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Review

Breeding Ecology of Mottled Ducks: A Review

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ABSTRACT Mottled ducks (*Anas fulvigula*) are endemic to the Gulf Coast of North America, and their range stretches from Alabama to the Laguna Madre of Mexico, with a distinct population in peninsular Florida and an introduced population in South Carolina. As one of the few non-migratory ducks in North America, mottled ducks depend on a variety of locally available habitat throughout the annual cycle, and threats to these landscapes may affect mottled ducks more acutely than migratory species. Annual population monitoring has revealed declines in mottled duck populations in Texas and Louisiana since 2008, and the genetic integrity of the Florida population has been muddled by the presence of large numbers of feral mallards (*Anas platyrhynchos*) resulting in hybridization. Similar to other closely related dabbling ducks, mottled duck populations are influenced by recruitment and breeding season survival, so changes in these factors may contribute to population decline. Accordingly, researchers have attempted to address various aspects of mottled duck breeding season ecology and population dynamics since the 1950s. We conducted a literature review on this topic by searching a combination of key terms using Google Scholar, including mottled duck, nesting ecology, habitat use, breeding incidence, nest success, brood, and breeding season survival, and followed citation trees to eventually aggregate information from nearly 50 publications on mottled duck breeding ecology. Our review concluded that mottled ducks use brackish and intermediate coastal marsh, including managed impoundments, and agricultural land during the breeding season. Their nests can be found in pastures, levees, dry cordgrass marsh, cutgrass marsh, spoil banks, and small islands. Nesting propensity and nest success estimates are often lower than other waterfowl species that are characterized by stable or increasing populations. Broods use wetlands composed of a mix of open water with submerged and emergent vegetation. Breeding season survival is higher for the Florida population than the western Gulf Coast population, but adult survival in both geographies is comparable to (or higher than) that of other dabbling duck species. Breeding habitat use, breeding season survival, and nest-site selection and success have been studied extensively in mottled ducks, whereas information on nesting propensity, renesting intensity, and post-hatch ecology is lacking.

KEY WORDS *Anas fulvigula*, coastal marsh, Florida, Gulf Coast, Louisiana, nest, survival, Texas, waterfowl.

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; Fig. 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 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,

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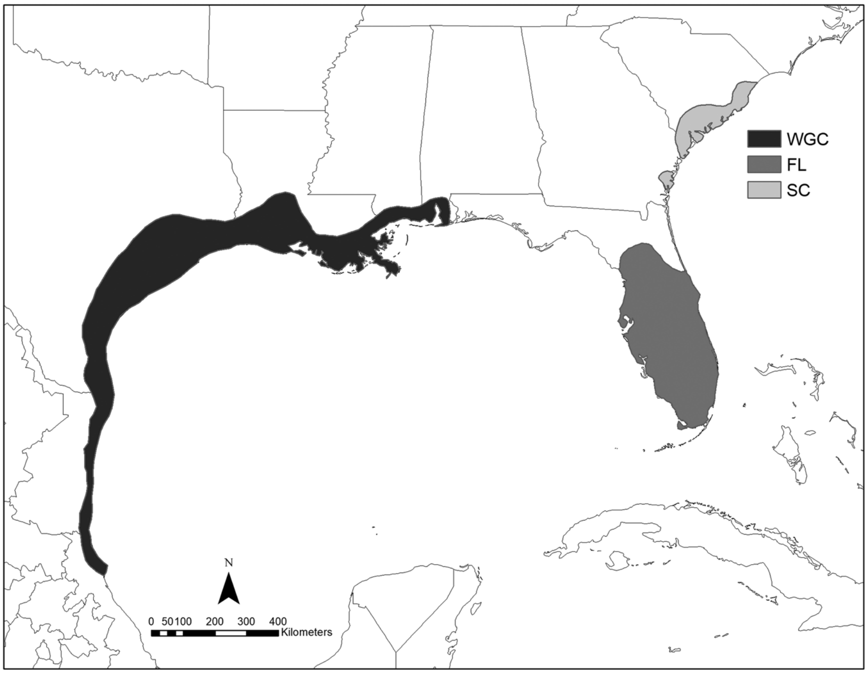

Figure 1. Mottled duck range in 2021, parsed by western Gulf Coast (WGC), Florida (FL), and south Atlantic (SC) populations.

