Colonial Nesting Wading Bird Tracking and Habitat Use Assessment

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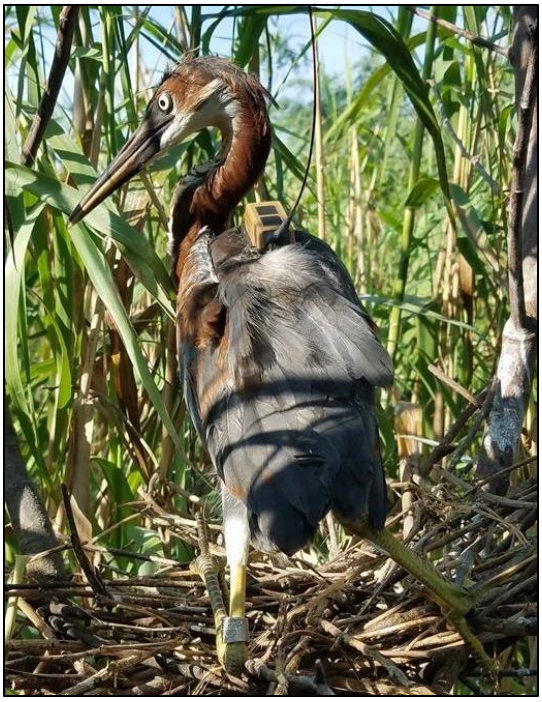
White ibis fitted with a satellite transmitter. Image credit: Atlee Hargis credit: Atlee Hargis



Tricolored heron fitted with a satellite transmitter. Image credit: Philipp Maleko

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EXECUTIVE SUMMARY

We assessed the movements, habitat use, and survival of tricolored herons (*Egretta tricolor*) and white ibis (*Eudocimus albus*) breeding in coastal Alabama, with the goal of supporting restoration and conservation planning in the aftermath of the Deepwater Horizon oil spill. We used satellite telemetry to mark 49 tricolored herons and 50 white ibis captured at coastal islands from 2020 to 2022, and tracked birds until July 2024. The data derived from satellite telemetry provided new insights into daily and seasonal movements, habitat use, and survival rates of these two colonial wading bird species.

Daily movement patterns from nesting colonies at Coffee, Marsh, and Gaillard islands showed that both species foraged primarily in nearby wetlands; birds from Coffee and Marsh islands foraged primarily at coastal sites on the mainland. Tricolored herons showed a strong dependence on emergent herbaceous wetlands, while white ibis demonstrated more flexibility, using not only wetlands but also human-modified landscapes including agricultural lands and a shellfish processing facility. Both species regularly relied on a mix of protected lands, including National Wildlife Refuges and State-managed tracts, as well as privately owned wetlands.

Seasonal tracking highlighted contrasting movement strategies. Tricolored herons showed true migratory behaviors, with a small proportion remaining as residents in coastal Alabama. Most migrants crossed the Gulf of America (formerly Gulf of Mexico; herein "Gulf"), with juveniles often staging first in Louisiana and adults flying directly to wintering areas in Mexico and Central America. Mortality during these crossings appeared high, underscoring the energetic challenges of migration, particularly across a large expanse of open water. In contrast to migratory tricolored herons, white ibis displayed more nomadic movements and remained largely within the southeastern United States year-round, shifting inland to freshwater and more developed habitats during the non-breeding season.

Survival analyses further underscored species differences. Estimated annual survival of tricolored herons was very low for both juveniles and adults, raising concerns for population resilience and long-term viability. However, 2020 was a year of high tropical cyclone activity in the Gulf, corresponding with high juvenile mortality that year. In contrast, estimated annual survival for white ibis was significantly higher than for tricolored herons, and was similar to survival rates found in other studies of ibis species.

Because of the differences between these two species, management implications diverge, particularly during the non-breeding seasons. Tricolored herons use wetlands not only in the northern Gulf, but also in Mexico and Central America in winter. However, there are proportions of both species that are present in coastal Alabama year-round. During the breeding season, nesting colonies on coastal islands depend on overlapping foraging areas, thus loss or degradation of wetlands poses risks beyond individual nesting sites. Protecting and restoring wetlands within 10–15 kms of active colonies may be important. In addition, many foraging areas lie outside of protected lands, thus conservation planning will require coordination among Federal, State, and local agencies as well as partnerships with private landowners. Continued restoration projects, such as those on Coffee and Marsh Islands, remain important for sustaining colony sites, while broader landscape-scale efforts are important to ensure connectivity and habitat availability. Finally, species-specific strategies should guide future restoration: tricolored herons would benefit from focused protection of specialized wetlands and migratory stopover areas, while white ibis management should account for their broader and more flexible use of both natural and human-modified landscapes.

INTRODUCTION

There are many information gaps about the metapopulations of several species of colonial wading birds that breed along the Alabama coast in the northern Gulf of America (formerly Gulf of Mexico, hereafter "Gulf"); filling these gaps would benefit the development of future bird restoration plans. Specifically, there is interest in better understanding the contributions of individual nesting colonies to the metapopulation of Ardeids, the daily and seasonal movements of adults and juveniles from these colonies, and habitat use (foraging sites, roosting/loafing sites, and nesting sites) during the breeding and non-breeding season to inform restoration of their populations within the coastal areas of Alabama and other regions in the southeastern United States.

With this study, we sought to inform and enhance future restoration planning for tricolored herons (*Egretta tricolor*) and white ibis (*Eudocimus albus*) populations that breed along the Alabama coast that were injured by the *Deepwater Horizon* (DWH) oil spill in the northern Gulf (refer to Table 4.7.3 in DHNRDAT 2016). In general, and at the scale of the Gulf, ecological processes affecting populations of tricolored heron and white ibis may be fairly similar (GoMAMN 2017, Frederick 2020), but due to differences in the two species' life histories, foraging strategies, and movement behaviors, management recommendations may be divergent. In addition, understanding the movements, dispersal, and habitat use of both species is important in the context of restoration planning, particularly with regards to scale (Frederick and Odgen 1997, Fuller et al. 2025).

Tricolored herons are distributed year-round along the Atlantic Coast from New England through the Caribbean and northeastern South America as well as the northern Gulf, from the southernmost coast of Texas to the Everglades in Florida (Frederick 2020). They typically breed in coastal habitats, often on islands surrounded by open water. The number of nests found during waterbird surveys along the Gulf varied annually from 2010-2021 (Capitolo et al. 2023), with the highest number of nests found in 2021 both Gulf-wide (14,471 nests) and in Alabama (157 nests; DHRTIG 2023). In Alabama, tricolored heron colonies have been monitored on Gaillard, Cat, Marsh, and Coffee (Isle aux Herbes) islands (DHRTIG 2023). The breeding biology of this species is better known than other aspects of its life cycle (Frederick 2020). We do know that tricolored herons cross the Gulf (Gleason et al. 2025), and banding records show they overwinter in Mexico, the Caribbean, and Central America (Melvin et al. 1999). However, little is known

about the overlap of breeding and wintering populations in North America, and while birds breeding north of South Carolina are migratory, their movement patterns (migratory routes, timing of migration, dispersal from natal sites) and fidelity to breeding or wintering areas are poorly understood (Frederick 2020). Finally, there is very little known about annual survival of this species, particularly for juveniles.

The distribution of white ibis is less extensive than for tricolored heron, with year-round populations present in the Gulf as well as in coastal Virginia south to Florida, the Caribbean, Central America, and northern South America (Heath et al. 2020). White ibis also nest in colonies throughout the Gulf, ranging from western Louisiana to south Florida (Capitolo et al. 2023). Most of the white ibis nesting colonies in the Gulf are in southeastern Louisiana within Breton and Delta National Wildlife Refuges (NWR; DHRTIG 2023). The number of white ibis nests found during waterbird surveys from 2010-2021 along the Gulf were substantially higher than for tricolored herons, with the highest number of nests (19,118 nests) found in 2021 Gulf-wide (DHRTIG 2023). Conversely, in Alabama the greatest number of white ibis nests were found in 2011 (13,438 nests) and the lowest in 2021 (2,000 nests). Similar to tricolored herons, ibis were found on Gaillard, Cat, and Marsh and Coffee (Isle aux Herbes) islands (DHRTIG 2023). The species is considered nomadic (Frederick and Odgen 1997), frequently moving across the landscape during the non-breeding season in response to fluctuating hydrological conditions (Kidd-Weaver et al. 2020). Band recoveries have shown white ibis moving from Gulf states to Mexico and the Caribbean (Mikuska et. al 1988, Melvin et al. 1999) but information about specific movement patterns and timing, natal dispersal, and fidelity to breeding and wintering sites is sparse (Heath et al. 2020).

Our overall objectives included determining daily and seasonal movements, home range size, and habitat use by juvenile and adult and tricolored herons and white ibis captured at colonies near Mobile Bay, Alabama. We used satellite telemetry to track movements, determine home ranges, and estimate survival of marked birds between 2020 and 2024. This information is critical for restoration planning and conservation of these two wading bird species, not only in Alabama, but across the Gulf region.

GENERAL METHODS

Capture Sites

We captured tricolored herons and white ibis from 2020-2022 (Table 1) at three nesting colonies in Alabama: Gaillard Island in Mobile Bay and Coffee Island (Isle aux Herbes) and Marsh Island in Portersville Bay (Figure 1), and tracked these birds through July 2024 (Appendix A and B). Gaillard Island is a large (526 ha) dredge-spoil island constructed by the Army Corps of Engineers in 1979, and is characterized by large colonies of nesting waterbirds with high species richness (Capitolo et al. 2023). In 2021, nesting waterbird surveys recorded 1,591 white ibis nesting on the island, but most nests were of brown pelican (*Pelecanus occidentalis*) and laughing gull (*Leucophaeus atricilla*; 6,614 and 4,641 nests, respectively; DHRTIG 2023). Both Coffee Island (3.6 ha) and Marsh Island (9.7 ha) are small barrier islands. Restoration projects efforts at Coffee Island included the creation of oyster reefs to limit erosion and protect marsh habitats (https://www.gulfspillrestoration.noaa.gov/project?id=141). Of the 19 nests found on waterbird surveys in 2021, there were no white ibis nests and only one was a tricolored heron nest; most nests were great egret (*Ardea alba*; DHRTIG 2023). In Portersville Bay, Alabama, restoration projects the DWH oil spill included placing sediments and planting native

Table 1. Capture and tagging summary for tricolored herons and white ibis captured at nesting colonies in coastal Alabama, during summers of 2020 – 2022.

Marker	White Ibis			Tricolored Heron		
	Juvenile	Adult/ Subadult	Total	Juvenile	Adult/ Subadult	Total
Satellite Transmitters						
2020	16	4	20	16	1	17
2021	9	11	20	12	10	22
2021	4	6	10	0	10	10
Color Bands						
2020	29	4	33	26	1	27
2021	16	19	35	27	10	37
2022	21	10	31	17	13	30
Total	95	54	**149**	98	45	**143**

vegetation on Marsh Island, 2016-2017 (https://www.gulfspillrestoration.noaa.gov/project?id=6). No waterbirds were recorded nesting on Marsh Island 2010-2015, but surveys found 404 white ibis and 130 tricolored heron nests there in 2021; however, most nests were those of laughing gull and royal tern (*Thalasseus maximus*; 2,229 and 1,227 nests, respectively; DHRTIG 2023, Capitolo et al. 2023). Restoration at Coffee Island included the creation of oyster reefs to limit erosion and protect marsh habitats (https://www.gulfspillrestoration.noaa.gov/project?id=141). Of the 19 nests found on waterbird surveys in 2021, there were no white ibis nests recorded and only one tricolored heron nest was recorded; most nests were great egret (*Ardea alba*; DHRTIG 2023).

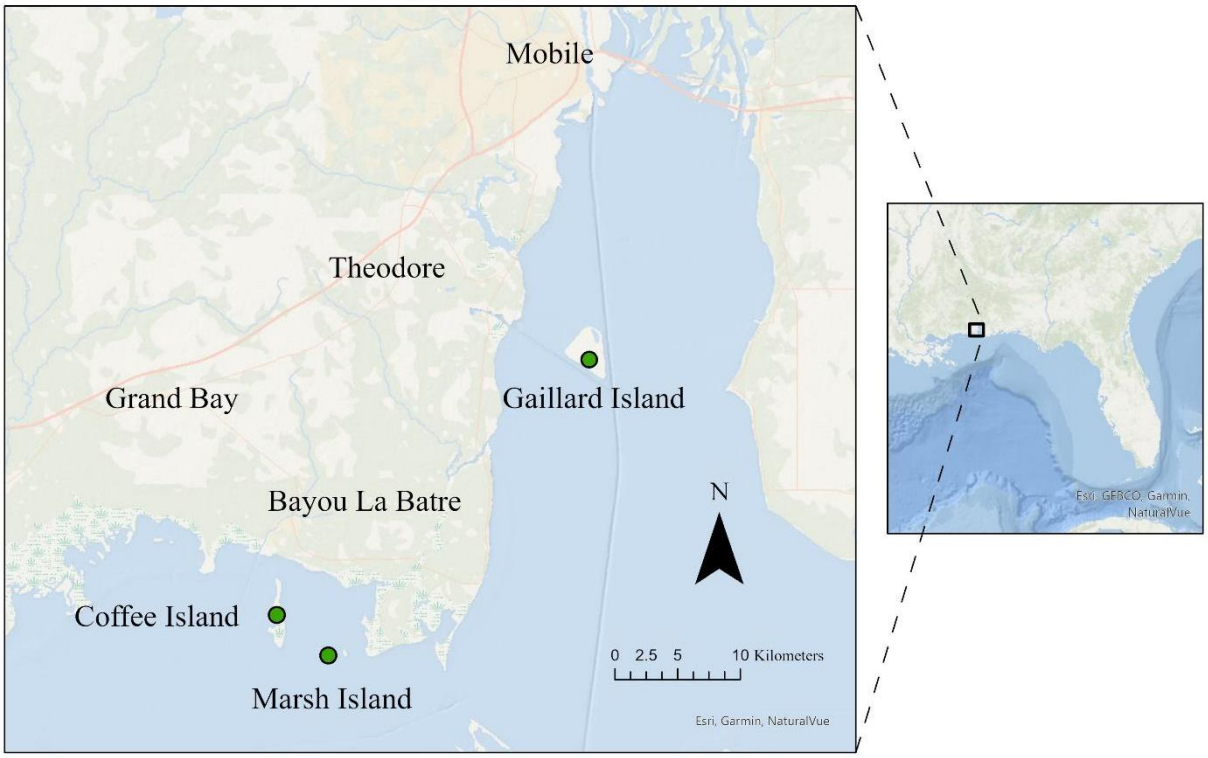

Figure 1. Capture sites (green circles) of tricolored herons and white ibis on Gaillard, Coffee (Isle aux Herbes), and Marsh Islands in coastal Alabama (2020 – 2022).

Capture and Marking

Capture and marking of birds took place from May through July 2020-2022 (Appendix A and B). To limit disturbing breeding colonies, we only visited each colony once per week (Frederick and Collopy 1989). We entered the colonies just after sunrise and left before noon, to avoid causing heat stress to nestlings, fledglings, and captured birds. We used three capture

methods to maximize our likelihood of sampling evenly across age classes (Frederick 1986, Keyes and Grue 1982, Perkins et al. 2010). To capture adult ibis, we deployed mist nests baited with wading bird decoys near colonies (Figure 2). We used self-tripping nest traps placed over nests to capture adult tricolored herons (Figure 2). We caught juveniles of both species by entering the colony and capturing them by hand or dip net. All bird capture and handling followed established scientific and safety protocols (Fair et al. 2023) and were conducted under the appropriate state and federal permits, as well as University of Florida Institutional Animal Care and Use Committee (#201910846).

Figure 2. Painted plastic flamingos used as decoys to attract white ibis, placed near mist nets (left) and self-tripping nest trap placed over the nest to capture adult tricolored herons (right). Image credits: Ke Zhang.

All birds were banded with a U.S. Geological Survey (USGS) metal band on the left tibiotarsus and a plastic alpha-numeric band on the right tibiotarsus (red bands on white ibis and blue bands on tricolored heron). We then recorded body mass by placing birds into a sanitized cotton pillowcase and weighing ($\pm$1g) them with a Pesola® spring scale. Tarsus width and length, culmen length, and nares width were measured with digital calipers (REXBETI® Digital

Caliper, ±1 mm) and wing chord length was measured using a flat meter stick (±1cm) (refer to Sutherland et al., 2004). To determine sex through genetic analysis we used tweezers to collect four breast feathers from the chest of each captured bird. We also used 25-g or 27-g needles to collect no more than 3 ml of blood from the medial metatarsal veins of captured birds (Owen 2011). We stored blood samples in DNA/RNA shield buffer (Zymo Research, California) and temporarily kept them in a -10℃ freezer, and transported samples to a -80℃ freezer for long-term storage after the field season. DNA extraction for gender determination is described in more detail in Zhang (2025).

We attached solar-PTTs (platform terminal transmitters; Microwave Telemetry Incorporated (MTI©, Columbia, Maryland)) to a subset of captured birds (Table 1) that met our weight requirements (described below) to track their movements, habitat use, survival, and breeding/natal site fidelity in subsequent years. We used 18 g PTTS for white ibis and 5.0 g and 9.5 g PTTs for tricolored herons, depending on the weight of the bird. We fitted PTTs to birds using a backpack-style harness made of Teflon ribbon and a round neoprene patch (approximately 2.5 cm in diameter and 0.5 cm thick). The PTT unit was placed on the bird's back, and two Teflon ribbons were aligned along the scapulars from the top of the harness. The ribbons crossed over a round neoprene patch positioned over the keel, then looped around humerus, and were secured back at the rear end of the transmitter. The harness was adjusted to be snug but not tight, allowing for potential tissue growth around the humerus. Once properly fitted, the ribbons were sewn onto the neoprene patch, trimmed, and sealed with adhesive at all sewn contact points. We ensured that each device plus the weight of the harness was < 3% of the bird's body weight (Geen et al. 2019). During all aspects of handling birds, we monitored air temperature and breathing rates of birds to prevent overheating. If we observed panting, we sprayed 95% ethanol on their legs and stopped processing for three minutes to cool them (Sutherland et al. 2004). All birds were released where they were captured; we aimed our processing time not to exceed 30 min to prevent capture-related mortality.

Data Processing

PTTs used on tricolored herons had duty cycles of 10 hrs on and 48 hrs off, while white ibis PTTs were on for 10 hrs and off for 24 hrs. We collected location data from Service Argos (https://www.argos-system.org); all data are stored in Movebank (movebank.org). Argos

estimates the exact error radius for each location and divides locations into six Location Classes (LC) based on the number of messages received per satellite pass and the estimated error of LC (Douglas et al. 2012): B (no accuracy estimated with 1 or 2 messages), A (no accuracy estimated with 3 messages), 0 (estimated error > 1500 m with 4 messages or more), 1 (500 m < estimated error < 1500 m with 4 messages or more), 2 (250 m < estimated error < 500 m with 4 messages or more), and 3 (estimated error < 250 m with 4 messages or more). To filter out unrealistic locations, we used the Douglas Filter (hybridization mode; Douglas et al. 2012).

ANALYTICAL METHODS

Due to the lack of resightings or reports of banded birds, birds marked only with colored leg bands (Table 1) are not included in any analyses. Of all of the banded (not tagged with transmitters) birds, one white ibis banded as an adult in 2022 was seen in Florida's Corkscrew Swamp Sanctuary in March 2025.

Defining Breeding versus Non-breeding Seasons

We defined the non-breeding season based on bird movements and roosting behavior. For all tracked individuals, the start of the non-breeding season was marked by departure from the natal/breeding colony and consistent use of a roost site located at least 5 km away for three consecutive duty cycles. For juveniles, which were not expected to breed the following summer, the non-breeding season was considered to end on 1 March of the following year or on the day they returned to the natal colony, whichever came first. For subadult and adult birds, the end of the non-breeding season was defined as the point when a bird remained at the same roost for four consecutive weeks between May and September, suggesting potential breeding activity. This marked the beginning of the breeding season, and the start of the next non-breeding season was set at the end of that period. For individuals that did not leave the natal/breeding colony or did not roost away for a sufficient number of consecutive days, the non-breeding season was defined as occurring from 15 July to 1 April. These definitions were informed by the known life history traits of white ibis and tricolored herons (Frederick 2020, Heath et al. 2020), as well as field observations from this study.

