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Temporal variation and landcover influence survival in adult female mottled ducks

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Abstract

Adult survival is a key driver of waterfowl population growth and is subject to temporal and spatial variation. Mottled ducks (*Anas fulvigula*) are native to the Gulf Coast and peninsular Florida, USA, and have suffered population declines over the past decade, especially in Texas and Louisiana, USA. Although the cause of this decline is not well understood, previous research concluded variation in survival contributed to nearly a third of variation in the species' population growth rate. We used global positioning system-groupe spécial mobile (GPS-GSM) transmitters to study temporal and spatial variation in survival of adult female western Gulf Coast mottled ducks in southwestern Louisiana, 2017–2020. We evaluated weekly survival models parameterized with combinations of hunted and non-hunted periods, biological seasons, and landcover types that were used by mottled ducks. There were 3 competitive survival models, and all contained 4 parameters that parsed the annual cycle into the non-hunted period, first part of the general waterfowl season, and second part of the waterfowl season, and included the proportion of GPS locations in agricultural lands. Weekly survival was 0.979 during the first part of the general waterfowl hunting season, and 0.996 during the second part of the general waterfowl season. Daily survival rate increased with an increasing proportion of locations logged in agricultural lands. Annual survival rates were similar to other waterfowl that are not experiencing population declines, which suggests survival is not limiting population growth of mottled ducks along the western Gulf Coast. Managers should ensure the availability of refuge areas where hunting is prohibited during the first part of the general waterfowl season, when mottled ducks are at an increased risk of mortality, in addition to the targeted conservation of agricultural lands that provide cover and forage.

KEYWORDS

agriculture, *Anas fulvigula*, coastal marsh, Gulf Coast, Louisiana, mortality, telemetry, waterfowl

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, 2006; Hoekman et al. 2002; Koons et al. 2006, 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, Lavretsky et al. 2014, Peters et al. 2016) 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 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., breeding 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).

We 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. Our objectives were to examine temporal and spatial variation in weekly survival of adult female WGC mottled ducks in southwestern Louisiana. We 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.

STUDY AREA

We conducted the study primarily in southwestern Louisiana, which includes Cameron, Vermilion, Jefferson Davis, Calcasieu, and Acadia parishes (Figure 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 we 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

