years because there were no renesting attempts in 2018. I used a Welch two sample t-test to examine differences in clutch size between first and second attempt nests.

3.4. Results

I deployed transmitters on 69, 58, and 21 individuals in 2017, 2018, and 2019, respectively, and monitored 34, 37, and 24 individuals over the course of the breeding season in 2018, 2019, and 2020, respectively. I located 5 nests that were initiated 13 March–5 June 2018 in addition to a dead female with an egg, 14 nests that were initiated 7 March–30 May 2019, and 9 nests that were initiated 30 March–5 July 2020, totaling 29 nest attempts during the entirety of the study (Figure 3.2). Seven of these nests were initially located after they were already depredated. When including unconfirmed but suspected nests, I observed an additional 2 nests in 2018. Throughout the entire study period, there were only 2 instances in which I suspected a nest and were unable to locate it, both in marsh habitat. In 1 case I was able to observe the marked female loafing at the site of the GPS coordinate indicating a loafing site as opposed to a nesting site, but at the other location I was unsure whether there was a nest. Average clutch size for incubated nests was 8.75 ± 1.34 eggs. Average number of eggshells located at nests that were previously depredated was 5.83 ± 1.72 eggshells.

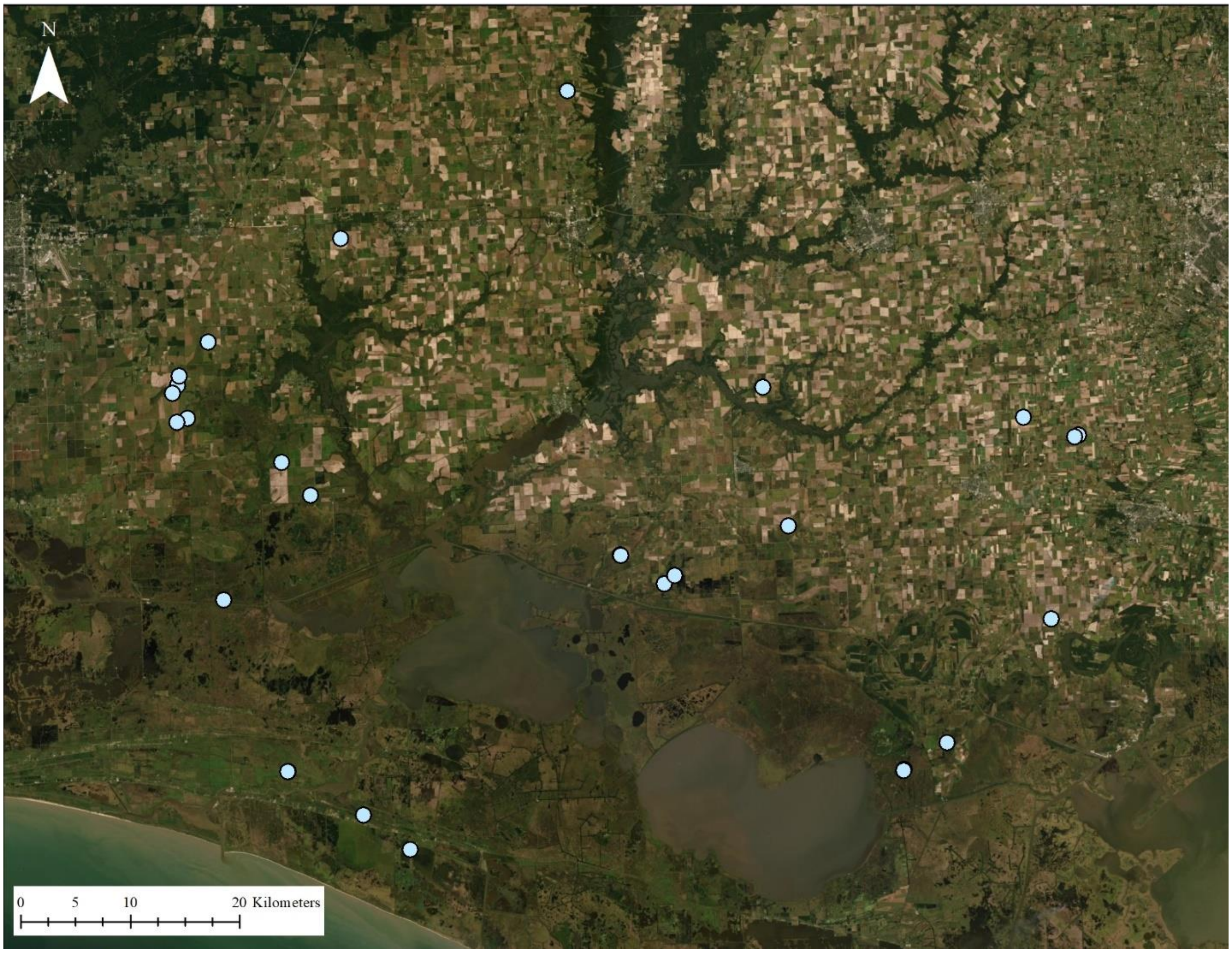

Figure 3.2. Location of nesting attempts by female mottled ducks monitored during this study in southwestern Louisiana, USA, 2018–2020.

3.4.1. Nesting propensity

Nesting propensity was 17.6% in 2018, 21.6% in 2019, and 25.0% in 2020, averaging 21.4% over the course of the study. When including unconfirmed but suspected nests, nesting propensity was 22.2% in 2018. Nesting propensity did not differ among years ($p = 0.632$).

3.4.2. Nest survival

I excluded 1 nest from survival analyses due to researcher-related abandonment and 1 because I was unable to locate the nest bowl. The cause of failure for all nests was depredation of the nest (n = 20) or nesting female (n = 2). Of the 27 nests included in the survival analysis, I identified 6 that failed during laying and 15 that failed during incubation.

The top model indicated that visual obstruction was the best predictor of nest survival (Table 3.1; $\beta = 0.240 \pm 0.114$), such that daily survival rate increased as visual obstruction increased (Figure 3.3). The daily survival rate for nests in this study was 0.965 ± 0.008, resulting in an overall nest success estimate of 0.284 for the 35-day nesting period. Although several other models were ≤ 2 ΔAIC_c, the additional parameters did not improve model fit and because the beta confidence intervals overlapped zero, they were designated uninformative parameters (Arnold 2010). The only other notable model was the model "wet," which differentiated between nests constructed overwater and those in upland habitats. The confidence interval overlapped zero, but the daily survival estimates for nests that were constructed overwater differed from those which were located in upland habitat. The daily survival rate for overwater nests was 0.991 ± 0.009, resulting in an overall nest success estimate of 0.729, while the daily survival rate for upland nests was 0.957 ± 0.010, resulting in an overall nest success estimate of 0.215.

Table 3.1. Model results within 2 ΔAIC_c, including corrected Akaike's Information Criterion (AIC_c), ΔAIC_c, AIC_c weights, and number of parameters (K), that best explains variation in daily survival of mottled duck nests in southwestern Louisiana, USA, 2018–2020. Parameters in competitive models include visual obstruction measurement (robel), patch size, whether the nest was located over water (wet), distance to water, presence or absence of cows (cows), and date of initiation (date).