Defining Resident versus Migrant Behavior

After the breeding season, we classified both juvenile and adult tricolored herons as either residents or migrants based on the maximum distance dispersed from their capture colonies. To classify individuals as residents or migrants, we excluded those with tracking durations shorter than one month and those whose locations remained exclusively on the capture islands without evidence of movement toward the mainland (assuming transmitter failure or mortality). Individuals that remained within Alabama or near the eastern Mississippi border (defined as the area bounded by 88.70° to 87.90° W and 30.13° to 30.90° N) were considered residents. All others were classified as migrants. We calculated the number of days each heron was tracked from the date it departed the capture colony to the last date of location transmission. We used kernel density estimation (KDE) to visualize the distribution of tracking lengths for residents and migrants of both age groups separately.

White ibis behavior is characterized by nomadic movements and frequent and unpredictable movements to different areas within their range. To account for the unpredictability of ibis movements, we considered an ibis to be philopatric if it was observed for at least 30 days in either coastal Alabama or the lower Mobile-Tensaw Delta, in at least one breeding season following its year of capture. However, a subset of tracked individuals did not survive long enough for us to verify either philopatric or dispersive behavior. When assessing philopatry, we truncated our data to only include individuals that survived at least 30 days into the breeding season in the year following capture.

Daily Movements from Nesting Colonies and Breeding Season Foraging Habitat

We used movement tracks of tagged individuals to quantify foraging flights and daytime foraging habitat use for white ibis and tricolored herons during the breeding season in coastal Alabama. We first combined multi-year satellite tracking datasets and filtered the data to include only high-quality Argos locations (location classes 1, 2, and 3) occurring between 1 April and 15 July. Relocations with estimated error radii >1,500 m or occurring outside the Gulf Coast study region were excluded. To eliminate duplicate fixes, we retained only the highest-quality location for each tag and timestamp combination based on Argos location class and error radius.

Solar position data (sunrise, sunset, night, and twilight times) were calculated for each point based on date and location. Each relocation was then classified as occurring during day,

dusk, dawn, or night. For each individual, a "day burst" was defined as beginning at dusk and continuing through all relocations until dusk on the following calendar day. Within each burst, we identified nighttime locations that occurred at known tricolored heron or white ibis breeding colonies in coastal Alabama. If a burst included at least one high-quality nighttime location (<500 m error radius) at a known colony, all daytime locations on the subsequent day were classified as potential foraging points.

Roost centroids were defined using the highest-quality nighttime location within each valid burst. Straight-line (Euclidean) distances were calculated between each daytime point and the associated roost centroid using an Albers Equal Area projection (EPSG 5070). National Land Cover Database (2019) raster values were extracted for each daytime location to characterize habitat use (Figure 3). Locations classified as open water or those occurring at the same colony as the previous night's roost were excluded from land cover summaries.

For each species and colony, we summarized the distribution of daytime foraging distances and proportional use of land cover types. Maps depicting straight-line commutes from nesting colonies to foraging sites during the breeding season were generated to visualize straight-line movements from colony roosts to daytime locations. Analyses were conducted separately for tricolored herons (Marsh Island and Coffee Island colonies) and white ibis (Marsh Island, Coffee Island, Gaillard Island, and a potential colony adjacent to a shellfish processing facility near Bayou La Batre). For each species and colony, we also identified focal foraging areas based on the spatial aggregation of daytime points.

Identifying Seasonal Movements

For migrant tricolored herons, we created trajectories from the end of the breeding season to the final non-breeding season location, and for some individuals, to the start of the next breeding season. For each migrant, we retained one high-quality Argos location per tracking period and connected these locations in chronological order to visualize movements between breeding and non-breeding ranges. We used kernel density plots rather than summary statistics (minimum, maximum, mean, and standard deviation) to better understand movement data for migrant and resident tricolored herons because of wide variation in tracking durations. An average value with a standard deviation would not capture these details, whereas the kernel density plots illustrate how many birds were tracked for different lengths of time, allowing us to

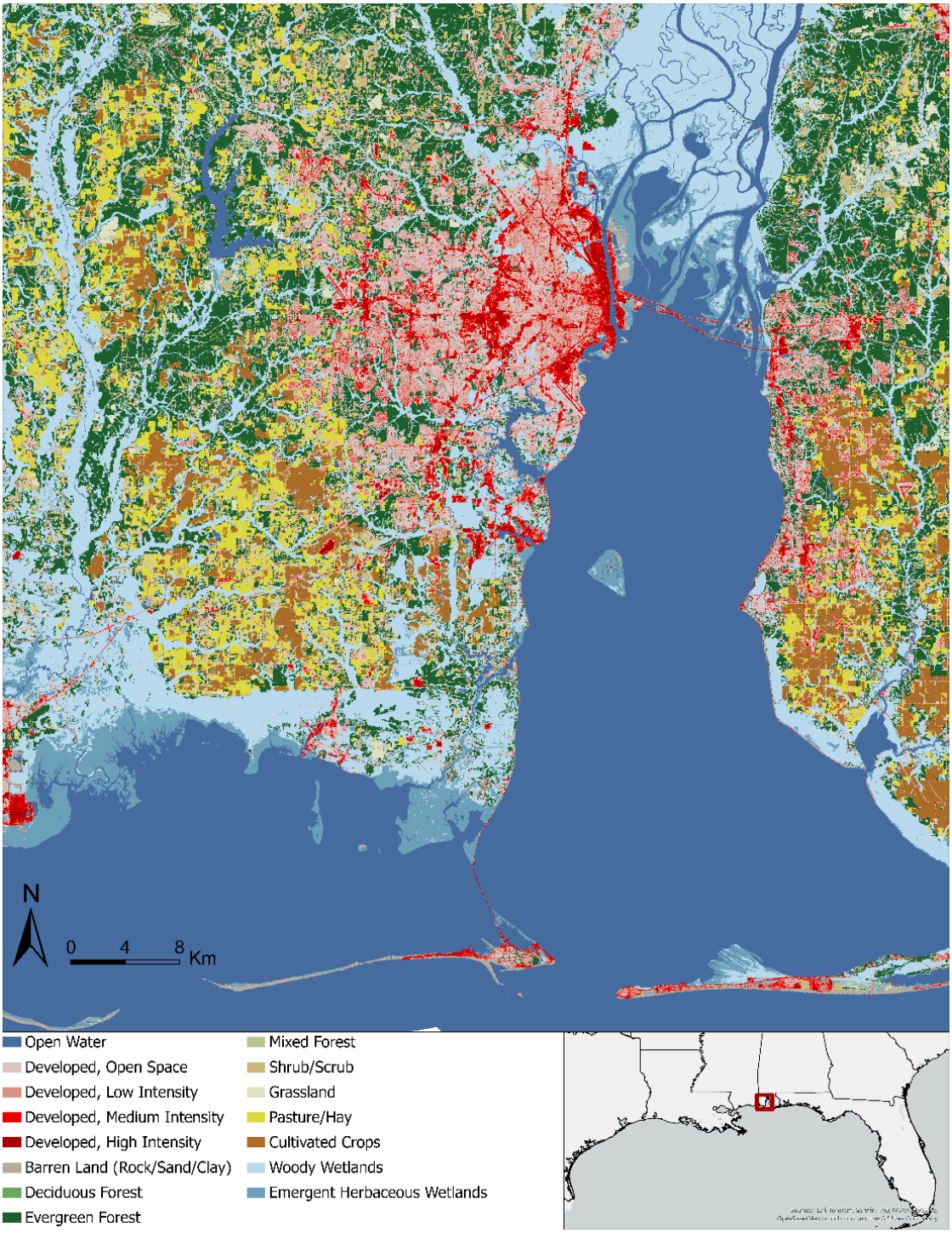

Figure 3. National Landcover Database (NLCD) raster, representing various landcover classes found in the vicinity of tricolored heron and white ibis capture sites in coastal Alabama and Mississippi. Land cover data: Multi-Resolution Land Characteristics Consortium (MRLC), National Land Cover Database (NLCD) 2019. Basemap source: Esri, HERE, Garmin, FAO, NOAA, USGS, EPA, NPS, USDA.

identify specific date ranges where most birds were tracked, which are visible as peaks in the plots.

To assess seasonal range shifts of white ibis, we subset telemetry data based on breeding and non-breeding periods. The breeding season was defined as 1 April–15 July, and the non-breeding season as 16 July–31 March. Only high-quality Argos locations (Location Class 1, 2, and 3) were retained for analysis. After filtering, we mapped all valid locations across both seasons from July 2020 through July 2024. Spatial distributions were visually compared to assess seasonal differences in regional use. Coastal and inland use patterns were evaluated qualitatively, and the number of individuals tracked per season was summarized.

Quantifying Philopatry and Dispersal

Due to the small number of tricolored herons that survived into the following year (Appendix A), philopatry and dispersal could not be quantitatively assessed in this study. We analyzed the trajectories of all tricolored heron individuals that survived into the next year to describe philopatry and dispersal behavior.

To identify philopatric behavior in tagged white ibis, and to determine regional space use and movement based on current age and age at capture we implemented the following methods. We first filtered for high-quality Argos locations (Location Class 3) and plotted spatial tracks for each tagged individual. These tracks were grouped by current age and capture age to allow visual inspection of 1) ontogenetic shifts in regional space use for birds tagged as juveniles, and 2) age- and cohort-related differences in general habitat use across all individuals. To classify philopatry for white ibis, we first established behavioral criteria. Individuals were considered eligible for assessing philopatric return only if they were tracked for at least 30 days into the breeding season following the year of capture (1 April–15 July). This decision reduced the likelihood of misclassifying mortality or short-term movements as failed returns. Among eligible individuals, we recorded: (1) whether they returned to the capture region during any subsequent breeding season, (2) their capture age and age at first philopatric return, and (3) the proportion of tracked breeding seasons in which they were philopatric. We also calculated each individual's maximum Euclidean dispersal distance and the time (in years) to first philopatric return.

For all philopatric ibis, we partitioned their movement tracks into a series of discrete home range movements, which were 1) distinct from long-distance movements (directed

movement steps with long step lengths and relatively straight turning angles, and 2) unique in space and/or time from other home ranging movements along that individual's track. On the resulting home range movements, we applied dynamic Brownian Bridge Movement Models (dBBMMs) to each discrete home range segment. dBBMMs estimate an individual's utilization distribution (UD) by incorporating both the location error and the time between successive fixes to account for movement uncertainty (Kranstauber et al. 2012). This method is particularly suited for high-resolution telemetry data with irregular time intervals. We extracted 95% isopleths from each UD to delineate core home range areas and mapped these to visualize spatial concentration of philopatric activity across the southeastern United States.

Lastly, we aimed to identify factors that influence ibis' displacement from the breeding colonies where ibis were originally captured. Telemetry data with high relocation frequency are susceptible to spatiotemporal autocorrelation, where successive relocations are not spatially and temporally independent of other locations along the movement track. If unaddressed, this autocorrelation can artificially inflate model confidence and increase the likelihood of type I error (Fletcher and Fortin 2018). To reduce this risk and ensure more reliable inference, we calculated the average weekly Euclidean displacement from the capture site for each individual and used these values in the regression models. Weekly intervals were chosen because white ibis are highly mobile and capable of long-distance movements over short time periods; in some cases, individuals moved hundreds of kilometers within a single week. Weekly averaging thus provided a balance between temporal resolution and statistical independence.

We then built models that included ibis' Euclidean displacement (km) as the response variable. This measure acted as a proxy for the distance each tracked ibis dispersed from coastal Alabama throughout its tracking period (Gulick 2025). Our predictor variables included sex and body mass. White ibis colonies are known for large fluctuations in the number of breeding pairs among years, and these fluctuations could drive density-dependent interactions with varying intensity across years and breeding cohorts (Ye et al. 2022). For this reason, we also included year and capture cohort as a variable in these models. Before modelling, we found that the response variable (Euclidean displacement) had a substantial positive skew which could not be remedied through removal of outliers or data transformations. We elected to model this relationship using a generalized linear model (hereafter, GLM) in the gamma family, with a log-

link function. This model type is suitable for overdispersed data with a strong skew (Forbes et al. 2010).

We assessed the variance inflation factors of response variables within multi-variable models to ensure that model terms were not collinear. Continuous variables with radically different ranges can lead to disproportionate model influence, where variables with larger ranges can falsely be weighted more heavily (Grueber et al. 2011). To avoid this, we scaled continuous variables (e.g., body mass) so that competing models with these values could be more accurately compared using model selection approaches.

Resource Selection During the Non-breeding Seasons

To assess resource selection (Manley et al. 2002) during the non-breeding season for both species, we first identified roost and foraging sites. For each bird and each functional period of the PTT, we used the highest-quality nighttime location to represent the roost site. The foraging site was defined as the farthest daytime location recorded during the same functional period following identification of the roost site visit. To calculate roost and foraging distance, we created two datasets: one linking each roost site to the farthest daytime location on the following day, defined as the foraging distance. The second links the farthest daytime location to the roost later that same day, defined as the roosting distance. We then calculated the straight-line distances between roost and foraging sites to represent roost and foraging distance. To mitigate bias from tracking device location error and from birds' stationary behaviors such as remaining at the roost site (e.g., delayed departure for foraging, early return, or resting at the roost during the day), we excluded foraging sites whose distance to the associated roost was smaller than the sum of their location error radii (Wiggins et al. 2024).

To assess resource selection for land cover type, we used land cover data from the National Land Cover Database (NLCD; Dewitz 2021) and refined wetland classifications using the National Wetlands Inventory (NWI; U.S. Fish & Wildlife Service 2018). Land cover types were reclassified into ten categories to reflect habitat characteristics relevant to the life histories of white ibis and tricolored herons (Kushlan 1977a, Strong et al. 1997, Beerens et al. 2011). We applied a Type III study design, in which both resource use and availability are defined at the individual level, and evaluated third-order selection, which reflects choices made within each bird's home range (Johnson 1980, Manly et al. 2002). "Used" locations were defined as

identified roost and foraging sites. Ratios of used to random points are often set between 1:2 and 1:5 in studies conducted at scales comparable to this study (Morries et al. 2016, Hefty and Stewart 2019). Baasch et al. (2010) found that assigning five random points per used location produced consistent and robust estimates of resource selection. For each used point, we generated ten random points within a buffer radius equal to the bird's roosting or foraging distance, representing available habitat. Land cover was classified based on the dominant type (highest proportion) within a 200-meter buffer around each location, reflecting the mean accuracy of location data. We clipped both used and random points within the Gulf, so no points over open water were included in the analysis, as these areas are not accessible for birds to land or forage. To evaluate selection, we calculated selection ratios as the proportion of used points in each land cover type divided by the proportion of random points; values > 1 indicate selection and values < 1 indicate avoidance (Manley et al. 2002).

To assess the selection for protected land, we used the Protected Areas Database of the United States (PAD-US 3.0; U.S. Geological Survey 2022), which includes an inventory of public and private terrestrial and marine protected areas. These areas were categorized according to International Union for Conservation of Nature (IUCN) protected area types, including nature reserves, wilderness areas, national parks, habitat/species management areas, and other conservation designations (Dudley 2008). We followed the same Type III and third-order design approach to assess selection of protected areas by our marked birds. For each bird, we calculated the proportion of its used locations that fell within protected areas. For availability, we generated ten random points per used location within the bird's average daily flight distance and calculated the proportion of random points located in protected areas. Selection ratios were calculated as the ratio of use to availability.

Modeling Annual Survival

Individuals were tracked between May 2020 and July 2024. Known-fate survival models consider three possible states for each individual in each time interval of the study. These include 00 (not observed in that interval), 10 (observed alive, but not observed dead during that interval) and 11 (observed alive at the start of the interval, and observed dead before the end of the interval; White and Burnham 1999). While Argos location data allow for high-frequency and accurate observations of an individual's movement, our transmitters were not equipped with

specific mortality censors. To assess the likelihood of mortality from movement data, we relied on a combination of auxiliary data transmitted from each PTT.

Termination of satellite tag transmissions can result from mortality, battery failure, tag detachment, or mechanical malfunction. To differentiate among these possibilities, we developed a decision framework based on sensor data and expected transmitter lifespan. First, individuals that showed no movement or activity post-release were censored, as their fate could not be reliably attributed to natural causes: this included six individuals. Post-release censorship represented a 1-week period after release. If we lost signal from a tagged individual during that time, we censored that individual from analysis. We did this to account for faulty transmitters and batter failure, dropped tags, and mortality that could be directly attributed to capture and release of the individual. Next, any individual whose tag ceased movement or activity for at least three days before the final transmission was classified as a mortality, consistent with Argos PTT documentation. Tags that failed more than three years post-deployment were assumed to have reached the end of their functional lifespan and were censored to avoid biasing adult survival estimates downward. For tags that stopped transmitting within three years but lacked signs of inactivity, we evaluated battery voltage data over the final three weeks. Tags exhibiting declining voltage or missed duty cycles were interpreted as battery failures. Transmitters that failed suddenly without any of these indicators were considered to reflect actual bird mortality.

We created one observation interval for each month that birds were tracked, which allowed us to account for the effect of month, season, and biological year on survival probability. The monthly observation intervals spanned from 15 July of one year to the same date in the following year, from 2020 to 2024. This period corresponds to general patterns of seasonal change for both species. If a tag stopped sending signals within seven days of the date that the bird was originally captured, tagged, and released we censored that bird from the analysis. This one-week window was chosen to account for potential capture- or tag-related mortality and resulted in the censoring of five tricolored herons and six white ibis from the analysis (Appendix A and B). We were unable to confirm suspected mortalities of ibis via direct observation, due to the large location errors for each tag. Additionally, the distant and remote nature of the mortality sites precluded any attempt to reach the suspected mortality in a timely and cost-efficient manner.

The effects of transmitters on survival are important to understand but uncertain, as no survival estimates exist for free-roaming white ibis without transmitters attached. Transmitters may increase mortality by adding weight to the bird or altering aerodynamics, both of which increase energy expenditure during flight (Barron et al. 2010, Fair et al. 2023). Tags may also influence survival by altering movement behavior, reducing foraging efficiency, or increasing time and energy spent preening (Barron et al. 2010). We attempted to account for this by including a censor period 7 d post-release. Before tagging, we also ensured the transmitter and harness accounted for <3% of all marked bird's body mass. While this is a commonly accepted threshold, the weight limit of transmitters may vary by species and among individuals. Additionally, an individual's mass may fluctuate widely throughout their life, which can dynamically change the weight burden of transmitters (Clark 1979). Still, we consider the 3% body mass threshold a conservative precaution that should have minimized potential transmitter effects on survival.

We fit staggered entry, monthly known-fate models to these data using package rMark (Laake 2013). We included two grouping variables in these models: capture year and capture age, to assess the effect of year since capture on individuals. We also created a time-varying individual covariate for tricolored herons and white ibis, which represented age class. White ibis exhibit delayed sexual maturity and undergo annual shifts across three age classes: hatch-year (HY), second-year (SY), and after-second-year (ASY). At each interval, individuals advanced to the subsequent age class until they reached adulthood (after-second-year). Tricolored herons were binned into two age classes, hatch-year (HY) and after-hatch-year (AHY), as they reach sexual maturity after their first annual interval. Using this covariate, we fit and compared single variable models of monthly survival to our data for each species (for details, refer to Gulick 2025). For both species, we included individual covariates including sex, as well as mass, tarsus length, culmen length, and wing chord at the time of capture. Tricolored herons were fitted with either 9.5 g or 5 g PTTs, which allowed us to model survival based on transmitter mass, as well as the mass of the transmitter relative to the body weight of the bird. We also included the effect of various time intervals on the probability of survival. This included season (breeding vs non-breeding season), month, and biological year (July through June of the following year). We included additive and multiplicative combinations of covariates as possible explanations of monthly survival. We did not assess overdispersion ($\hat{c}$) or model fit using residuals, as this is not

a recommended approach for known-fate survival models (White and Burnham 1999). While survival probability was estimated at the monthly scale, we used the delta method to extrapolate these estimates to the annual scale, for ease of interpretability (Powell 2007). For each species, we included all models in an AIC framework along with a non-explanatory null model, to assess the relative fit of each model to the data. In lieu of (ĉ) or residuals, we used this null model as a baseline to assess overall model fit.

Finally, we identified ibis and heron mortalities that occurred near the tropical cyclones that made landfall in the northern Gulf from 2020-2024. For each storm, we used National Hurricane Center (NHC) best-track GIS layers, including cumulative wind-swath polygons at 34, 50, and 64 knots. These swaths delineate areas that experienced sustained gale-, storm-, or hurricane-force winds at any point during the storm's lifetime. For each bird mortality, we recorded whether the its locations intersected any of the storm's wind-swath thresholds; if not, we calculated the Euclidean distance from the bird's locations to the nearest wind-swath boundary. However, absence of overlap with a wind swath does not imply absence of storm effects; storm surge, heavy rainfall, and flooding can raise energetic costs (e.g., thermoregulation; Wilson et al. 2004) and degrade foraging conditions by increasing water depth and turbidity (Cezilly 1992, Lantz et al. 2011). This may be especially impactful to sight-foraging wading birds such as tricolored herons. In addition, high speed wind gusts and sub-tropical-storm sustained winds can occur outside the ≥34-kt swath, and have the potential to negatively affect wading birds in these areas (Webster and Weathers 1988).