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 (Fig. 2).

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 breeding propensity ($r^2 = 0.322$) and nest success ($r^2 = 0.200$) were the most important components. Recruitment of mottled ducks is low compared

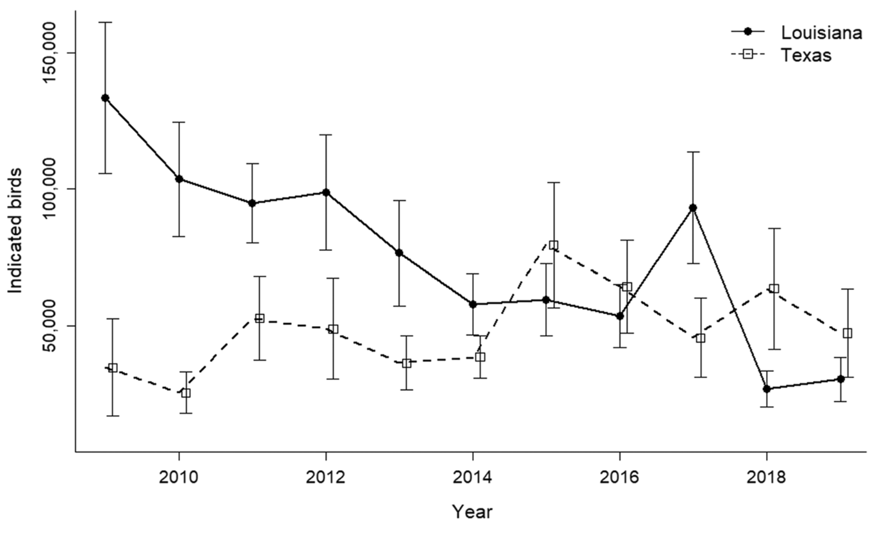

Figure 2. Western Gulf Coast mottled duck population estimates during the breeding population survey, 2009–2019 (excludes the Laguna Madre region of TX; U.S. Fish and Wildlife Service 2019).

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.

We reviewed the literature on mottled duck breeding ecology. Our 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.

STUDY AREA

The range of the mottled duck is restricted to the southern United States. The Florida 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).

METHODS

We conducted our 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. We followed citations 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.

RESULTS

Breeding Habitat Use

Second-order habitat selection (i.e., home range; Johnson 1980, Eicholz and Elmberg 2014) for breeding dabbling ducks is shaped by habitat availability and territoriality (Lokemoen et al. 1984, Eicholz and Elmberg 2014). Thus, habitat selection may be constrained for species in some geographies, forcing pairs into suboptimal 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 land cover, 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.

We 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.

Nesting Ecology

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).

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 our 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.

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).

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).

Nest success.—Mayfield nest success for mottled ducks ranges from 5.0% (Baker 1983) to 57.0% (Stieglitz and Wilson 1968; Table 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

Table 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 (%)		Reference
			Mayfield	Apparent	
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).

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) 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 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.

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.

Brood Ecology

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).

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 our knowledge of what constitutes suitable brood habitat and which land cover types are avoided, we can improve our understanding of which wetlands should be prioritized for conservation.

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 mottled ducks in Florida, 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). Mottled ducks in Florida 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 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

Table 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 Mar–31 July	0.97	0.86	Bielefeld and Cox (2006)
South Florida-rural	2009	1 Mar–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–Jul 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 Jun	0.94	0.76	Rigby and Haukos (2012)
Texas	2007–2009	1 Mar–14 Jul	0.93	0.70	Wehland (2012)
Louisiana	2007–2009	1 Mar–14 Jul	0.94	0.76	

[a] Encompasses breeding and brooding period.

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 we assign to breeding season survival rates.

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). Mottled ducks in Florida 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).

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.

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