Model	AIC_c	ΔAIC_c	AIC_c weight	K
Robel	164.4	0.00	0.237	2
Robel + patch size	166.0	1.60	0.107	3
Wet	166.3	1.89	0.092	2
Wet + robel	166.4	1.97	0.089	3
Robel + distance water	166.4	1.98	0.088	3
Robel + cows	166.4	1.98	0.088	3
Robel + date	166.4	2.00	0.087	3
Null	168.0	3.60	0.039	1

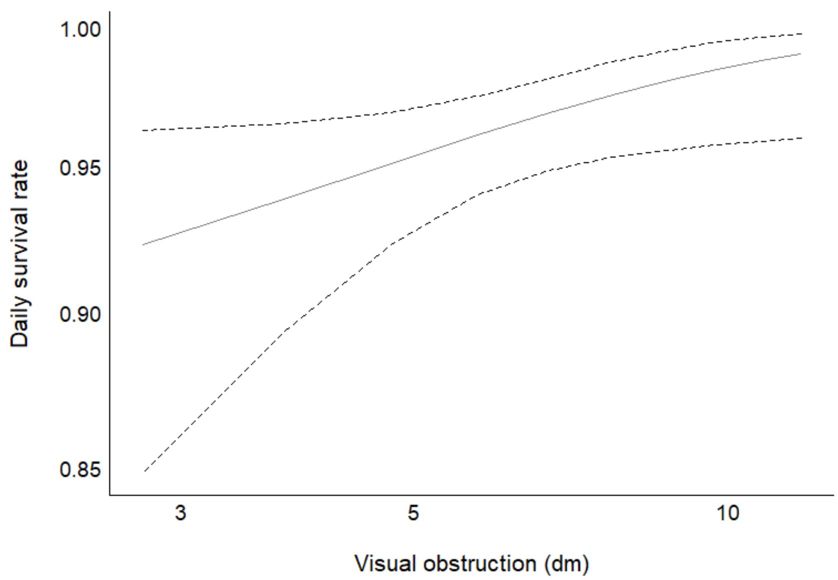

Figure 3.3. Relationship between visual obstruction measurements (dm) and daily survival rate of mottled duck nests in southwestern Louisiana, USA, 2018–2020.

3.4.3. Renesting propensity

I documented 7 individuals that initiated renesting attempts, resulting in 8 second attempt nests (Figure 3.4). Partitioned among years, I recorded 0, 5, and 3 renest attempts in 2018, 2019, and 2020, respectively, resulting in renesting rates for unsuccessful females of 0.0, 0.71, and 0.75. The probability of renesting was best explained by how far into incubation the female was when the initial nest failed (Table 3.2). Females that were at a later incubation stage at the time of nest failure were less likely to renest (Figure 3.5; $\beta = -0.2287 \pm 0.1323$, $p = 0.08$). The renesting interval between failure of the first nest and initiation of the second nest ranged from 14 to 38 days, averaging 26 ± 8.3 days. I found no association between the age of the first nest at the time of failure and renesting interval ($p = 0.76$) and no difference in the average clutch size of first and second nests ($p = 0.58$).

Table 3.2. Model results, including AIC_c, ΔAIC_c, AIC_c weights, and number of parameters (K), that best explains variation in renesting propensity of mottled ducks in southwestern Louisiana, USA, 2018–2020.

Model	AIC_c	ΔAIC_c	AIC_c weight	K
Incubation stage at failure	19.8	0.00	0.500	2
Null	21.5	1.66	0.218	1
Initiation date	22.8	3.03	0.110	2
Incubation stage at failure + initiation date	22.8	3.04	0.109	3
Clutch size	24.0	4.17	0.062	2

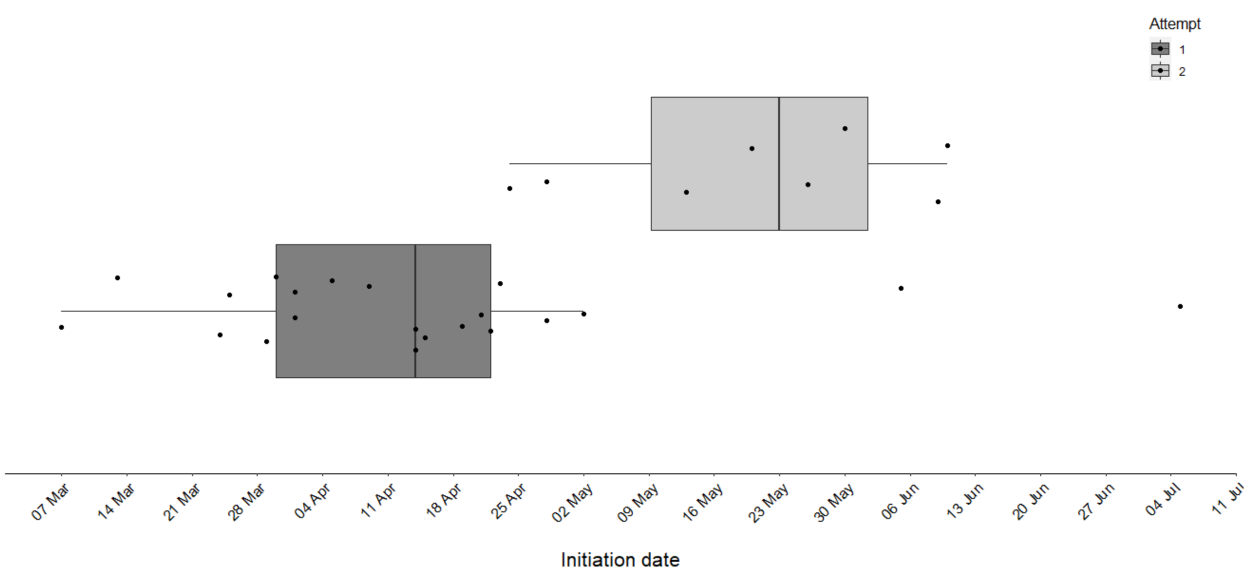

Figure 3.4. Nesting chronology for first and second nest attempts by mottled ducks in southwestern Louisiana, USA, 2018–2020. First attempt nests peaked on ~15 April and second attempt nests peaked on ~28 May.

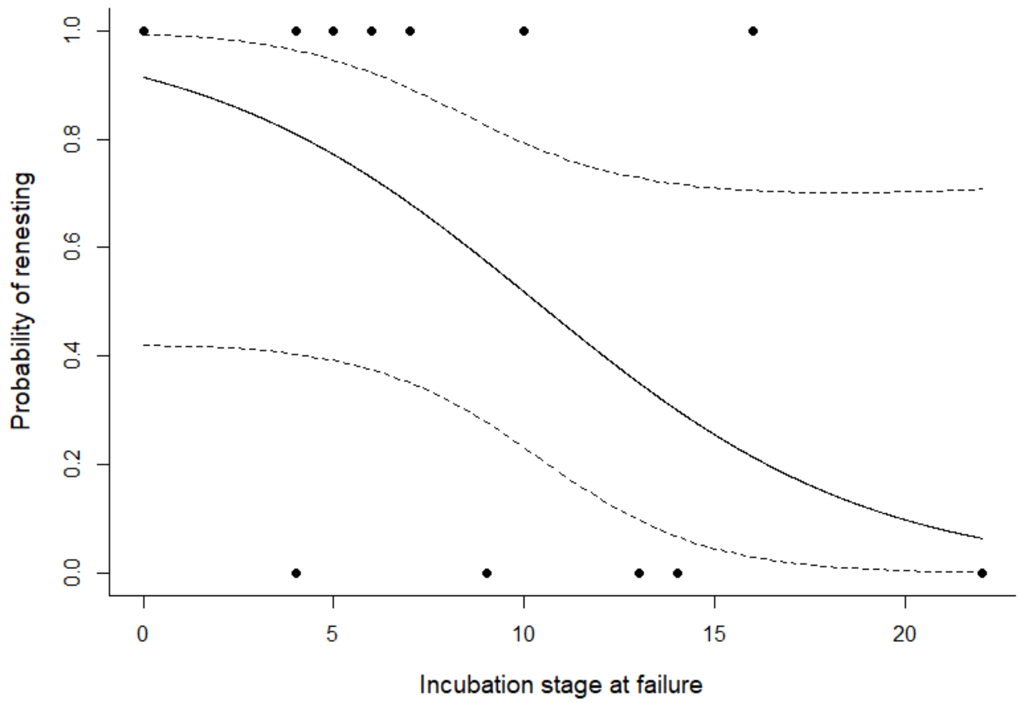

Figure 3.5. Relationship between the probability of renesting and the incubation stage at which first nests failed for mottled ducks in southwestern Louisiana, USA, 2018–2020. The dashed line represents the 95% confidence interval.