TRICOLORED HERON

Daily Movements and Habitat Use During the Breeding Season

We tracked tricolored herons (n = 15) breeding at two colonies in coastal Alabama (Marsh Island and Coffee Island) during the 2020–2024 breeding seasons. Daytime foraging locations were linked to the nearest preceding nighttime roost associated with a communal breeding colony in coastal Alabama, and straight-line (Euclidean) distances were calculated between each roost–forage pair. Movements terminating over open water or at the roost colony were excluded from the analysis, resulting in a dataset of 1,425 movements. All 15 tricolored herons in our sample visited Marsh Island, and seven of these individuals also visited Coffee Island. The average one-way daily commute distance across all individuals and colonies was 9.0

km (SD = 7.1 km, median = 5.5 km, 90th percentile = 22.2 km). We interpret these as breeding season movements because they occurred while birds were roosting at known breeding colonies during the breeding season. However, due to Argos location error, limited visibility at densely packed colonies, and the potential for undetected early nest failures, we could not confirm that each roosting observation actually represented an active nesting attempt. Nonetheless, because individuals present at a colony during the breeding season may contribute indirectly to colony success (e.g., by attracting conspecifics and maintaining colony cohesion), we treat these as breeding season movements for the purposes of this analysis.

Movement patterns appeared to differ by breeding colony. Birds using Marsh Island exhibited shorter movements overall, with an average distance of 8.0 km (SD = 7.2 km, median = 4.9 km, 90th percentile = 23.0 km) based on 1,096 movements from 15 individuals. Marked birds flying from Coffee Island displayed a mean foraging flight distance of 12.6 km (SD = 5.3 km, median = 12.0 km, 90th percentile = 21.1 km) across 329 movements from seven individuals.

Land cover used by foraging birds also appeared to differ by breeding colony. Marsh Island herons foraged predominantly in emergent herbaceous wetlands (91%), with minor use of woody wetlands (4%), and other classes (< 3%; Figure 4). These birds concentrated their activity in three privately-owned wetland complexes east of Pascagoula, west of Heron Bay, and in portions of Dauphin Island. Additionally, herons frequently visited five protected areas, including Grand Bay National Wildlife Refuge, Coffee Island, Heron Bay Wetlands Tract, and a Mississippi barrier island managed by Gulf Islands National Seashore. Herons roosting at the Coffee Island breeding colony used a broader array of land cover types for foraging (Figure 5). These included emergent herbaceous wetlands (59%), woody wetlands (12%), pasture lands (9%), evergreen forest (5%), and croplands (5%). They foraged within four protected areas: Grand Bay National Wildlife Refuge, Grand Bay Savanna Community Hunting Area, Fowl River Mitigation Bank, and a barrier island managed by the Gulf Islands National Seashore. They also foraged in three privately-owned areas, including wetlands east of Pascagoula, Mississippi, emergent wetlands west of Heron Bay, and wetlands immediately outside of Grand Bay, Alabama.

Seasonal Movements from Breeding Colonies to Wintering Areas

A total of 42 tricolored herons, consisting of 22 juveniles and 20 adults, transmitted sufficient data to allow classification as either residents or migrants. One juvenile survived for over a year, allowing for tracking into its second year as an adult, resulting in a total sample size of 21 adults. Among juveniles, five (23%) individuals remained near the colony and were classified as residents, while 17 (77%) dispersed from the colony area and were classified as migrants. Among adults, five (24%) individuals were residents and 16 (76%) were migrants.

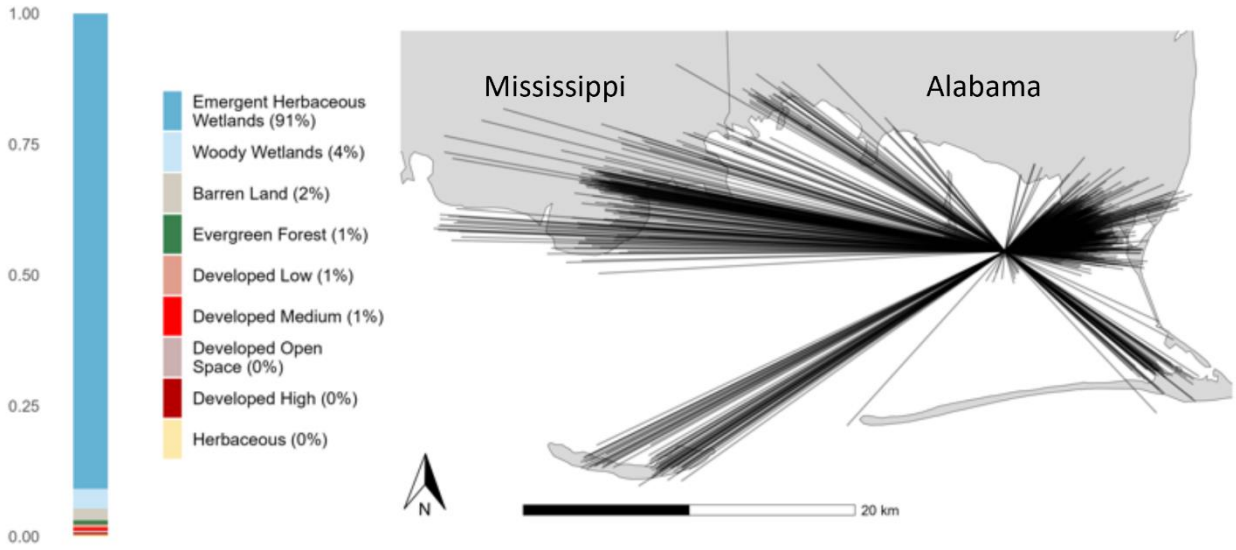

Figure 4. Straight-line movements of tricolored herons from 2020 – 2024 from the Marsh Island communal nesting colony to foraging locations during the breeding season. Each black line represents a single movement from a roost to a foraging site. The adjacent bar chart displays the relative use of different land cover types, primarily emergent herbaceous wetlands. Land cover classification is based on the 2019 NLCD raster. Geographic boundary data: U.S. Census Bureau, 2020 TIGER/Line Shapefiles.

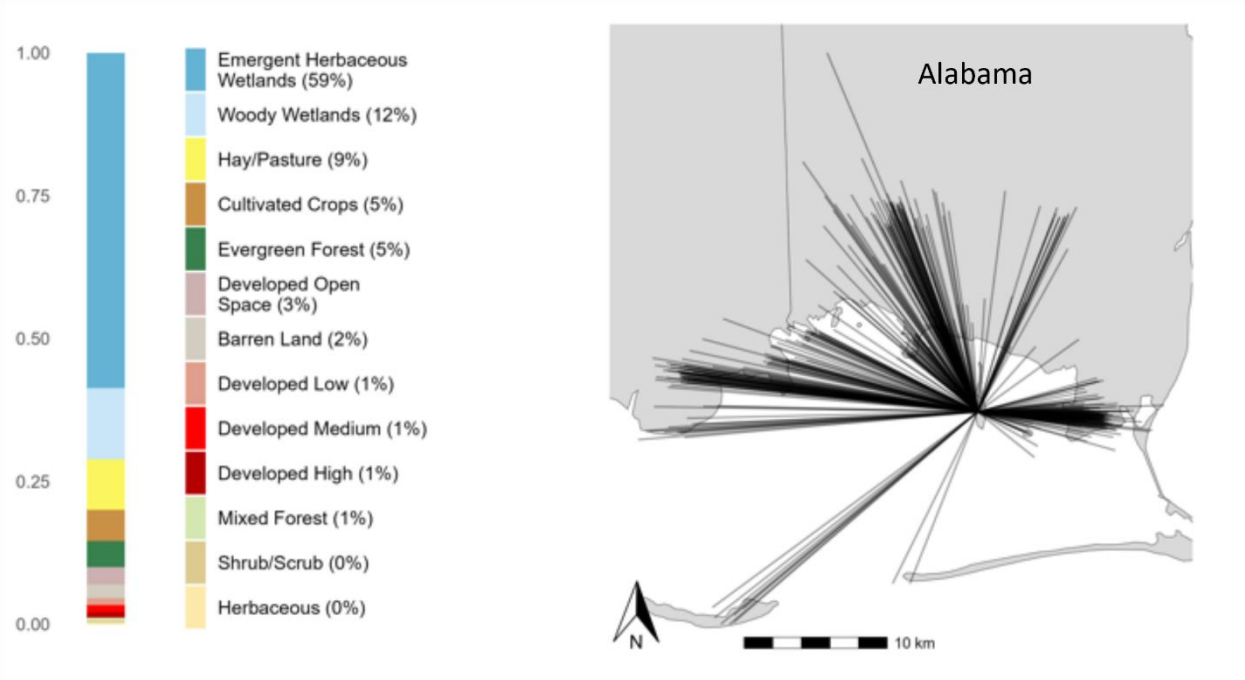

Figure 5. Straight-line movements of tricolored herons from 2020 – 2024 from the Coffee Island communal nesting colony to foraging locations during the breeding season. Each black line represents a single movement from a nighttime roost location to a subsequent daytime location. The adjacent bar chart shows the proportion of each land cover class at foraging sites, based on the 2019 National Land Cover Database (NLCD). Emergent herbaceous wetlands made up the majority of used habitat types. Geographic boundary data: U.S. Census Bureau, 2020 TIGER/Line Shapefiles.

For juvenile tricolored herons, the peak tracking duration (highest probability density) occurred at 93 days for migrants and 100 days for residents (Figure 6). Among adults, the peak was 112 days for migrants and 128 days for residents (Figure 7). These peaks correspond with the timing when birds attempted to cross the Gulf. The decline in relative probability following the peak indicates that many birds likely died during these crossing attempts.

Tricolored herons exhibited two major migration routes, crossing the Gulf into Mexico and Central America, or moving west into Louisiana (Figure 8). For the birds that migrated across the Gulf, adult birds left directly from the breeding colonies in Alabama. In contrast, most juvenile herons first moved west to estuaries in coastal Louisiana where they remained for several weeks before crossing the Gulf. One individual, however, departed from the Texas coast. The remaining individuals that did not cross the Gulf spent the winter in coastal Louisiana (Figure 8).

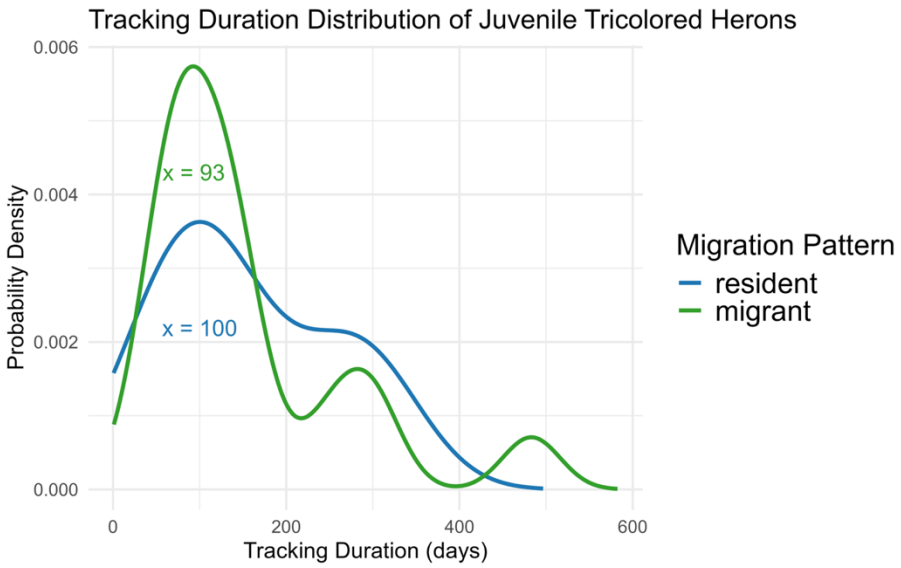

Figure 6. Probability density of tracking durations (in days) from 2020 – 2024 for juvenile tricolored herons by migration pattern. Density curves represent the probability density for individuals classified as residents (blue) and migrants (green). For each curve, the x-value at the highest density (peak) is labeled to indicate the most frequent tracking duration.

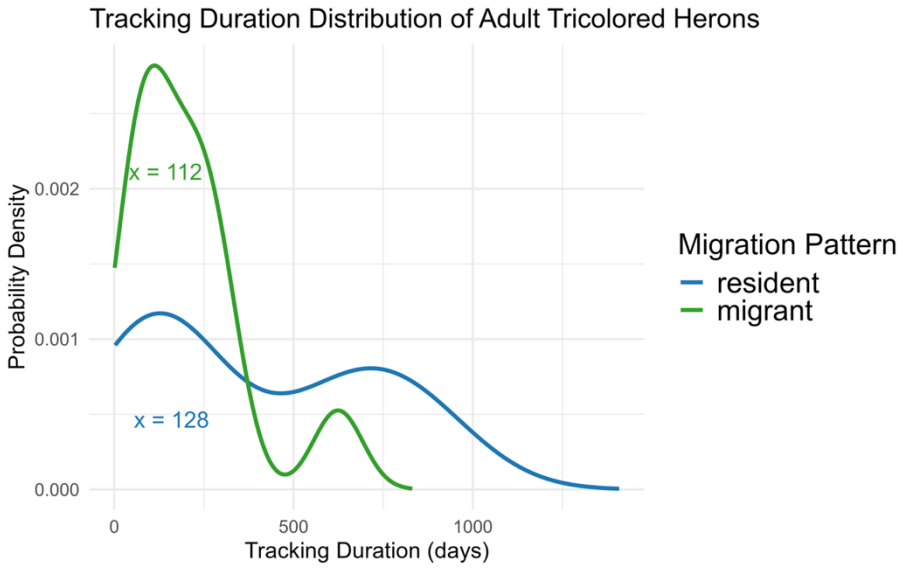

Figure 7. Probability density of tracking durations (in days) from 2020 – 2024 for adult tricolored herons by migration pattern. Density curves represent the probability density for individuals classified as residents (blue) and migrants (green). For each curve, the x-value at the highest density (peak) is labeled to indicate the most frequent tracking duration.

For those juvenile tricolored herons that migrated, the timing of departure from natal colonies was relatively consistent, occurring between mid-July and August (Figure 9). Six juveniles attempted to cross the Gulf, five of which successfully landed on the northern Yucatán Peninsula, while one failed to complete the crossing. Before attempting to cross the Gulf, four of these juveniles first moved to stopover sites in coastal Louisiana within a week of leaving the colony, one first stopped in Louisiana but eventually moved to coastal Texas and spent nearly three months there, and one departed directly from the capture colony area. For the juveniles that successfully crossed the Gulf, the time between their last recorded locations in the northern Gulf states (prior to crossing the Gulf) and their first locations in the Yucatán Peninsula (after crossing) was > 48 hrs; however, this is likely due to the 48-hr off duty cycles of the PTTs. Two individuals had locations recorded during part of the Gulf crossing, suggesting that the actual flight time may have been <24 hrs. Departure dates ranged from early October to mid-November, with four of the six individuals departing in late October to early November. In general, crossing the Gulf by juveniles occurred on average about 90 days after leaving the colony, which corresponded with the peak of tracking duration (Figure 6). Although landing sites varied, all five juveniles that successfully crossed the Gulf ultimately arrived along the coast of

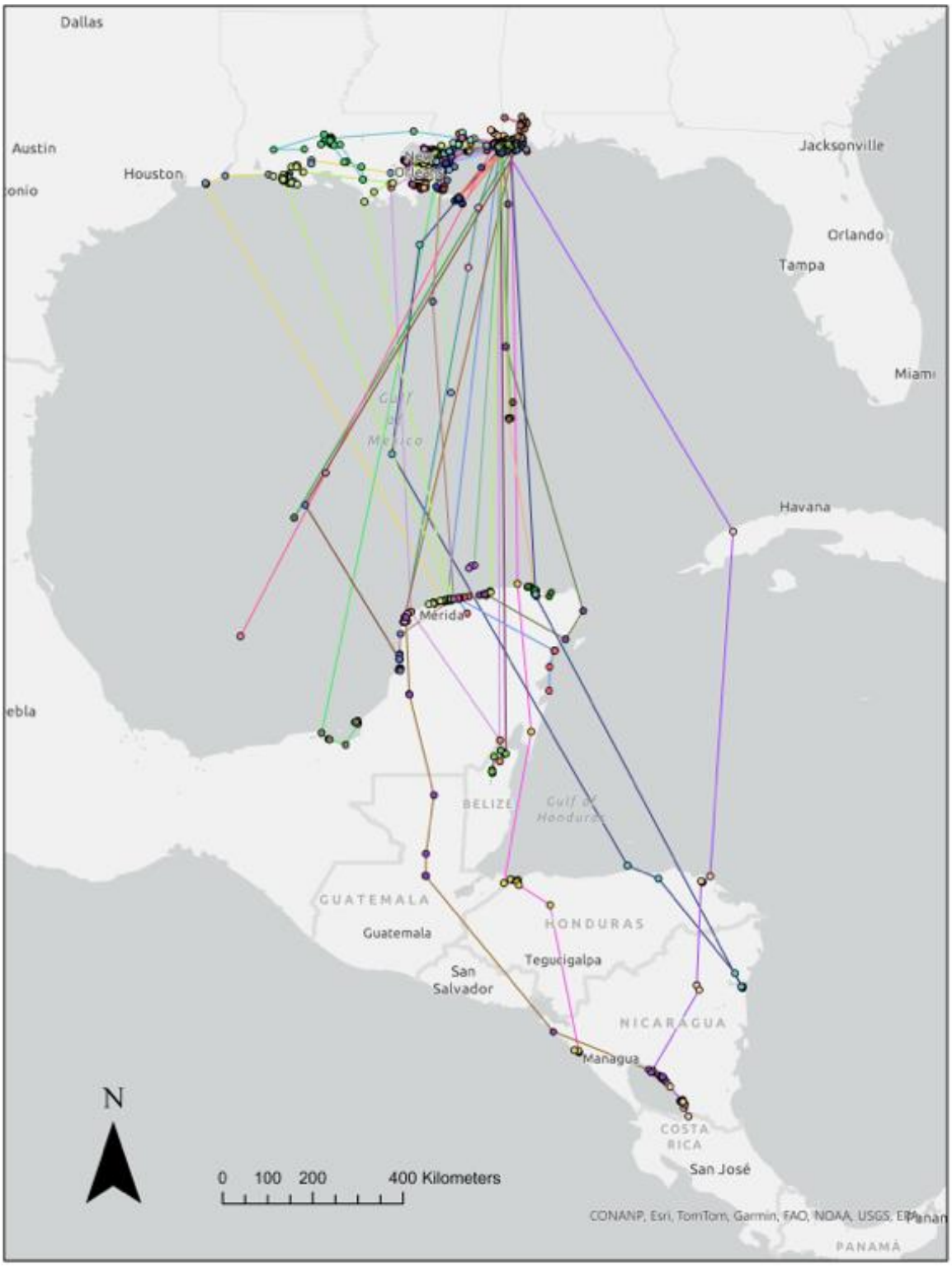

Figure 8. Migration routes of tricolored herons captured in coastal Alabama, 2020 – 2022. Each dot represents one location per bird per tracking period. Lines connecting the dots infer migration routes.

the Yucatán Peninsula and did not disperse to other countries before their tracking data ended. Only one migrant juvenile survived its first winter after crossing the Gulf. It returned to the same stopover site in the northern Yucatán region of Mexico for a week before flying north back across the Gulf and arriving near the colony area at the end of the following April. For the 11 migrant juveniles whose tracking ended in estuaries in Louisiana, ten arrived within a week after leaving their natal colonies, and one individual spent approximately two weeks in transit, stopping at several estuaries along the route to Louisiana. Tracking data for all eleven of these migrant juveniles ended during their first winter. Of the five juveniles classified as residents, one individual that was tagged on Gaillard Island spent the winter in the Mobile–Tensaw River Delta before its transmitter stopped sending location data. The remaining juvenile residents mostly used estuaries along the coasts of Alabama and Mississippi, including the Heron Bay Wetlands Forever Wild Tract and Grand Bay National Wildlife Refuge in Alabama, as well as the Grand Bay National Estuarine Research Reserve and Cat Island in Mississippi (Figure 8).