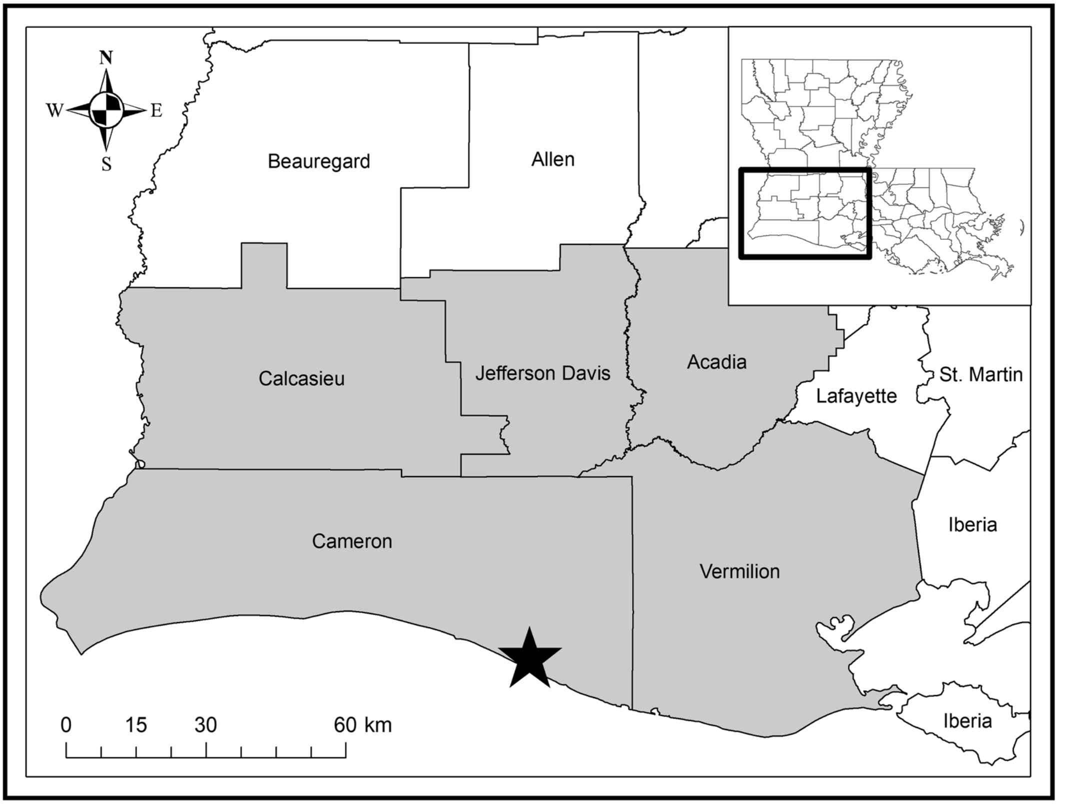

FIGURE 1 The core study area was southwestern Louisiana, USA, highlighted by the shaded area. The star denotes where we captured mottled ducks around Rockefeller Wildlife Refuge in 2017–2019.

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 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.

METHODS

We 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 we selected was ≥690 g, to ensure transmitters were ≤3% of body mass. We 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. We 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, we 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. We 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. We 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. We 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. We recorded individuals as mortalities when transmitters recorded little or no activity. We confirmed and recovered all mortalities in the field when possible.

We 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). We built encounter histories in weekly increments using a live-dead format. To evaluate temporal trends in survival, we 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). We 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, we labeled the week as a hunt period (Table 1). We 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). We labeled the non-hunted and biological periods according to which period comprised the majority of the week (Tables 1 and 2). We observed considerable temporal overlap of nesting and brood rearing, so we combined these time periods into the breeding season.

We 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

TABLE 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.

	2017–2018		2018–2019		2019–2020		2020–2021	
Season	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 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		

locations in agriculture ($r = -0.96$); we retained agriculture in our modeling because survival in agricultural lands is of management interest. We also investigated models that included the latitude of last known location (essentially the location at the time of mortality), which we used as a proxy for gradation of landscape characteristics like anthropogenic disturbance and fragmentation, both of which increase with latitude in southwestern Louisiana. We developed our 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). We 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. We used corrected Akaike's Information Criterion (AIC_c) to rank resulting models (Burnham and Anderson 2002, Arnold 2010). We then used competitive temporal models ≤2 ΔAIC_c, plus our strictly biological model, to explore the influence of spatial covariates. We used ΔAIC_c to rank the remaining models and deemed models ≤2 ΔAIC_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, we conducted an additional analysis when those individuals were not censored from the data. We 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. We 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).

RESULTS

We 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. We censored 23 individuals from our 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. We documented 51 mortalities, 21 of which were recovered. For transmitters that we 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. Our 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 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. Our 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) and survival increased as proportion of GPS locations in agricultural lands increased

TABLE 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. We used corrected Akaike's Information Criterion (AIC_c), ΔAIC_c, AIC_c weights, and number of parameters (*K*) to rank models. We present models with $\Delta AIC_c < 2$ 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

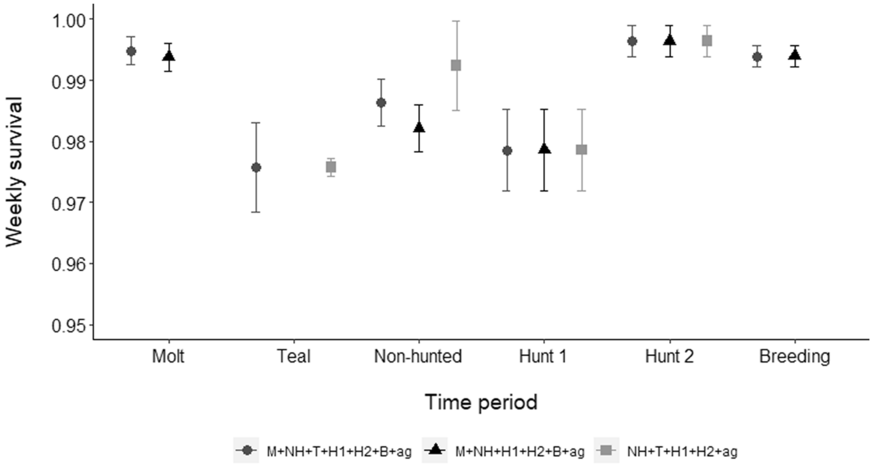

FIGURE 2 Estimated weekly survival rates, with standard error, of female mottled ducks in southwestern Louisiana, USA, 2017–2020, from supported models, which included combinations of molt (M), teal season (T), non-hunted period (NH), first split of the general waterfowl season (H1), second split of the general waterfowl season (H2), breeding season (B), and proportion of locations on agricultural lands (ag).