3.5. Discussion

Nesting propensity estimates for adult mottled ducks in southwestern Louisiana were low (21.4%) and fall far below the 95–100% expected in adult mallards when conditions are favorable (Hoekman et al. 2002, Hoekman et al. 2006). The two highest estimates of this parameter ever documented for WGC mottled ducks across their range were 77% and 63%, on the mid and upper Gulf Coast of Texas respectively, (Finger et al. 2003, Rigby and Haukos 2012), which are similar to that of mallards in poor body condition (Devries et al. 2008). The low nesting propensity rates observed in mottled ducks marked by transmitters were contrary to those from a small number of mottled ducks marked with geolocators. In the summer of 2018, researchers in southwestern Louisiana marked mottled ducks with leg-mounted geolocators to obtain nesting propensity estimates without the potentially detrimental effects associated with transmitters. Although only 3 geolocators were recovered containing breeding season data, all 3 geolocators showed nest attempts, resulting in a nesting propensity estimate of 100% (Ringelman et al. 2022). Given the high predation risk associated with nesting (Sargeant and Raveling 1992) and nutrient reserves necessary for egg production and incubation in waterfowl (Alisauskas and Ankney 1992), previous studies hypothesized a tradeoff between nesting propensity and survival in mottled ducks (Bielefeld and Cox 2006, Rigby and Haukos 2012). My sample of marked mottled ducks in southwestern Louisiana exhibited high survival (see Chapter 2), which may be linked to the low nesting propensity observed over the course of this study.

Nesting propensity is also linked to environmental conditions (Warren et al. 2014), and although 2018 was a year of moderate drought in the southwest part of Louisiana, average moisture levels were maintained until May (National Oceanic and Atmospheric Administration, National Centers for Environmental Information [NOAA, NCEI] 2021*b*), which is beyond the peak of the mottled duck nesting season. Although the reasons for low nesting propensity in mottled ducks are not well understood, one possibility is that habitat conditions may fail to exceed certain thresholds of quality (Johnson 2009, Rigby and Haukos 2012). Mottled ducks may initiate nesting activity in response to environmental conditions such as temperature and precipitation, or specific habitat characteristics such as vegetation density or water depth that are necessary to fulfill their needs during the nesting and brood-rearing periods. Previous studies observed high variability in nesting propensity (Table 3.3), identifying it as a potential target for management activities that might induce mottled ducks to nest (Rigby and Haukos 2012). Based on the low and invariant nesting propensity estimates observed in this study, there remains an emphasis on obtaining a robust estimate of nesting propensity across the mottled duck range and identifying environmental conditions associated with high nesting propensity where it occurs, and how management actions can consistently provide those conditions.

Table 3.3. Comparison of nesting propensity estimates of mottled ducks across its range.

Geography	Years	Nesting propensity	Reference
Interior Florida	1997–1999	0.22–0.56	Dugger et al. (2010)
Florida	1999–2002, 2009–2011	0.25–0.56	Varner et al. (2013)
Texas mid-Gulf	2000–2002	0.30–0.77	Finger et al. (2003)
Texas upper Gulf	2006–2008	0.15–0.63	Rigby and Haukos (2012)
Southwestern Louisiana	2017–2020	0.18–0.25	This study

Depredation of the nest was the primary cause of nest failure in this study, as it is for most nesting birds (Ricklefs 1969, Greenwood et al. 1995). As a result, individuals choose nest sites to reduce predation risk, often concealing nests in tall, dense vegetation (Martin 1993, Borgo and Conover 2016). I found that daily survival rate increased as visual obstruction measurements increased, a trend that is inconsistent in the waterfowl literature. Although many studies found no relationship between nest survival and visual obstruction (Ackerman 2002, Koons and Rotella 2003, Varner et al. 2013, Péron et al. 2014, Ringelman et al. 2014), others have found a positive or quadratic relationship with survival (Durham and Afton 2003, Grisham et al. 2014, Raquel et al. 2015, Ringelman et al. 2018, Lawson et al. 2021). Durham and Afton (2003) found that successful mottled duck nests were associated with higher vegetation density measurements and a greater number of plant species on agricultural lands in southwestern Louisiana. Coupled together, these characteristics likely added complexity to the vegetation structure and increased nest concealment (Durham and Afton 2003). Although mottled duck nest success was highest during a wet year compared to the drier years on the mid-Gulf Coast of Texas, which may be due to increased plant growth (Finger et al. 2003), nest survival did not vary by year in this study likely because, similar to nesting propensity, the observed period of drought in 2018 occurred after peak mottled duck nesting. Contrary to previous research, nest survival did not vary with distance to water (Durham and Afton 2003); however, the nests I monitored were located across various landscape types and included overwater nests, which were all within 1 m of water. Whether a nest was constructed overwater was also identified as a competitive model and although not significant, nest survival was higher at overwater nests than upland nests. A variety of mammalian, avian, and reptilian predators are known to cause mottled duck nest failure (Stieglitz and Wilson 1968, Baker 1983, Stutzenbaker 1988, Durham and Afton 2003, Finger et al. 2003, Dugger et al. 2010, Kneece 2016); however, more information is needed to understand which predators most commonly depredate nests in southwestern Louisiana and how these predators interact with landscape characteristics such as habitat composition and the density of mottled ducks and other prey species.

Given the apparent relationship between dense vegetation and mottled duck nest survival, land management practices could be tailored to promote successful mottled duck nesting. Currently, most large tracts of upland habitat, characterized by bunch grasses and limited flooding, in southwestern Louisiana are heavily managed and practices such as cattle grazing, haying, and prescribed burns may preclude the production of tall, dense stands of vegetation that is associated with higher nest survival rates, especially when those management activities are not timed to benefit ducks. Prescribed burns are commonly used to reset succession and promote desired plant species when timed in the fall or winter and on a rotational schedule, but when burned too late in the year the vegetation growth may not rebound in time for the breeding season or nests and young may be destroyed (Nyman and Chabreck 1995). Ecological traps may occur when mottled ducks are attracted to the tall, dense stands of vegetation used for haying and cattle forage as an optimal nest site, only for their nests to be destroyed by mowing as the season progresses (Dugger et al. 2010, Bonczek and Ringelman 2021). Most of southwestern Louisiana is privately owned, so to conserve important mottled duck nesting habitat, it is crucial to educate landowners on best management practices that benefit vegetation growth, such as using light cattle stocking rates, burning on a rotational schedule, and timing burns and haying to avoid destroying mottled duck nests and degrading nesting habitat. Moreover, without a complete understanding of how much habitat is needed to support desired population levels, it is important for managers to improve on the current conservation practices used to manipulate mottled duck habitat.

This study provides the first renesting propensity estimates for mottled ducks. The renesting rates observed in 2019 and 2020, 0.71 and 0.75 respectively, were higher than those of other dabbling duck species. Mallards and northern pintails (*Anas acuta*) both renest at a rate of about 0.56 (Grand and Flint 1996, Arnold et al. 2010). Mottled duck renesting propensity declined as the number of days spent incubating the previous clutch increased, similar to other waterfowl species (Krapu et al. 1983, Fondell et al. 2006). Nesting birds must obtain at least a minimum threshold level of nutrient reserves to produce a clutch (Alisauskas and Ankney 1992) and the reduced foraging associated with incubation likely causes a decline in body condition (Hepp et al. 2005), therefore reducing the chance of additional nesting attempts. Initiation date of the first nest was the most important variable influencing renesting propensity in mallards in the Canadian Prairie Parklands (Arnold et al. 2010) and northern pintails on the Yukon-Kuskokwim Delta, Alaska (Grand and Flint 1996). However, I found that initiation date did not influence renesting propensity in mottled ducks; this seems logical, because mottled ducks have a longer nesting window that extends from February through August (Dugger et al. 2010, Walters 2000) and individuals are not as constrained by changes in temperatures or impending autumn migration.

The mottled duck renesting interval, which averaged 26 days, was much longer than that found in mallards, which averaged 5.5 days for females that failed during laying and 10.7 for females that failed during incubation (Arnold et al. 2010). Mallard females renested almost immediately if their nest failed during the laying period (Arnold et al. 2002); in this study, the 2 mottled ducks that lost their nests during laying did not renest for ≥23 days. This suggests either a scarcity of resources to recoup nutrients lost during egg production, less phenological pressure to renest quickly, or both. Given the high renesting propensity found in this study in years of average moisture (2019 and 2020), this vital rate has the potential to help bolster low nest success resulting in a higher hen success rate (Cowardin and Johnson 1979). The large fluctuation observed in renesting propensity among years identifies it as a potential target for management. Renesting was absent in 2018, the year with below average moisture, (National Oceanic and Atmospheric Administration, National Centers for Environmental Information [NOAA, NCEI]*b*) and maintaining water on the landscape in years of drought may promote renesting behavior.