The timing of departure of adult herons from the breeding colonies ranged from early June to mid-October (Figure 10). Of the 16 migrant adults, 15 attempted to cross the Gulf, while one migrated only as far as Louisiana. Among the 15 adult migrants that attempted the crossing, 14 departed from colonies in coastal Alabama and crossed the Gulf to their wintering grounds, and one departed from coastal Louisiana. Departure dates were concentrated between late September and early November. Eleven adults successfully crossed the Gulf (Figure 10). Among the eleven adult migrants that crossed the Gulf, eight had a time gap >48 hrs between their last location in the northern Gulf and their first location in the Yucatán Peninsula, due to 48-hr off cycles of the PTTs. One individual had a gap of over 24 hrs and briefly stopped in Cuba for approximately four hrs during the crossing. The remaining two individuals had time gaps < 24 hrs. All adult Gulf-crossing individuals flew directly over open water and landed in the Yucatán Peninsula before further dispersing into other countries, including Belize, Guatemala, Honduras, and Nicaragua, except for the one bird that stopped in Cuba (Figure 8). This bird flew over Cuba, spent approximately five hours there, then continued to eastern Honduras and eventually settled near Lake Nicaragua (Figure 8). Another heron also overwintered along the shores of Lake Nicaragua but took a more westerly route, landing in northwestern Yucatán Peninsula and traveling through Guatemala and El Salvador (Figure 8). In general, crossing the Gulf by adults occurred on average about 60 days after leaving the colony, which was before the peak of

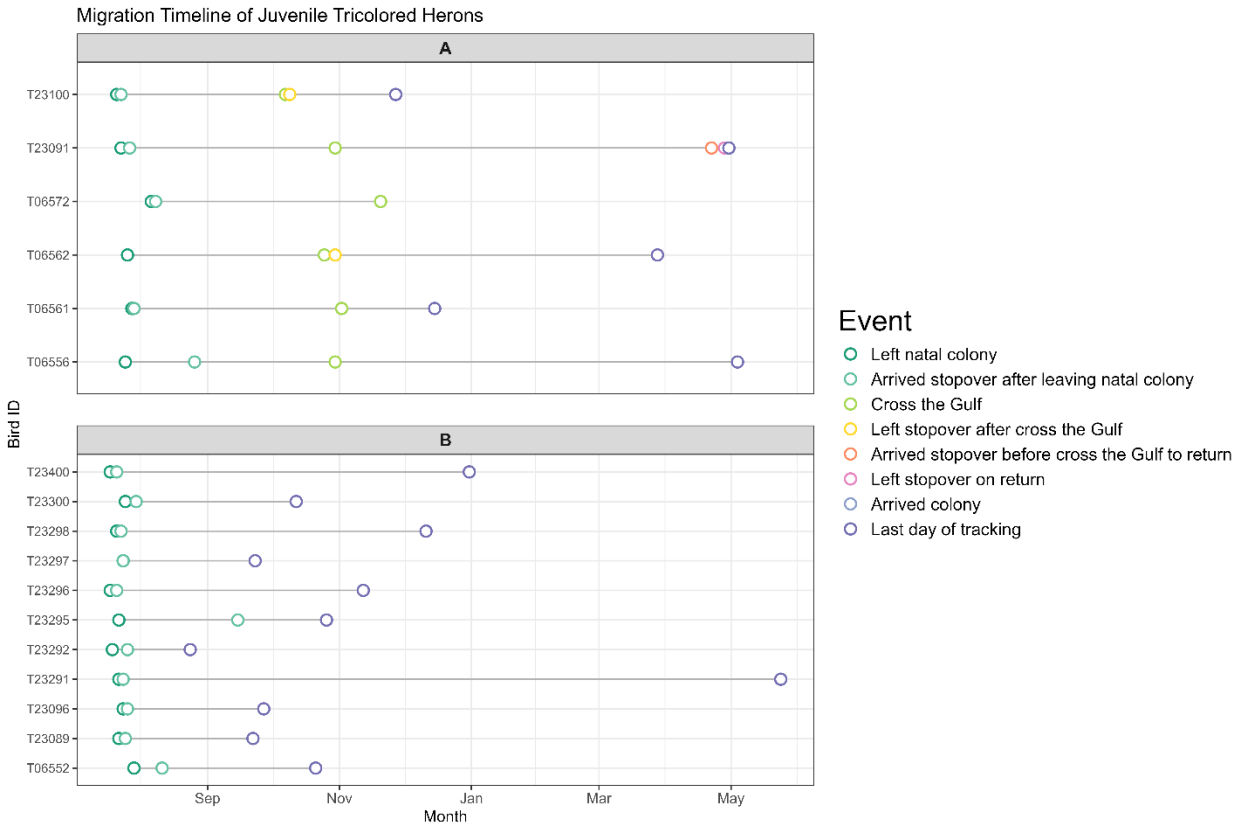

Figure 9. Timing of movements and migration status of tricolored herons captured as juveniles in coastal Alabama, 2020 – 2022. Group A includes five individuals that successfully crossed the Gulf and one individual that attempted the crossing but failed. Group B consists of 11 individuals that reached a stopover or possible wintering site, but without evidence of an attempt to cross the Gulf before the end of transmissions from the platform transmitting terminals (PTTs).

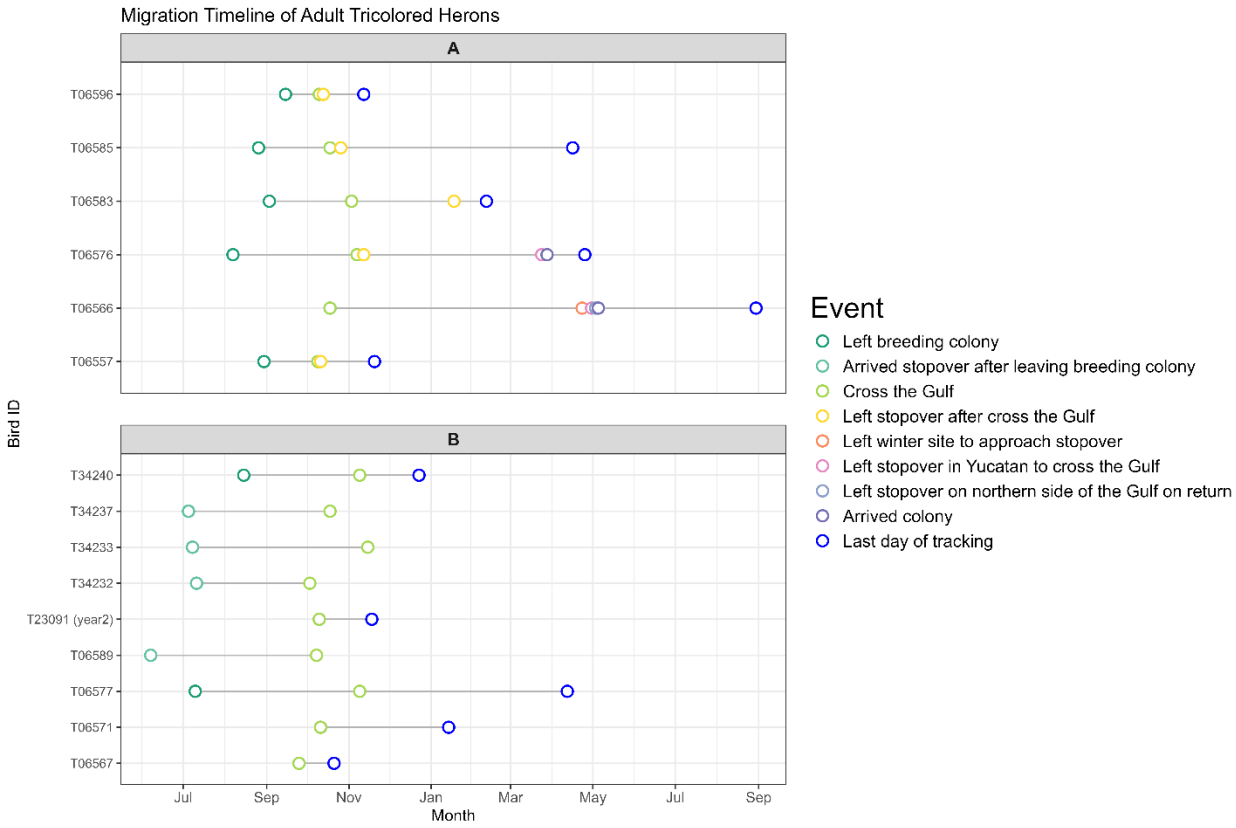

Figure 10. Timing of movements and migration status adult tricolored herons captured in coastal Alabama, 2020 – 2022. Group A includes six individuals that crossed the Gulf and continued migrating to other countries in Central America after a stopover in the Yucatan Peninsula. Group B consists of five individuals that crossed the Gulf but remained in the Yucatan region before the end of transmissions from the platform transmitting terminals (PTTs), and four individuals that attempted to cross the Gulf but failed.

tracking duration (Figure 7). Only two Gulf-crossing adults survived the winter and returned to coastal Alabama during the breeding season. They used the northern Yucatán as a stopover site for less than a week before crossing the Gulf again and arriving in coastal Alabama between late March and early May. One migrant adult didn't attempt to cross the Gulf, and it wintered in coastal Louisiana for two consecutive years. Five adults remained as residents. These individuals primarily used coastal areas of Alabama and Mississippi, especially the Heron Bay Wetlands Forever Wild Tract and Grand Bay National Wildlife Refuge in Alabama, as well as the Grand Bay National Estuarine Research Reserve in Mississippi (Figure 8).

Fidelity and Dispersal

One juvenile and five adults survived for more than a year. Among them, one juvenile and one adult wintered in Central America and returned to their natal or breeding colony the following year, while the remaining individuals stayed in the colony area as residents. In addition, one adult did not survive beyond a year but also wintered in Central America and returned to the capture colony before transmission ceased. Because of high mortality rates, our sample size was insufficient to make inferences about philopatry.

Daily Movements and Habitat Use During the Non-Breeding Season

During the non-breeding season, tricolored herons moved from their daytime foraging sites to their nighttime roost an average distance of 3.30 km (SD = 0.93 km). From their roost sites, they moved an average distance of 3.76 km (SD = 1.00 km) to their foraging sites. Tricolored herons primarily selected estuarine and marine wetlands for foraging (Figure 11), and both estuarine and marine wetlands as well as open water (river, pond, and lake) habitats for roosting (Figure 12). Tricolored herons showed strong preference toward protected land, with a selection ratio of 3.37 (SD = 5.17). They primarily used coastal habitats, during both the breeding and non-breeding seasons, leading to frequent use of protected estuarine habitats. Within the United States, they frequently used sites including the Mobile-Tensaw Delta Wildlife Management Area, Heron Bay and Portersville Bay Wetlands Forever Wild Tracts, Grand Bay Savanna Wildlife Management Area, and Grand Bay National Wildlife Refuge in Alabama; Grand Bay National Estuarine Research Reserve, Grand Bay Savannah, Pascagoula River Marsh, Wolf River Marsh, and Hancock County Marsh Coastal Preserves in Mississippi; Biloxi State Wildlife Management Area, Pearl River Wildlife Management Area, Big Branch Marsh National Wildlife Refuge, Jean Lafitte National Historical Park and Preserve, Pass A Loutre State Wildlife Management Area, and Rockefeller Wildlife Refuge in Louisiana; and McFaddin National Wildlife Refuge in Texas. We could not determine selection ratios for protected lands for those herons that migrated to Central America for the winter; however, several protected coastal areas were used as stopover or wintering sites. Herons that crossed the Gulf frequently stopped in protected areas along the Yucatán Peninsula in Mexico, including Ría Lagartos

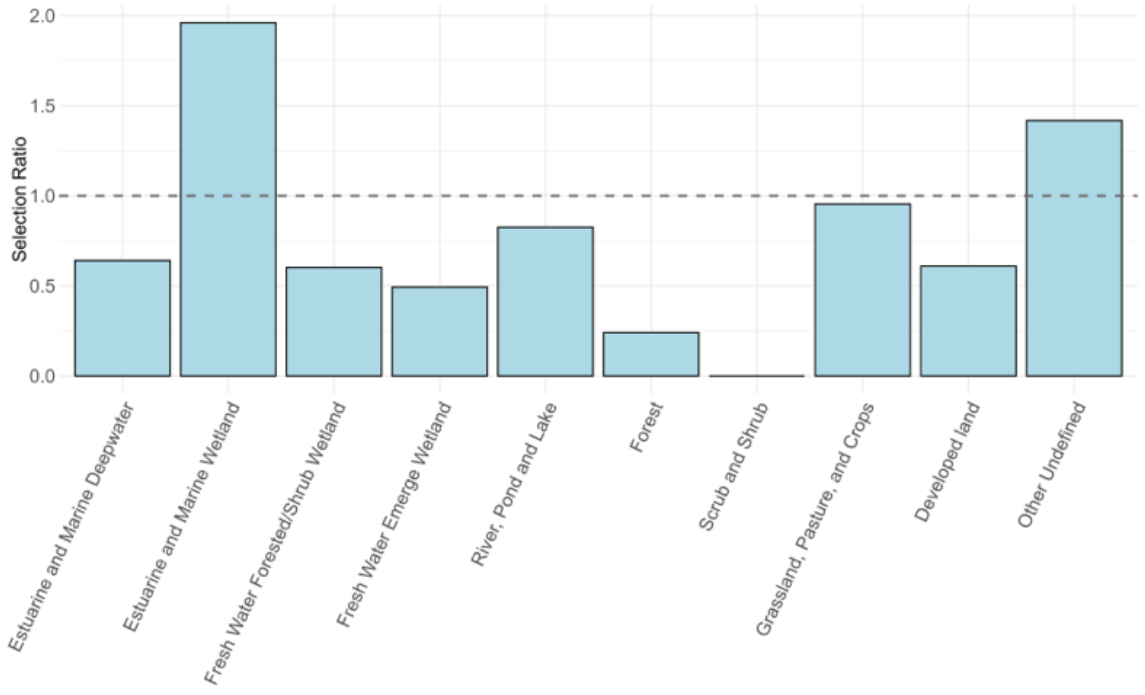

Figure 11. Selection ratios for land cover at the local scale (200 m) of foraging sites used by tricolored herons in the northern Gulf States during the non-breeding season from 2020 – 2024. Values > than 1 indicate selection, while values < 1 indicate avoidance.

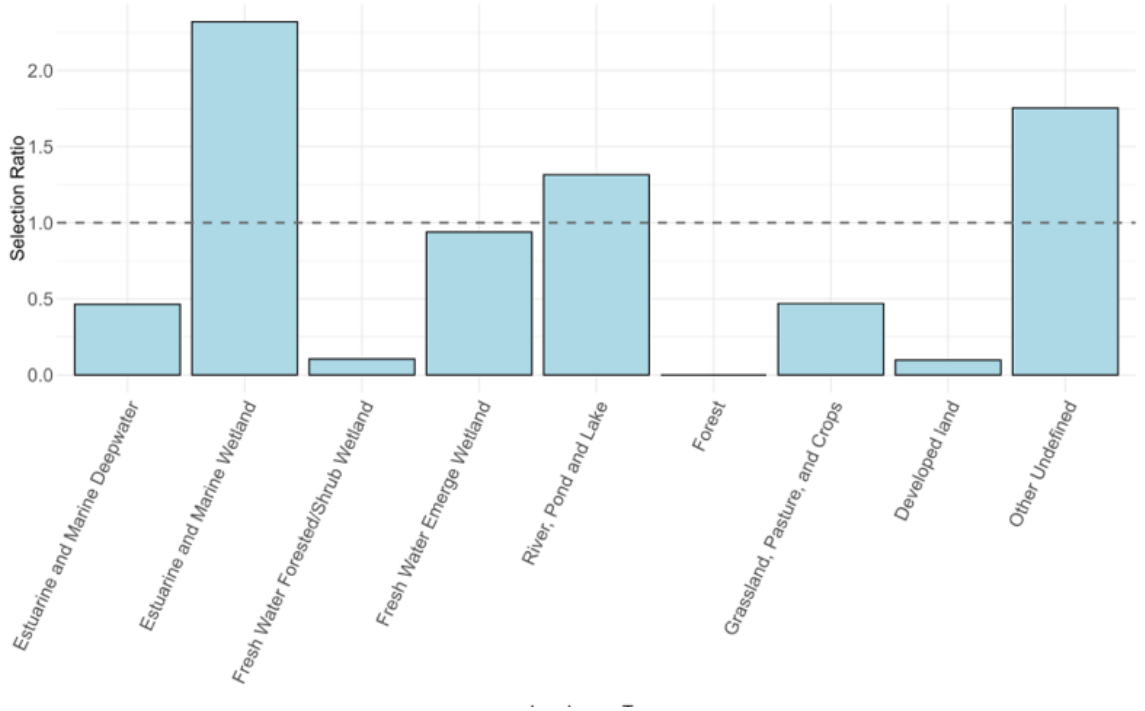

Figure 12. Selection ratios for land cover at the local scale (200 m) of nighttime roosts used by tricolored herons in the northern Gulf States during the non-breeding season from 2020 – 2024. Values > 1 indicate selection, while values < 1 indicate avoidance.

Natural Park, San Diego and San Felipe Las Barras National Park, El Palmar State Reserve, and Ría Celestun Biosphere Reserve.

Annual Survival Estimates

We included 24 juvenile and 21 adult tricolored herons in our survival analysis (Appendix A). We tracked 21 tricolored herons that were captured as hatch-year individuals for a single annual interval. An additional three birds were tracked for two consecutive years, contributing one hatch-year interval and one after-hatch-year interval each. In total, this resulted in 27 bird-years of data from individuals captured as hatch-year, comprising 24 hatch-year intervals and 3 after-hatch-year intervals. Among the 15 birds captured as after-hatch-year, 15 contributed one annual interval, four contributed two intervals, and two individuals were tracked for three years, totaling 29 bird-years from after-hatch-year tagged individuals. Across all tricolored herons in the study, we analyzed 56 total bird-years of data: 32 after-hatch-year intervals and 24 hatch-year intervals.

Survival estimates for tricolored herons varied by year and age class (Table 1). Annual survival probability for hatch-year birds was 0.13 (SE: 0.06; 95% confidence interval (CI): 0.009–0.24; Figure 13), and 0.35 (SE: 0.08; 95% CI: 0.20–0.50) for after-hatch-year birds (Figure 13). Across the study, annual survival during each year varied (Figure 14). Annual survival across all age classes was 0.07 (SE: 0.05; 95% CI: 0.00–0.17) in 2020, 0.31 (SE: 0.10; 95% CI: 0.12–0.50) in 2021, 0.30 (SE: 0.11; 95% CI: 0.08–0.52) in 2022, and 0.62 (SE: 0.21; 95% CI: 0.20–1.00) in 2023. Across the study, annual survival probability was 0.19 (SE: 0.07; 95% CI: 0.06–0.32) for males, and 0.33 (SE: 0.09; 95% CI: 0.16–0.50) for females.

Within seasons, monthly survival was 0.90 (SE: 0.04; 95% CI: 0.78–0.96) for the breeding season and 0.89 (SE: 0.02; 95% CI: 0.85–0.92) for the nonbreeding season. Among the hatch-year birds, only three individuals survived for more than a year. Two remained residents in coastal Alabama and Mississippi throughout their tracking period, and one overwintered in the Yucatán Peninsula for two consecutive winters and returned to the northern Gulf region during the summer. Its transmitter stopped functioning during the second winter. Among the adults, six individuals survived for more than one year, and two of those survived into a third year. Notably, only one of the adults that survived beyond the first year exhibited Trans-Gulf migration; this

Table 2. Model selection results for monthly apparent survival of tricolored herons captured at coastal Alabama breeding colonies and tracked between 2020 – 2024. Models with ΔAICc ≤ 2 indicate comparable explanatory support.