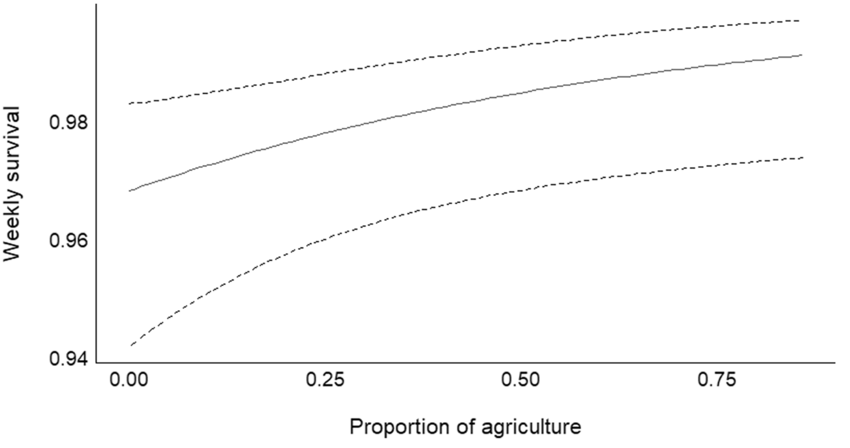

FIGURE 3 The relationship between the proportion of locations in agricultural lands and weekly survival during the teal season for mottled ducks in southwestern Louisiana, USA, 2017–2020. The dashed lines represent the 95% confidence intervals.

(Figure 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, we documented 88 suspected mortalities. The top models of this analysis were similar to those based on confirmed mortalities (Table 4), including the periods of lowest survival (Figure 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 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 we labeled those individuals that lost signal as mortalities. We used corrected Akaike's Information Criterion (AIC_c), ΔAIC_c, AIC_c weights, and number of parameters (K) to rank models. We 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

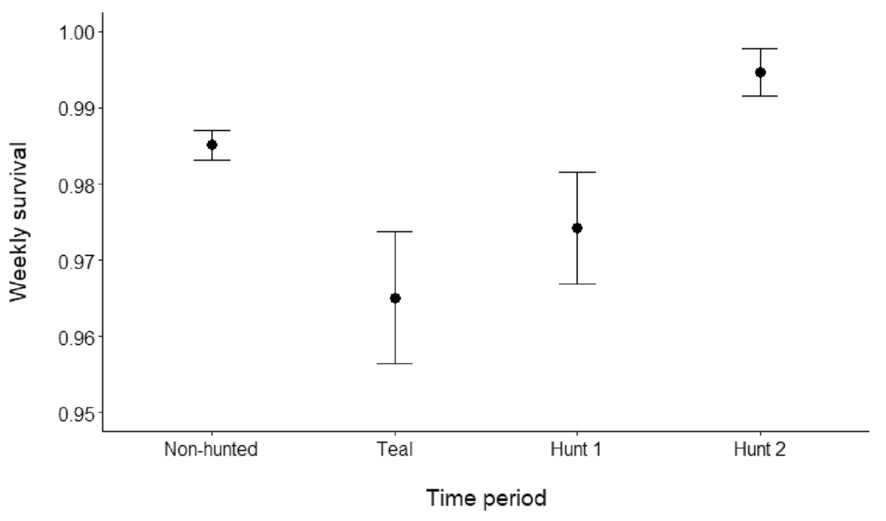

FIGURE 4 Estimated weekly survival rates, with standard error, of female mottled ducks in southwestern Louisiana, USA, 2017–2020, from our top model representing a worst-case scenario, containing the non-hunted period, teal season, first split of the general waterfowl season (Hunt 1), and second split of the general waterfowl season (Hunt 2).

DISCUSSION

We 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, we 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 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 we 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.

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 our 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

FIGURE 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.

(Cowardin et al. 1985, Bielefeld and Cox 2006, Varner et al. 2014), 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 breeding propensity ranging from 17.6–25.0% (E. S. Bonczek, Louisiana State University, unpublished data), which was similar to the low breeding propensity and high breeding season survival reported in previous studies (Finger et al. 2003, Bielefeld and Cox 2006, Wehland 2012, Varner et al. 2014). 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 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

TABLE 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)

during the reproductive period (i.e., nest success, nesting propensity, brood survival) are likely factors influencing mottled duck population dynamics. Our 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 our understanding of reproductive parameters, factors that influence them, and how they drive population dynamics.

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.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

Procedures were approved by Louisiana State University Institutional Animal Care and Use Committee under permit A2016-27 and federal bird banding permit 06669.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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