Although transmitters allow us to follow a representative sample of individuals with great precision, there are still limitations and tradeoffs between the logging interval and battery life resulting in the absence of complete information. These nesting propensity estimates may be biased low if nests commonly failed during laying and the female did not log enough locations at the nest for us to detect an attempt. Similarly, nest success estimates may be biased high if I was not able to identify all nests which failed early. Nest success for mottled ducks in this study was above the 15% required for midcontinent mallards to maintain a stable population (Cowardin et al. 1985). Given that many of the nests I located failed during the laying period, I likely missed the discovery of other nests depredated during laying; therefore, the nest success estimate of this marked population would be lower than reported herein, potentially below 15%, although the high renesting rates may help offset low nest success (Cowardin and Johnson 1979). Additionally, the effects of marking mottled ducks with backpack transmitters and a harness attachment may be so great that individuals did not nest at all. Mallards marked with backpack transmitters with a harness attachment weighed less and spent less time in the water than birds without transmitters (Garrettson et al. 2000, Kesler et al. 2014). Female mallards with backpack transmitters allocated fewer days for reproductive behavior and initiated fewer nests than those marked with abdominal implant transmitters (Paquette et al. 1997). Although using transmitters afforded us the opportunity to locate and monitor nests across the landscape, I acknowledge my limited sample size and more extensive and longitudinal studies may uncover variability in breeding parameters not observed in this study. Additionally, other methods, such as geolocators or different attachment methods, may offer a less intrusive way to examine the reproductive parameters that may be more sensitive to transmitter effects, such as nesting propensity.

These results provide additional evidence that mottled ducks in southwestern Louisiana exhibit low nesting propensity, even considering the potential transmitter bias associated with these estimates. Daily survival of mottled duck nests is influenced by visual obstruction such that taller, denser vegetation is associated with higher nest survival. Additionally, I observed high renesting during years of average moisture, which may produce favorable conditions. Thus, management actions should seek to conserve and promote areas with tall, dense stands of vegetation and time various land management strategies in a manner that does not make them an ecological trap, such as conducting prescribed burns in the fall or early winter on a 3–5 year burn cycle and lengthening mowing intervals. Management strategies that keep water on the landscape provide foraging and brood rearing areas which may encourage females to nest and renest. Future research should continue to work to obtain more reliable estimates of reproductive vital rates such as nesting propensity, nest success, and renesting propensity, in addition to duckling survival to fully understand the variation in recruitment by region (Greenwood et al. 1987, Mauser and Jarvis 1994) and across the mottled duck range.

Chapter 4. Nest Site Selection in Mottled Ducks

4.1. Introduction

Breeding habitat selection in North American waterfowl is a hierarchical process (Johnson 1980): at large scales, first- and second-order selection are for latitude and habitat type, and at local scales, third- and fourth-order selection are for breeding home range and for a specific nest location (Kaminski and Elmberg 2014). First- and second-order selection are largely constrained by evolutionary history or broad landscape-level processes (e.g., drought). On the other hand, nest survival is the predominant parameter affecting the population dynamics of many duck species (Hoekman et al. 2002, Johnson et al. 1992), and so much attention has been paid to cues that shape third- and fourth-order selection, because this process should be adaptive to minimize risks of nest failure and increase fitness (Clark and Shutler 1999). Habitat selection at these local scales is generally driven by food availability and predator avoidance and the extent to which such cues can be reliably distinguished by nesting ducks (Eichholz and Elmberg 2014).

Predation is the most common source of nest failure in ducks (Klett et al. 1988), and so nest sites should be selected to minimize this risk of failure. For example, ducks may select nest sites based on patch size (Clark and Nudds 1991, Reynolds et al. 2001) or distance to wetlands (Duncan 1987, Greenwood et al. 1995, Shutler et al. 1998, Larivière and Messier 2000), which may be related to local predator abundance. Nest sites may be selected based on a favorable microclimate for incubation (Gloutney and Clark 1997, Hepp et al. 2006) or vegetation species, height, or density (Lokemoen et al. 1990, Clark and Shutler 1999, Setash et al. 2020) that may conceal the nest from predators. Ducks may also be able to directly assess predator or alternative prey abundance (Ackerman 2002, Dassow 2012) and select nest sites accordingly. Finally, ducks use prior experience (nest success, or failure from predation or flooding) (Greenwood et al. 1982, Lindberg and Sedinger 1997, Öst et al. 2011, Ringelman et al. 2017) to make more adaptive choices in the future. Over time, individuals may alter their behavior based on positive and negative previous experiences (Chalfoun and Schmidt 2012) in favor of nest sites that confer the greatest opportunity for reproductive success (Gavin and Bollinger 1988, Marzluff 1988).

Most ducks are migratory and have little time to evaluate a temporally unpredictable landscape and select nest sites. In contrast, mottled ducks are a non-migratory resident species found along the Gulf Coast of the southern United States (Baldassarre 2014). Because mottled ducks can constantly evaluate relatively less variable habitats to make adaptive choices, mottled ducks should theoretically make well-informed nest-site selection decisions, and yet, nest success is wildly variable among habitats and years (Baker 1983, Stutzenbaker 1988, Holbrook et al. 2000, Durham and Afton 2003). Mottled duck nest success on the western Gulf Coast varies widely depending on the landscape and region; the lowest Mayfield nest success observed was 5.0% in southwestern Louisiana (Baker 1983), compared to the highest estimate of 30.6% observed in the Atchafalaya River Delta (Holbrook 1997), where the differences in these two landscapes are likely to influence this vital rate. Depredation of the clutch or the incubating hen was the primary cause of failure for mottled duck nests (Stutzenbaker 1988, Durham and Afton 2003, Finger et al. 2003). Mammalian predators are expected to be the most frequent mottled duck nest predators, most notably raccoons (*Procyon lotor*; Stutzenbaker 1988, Holbrook 1997, Walters 2000, Dugger et al. 2010, Shipes 2014, Kneece 2016), but also coyote (*Canis latrans*) and striped skunk (*Mephitis mephitis*; Durham and Afton 2003). In addition, snakes (Baker 1983, Finger et al. 2003) and American alligators (*Alligator mississippiensis*) may cause partial or complete clutch loss. Other causes of nest loss include flooding (Finger et al. 2003, Caillouet

2015), mowing/plowing (Dugger et al. 2010), trampling by cattle (Durham and Afton 2003), and abandonment due to disturbance (Walters et al. 2001) or partial clutch loss (Finger et al. 2003).

Previous studies on mottled duck nesting ecology have documented nests in a variety of landscape types, including cordgrass prairie, tallgrass prairie, idle rice fields, cattle pasture, salt marsh (Stutzenbaker 1988, Finger et al. 2003), and freshwater marsh (Bonczek and Ringelman 2019) in Texas and southwestern Louisiana, and on dredge spoil islands, canal banks, and levees along the river deltas of Louisiana (Holbrook et al. 2000, Walters et al. 2001). In the agricultural lands of southwestern Louisiana, females choose to nest in permanent pastures with knolls or idle fields and select sites with taller vegetation (Durham and Afton 2003). Similarly, on the mid-coast of Texas, nests were also found in vegetation >60 cm tall with >75% canopy cover (Finger et al. 2003). Mottled ducks may elevate their nests when nesting in areas prone to flooding (Finger et al. 2003). Nests were located "within several hundred feet," or up to 1.5 km in a drought year, from temporary or permanent water bodies (Stutzenbaker 1988) expected to function as brood rearing habitat.