Model	Parameters	AICc	ΔAICc	Weight	Deviance
Year	4	259.82	0	0.2	77.99
Age Class	2	259.99	0.16	0.18	82.23
Sex + Year	5	261.03	1.21	0.11	250.87
Sex + Age Class	3	261.3	1.48	0.1	255.24
Age Class + Year	5	261.62	1.79	0.08	77.73
Age Class + Season	3	261.82	2	0.07	82.03
[PTT Mass / Body Mass] + Age	3	262	2.18	0.07	255.94
Culmen Length	4	262.22	2.4	0.06	254.11
Null	1	262.46	2.63	0.05	86.72

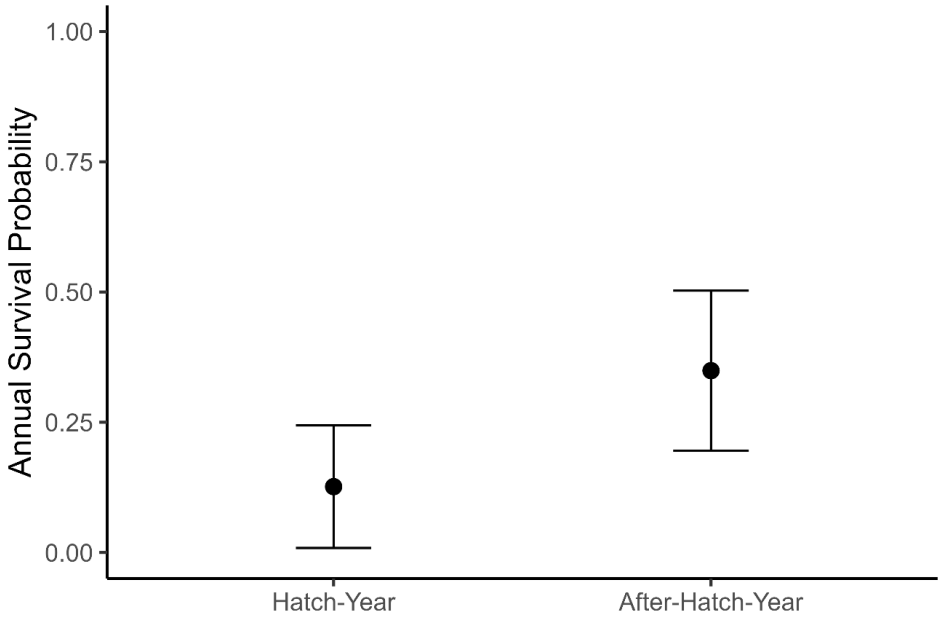

Figure 13. Annual survival estimates of platform terminal transmitter (PTT)-tagged tricolored herons, tracked from July 2020 – 2024, based on age class. This includes 24 individuals tracked as adults (21 tagged as adult, 3 tagged as juvenile), and 24 individuals tracked as juveniles.

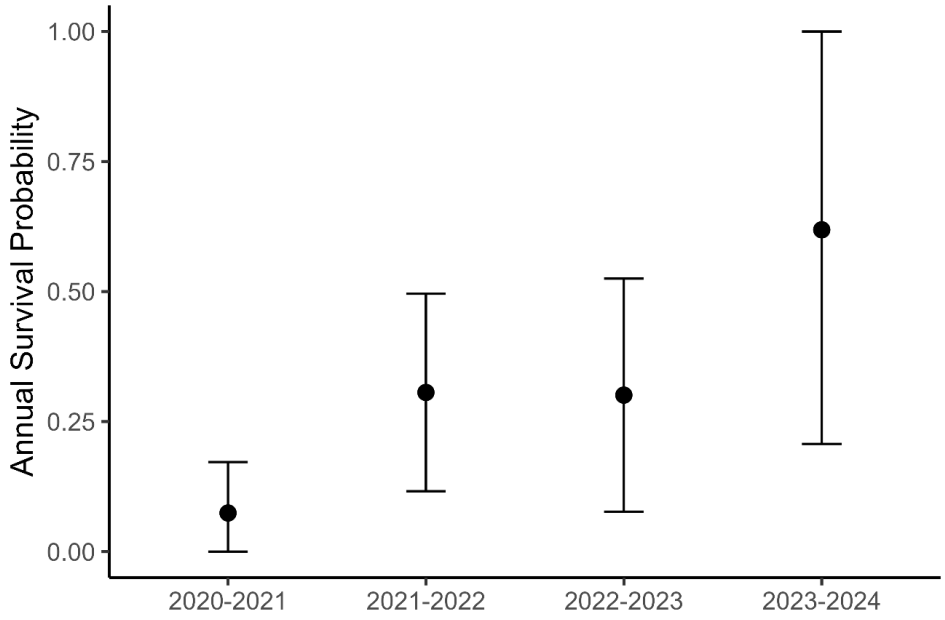

Figure 14. Annual survival estimates of platform terminal transmitter (PTT)-tagged tricolored herons tracked from July 2020 – 2024, based on biological year (July through June of the following year).

individual overwintered in Belize and returned to coastal Alabama in the following breeding season. The other five adults overwintered exclusively in the northern Gulf region. The small sample size and very low survival rate during the first year after transmitter deployment limited our ability to conduct statistical modeling on factors influencing survival.

During the period of this study, several hurricanes made landfall in 2020 including Laura (Category 4), Delta (Category 2), and Zeta (Category 3) in coastal Louisiana, and Sally (Category 2) in coastal Alabama. Ida (Category 4) hit coastal Louisiana in 2021 (refer to Figure 2 and Table 1 in Vasseur et. al, 2023). We found a total of 11 mortality events of juvenile tricolored herons that were associated with hurricanes in 2020. Of the storms centered around coastal Louisiana, one mortality was associated with Laura (~ 41 km from the wind swath), one with Marco (~22 km of the wind swath), one with Delta (within 71 km from the wind swath), and three within the 64-kt wind swath of Zeta. Hurricane Sally made landfall at Gulf Shores, Alabama, and five juveniles died during that storm; two within the 34-kt wind swath and three within 58 km.

Discussion

During the breeding season, tricolored herons nesting at Marsh and Coffee Islands in coastal Alabama relied heavily on emergent wetland habitats (primarily coastal) across a spatially diverse landscape. While the average commute distance across both colonies was approximately 9 km, we observed considerable variation among individuals and between colonies, with herons from Coffee Island traveling farther on average than those from Marsh Island. These distances could reflect both local habitat availability and the location of each colony within the context of the surrounding landscape. Across both colonies, emergent herbaceous wetlands were the dominant land cover class used during daytime foraging, comprising 91% of used points for Marsh Island birds and 59% for Coffee Island birds. This highlights the importance of maintaining a diversity of shallow, vegetated wetland habitats available during the breeding season (Gawlik and Crozier 2007). Woody wetlands, pastures, croplands, and forested areas were also used, particularly by birds commuting from Coffee Island. The broader diversity of land cover types used by herons roosting at Coffee Island may reflect differences in landscape context. Coffee Island is situated farther from the relatively homogeneous marsh complexes west of Heron Bay and nearer to a more varied landscape north of Bayou La Batre, which includes forested tracts, pasture, and low-density development. These differences may explain the greater commute distances and habitat diversity observed in herons from Coffee Island, though we cannot rule out the influence of sample size, individual preferences, social cues, or variation in prey availability (Gawlik and Crozier 2007, Bereens et al 2015). Herons consistently used both protected and privately owned lands, with foraging sites spanning national wildlife refuges, state-managed conservation areas, and privately held marshes and uplands. For instance, birds from both colonies regularly visited wetlands east of Pascagoula, west of Heron Bay, and in the Grand Bay region—areas that include both protected and private properties. This suggests that conservation strategies focused solely on protected lands would overlook large portions of the actual foraging landscape during the breeding season.

Our findings underscore the importance of habitat protection within commuting distance (~10–15 km) of active breeding colonies. Although birds from different colonies varied in their movement distances and habitat use proportions, they exhibited substantial spatial overlap in foraging areas, including several key wetland complexes and protected sites. This overlap, coupled with the close proximity of colony sites (~3 km apart), suggests that breeding birds from

different colonies are drawing from the same foraging habitats. As a result, degradation of foraging habitat may pose a greater risk to the regional population than colony-specific nesting site declines, especially given the availability of alternative breeding colonies but the relative irreplaceability of shared foraging areas. Finally, the spatial breadth of foraging areas, often crossing jurisdictional boundaries and management authorities, emphasizes the importance of inter-agency collaboration in wading bird conservation (Kushlan 2012). Our data indicate that coordinated efforts among Federal, State, and private landholders to maintain wetland function and landscape connectivity across the northern Gulf Coast would likely benefit this suite of species. Conservation actions that protect both colony-adjacent wetlands and key foraging hotspots, particularly those outside formal state or federal protection, may be vital to sustaining tricolored heron populations in this region.

After the breeding season, tricolored herons either remained near their colonies or dispersed westward. Many juveniles stopped in coastal Louisiana, with some staying there for the entire winter and others continuing south across the Gulf, while most adults crossed the Gulf directly from Alabama. The frequent use of Louisiana estuaries, particularly by juveniles, suggests these areas are important for the survival of young birds, providing opportunities to build fat reserves and improve body condition before the open-water Trans-Gulf migration. The timing of Gulf crossings was relatively consistent, likely reflecting the need to wait for favorable environmental conditions (Rappole and Ramos 1994, Eikenaar et al. 2017, Burnside et al. 2021). The crossing itself is nearly 2,000 km, and mortality during this flight is likely high, as indicated by tracking data from at least two birds that stopped transmitting mid-crossing. This interpretation is further supported by the alignment between the timing of Trans-Gulf migration and the peak of tracking duration, suggesting that many individuals did not survive. After crossing the Gulf, the Yucatán Peninsula was the first stopover site for most birds and also served as a stopover for the few that survived the winter and returned back north to Alabama, highlighting the importance of the northern Yucatán as an important area for migratory tricolored herons. Migratory tricolored herons spent in coastal Mexico and Central America, but also along the shores of Lake Nicaragua, which overlaps with previous band-recovery data (Mikuska et al. 1998, Melvin et al. 1999); however, the importance of the northern Yucatán Peninsula as a stopover site for both spring and fall migration was unknown before this study.

Daily movements during the non-breeding season appeared, on average, shorter than daily movements during the breeding season. This contrasts with the expectation that breeding-season birds, being tied to nests, would travel shorter distances, while non-breeding birds could range farther to forage. The relatively long foraging distances during the breeding season may be explained by breeding colony locations, which were on coastal islands and thus, inherently farther from foraging areas. In the non-breeding season, roosts were located on the mainland, allowing birds to remain closer to foraging sites. During the non-breeding season, tricolored herons generally stayed along coastal areas, using estuaries, freshwater wetlands, and open water for both roosting and foraging. However, their roost–foraging relationships were variable, including patterns such as central-place foraging and multiple-central-place foraging, and were possibly shaped by heterogeneous resource distribution (Zhang 2025).

Tropical storms are a common occurrence in Gulf states, and tricolored herons likely evolved in an environment where these storms occurred regularly. However, some evidence suggests that severe tropical storms are expected to become more frequent in the Gulf (Balaguru et al. 2023, Radfar et al. 2024). This could have variable and complex effects on tricolored heron survival and population dynamics. On one hand, tropical storms deposit large amounts of freshwater, which can replenish short-hydroperiod wetlands. While flooding reduces habitat quality in the short term, it can increase the amount of habitat available to wading birds in the long term (Cocoves et al. 2021). On the other hand, these storms can also cause severe destruction of conservation lands, which may degrade or destroy island nesting colonies and foraging habitat. Further, the impacts of the storms (e.g., strong winds, heavy rainfall, severe inundation) could directly lead to decreased individual survival, a phenomenon that that may be responsible for widespread juvenile tricolored heron mortality during the hurricane seasons of 2020 and 2021. Ultimately, it would be difficult to manage for this phenomenon in anything but a reactive capacity. However, increasing (or maintaining) the quantity and quality of foraging habitat in the northern Gulf may offset direct mortality caused by tropical storms. Additionally, efforts to protect or restore inshore islands could help maintain the ability of this species to readily breed at communal colonies in coastal Alabama.

There were four major tropical storms in the northern Gulf in 2020. Most of these storms occurred before migratory tricolored herons departed for fall migration across the Gulf and after birds that might have remained in Louisiana for winter had arrived. To compound the effects of

these storms, we specifically targeted juvenile herons to tag in 2020, anticipating we could attain 2-4 years of movement data from these individuals. Unfortunately, the four major hurricanes that year overlapped with areas used by these birds, and 11 out of 16 (69%) juveniles died in August through October. Laura, Ida, Beta, and Sally all made landfall only ~1-2 months after juvenile herons had fledged, so these birds were particularly inexperienced. In addition to the low survival of hatch-year (juvenile) herons, our survival estimates were associated varied significantly by year, with the lowest survival in 2020, coinciding with the frequent severe weather in the Gulf.

Carrying transmitters can also have a negative effect on the survival of birds (Geen et al. 2019). We only attached transmitters to individuals if the combined weight of the transmitter and harness was < 3% of the bird's body mass. This is a commonly cited benchmark for limiting negative effects of transmitters on birds (Geen et al. 2019) and relatively easily implemented at capture. However, this weight standard may not hold true for all bird species. Beyond weight, transmitters may alter the aerodynamic profile of flying birds, which could thereby increase the energetic cost of movement (Barron et al. 2010, Fair et al. 2023). While it is a possibility that transmitter effects could have influenced survival for our marked sample of tricolored herons, we took precautions (e.g. one-week censor period post-release) to decrease the likelihood that this influenced our results. We also included transmitter mass and proportionate transmitter mass as variables in our survival models and found the results to be uninformative. Further, despite our efforts to band and resight captured birds, no other means of assessing annual survival (e.g., capture-mark-resight, capture-mark-recapture, e.g., Gilroy et al. 2012, Lindberg 2012) has proven to be effective. Therefore, we currently lack a baseline that we could use to assess the effects of transmitters on this species.

Finally, the migration across the Gulf is inherently risky, particularly during autumn when wind conditions can be variable and at times dangerous (Ward et al, 2018, Newton 2025). Of the juvenile herons that attempted to cross the Gulf during fall migration, 5 out of 6 (83%) were successful. For adult herons during the fall migration, 11 out of 15 (73%) that crossed the Gulf were successful. However, of all the herons that migrated to Mexico and Central America, only one juvenile and two adults migrated back to the United States in spring; the rest of the birds appeared to have died during the winter. We are unable to determine causes of mortality during this time, but herons may be hunted in many of these regions (Frederick 2020).

Despite the large variation in our estimates of juvenile survival, they overlapped the one mortality estimate derived from band recoveries over a 50-year time period (21% survival for the first year; Telfair 1979). While large variation in apparent survival estimates is typical for juvenile birds in general (Maness and Anderson 2013, Bates et al. 2015, Beauchamp 2023), the low survival rate we documented for tricolored herons could represent a real and pervasive obstacle to recruitment in this population. The importance of coastal wetlands in Louisiana to juvenile herons is also highlighted by their use of this area both prior to migration as well as for overwintering. In addition to ongoing loss of estuarine habitat in this region (Reed et al. 2020), it is also located in an area frequently impacted by tropical storms (Vasseur et al. 2023) during the period juveniles are present. The low adult survival rates we documented indicate that the population of breeding tricolored herons in coastal Alabama could be declining, however, the only other survival estimation for this species (based on band recovery) was a life expectancy of 1.16 years after fledging (Telfair 1979). While these low survival rates could be offset by high fecundity or immigration of herons from other breeding populations, further study could help to better understand the population status of tricolored herons in Alabama, as well as across all Gulf-adjacent states.

WHITE IBIS

Daily Movements and Habitat Use During the Breeding Season

We tracked ibis moving from four different breeding colonies in coastal Alabama during the breeding seasons of 2020-2024; Marsh (Figure 14), Coffee (Figure 15), and Gaillard islands (Figure 16), and an impoundment adjacent to a shellfish processing facility (30.40281, -88.26683) on the mainland (Figure 17). This facility, the Gulf Coast Agricultural and Seafood Co-op, stores seafood waste (e.g., crab shells, shrimp tails) and processes this waste into fertilizer. Because of this, large piles of seafood waste are available on site throughout the breeding period and these piles are frequented by foraging white ibis. We interpret these movements as breeding season movements because they originated from roosts at known breeding colonies during the breeding season. However, due to Argos location error, limited visibility at crowded colonies, and the possibility of undetected early nest failures, we could not confirm that each roosting event at a breeding colony represented an actual nesting attempt. Nevertheless, individuals present at a colony during the breeding season may contribute

indirectly to colony function (e.g., by attracting conspecifics and reinforcing colony cohesion), so we treat these as breeding season movements for the purposes of this analysis. After excluding daily movements from colonies to foraging sites that ended over open water or at the roost colony from the prior night, we retained a total of 2,443 movements made by 22 individual birds. The average commute distance across all individuals and colonies was 3.2 km (SD = 5.0 km, median = 1.0 km, 90th percentile = 9.4 km).

Movement patterns varied by breeding colony. Birds roosting at the breeding colony near the shellfish processing facility exhibited the shortest movements overall, with an average distance of 1.4 km (SD = 2.21 km, median = 0.7 km, 90th percentile = 2.6 km) based on 1,754 movements from 10 individuals. In contrast, birds from Coffee Island showed the longest average movement distances, with a mean of 9.0 km (SD = 7.7 km, median = 7.4 km, 90th percentile = 19.8 km) across 191 movements from 12 individuals. Marsh Island birds had intermediate movement distances (mean = 8.0 km, SD = 3.1 km, median = 8.3 km, 90th percentile = 10.3 km; 386 movements, 14 individuals), while those from Gaillard Island had a mean movement distance of 4.4 km (SD = 12.4 km, median = 0.5 km, 90th percentile = 20.9 km) based on 112 movements from 5 individuals. These results highlight considerable variation in foraging movement distances among colonies, which may reflect differences in local landscape context, foraging habitat availability, or colony-specific foraging strategies.

White ibis roosting at the Marsh Island colony during the breeding season traveled to five primary foraging areas during daylight hours (Figure 15). These included two protected areas, Coffee Island and the Grand Bay Savanna Community Hunting Area, as well as three privately-owned sites: the shellfish processing facility, wetlands near Heron Bay, and developed areas within the town of Bayou La Batre. Land cover use was dominated by emergent herbaceous wetlands (41%) and woody wetlands (24%). A mix of developed landscapes, including low, medium, and open space classifications, accounted for 2–7% of points. Other land

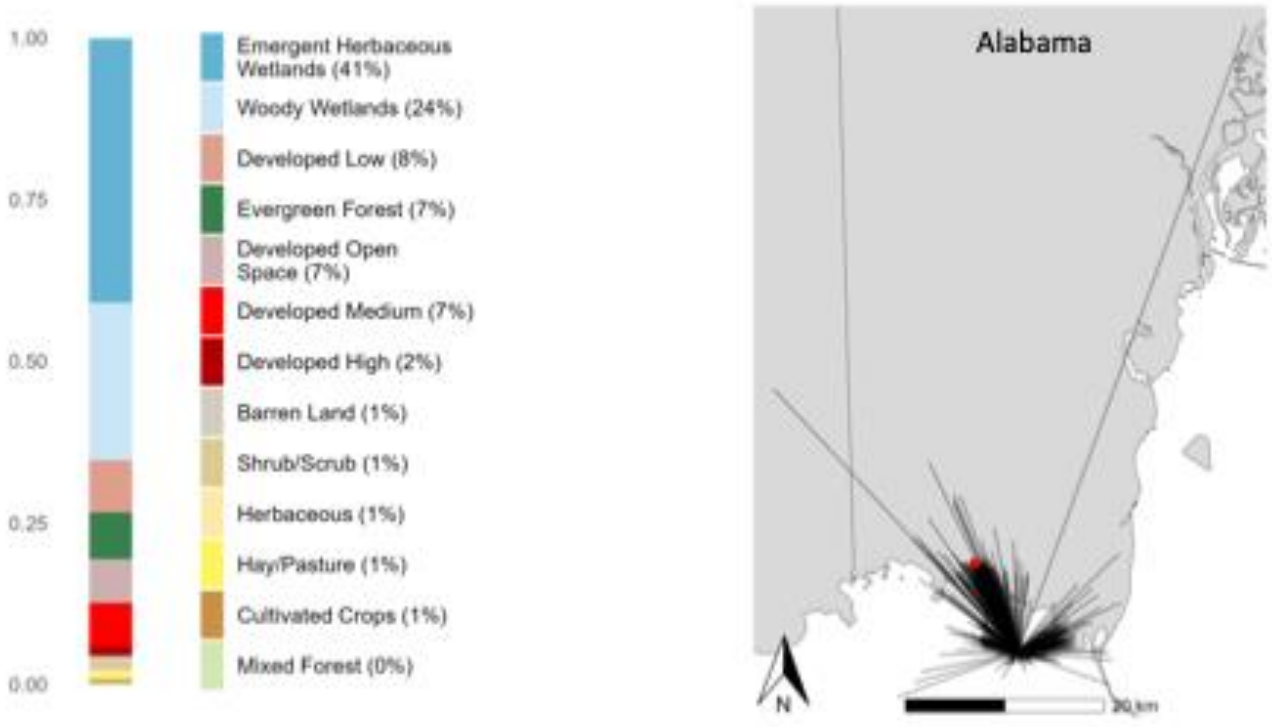

Figure 15. Straight-line movements from 2020 – 2024 of white ibis from the Marsh Island communal nesting colony to daytime foraging locations during the breeding season. Each black line represents a movement from a nighttime roost to a subsequent daytime point. The red dot indicates the shellfish processing facility, a primary area used by ibis that roosted at Marsh Island. The stacked bar chart shows the proportion of land cover types at daytime foraging locations, based on the 2019 National Land Cover Database (NLCD). Emergent herbaceous and woody wetlands were the dominant habitat types used. Geographic boundary data: U.S. Census Bureau, 2020 TIGER/Line Shapefiles.

cover types were used in relatively low proportions, with evergreen forest comprising 7%, and all other NLCD categories representing <2% of foraging locations. These findings indicate that ibis nesting at Marsh Island make frequent use of both public and private wetland complexes in the surrounding landscape and may rely on a mix of natural and human-modified environments during the breeding season.