Although previous research examined the landscape characteristics that influence nest survival, very few studies have investigated the factors that influence nest site selection in mottled ducks. Additionally, previous studies have located mottled duck nests by searching targeted habitats or observing nesting females return to their nests after morning incubation breaks. These techniques may therefore limit our understanding of which landscapes mottled ducks prefer across the region as mottled ducks may nest in landscapes not under observation. Here, I used GPS-GSM transmitters to monitor nesting mottled ducks across southwestern Louisiana, a stronghold for breeding WGC mottled ducks. Understanding which landscapes mottled ducks prefer and how landscape characteristics are associated with nest site selection can be used to inform and prioritize habitat conservation decisions. The objective of my study was to determine how landscape-level characteristics influence nest site selection. In concordance with previous research, I expected mottled ducks to choose nest sites with taller and denser vegetation than available sites.

4.2. Study area

Our primary mottled duck capture site was at Rockefeller Wildlife Refuge (hereafter Rockefeller) in southwestern Louisiana, a roughly 29,000 ha property managed by the Louisiana Department of Wildlife and Fisheries. Rockefeller is located in Cameron and Vermilion Parishes at the lower end of the Mermentau River Basin near Grand Chenier, Louisiana; Rockefeller borders the Gulf of Mexico and extends inland about 10 km. Rockefeller contains both managed and unmanaged wetland impoundments of varying salinity from fresh to saline, and moist soil management units (Selman et al. 2011). Marked birds nested across southwestern Louisiana in Cameron, Vermilion, Calcasieu, and Jefferson Davis parishes. The average breeding season temperature 2017–2020 in parishes in which nests were commonly found was 23.4°C in Cameron Parish, 23.3°C in Vermilion Parish, and 22.9°C in Jefferson Davis Parish, and average monthly precipitation was 13.0 cm, 13.3 cm, and 13.1 cm respectively (National Oceanic and Atmospheric Administration, National Centers for Environmental Information [NOAA, NCEI] 2021*a*).

4.3. Methods

I captured adult female mottled ducks on Rockefeller and adjacent private land during the summers of 2017–2019 from airboats at night by hand when the birds were molting and unable to fly (Cummings and Hewitt 1964) in conjunction with annual waterfowl banding activities conducted by Louisiana Department of Wildlife and Fisheries. Captured individuals received a

U. S. Geological Survey aluminum or incoloy leg band and some individuals received 21 g solar-powered Saker-L GPS-GSM transmitters (Ecotone Telemetry, Gdynia, Poland) which use the cellular network to transmit locations. The body mass of birds I selected was ≥ 690 g, to ensure transmitters were ≤ 3% of body mass. I prioritized deploying transmitters on mottled ducks that had already completed molt and were flight capable, or individuals that were furthest along in molt, as I reasoned that these birds would be less vulnerable to predation and less energetically stressed as they grew accustomed to the transmitter. I attached the transmitters in a modified Dwyer style configuration (Dwyer 1972) with two separate loops— one around the body behind the wings and one around the neck which sat at the base of the furcula; these loops were secured with knots and epoxied. I used Conrad-Jarvis 6 mm black nylon automotive elastic with neoprene elastomer (Casazza et al. 2020) and tightened until the tip of the thumb fit under the unit. I released marked birds within 12 hours back to location of capture. Transmitters logged GPS coordinates every 2 hours during daylight and were accurate to 30 m. I obtained transmitted data from the manufacturer-designed web-based Ecotone data management panel. From this panel, I could obtain transmitter metrics, such as battery level, activity level, temperature, and date of most recent GPS location, and download individual kmz files with monthly GPS locations to be input into Google Earth or .csv files of bird locations for further analysis. My procedures were approved by Louisiana State University Institutional Animal Care and Use Committee under permit A2016-27 and federal bird banding permit 06669.

Monitoring began 1 Feb 2018–2020. I examined the locations and movements of each individual every 3 days using the Google Earth kmz file obtained from the web-based Ecotone data management panel. Once I identified an individual that logged locations in the same area consecutively (Fig. 1), I waited 10 days from the inferred date of nest initiation, which was determined by the first date the female was observed at the presumed nest site, to ensure the female had begun incubating and visited the site on foot to confirm the presence of a nest. The use of a dog was extremely helpful in locating nests (Glover 1956, Keith 1961) when they were unable to be located by researchers alone, especially for nests where the female was not present or had already failed at the time of discovery. At the initial nest visit I collected clutch size and incubation stage by candling (Weller 1956). At the landscape scale, I recorded the habitat type, which I defined as pasture, old field (lightly grazed or ungrazed), emergent marsh, idle rice, or crawfish (*Procambarus* spp.) pond levee. At the nest site scale, I recorded height of the tallest vegetation adjacent to the nest bowl, visual obstruction, and the top 3 dominant plant species and percent cover within a 4 m radius around the nest bowl. I used visual obstruction as an index of vegetation density, which was measured using a Robel pole at a height of 1 m and a distance of 4 m from the nest bowl in each cardinal direction (Robel et al. 1970). At the final visit to determine nest fate, I collected elevation using a Hiper II dual-frequency Real Time Kinematic and static GNSS receiver from Topcon systems, used in static mode on a 1.6 m range pole with support bipod. The receiver was set to log all available GNSS satellite signals at 1-second intervals to an internal microSD card, and each static occupation was a minimum of 15 minutes. I was unable to collect elevation in 2020 because of complications obtaining the equipment. From satellite imagery and ArcMap, I measured patch size, distance to water, type of nearest water, distance to main road (defined as public access roads), distance to road (included two-tracks and driveways), distance to path (e.g., patch edge, levee, etc.), and distance to nearest croplands as defined by the 2019 National Land Cover Database (United States Geological Survey, Multi-Resolution Land Characteristics Consortium 2019). I used transitions between cover types to designate patch borders. For every nest site, I selected 4 matched random points and visited them as close to the date of the initial nest site visit as possible; however, because of landowner permission and private land access, I was not able to obtain 4 random points for all nests. I selected these random points in R by generating an 80% minimum convex polygon home range of the nesting female for the 6 days prior to nest initiation. I used a 6-day window because this is the timeframe in which rapid follicular growth occurs in mottled ducks (Alisauskas and Ankney 1992), so I assumed females would be prospecting for a nest site at this time. Using the home range of the female allowed us to examine nest site selection at a biologically-relevant scale. I took identical measurements at the random points as I did at the nest site. Landscape types that characterized random points were classified in the same way as nests, in addition to an "other" category that encompassed open water, croplands, and forest.

I used generalized linear models to check for differences between the nest sites and random points, where "1" and "0" designated used and available, respectively. I defined salinity based on a marsh vegetation type classification layer from the U.S. Geological Survey (Enwright et al. 2015), which delineated coastal marsh vegetation communities into saline, brackish, intermediate, freshwater marsh, and other. Areas classified as "other" I assumed to be fresh because of their inland location, and those classified as open water I determined to be the salinity of the nearest designation. Visual obstruction and vegetation height were correlated as were distance to main road, road, path, and patch size. Therefore, I included only visual obstruction and distance to path in our models. I included the quadratic term of visual obstruction because previous studies found that nesting ducks may select an intermediate level of vegetation height and density (Götmark et al. 1995). I created a candidate set of 9 univariate models and added models with multiple covariates when I determined the combination of covariates was biologically meaningful. I used corrected Akaike information criterion (AIC_c) to rank the resulting models (Burnham and Anderson 2002, Arnold 2010), whereas models ≤ 2 ΔAIC_c were competitive.

4.4. Results

I located 30 nest attempts by 17 females from 2017–2021. I initially excluded 2 nests from analysis due to the inability to locate the nest bowl. One excluded attempt was a dead female with 1 egg and the other attempt was excluded because I was only able to locate eggshell fragments among extremely tall and dense vegetation. Mottled ducks nested across southwestern Louisiana (Figure 4.1) in various landscape types. Of the 28 nest bowls I located, most nests were found in old fields (39.3%), followed by pasture (28.6%), emergent marsh (14.3%), idle rice (10.7%), and crawfish pond levees (7.1%; Table 1). Elevations at nest sites ranged −0.068–6.221 m, averaging 2.215 ± 2.068 (SD) m. Patch size ranged 0.6–2,831 ha, averaging 515 ± 1,067 ha. I removed an additional 3 nests from the nest site selection analysis because land access restrictions in 2020 prevented me from obtaining random points, resulting in a total of 25 nests included in analysis. Nest site selection in mottled ducks was best explained by landscape type and visual obstruction measurement, and no other models were competitive (Table 4.2). The probability of use was highest in old fields ($\beta = 2.452 \pm 1.462$, $p = 0.094$) and lowest in marsh ($\beta = -4.133 \pm 1.764$, $p = 0.019$; Figure 4.2). The probability of use was positively associated with visual obstruction ($\beta = 0.658 \pm 0.178$ [SE]; Figure 4.3).