White ibis roosting at the Coffee Island colony during the breeding season traveled to five main foraging areas during daylight hours (Figure 16). These included Marsh Island, emergent marshes near Heron Bay, developed zones around Bayou La Batre, coastal wetlands near

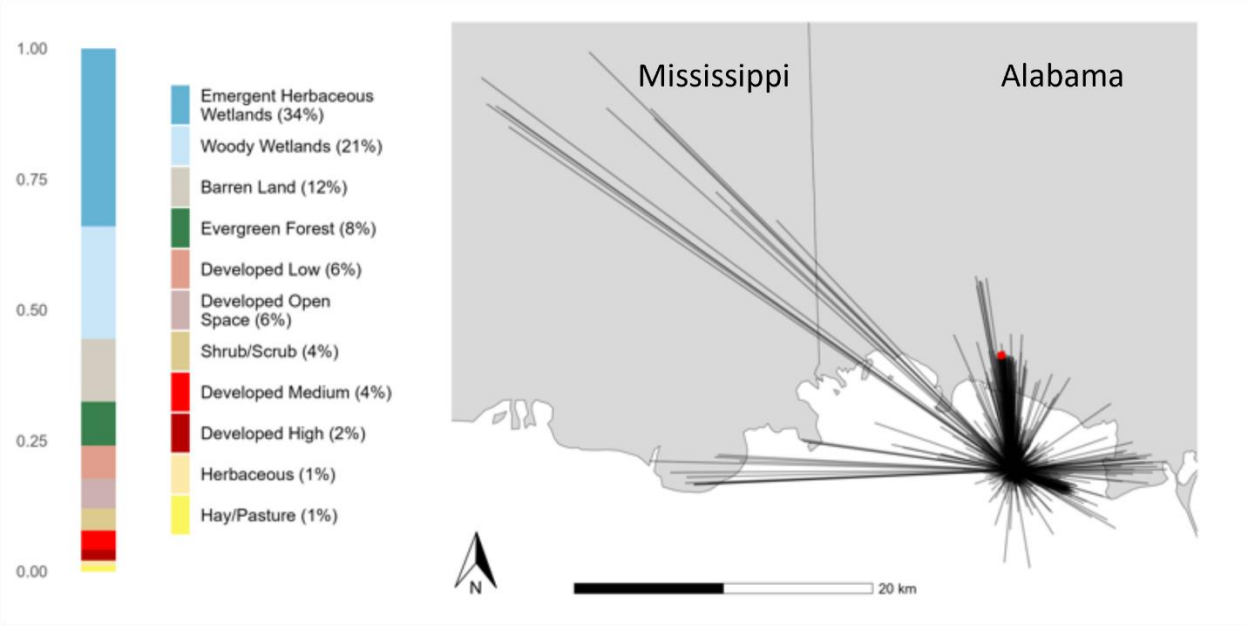

Figure 16. Straight-line movements from 2020 – 2024 of white ibis from the Coffee Island communal nesting colony to daytime foraging locations during the breeding season. Each black line represents a movement from a nighttime roost to a daytime location in the following day. The red dot represents a shellfish processing facility that was used heavily by ibis during the breeding season. The stacked bar chart shows the proportion of land cover types at foraging sites, based on the 2019 National Land Cover Database (NLCD). Emergent herbaceous and woody wetlands were the primary land cover types used, followed by barren land and mixed developed areas. Geographic boundary data: U.S. Census Bureau, 2020 TIGER/Line Shapefiles.

Pascagoula, and the vicinity of a shellfish processing facility near Bayou La Batre. All these areas are privately owned. Foraging locations were primarily situated in emergent herbaceous wetlands (34%) and woody wetlands (21%), followed by barren land (12%), which likely reflects use of exposed shoreline and mudflats. Additional land cover types included evergreen forest (8%), developed landscapes (2–6%), and shrub/scrub habitats (4%). All other NLCD classes each accounted for <3% of foraging points. Ibis relied on a mix of natural and altered habitats across a broad area, most of which lies outside formally protected lands.

White ibis roosting at Gaillard Island during the breeding season foraged locally, with most daytime locations occurring near the colony itself or within wetland areas west and north of Mobile Bay (Figure 17). Land cover at foraging points was dominated by emergent herbaceous wetlands (62%) and woody wetlands (30%), indicating a strong reliance on shallow wetland complexes. All other NLCD classes accounted for less than 3% of used locations combined.

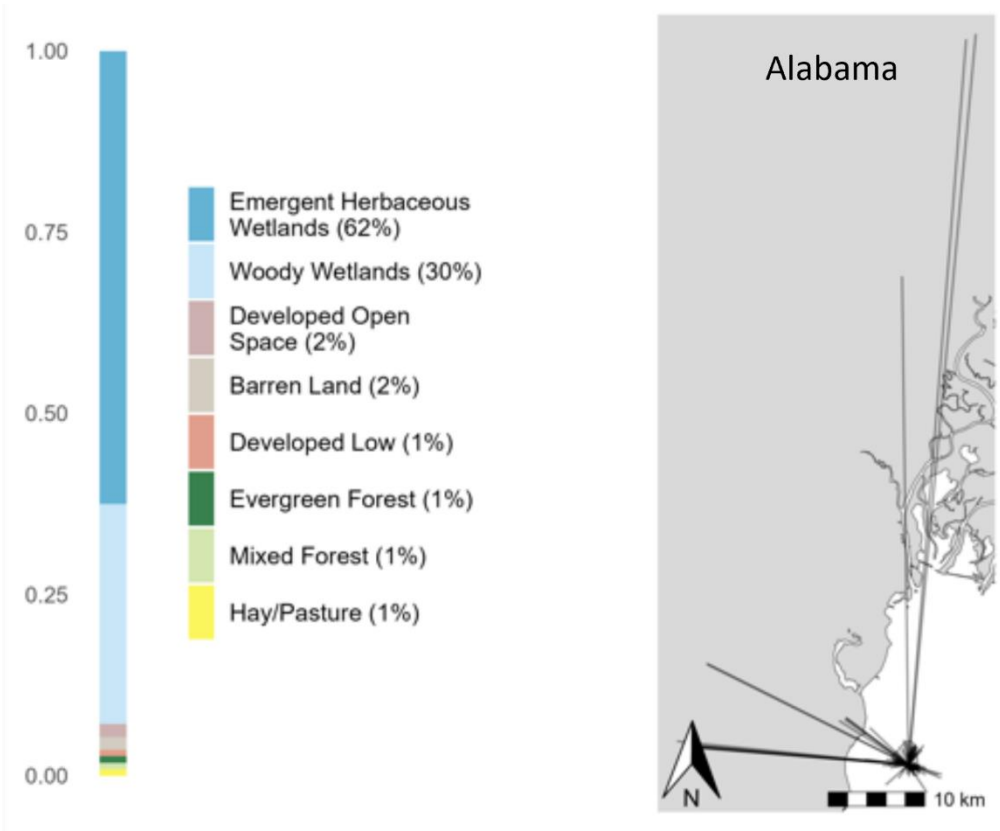

Figure 17. Straight-line movements from 2020 – 2024 of white ibis from the Gaillard Island communal nesting colony to daytime foraging locations during the breeding season. Each black line represents a movement from a nighttime roost to a subsequent daytime location. The stacked bar chart shows the proportion of land cover types at foraging sites, based on the 2019 National Land Cover Database (NLCD). Most daytime locations occurred in emergent herbaceous and woody wetlands within and around Mobile Bay. Geographic boundary data: U.S. Census Bureau, 2020 TIGER/Line Shapefiles.

White ibis roosting at the breeding colony near the shellfish processing facility in coastal Alabama foraged primarily in the immediate vicinity of the facility, with some individuals also traveling to Coffee Island, Marsh Island, and adjacent privately owned wetlands west of Mobile Bay (Figure 18). Foraging habitat was dominated by woody wetlands (40%) and emergent herbaceous wetlands (15%), indicating a preference for wetland-rich environments even in a highly modified landscape. Other frequently used classes included evergreen forest (9%), medium intensity developed areas (9%), developed open space (8%), and low intensity developed areas (8%). Minor use was observed in barren land (6%) and other categories (<5%).

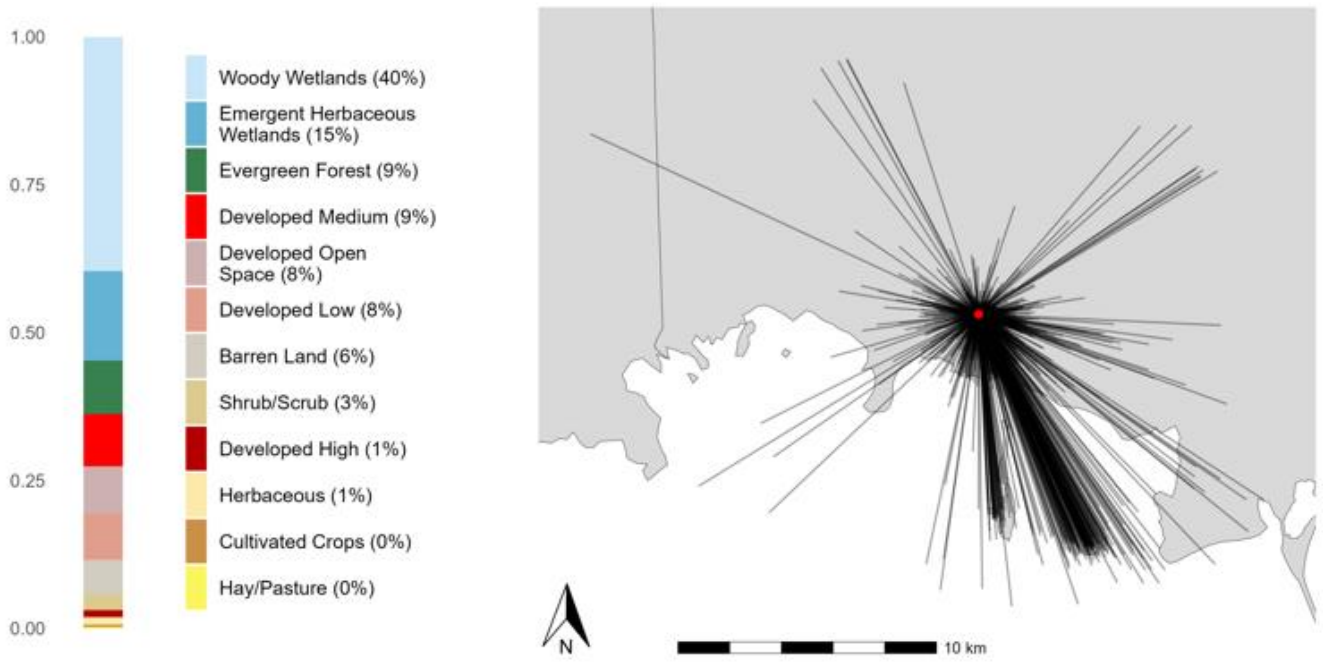

Figure 18. Straight-line movements from 2020 – 2024 of white ibis from a communal nesting colony near a shellfish processing plant in coastal Alabama to daytime foraging locations during the breeding season. Each black line represents a movement from a nighttime roost to a daytime point. The stacked bar chart shows the proportional use of land cover types at foraging sites, based on the 2019 National Land Cover Database (NLCD). Woody and emergent wetlands were the most frequently used habitat types. Geographic boundary data: U.S. Census Bureau, 2020 TIGER/Line Shapefiles.

Despite being located near a developed area, this colony supported high levels of foraging activity in at the nearby shellfish processing plant.

Seasonal Movements from Breeding Colonies to Wintering Areas

We tracked a total of 41 white ibis between 2020 and 2024. Of these, 35 marked birds contributed high-quality locations during the breeding season (1 April–15 July), and 39 were tracked during the non-breeding season (16 July–31 March). While not showing classic migration behavior, white ibis exhibited a clear latitudinal range shift between seasons. During the breeding season, birds occupied a more northerly distribution, including interior lowlands and floodplain systems such as the upper Mississippi River Delta and Atchafalaya Basin (Figure 19). Coastal breeding-season use areas included southern Louisiana, Mississippi, Alabama, the

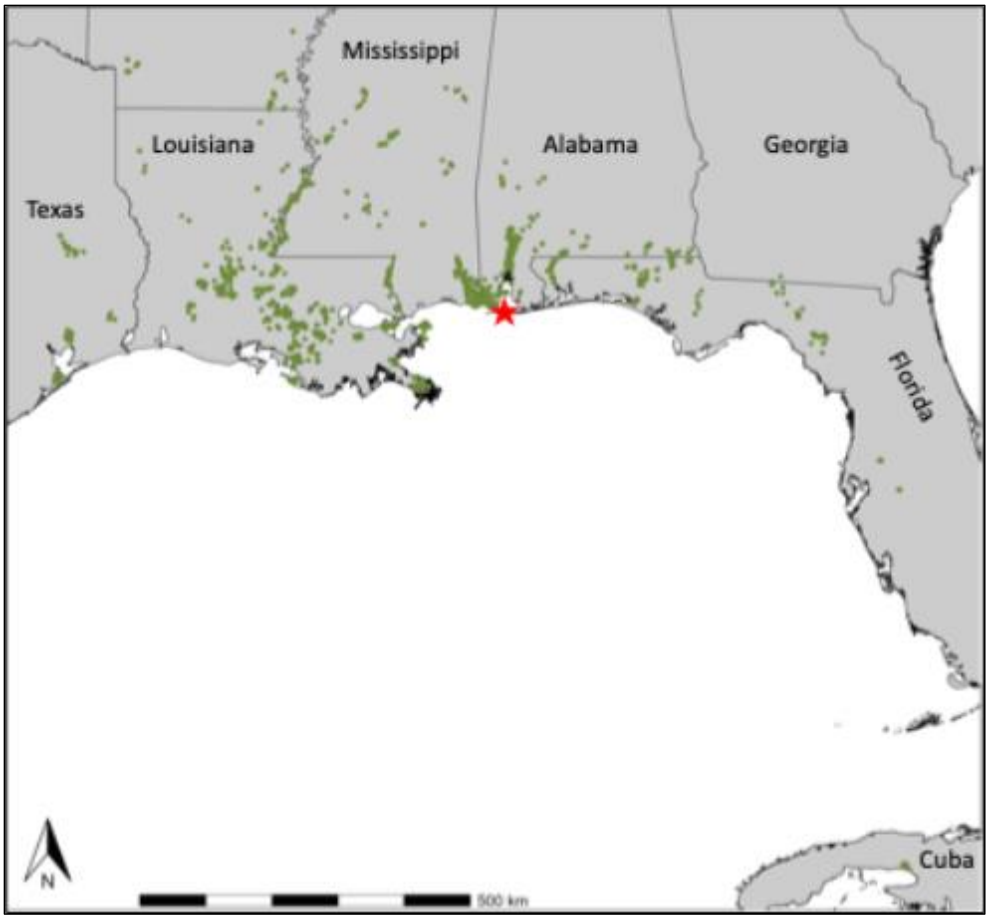

Figure 19. White ibis breeding season (1 April – 15 July) locations recorded from July 2020 through July 2024. Each point represents a high-quality Argos location (LC 1–3). Birds used coastal and interior lowland areas throughout the southeastern United States, with concentrations in Louisiana, coastal Alabama and Mississippi, and the Florida Panhandle. Red star denotes general capture area. Geographic boundary data: U.S. Census Bureau, 2020 TIGER/Line Shapefiles.

Florida panhandle, and coastal Texas. Additionally, one individual spent one non-breeding season and part of a breeding season in coastal Cuba.

In contrast, regional distribution shifted southward during non-breeding (Figure 20). Ibis concentrated in the central and southern portions of peninsular Florida, as well as along coastal zones throughout the Gulf, including Louisiana, Texas, and the Florida Gulf Coast. Coastal areas of Alabama, Louisiana, Texas, Mississippi, and the Florida Panhandle were used during both seasons, indicating regional importance across seasons. Overall, breeding-season locations were

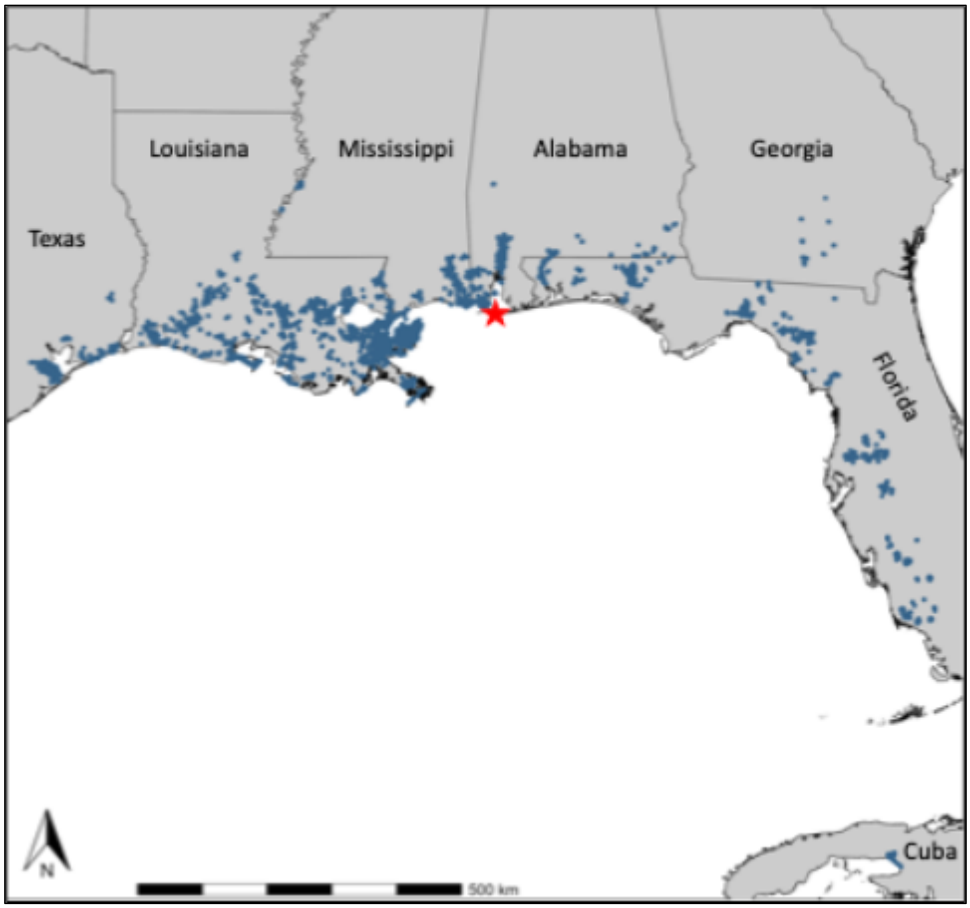

Figure 20. White ibis non-breeding season (16 July – 31 March) locations recorded from July 2020 through July 2024. Locations were concentrated in southern peninsular Florida, Cuba, and along the Gulf Coast, with reduced use of interior lowlands compared to the breeding season. Red star denotes general capture area. Geographic boundary data: U.S. Census Bureau, 2020 TIGER/Line Shapefiles.

more broadly distributed across both coastal and inland wetland systems, whereas non-breeding-season ranges were more coastal and southerly, particularly in Florida and Cuba.

Fidelity and Dispersal

Philopatric white ibis established home ranges not only in coastal Alabama but also in Arkansas, Texas, Louisiana, Mississippi, Georgia, and Florida (Figure 21). Notable areas of concentrated space use included coastal Louisiana near the mouth of the Mississippi River, coastal Mississippi, the Pensacola River basin, and wetland systems of southwest Florida.

Figure 21. Home ranges of all philopatric white ibis tracked from May 2020 – July 2024 (*n* = 14). Ibis were considered philopatric if they returned to coastal Alabama ≥ 30 days during a subsequent breeding season following capture. Utilization distributions (95% contours) were estimated using dynamic Brownian bridge movement models. Red star denotes general capture area. Geographic boundary data: U.S. Census Bureau, 2020 TIGER/Line Shapefiles.

White ibis tagged as juveniles exhibited shifting space-use patterns across life stages (Figure 22). During their first year, movements were concentrated in coastal Alabama, Mississippi, and Louisiana. Additional areas of use included the Atchafalaya Basin (Louisiana), the Pensacola Bay, Choctawhatchee River, and Apalachee Bay regions of the Florida Panhandle, as well as wetland complexes in central Florida (Figure 22). As these individuals transitioned into their second year (subadult stage), movement generally decreased relative to juvenile and adult stages. Focal areas of space use during this period included coastal Louisiana, southern Mississippi and Alabama, the Pensacola and Choctawhatchee River systems, and wetlands in peninsular Florida (Figure 22). Movement tended to increase following their second year. Some individuals returned to coastal Alabama, while others established home ranges in southern and coastal Louisiana, the Florida Panhandle, and southeast Texas.