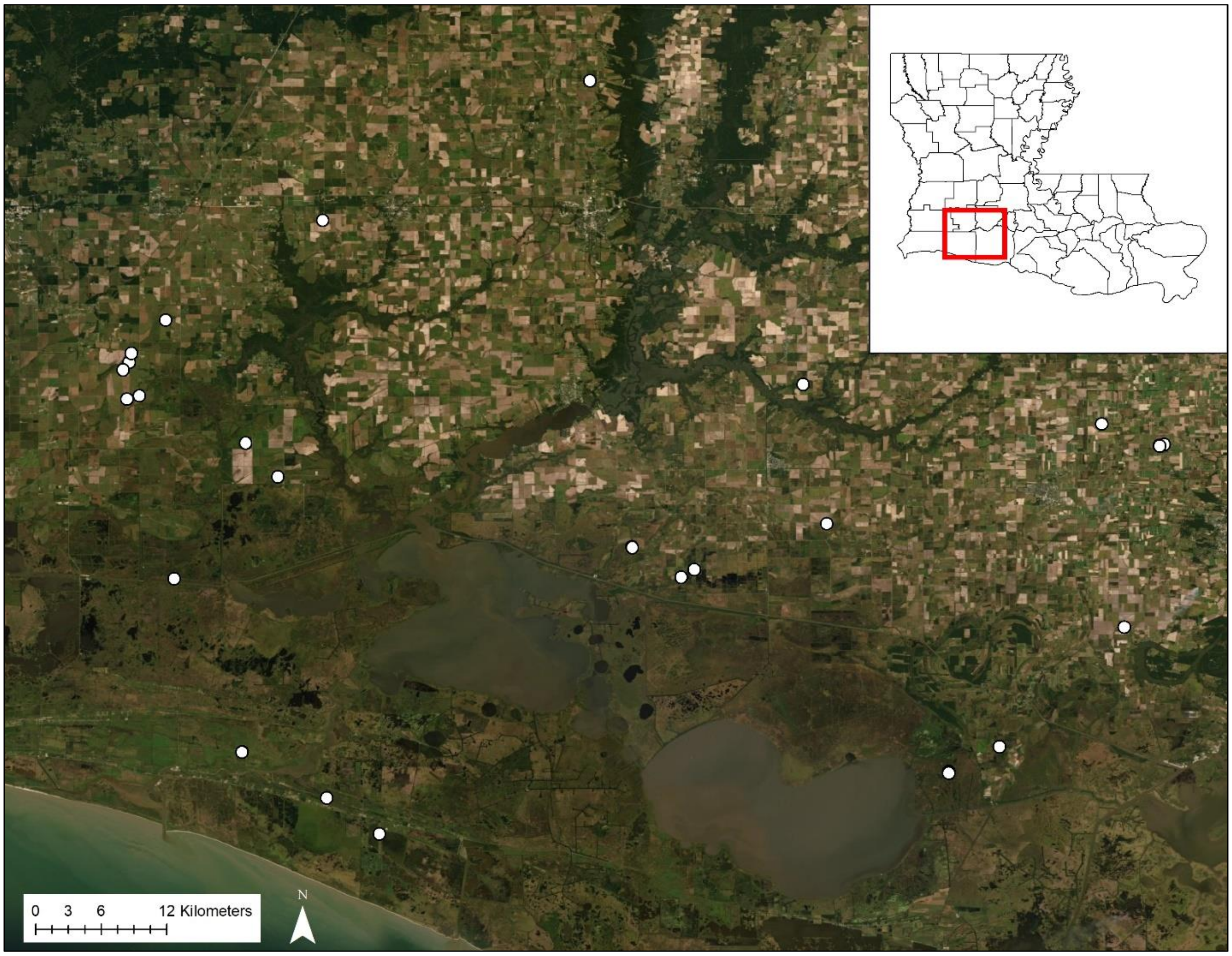

Figure 4.1. Location of mottled duck nests monitored in southwestern Louisiana, USA, 2017–2021.

Table 4.1. Average visual obstruction measurement (dm) and common plant species by landscape type at the nest sites of mottled ducks in southwestern Louisiana, USA, 2017–2021.

Landscape type	Average visual obstruction (dm)	Common plant species
Old fields	6.3	*Andropogon* spp., *Paspalum* spp., *Eleocharis* spp.
Pasture	4.8	*Paspalum* spp., *Axonopus fissifolius*, *Spartina patens*, *Eleocharis* spp.
Emergent marsh	10.9	*Zizaniopsis milliaceae*, *Sagittaria* spp.
Idle rice	4.3	*Eleocharis* spp., *Iva* spp.
Crawfish pond	3.5	*Panicum* spp., *Cynodon dactylon*

Table 4.2. Model results that best explained nest site selection of female mottled ducks in southwestern Louisiana, USA, 2017–2021. I used corrected Akaike's Information Criterion (AIC_c), ΔAIC_c, AIC_c weights, and number of parameters (K) to rank models. I included the next best model, univariate models of the top-ranked model, and null model for comparison.

Model	AIC_c	ΔAIC_c	AIC_c weight	K
Robel + habitat type	78.9	0.00	1	7
Robel + distance water	95.0	16.05	0	3
Habitat type	101.1	22.20	0	6
Robel	109.9	30.99	0	2
Null	123.9	44.99	0	1

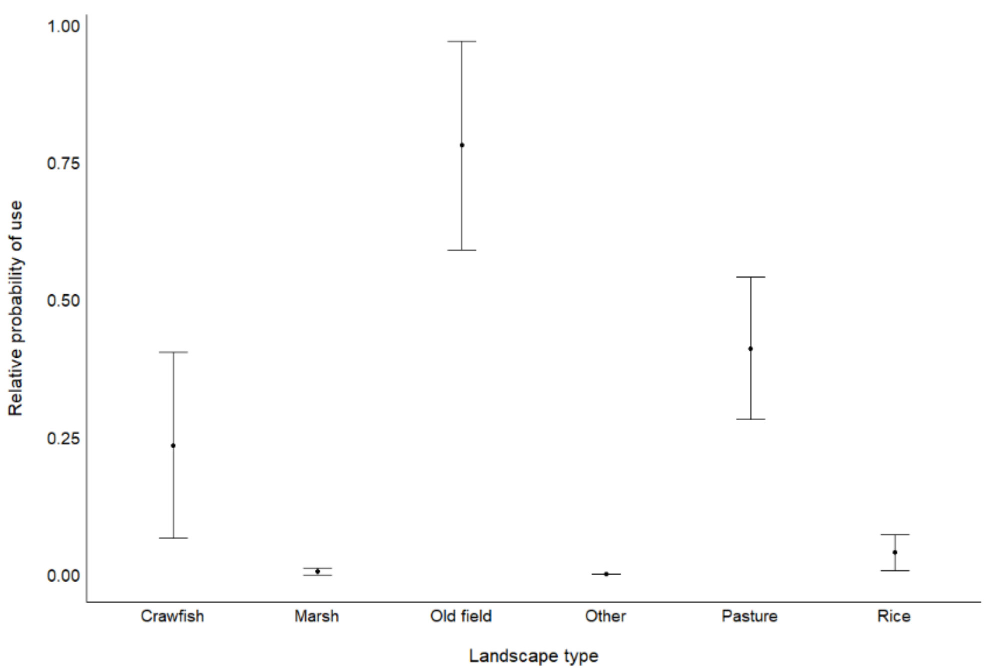

Figure 4.2. Relationship between the probability of use and landscape type for mottled ducks choosing nest sites in southwestern Louisiana, USA, 2017–2021. Error bars denote standard error.