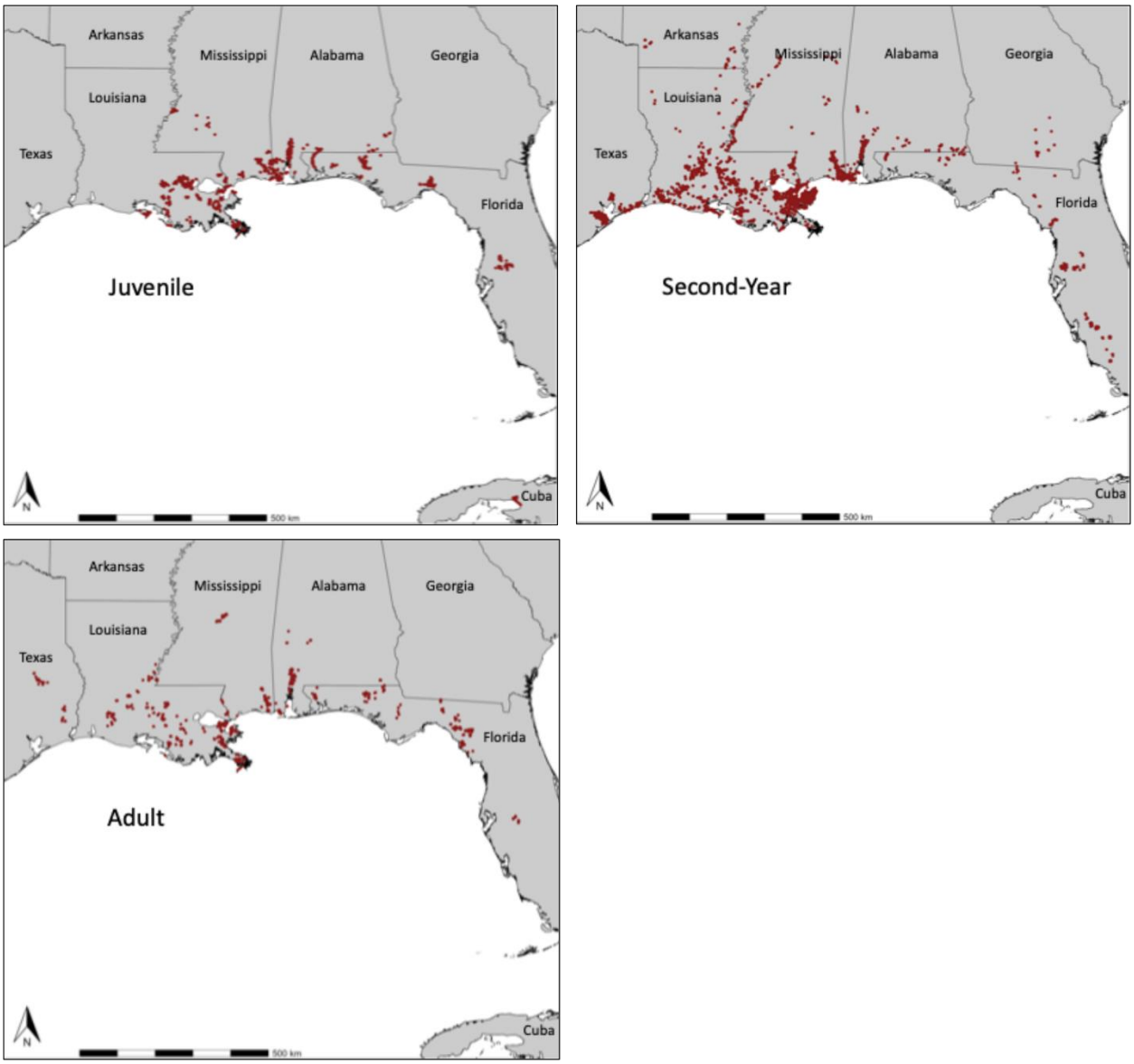

Figure 22. Locations of white ibis tagged as juveniles from 2020 – 2022, during their first, second, and third year after capture. Geographic boundary data: U.S. Census Bureau, 2020 TIGER/Line Shapefiles.

Individuals tagged after their hatch year (AHY) also concentrated movements in coastal Alabama, Mississippi, and Louisiana (Figure 23). Compared to juveniles, AHY individuals spent less time in the Florida Panhandle and more time in coastal Texas, the upper Mississippi River delta, and agricultural regions of southern Louisiana. Several individuals also established home ranges in southern Florida, Georgia, and Arkansas (Figure 23).

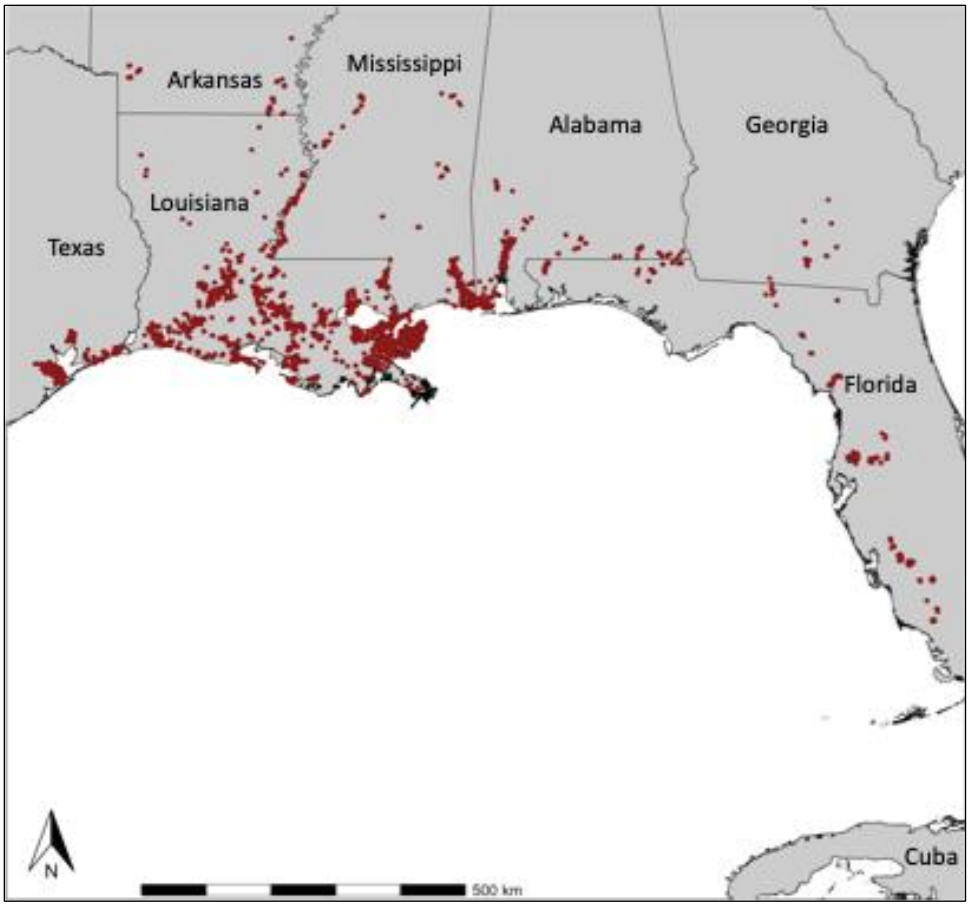

Figure 23. Locations of white ibis from 2020 – 2024 that were tagged after their hatch year (including both subadults and adults). Geographic boundary data: U.S. Census Bureau, 2020 TIGER/Line Shapefiles.

Average weekly displacement of tracked ibis ranged from 0.37 km to 1,081.97 km (mean = 204 km, SD = 210 km). The top model was an interactive model that incorporated sex and body mass (Figure 24). This model indicated that, while accounting for sex, birds with greater body mass had lower displacement distances ($\beta = -0.005$, $SE < 0.001$, $p < 0.01$). Across the range of body masses, males showed a marginally greater displacement from coastal Alabama when compared to females ($\beta = -0.51$, $SE = 0.28$, $p = 0.08$). However, the relationship between mass and displacement varied by sex ($\beta = 0.002$, $SE < 0.001$, $p < 0.01$); the relationship between displacement and mass was significantly stronger for males than females (Figure 24).

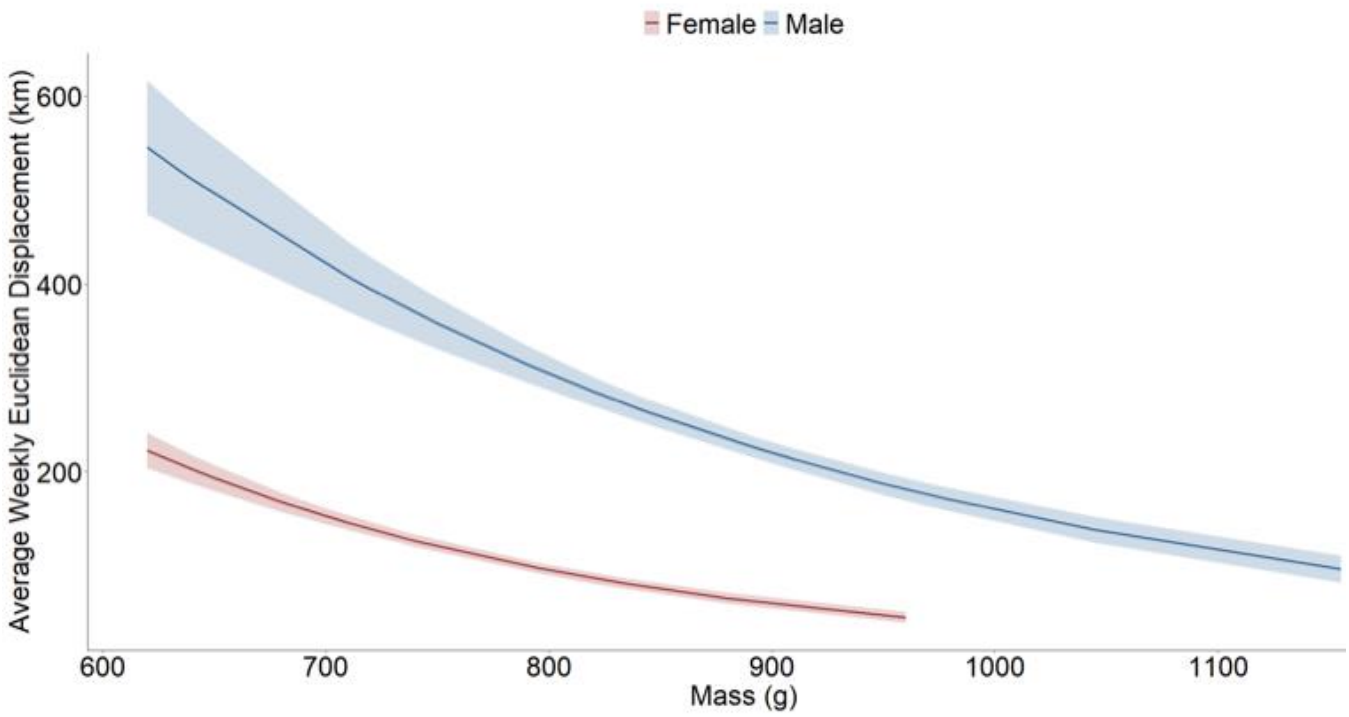

Figure 24. Model explaining Euclidean displacement of ibis from coastal Alabama breeding colonies from 2020 – 2024. Larger individuals were less likely to be displaced from coastal Alabama. Additionally, males traveled farther from coastal Alabama compared to females.

Philopatry patterns varied by age at capture and tagging. Of the seven birds tagged as juveniles that survived long enough to determine philopatry in the following year, only 2 (29%) later returned to the capture region. One subadult (50%) and 11 of 14 eligible adults (79%) exhibited philopatric behavior at least one year post-release. For eligible birds tagged as juveniles, only one out of seven (14%) returned to coastal Alabama during their subadult year. For eligible birds that were tracked during adulthood, 19 of 45 adult-years (42%) involved a return to coastal Alabama. Among individuals that did return to coastal Alabama, the average time to first return was 1.5 years for juveniles (SD = 0.7), 1.0 year for subadults (SD = 0.0), and 1.1 years for adults (SD = 0.3). Of all tracked individuals that survived at least 30 days into the breeding season following capture, only one remained resident in coastal Alabama through the entirety of its tracking period.

Daily Movements and Habitat Use During the Non-Breeding Season

During the non-breeding season, white ibis moved an average distance of 4.82 km (SD = 0.73 km) from their diurnal foraging areas to their nighttime roosts. They moved an average distance of 4.56 km (SD = 0.65 km) from their roost sites to the next day's foraging areas.

White ibis selected estuarine and marine wetlands, freshwater forested/shrub wetlands, freshwater emergent wetlands, scrub/shrub, and open water (rivers, ponds, and lakes) for foraging (Figure 25). For roosting, they primarily used estuarine and marine wetlands, freshwater forested/shrub wetlands, and open water (Figure 26).

White ibis showed a selection ratio of 1.13 (SD = 1.17) toward protected conservation lands. Compared to tricolored herons, white ibis used a broader range of habitats and spent more time in inland areas rather than remaining exclusively along the coast. Their use of protected areas included both estuarine and freshwater sites. In Florida, these included Big Cypress National Preserve, Fakahatchee Strand Preserve State Park, Picayune Strand State Forest, Babcock Ranch Preserve, Fred C. Babcock/Cecil M. Webb Wildlife Management Area, Richloam Wildlife Management Area, Green Swamp West Unit, Steinhatchee Springs, Mallory Swamp, Aucilla, and Saint Marks River Wildlife Management Areas, as well as Choctawhatchee and Holmes Creek Water Management Area and Escambia and Yellow River Wildlife Management Areas. In Alabama, protected areas used included Upper Delta and Mobile-Tensaw Delta Wildlife Management Areas, Heron Bay and Portersville Bay Wetlands Forever Wild Tracts, Grand Bay

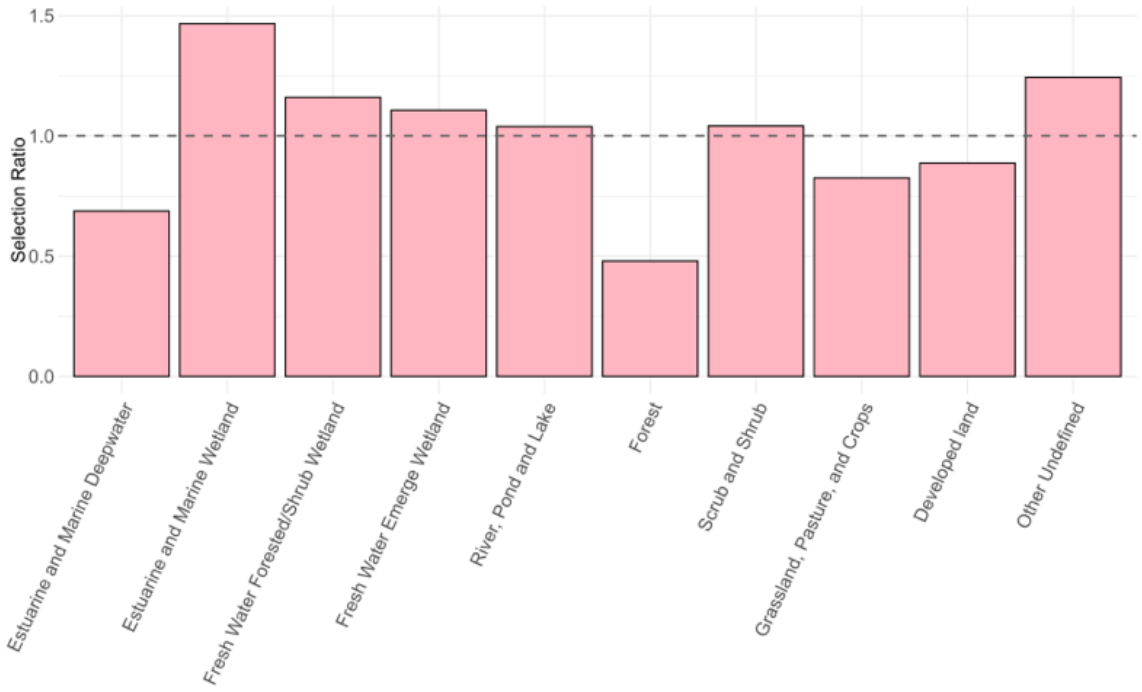

Figure 25. Selection ratios for foraging land cover at the local scale (200 m) by white ibis in the northern Gulf States during the non-breeding season from 2020 – 2024. Values > 1 indicate selection, while values < 1 indicate avoidance.

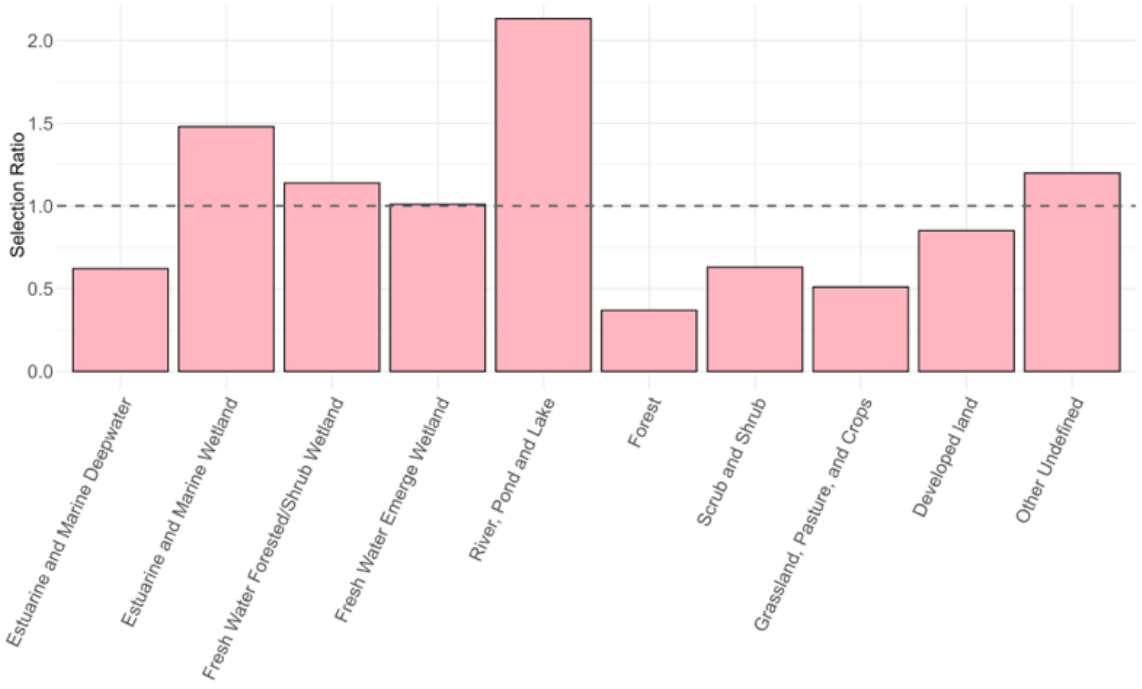

Figure 26. Selection ratios for roost land cover at the local scale (200 m) by white ibis in the northern Gulf States during the non-breeding season from 2020 – 2024. Values > 1 indicate selection, while values < 1 indicate avoidance.

Savanna Wildlife Management Area, and Grand Bay National Wildlife Refuge. In Mississippi, ibis used Grand Bay National Estuarine Research Reserve, Grand Bay Savannah Coastal Preserve, and Pascagoula River State Wildlife Management Area. In Louisiana, they used Pearl River Wildlife Management Area, Bogue Chitto and Bayou Sauvage National Wildlife Refuges, Biloxi State and Pass-a-Loutre State Wildlife Management Areas, Jean Lafitte National Historical Park and Preserve, and Maurepas Swamp, Joyce, Manchac, and Marsh Island Wildlife Areas. In Texas, they used McFaddin and Jocelyn Nungaray National Wildlife Refuges.

Annual Survival Estimates

The top model explaining white ibis monthly survival included age class (Table 3). Two additive models were within 2 ΔAICc of the top model, one including the effects of age class and sex, and the other including the effects of age class and season. While these models received marginal support, the effects of sex and season were not significant in their respective models. Given that age class was in the top three models, this factor appears to have the strongest influence on white ibis survival.