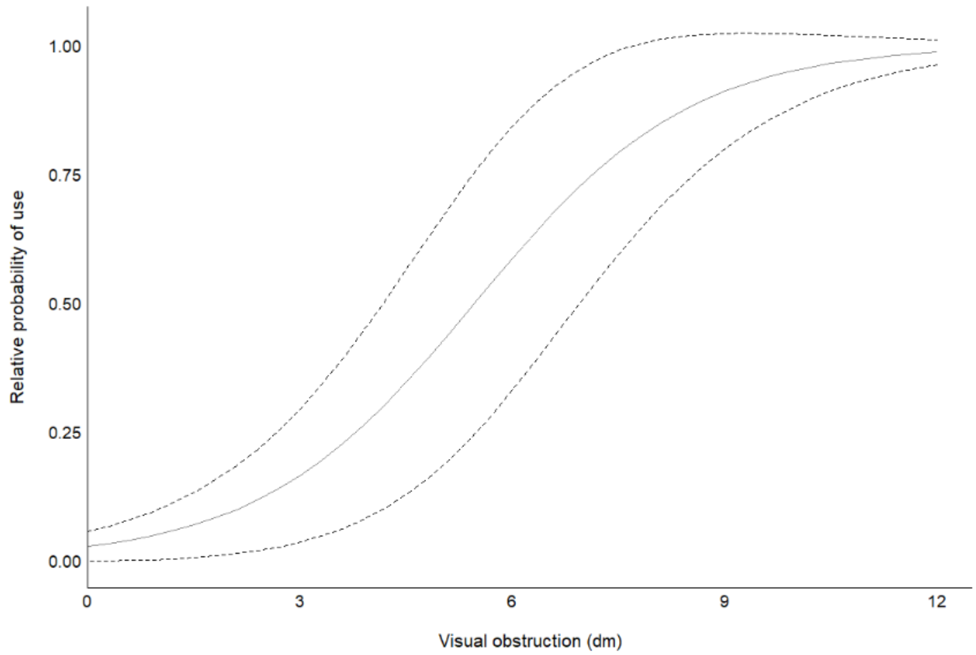

Figure 4.3. Relationship between the probability of use and visual obstruction measurement (dm) for mottled ducks choosing nest sites in southwestern Louisiana, USA, 2017–2021. The dotted line represents the 95% confidence interval.

4.5. Discussion

Selection of a higher-quality nest site should confer reproductive advantages (Clark and Shutler 1999), so it is critical to understand the factors that influence this process. Although qualitative data exist, few studies have quantitatively examined nest site selection in mottled ducks despite the importance of breeding habitat conservation for this declining species. By marking females during molt, I obtained a more representative sample of utilized nest sites because I followed individual females and observed their nesting behavior, rather than searching for nests in researcher-selected landscapes and locations. Previous studies monitored nesting mottled ducks in certain landscapes or within distinct study area boundaries (Stutzenbaker 1988, Durham and Afton 2003, Holbrook et al. 2000), which precluded the observation of all possible nesting habitats. I found that mottled ducks nested in various landscape types, including nests that were constructed overwater in emergent marsh (Bonczek and Ringelman 2019). Mottled ducks were most likely to nest in old fields, which were ungrazed and often appeared to be lacking current land use activities. However, there may have been a bias associated with the discovery of mottled duck nests in upland landscapes identified from telemetry data. An individual that spends time in dry areas, such as overgrown fields or pastures that lack wetlands, presents a more obvious nest attempt compared to an individual that nests in flooded areas they frequent regardless of nesting status (e.g., for foraging or loafing), such as cordgrass meadows or emergent marsh. Previous work in agricultural lands in southwestern Louisiana found that mottled ducks preferred nesting in permanent pasture with knolls and idle areas, which were ungrazed or lightly to moderately grazed and characterized by dense perennial grasses and scattered shrubs (Durham and Afton 2003), similar to old field and pasture designations in this study. Mottled ducks on the Atchafalaya River Delta nested in shrub-moderate habitat, where ground cover was $> 30\%$ and cover at 1.5 m was $\geq 10– < 50\%$, and avoided shrub-sparse, where ground cover was $\geq 10– \leq 30\%$ and cover at 1.5 m was $< 10\%$, and marsh habitat (Holbrook et al. 2000). Mottled ducks may avoid nesting in areas such as marsh if they are regularly inundated (Baker 1983, Stutzenabker 1988) because of flood risk to the nest. Although this may be true, I observed a female add new material and increase the elevation of the nest bowl in response to light flooding from a rain event, suggesting mottled ducks can adapt to some changes in conditions during nesting. Emergent marsh was also the least likely landscape type mottled ducks selected for nesting in this study. This may be because the marsh landscape was so vast that the characteristics of the vegetation and physical environment were relatively homogenous within the home range of marsh-nesting females, thereby resulting in similarity between the nest site and random points. Nest survival is positively associated with visual obstruction in mottled ducks (Durham and Afton 2003, Chapter 3) and vegetation height and density in emergent marsh in southwestern Louisiana (Table 4.1) were typically favorable for nest survival; thus, I expected a higher probability of use in this landscape.

The probability of use increased as visual obstruction increased, and nest sites chosen by mottled ducks were characterized by taller and denser vegetation than available sites. Durham and Afton (2003) examined the nesting ecology of mottled ducks in agricultural lands of southwestern Louisiana, and they similarly found that mottled ducks selected nest sites with taller vegetation than available sites. Although this vegetation structure is not likely to conceal nests from mammalian predators, which typically use olfactory cues in foraging (Nams 1997, Clark and Wobeser 1997), vegetation height and density may impede the movement of predators or block scent, thereby providing some protection (Elton 1939, Hines and Mitchell 1983). The effects of visual obstruction on nest survival are inconsistent for waterfowl overall (Ackerman 2002, Koons and Rotella 2003, Varner et al. 2013, Péron et al. 2014, Ringelman et al. 2014, Raquel et al. 2015, Ringelman et al. 2018, Lawson et al. 2021); however, previous research found visual obstruction positively influenced nest survival in mottled ducks (Durham and Afton 2003, this study), so this preference may be adaptive.

Previous mottled duck research concluded certain landscape features were important for nesting mottled ducks, but not all of them were identified as significant in this study. Patch size where nests were found in southwestern Louisiana ranged widely. Current management recommendations focus on conserving large tracts of land for nesting mottled ducks (Hartke 2013); however, I observed that mottled ducks still use small tracts of habitat successfully, and thus they should not be discounted in conservation measures. Old fields, the most frequently used landscape type, averaged only 14 ha, although current management guidelines identified tracts of < 16 ha as unsuitable habitat (Hartke 2013). Distance to nearest water was another variable that was not competitive, despite the risks associated with overland brood movements and the foraging opportunities provided to the incubating female. I was able to follow 5 successful females to their brood rearing area. Nest sites were located an average of 2,440 ± 1,600 m straight-line distance from the nest site to the final brooding area, which was designated as the area at which the female made no further movements outside of the patch. These observations suggest that broods travel greater distances for brood rearing areas than previously thought. For example, nesting areas >1.6 km from potential brood rearing areas were deemed unsuitable for mottled ducks due to the distance (Krainyk et al. 2019), but my observations suggest that making such a designation may exclude nesting habitat and thus deprioritize areas for conservation that are in fact useful. When calculating the exact distance traveled, rather than the straight-line distance of the brood area from the nest, one female traveled 7.8 km over almost 72 hours. On the way to the final brood rearing area, females bypassed or only briefly used other shallow wetlands with emergent vegetation, some of which appeared similar to the final destination, highlighting how little is understood about the brood rearing needs and selection process of this species. Dabbling ducks in the central valley of California also escorted their broods to ponds further from the nesting site than the closest available brood pond (Casazza et al. 2020). Mottled duck females seemed to know exactly where they wanted to take their broods, as evidenced by two instances of prospecting the day before hatch. Having prior knowledge of wetland conditions such as water level, vegetation cover, and food resources likely benefits broods and minimizes the risks associated with bringing a brood to a novel wetland (Casazza et al. 2020).

I documented nest attempts in multiple years for 4 females, 3 of which nested in close proximity (23, 39, and 106 m) to the nest site of the previous year. The remaining female nested

7.2 and 19.4 km from previous nest sites. These results suggest that mottled ducks may exhibit high nest site fidelity, and perhaps more so when the clutch of the previous year hatched successfully. Of the females that nested near the site of the previous year, 2 experienced success on their first documented nest attempt, while 1 was unsuccessful on her first documented attempt but successful the subsequent year.

Mottled ducks in southwestern Louisiana select nest sites with tall, dense vegetation and prefer to nest in old fields, whereas they are least likely to nest in emergent marsh. Land use practices that influence vegetation growth, such as grazing and haying, should be minimized during the mottled duck breeding season to promote ideal vegetation conditions for nesting birds. Additionally, the timing of prescribed burns should be conducted to allow for sufficient regrowth of desired species prior to the nesting season, and parcels on which burns occur should be rotated to provide areas not affected by burns. Future studies should investigate the dominant predators of mottled duck nests and the role that nest density of mottled ducks and other nesting birds may have on nest-site selection and predator-prey dynamics. Birds may be able to assess the predator community and make behavioral decisions based on that knowledge (Eicholz and Elmberg 2014), so by understanding which predators are most common, researchers can pinpoint selected nest site characteristics that influence predator foraging behavior (e.g., for olfactory predators, specific characteristics may influence the scent cone of the nest; Conover 2007). Improving the understanding of mottled duck nest site selection and drivers of nest survival will help guide targeted conservation measures to provide quality habitat for nesting mottled ducks.

Chapter 5. General Conclusions

As one of the few non-migratory ducks in North America, mottled ducks depend on the coastal marsh and other locally available habitats throughout the annual cycle, and threats to these landscapes may affect mottled ducks more acutely than migratory species. Western Gulf Coast mottled duck numbers have declined over the past few decades. Threats to the population include habitat loss and degradation, changes in predator populations and distribution, variation in precipitation, land use changes, lead exposure, and harvest (Wilson 2007). Survival and fecundity drive population dynamics, thus declines are related either to survival or recruitment. Furthermore, evidence for range-wide variation in mottled duck demographic parameters may indicate the need for management efforts on a more regional scale. This project was initiated in response to declines in the WGC mottled duck population. I examined mottled duck demographic parameters in southwestern Louisiana, the stronghold of the Louisiana breeding mottled duck population, and what factors influenced these rates.

Maximum partitioning of the year into the hunted periods and biological season best explained temporal variation in mottled duck survival. Competing models varied slightly, but all contained the hunted and non-hunted periods. The periods of lowest survival were the teal season and the first split of the hunting season, and the period of highest survival was the second split of the hunting season. Similarly, the hunting seasons best explained variation in survival in the Chenier Plain of Texas (Moon et al. 2017). Although illegal harvest was observed in Texas, the increased mortality associated with the teal season in this study, may have been a delayed transmitter effect, as result of poor body condition following molt, or an interaction between the two. The vast majority of marked mottled ducks harvested during this study occurred in the first split of the hunting season. The mottled duck season is closed in Texas during the first 5 days of the season and my results corroborate that mottled ducks may be more vulnerable to harvest during this time. Survival was also explained by the proportion of GPS locations in agricultural land, which exhibited a positive relationship. Agriculture may provide a more abundant or better-quality food source or there may be different predator communities or abundance in this landscape compared to other landscape types. Annual survival during this study was one of the highest estimates for WGC mottled ducks.

Reproductive parameters central to recruitment include nesting propensity, nest survival, and renesting propensity. The nesting propensity rate observed in this study was extremely low compared to what is expected for waterfowl when conditions are favorable. Given the high risk of predation associated with nesting there may be a tradeoff between nesting propensity and survival; however, further research should be conducted to identify environmental conditions that are associated with high nesting propensity rates in mottled ducks and how managers can provide for those conditions. Nest survival estimates during this study were among the highest for WGC mottled ducks and nest survival varied positively with visual obstruction. Tall, dense vegetation likely provides the vegetation structure needed to conceal nests from predators. Renesting propensity during this study was high during years with average moisture, but low during a moderate drought year, indicating that environmental conditions may play a role in the decision of females to renest. Additionally, renesting propensity decreases as the stage at which nests fail increases, suggesting that mottled ducks females which invest more effort in their previous clutch, and thus use more nutrient reserves, may not be willing or cannot recoup the reserves necessary for additional egg production. Although transmitters allowed us to gather unprecedented nesting data, there may also be some bias associated with the use of transmitters. When females lay eggs, they only spend a short amount of time at the nest, so if nests are depredated before I was able to identify a nest attempt, they are not accounted for. The presence of unidentified nest attempts would bias nesting propensity low and nest survival high.

Nest site selection should minimize risks of failure in order to increase fitness and is driven by predator avoidance and food availability. Mottled ducks in southwestern Louisiana nested in a wide range of habitats across the region, including old fields, pasture, emergent marsh, idle rice fields, and crawfish levees. Nest site selection in mottled ducks was best explained by habitat type and visual obstruction measurement. Mottled ducks were most likely to use old fields and least likely to use emergent marsh for nesting. The probability of use also exhibited a positive relationship with visual obstruction, which follows given that nest survival is positively associated with visual obstruction. I expected a higher probability of use in emergent marsh since vegetation height and density in emergent marsh were generally favorable for nest survival. However, the marsh landscape was expansive, and the characteristics of the vegetation and physical environment were often similar between the used nest sites and the unused locations. Lastly, nest attempts in fields and other dry areas were much more obvious than nest attempts in wetlands because locations transmitted at short-lived nests in emergent marsh could have been mistaken for foraging or loafing activity. This may have resulted in a transmitter bias of being more likely to identify nest attempts in upland habitat.

The use of GPS-GSM transmitters allowed us to answer a range of critical questions to better understand population dynamics of mottled ducks. Annual survival in this study was within the range of other dabbling duck species not experiencing declines, indicating that survival rates are likely not limiting WGC mottled ducks in southwestern Louisiana. However, if managers would like to take action to decrease mottled duck mortality, further research should investigate the effects of the delayed harvest window and how it influences harvest numbers and a similar limited mottled duck season could be enacted in Louisiana. Instead of survival, the decline is likely related to components of recruitment. Both nest survival and nest site selection are related to vegetation density, so landowners managing for breeding mottled ducks should keep cover on the ground throughout the breeding season and minimize burning, mowing, and grazing to prevent quality patches from becoming ecological traps. Lastly, as technology advances, new methods may reveal a deeper insight into the reproductive parameters which have traditionally been difficult to estimate, such as nesting and renesting propensity.

Appendix. Publishing Agreement

Using previously published JWM articles in dissertation

Elizabeth Bonczek <lizzi.bonczek@gmail.com> Mon, May 16, 2022 at 2:11 PM
To: permissions@wiley.com

Hi,

I am the first author on two articles that have been published in the Journal of Wildlife Management over the past few years (see below for article titles). I am putting together my dissertation, and was hoping to include those manuscripts, but am not sure the exact steps I should take to make this happen. Where can I go to access the publishing agreement? Or do I have to submit a permissions request?

Bonczek, E. S., K. M. Ringelman, J. R. Marty, and S. A. Collins. Temporal variation and landcover influence survival in adult female mottled ducks. *In print*.

Bonczek, E.S. and K. M. Ringelman. 2021. Breeding ecology of mottled ducks: a review. Journal of Wildlife Management 85:825-837.

Thank you for any assistance you can provide on this!

Thanks,

Lizzi Bonczek

--
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Using previously published JWM articles in dissertation

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Vita

Elizabeth “Lizzi” S. Bonczek was born in Fitchburg, MA. She graduated from the University of Maryland in 2013, where in her last year she started work at the captive seaduck colony at Patuxent Wildlife Research Center and fell in love with ducks. After graduation, she worked seasonal jobs focused on a variety of waterfowl species, on the breeding, wintering, and staging grounds around the country. Observing graduate students and researchers explore research questions was a great motivator in her decision to pursue a future in waterfowl research. Lizzi began her PhD at Louisiana State University examining the breeding ecology of mottled ducks in January 2017. Following the completion of her degree, Lizzi hope to continue her work with waterfowl and use research to make applied management decisions.