Table 3. Model selection results for monthly apparent survival of white ibis captured at coastal Alabama breeding colonies and tracked between 2020 – 2024. Models with ΔAICc ≤ 2 indicate comparable explanatory support.

Model	Parameters	AICc	ΔAICc	Weight	Deviance
Age Class	3	199.10	0.00	0.36	90.69
Age Class + Sex	4	199.48	0.38	0.29	191.43
Age Class + Season	4	200.86	1.77	0.15	90.44
Age Class * Sex	6	201.85	2.75	0.09	189.75
Age Class * Season	6	202.25	3.15	0.07	87.77
Age Class + Year	6	203.81	4.71	0.03	89.33
Age Class * Year	12	207.09	7.99	0.01	80.32
Sex + Year	5	212.51	13.41	0.00	202.43
Year	4	214.58	15.49	0.00	104.16
Sex	2	215.80	16.71	0.00	211.79

Annual survival probability of white ibis increased substantially with age (Figure 27). Juvenile ibis exhibited the lowest apparent annual survival at 0.29 (SE: 0.09, 95% CI: 0.11–0.47), while subadults had markedly higher apparent annual survival at 0.89 (SE: 0.10, 95% CI:

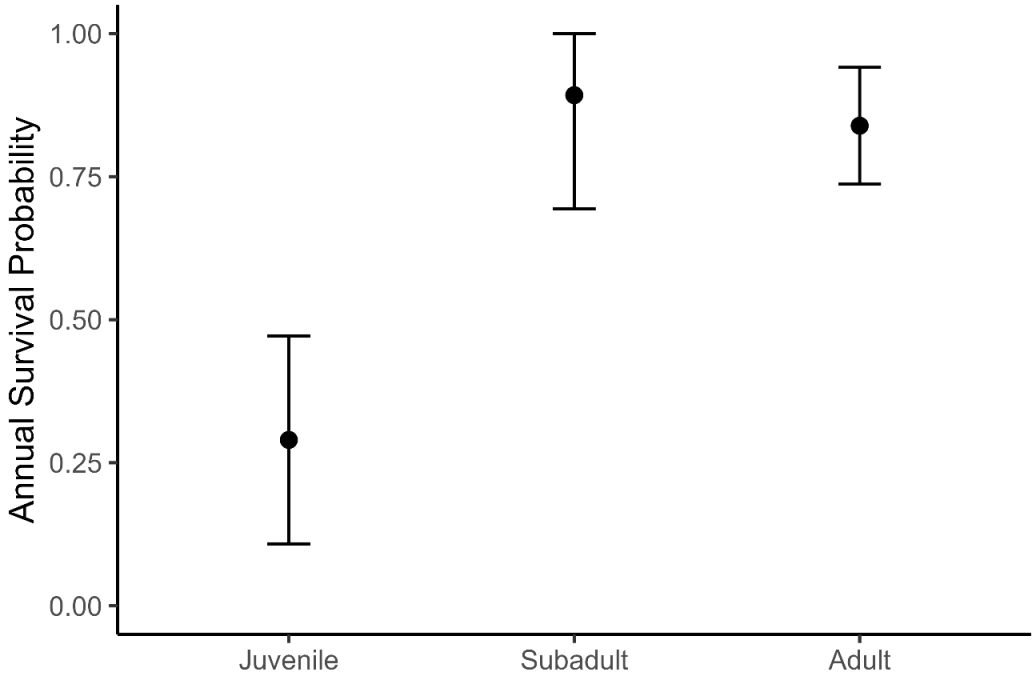

Figure 27. Annual survival estimates (± 95% confidence intervals) for white ibis, grouped by age class. Survival increased with age, from 0.33 (95% CI: 0.15–0.59) in juveniles, to 0.75 (95% CI: 0.45–0.92) in subadults, and 0.82 (95% CI: 0.70–0.90) in adults. Estimates are derived from known-fate models fitted using annual intervals, based on satellite-tagged individuals tracked between 2020 – 2024.

0.69–1.00). Adult birds had the highest estimated apparent annual survival of 0.84 (SE: 0.05, 95% CI: 0.73–0.94). The wide confidence intervals associated with juvenile survival reflects greater variability in outcomes for young birds, while the narrower confidence interval around adult estimates indicates more consistent survival among mature individuals. These results highlight a steep ontogenetic increase in annual survival, consistent with age-related improvements in foraging efficiency and spatial familiarity (Bildstein 1993, Votier et al. 2017, Grecian et al. 2018).

Within age classes, females tended to show slightly greater apparent survival compared to males. However, these differences were small and not statistically significant. Annualized estimates from this model were 0.24 (SE: 0.09, 95% CI: 0.06–0.42) for juvenile males, and 0.45 (SE: 0.17, 95% CI: 0.12–0.78) for juvenile females. For subadults, male survival probability was 0.87 (SE: 0.12, 95% CI: 0.63–1.00), and female survival probability was 0.93 (SE: 0.08, 95% CI:

0.78–1.00). Adult male survival probability was 0.80 (SE: 0.07, 95% CI: 0.66–0.94), and adult female survival probability was 0.88 (SE: 0.05, 95% CI: 0.78–0.98).

Similar to sex, seasonal differences were not statistically significant, and small relative to the variation in survival based on age. Monthly survival of subadults was 0.99 (SE: 0.01, 95% CI: 0.899–0.999) during breeding, vs. 0.99 (SE 0.01, 95% CI: 0.94–1.00) during nonbreeding. Adult monthly survival was 0.98 (SE 0.01, 95% CI: 0.94–0.99) during breeding and 0.987 (SE 0.01, 95% CI: 0.97–0.99) during nonbreeding. Monthly survival of juveniles during the nonbreeding season was 0.90 (SE: 0.02, 95% CI: 0.84–0.94). Juveniles were captured at the end of the breeding season in which they hatched, and transitioned to subadults at the beginning of the following breeding season. Therefore, no breeding season estimate for juveniles is presented.

We found a total of three mortality events for juvenile white ibis that occurred within or near hurricanes in Louisiana in 2020: one within the 50-kt swath and one within 64-kt wind swath of Zeta, and one within the wind swath of Laura. In 2021, one adult white ibis mortality occurred within the 64 kt wind swath of Hurricane Ida in 2021.

Discussion

White ibis breeding in coastal Alabama exhibited considerable variation in foraging behavior across four colony sites during the 2020–2024 breeding seasons. Despite differences in movement distances and local landscape context, birds at all colonies relied heavily on wetland habitats during the breeding season. Emergent herbaceous and woody wetlands together accounted for most foraging locations at each colony, highlighting the importance of these habitat types for foraging during the breeding-season. Average foraging distances varied widely among colonies, ranging from 1.4 km for ibis roosting at a shellfish processing facility to over 9.0 km for those using Coffee Island. Mean foraging flights from all coastal Alabama breeding colonies were generally consistent with previous observations across the species' range (e.g., <10 km; Ogden 1994). In North Carolina, white ibises typically foraged within 8 km of the nest during early breeding, expanding up to 50 km post-hatching (Pennycuick & de Santo 1989). The daily distances moved between the colonies and foraging areas in our study were also within the ranges seen in closely related Australian white ibis (*Threskiornis molucca)* in urban settings (67% moved an average of 2 – <10 km, 27% moved from 10 – < 20 km; Martin et al. 2011). Differences in foraging distances from nesting colonies likely reflect variation in local habitat

configurations rather than colony-specific foraging strategies. For example, birds nesting near the shellfish facility were located adjacent to a processing plant that stored the remains of crab and shrimp in large open-air piles before processing. This likely provided a consistent and readily available food source for the individuals roosting nearby. Ibis from other colonies, like Coffee Island, were farther from this shellfish facility, as well as from Heron Bay wetlands, which likely resulted in longer commute distances. Nonetheless, there was substantial overlap in foraging locations among colonies, particularly among birds using Marsh Island and Coffee Island, suggesting that colony location alone does not determine access to key foraging areas.

Across all colonies, ibis used a mix of protected and privately owned lands. Some of the most heavily used areas included the shellfish processing facility, Bayou La Batre, and wetlands near Heron Bay and Pascagoula. These areas are outside the boundaries of formal conservation areas. In addition, regular use of developed landscapes, including low- and medium-intensity development, further illustrates their capacity to facultatively forage in human-modified environments (e.g., Murray et al. 2018). These movements between colonies and foraging areas emphasize the likely benefit of conservation strategies that extend beyond public lands and include conservation partnerships with private landowners and industry stakeholders.

Despite Gaillard Island's distance from the mainland, white ibis using this site during the breeding season exhibited relatively short commute distances, with most foraging flights remaining on or near the island. While a few individuals traveled to wetlands north and west of Mobile Bay, most movements were highly localized. Gaillard Island is large, well-protected from erosion, and contains extensive interior wetland habitat. This likely reduces the need for long-distance foraging flights and may contribute to the island's long-term suitability as a breeding colony. The persistence of white ibis nesting at Gaillard may be directly linked to the availability and quality of within-island foraging habitats. Over the long-term, foraging site quality alone is unlikely to fully explain patterns of colony persistence. Marsh Island and Coffee Island, for example, are separated by just three kilometers and share many foraging zones yet may differ in long-term viability due to differences in island-specific characteristics such as elevation, vegetation structure, erosion exposure, or predator access. These findings underscore the importance of managing both colony-adjacent foraging landscapes and the physical and ecological conditions of the colony sites themselves, particularly colonies located on islands.

The spatial and habitat use patterns observed in this study highlight several factors that may be relevant to conservation planning. Emergent and forested wetlands located within 5–10 km of active colonies comprised a substantial proportion of foraging activity across all sites, suggesting these habitats contribute meaningfully to breeding-season resource use. Certain wetland complexes, such as the Heron Bay marshes and the Grand Bay region, were used by birds from multiple colonies, indicating their potential importance as shared foraging site hubs. In addition, observations from the shellfish processing facility colony illustrate that developed landscape patches can still support breeding season foraging when consistent resources are available in those areas.

Directly comparing daily foraging distances between breeding and non-breeding seasons is difficult because breeding-season distances varied greatly among the three nesting colonies. However, similar to tricolored herons, white ibis in the non-breeding season were not strongly tied to specific roost sites. Their roost–foraging relationships were more dynamic, including central-place foraging, multiple-central-place foraging, and nomadic patterns, in which birds frequently shifted roost and foraging sites without maintaining stable home ranges (Zhang 2025). Most adult white ibis tracked for at least two years returned to their original capture site in subsequent breeding seasons, suggesting strong breeding site philopatry in this population, particularly within 2–4-year intervals. These data coupled with long-term observations of regional shifts in breeding distribution in this species support the hypothesis that white ibis are not uniformly nomadic from year-to-year. Instead, this species may function as facultative irruptive nomads over longer timescales, dispersing in response to large spatial-scale environmental conditions (e.g., Frederick et al. 1996). Philopatric behavior in this population appears to be shaped in part by intrinsic traits associated with breeding competition and sexual selection, implying that site fidelity may offer competitive advantages for breeding adults. Consequently, nomadism may be the exception when local breeding conditions are favorable but may become more common when local-scale habitat and environmental conditions fall below critical thresholds. This aligns with long-term colony monitoring, which has documented large fluctuations in breeding numbers across years (Ogden 1994, Keeler 1956, Dusi and Dusi 1987, Shepherd et al. 1991, Capitolo et al. 2023). Such variability may stem from density-dependent factors, such as competition for food or nest sites, that influence the benefits of remaining site-faithful (Cocoves et al. 2021). While some colonies have hosted breeding ibis continuously for

over two decades (Frederick et al. 1996), the average colony lifespan is closer to 10 years, with shorter durations more common in larger colonies. Due to the limitations of earlier band-resight data, it has remained unclear whether the same individual marked white ibis returned to breeding sites across years. Our work using satellite telemetry shows that many adult white ibis do exhibit multi-year fidelity to colony sites, at least when environmental conditions remain sufficiently favorable.

Philopatric behavior varied considerably by age-at-capture. Philopatry was relatively rare among tagged juveniles but far more common among tagged adults. Notably, juvenile-tagged individuals tended to only return to coastal Alabama upon reaching adulthood. Therefore, many juvenile-tagged ibis that survived into their second year but were not considered philopatric may have displayed philopatric behavior had they actually survived to reach the adult age-class. From an ecological perspective, these patterns highlight the potential importance of maintaining stable local habitat conditions for adult white ibis, independent of where they were hatched. If adult white ibis consistently return to previously used colonies, even when hatched elsewhere, the continued availability of local breeding and foraging habitat could play a critical role in sustaining multi-year site fidelity. Maintaining these conditions may, in turn, support reproductive success and colony persistence over time.

White ibis exhibited pronounced ontogenetic shifts in movement patterns and space use. Individuals tagged after fledging tended not to return to the capture region until adulthood, and their early life stages were marked by broad regional movements. This behavior is likely consistent with exploratory dispersal (Yu et al. 2010), during which young birds may sample a wide array of potential breeding and foraging habitats across the southeastern U.S. Such exploration may confer adaptive benefits (Paradis et al. 1998) by allowing individuals to assess habitat quality and build a repertoire of suitable locations for future reproduction. Dispersal in early life could also be influenced by age-based competition, in which juveniles or subadults move away from breeding colonies to avoid displacement or exclusion by older, more competitive conspecifics. In either case, these patterns imply that survival during the post-fledging period and early dispersal phase may depend on a broader network of suitable habitats well beyond the region in which a bird was hatched. If increasing survival among younger age classes becomes a management priority, environmental conditions prior to fledging and the quality of out-of-region habitats may represent key areas of focus.

While coastal Alabama served as a consistent focal point for many philopatric individuals, several regions away from the capture site were also used extensively. These areas likely play important roles in the seasonal ecology of this white ibis population. Notably, coastal Louisiana, the Atchafalaya Basin, the Tampa Bay region of Florida, coastal Mississippi, and the Pensacola River basin emerged as recurrent areas of space use by our marked sample. These regions may serve as important non-breeding or migratory habitats and these areas appear to support movements and/or settlement of ibis returning to coastal Alabama. The presence of home ranges spanning multiple states highlights the extent to which this population utilizes a regional network of wetlands (Lang et al. 2024). This highlights the value of coordinating across stakeholders for habitat protection and conservation efforts across the southeastern U.S.

We found that intrinsic traits such as body mass and sex were associated with variation in Euclidean displacement from the capture site. Lighter individuals dispersed farther, with this dispersal pattern particularly pronounced in males. This trend is consistent with strong male–male competition, where larger males may gain better access to mates or nesting sites through direct contest (Frederick 1986, 1987b; Babbitt and Frederick 2007). Body mass and culmen length have been shown to play key roles in these contests (Frederick 1987a, 1987b; Heath et al. 2020), supporting the idea that body condition influences spatial distribution associated with movement behaviors. Notably, male white ibis dispersed farther, on average, than females regardless of mass, and the relationship between mass and displacement was stronger for males, suggesting that competition may be more intense among males. Male-biased dispersal is uncommon among birds but has been reported in some waterbirds (Peters et al. 2012, Li and Kokko 2019). In many bird species, male philopatry is favored by territory-based competition, while female-biased dispersal is more common in species where mating competition is less direct (Greenwood 1980). The pronounced sexual size dimorphism in white ibis (Bildstein 1993), in which females are 74% the mass and 78% the bill length of males (Kushlan 1977b), suggests that sexual selection may have acted more strongly on males. While it is possible that mate choice contributes to these patterns, current evidence points more strongly to male–male competition as the driving force. Because females are typically the limiting sex in population growth models, understanding the spatial patterns of female movement has implications for long-term population dynamics. Female white ibis in this study exhibited shorter displacement distances than males, suggesting females may be more reliant on areas near the capture location. If improving female

survival is a conservation priority, maintaining the quality and availability of habitat in and near core breeding areas could support that goal. Meanwhile, the observed behavioral flexibility among individuals, many of whom alternated among philopatry, and dispersal across years, highlights the behavioral plasticity of this species and its ability to respond dynamic environmental conditions. While philopatry was prevalent, nearly half of the individuals tracked for at least two years displayed non-philopatric behavior in at least one year, suggesting that movement strategies are plastic and context dependent. This behavioral flexibility likely enhances individual fitness and may buffer populations against localized environmental disturbances (Kushlan 1979, Martin et al. 2012, Herring and Gawlik 2013).

Seasonal movement patterns of white ibis in the northern Gulf region suggest strong seasonal plasticity in habitat use, consistent with partial migratory behavior. During the breeding season, birds expanded into more northerly and inland areas, likely exploiting seasonal wetland productivity in floodplains and agricultural landscapes. Use of expansive systems like the Atchafalaya Basin and upper Mississippi Delta may reflect some combination of high foraging efficiency and seasonal resource pulses at or immediately adjacent to these sites (e.g., Binkley et al. 2019). In contrast, non-breeding ranges were more concentrated in southerly coastal areas, particularly in Florida and along the Gulf Coast proper. This southward shift aligns with expectations for winter habitat selection in this species, which tends to favor more stable hydrologic conditions and less seasonally variable wetlands during the non-breeding period. The repeated use of coastal areas such as Alabama and Mississippi across both seasons underscores the importance of these habitats as year-round resources for some individuals. These findings highlight the importance of considering both seasonal dynamics and regional habitat heterogeneity when planning conservation actions for wide-ranging wetland-dependent birds. While inland floodplains may support breeding efforts during high water years, coastal wetlands provide essential overwintering habitat and should remain a focus for habitat protection and restoration.

This study fills a critical gap in our understanding of white ibis demography and life history (Frederick et al. 1996, Cezilly 1997). Past research has analyzed survival in captivity and before fledging (Adams and Frederick 2009, Frederick et al. 2011), but the species' long-distance movements and nomadic behavior have precluded estimation of survival using traditional banding and mark-recapture techniques (Bildstein 1993, Frederick et al. 1996, Melvin

et al. 1999, Frederick 2002). We provide the first estimates of post-fledge annual survival for free-ranging American white ibis.

White ibis apparent survival increased with age, and the variation about survival estimates declined with age. This is common for long-lived species that exhibit delayed sexual maturity (Hafner et al. 1998). Low juvenile survival is a well-documented phenomenon in birds and is sometimes underestimated due to natal dispersal (Beauchamp 2023). However, in this study, dispersal-related declines in detection can be definitively ruled out, as transmitter-based known-fate models assume perfect detection regardless of dispersal distance. Nevertheless, this behavior may still contribute to decreased juvenile survival. Natal dispersal is energetically costly and exposes individuals to potentially unsuitable habitat, increasing their risk of mortality even when detection probability remains unaffected (Bonte et al. 2012). Compared to older individuals, juveniles may also be less effective at both locating and capturing prey in short hydroperiod wetlands, which tend to be highly variable and unpredictable. Ibis possess several adaptations that are likely to facilitate efficient foraging, including memory and reliance on environmental cues; these qualities may improve with age (Beauchamp and Heeb 2001, Ward and Zahavi 1973, Delgado et al. 2009, Bracis et al. 2015, Davies et al. 2024). Juveniles, lacking the memory and experience of older birds, may be unable to consistently acquire prey as efficiently or proficiently as adults (Bildstein 1993, Hand et al. 2010). High energetic costs of dispersal, limited experience, and competition with older conspecifics may explain the heightened juvenile mortality observed in this study.

CONCLUSIONS

Wading birds from different breeding colonies varied in their foraging habitats but frequently overlapped at several key sites. These included privately owned wetlands near Heron Bay, Grand Bay National Wildlife Refuge, and a shellfish processing facility on the mainland. Use of the shellfish facility was especially common among ibis from multiple colonies, suggesting it serves as a strong attractant. The net effect of this site on breeding ibis remains uncertain. Potential drawbacks include low-quality food, increased disease risk, and overreliance on a single foraging resource, while potential benefits include a highly predictable food supply during the breeding season, which could be particularly beneficial for breeding ibis. One notable exception to these patterns were ibis from the Gaillard Island colony, which is consistently the

most populated ibis breeding colony in coastal Alabama. These birds foraged primarily at or near the island, with relatively few long-distance movements to the mainland, indicating that local habitat conditions at Gaillard Island may be particularly influential for the breeding success of this group. Conversely, tricolored herons' foraging habitat was primarily centered on herbaceous wetlands near Heron Bay and Grand Bay National Wildlife Refuge. Tricolored herons focused foraging in these areas, regardless of which breeding colony they used.

In the non-breeding season, white ibis used similar habitat types as during the breeding season. However, unlike tricolored herons, white ibis did not remain primarily in coastal areas, rather many moved farther inland occupying more freshwater wetlands and terrestrial upland habitats. This subsequently reduced their selection ratio for protected land, as much of the inland habitat they used consisted of human-developed areas, including residential zones, associated water bodies, and grasslands. This does not suggest that protected areas are unimportant for the species; rather, it suggests that white ibis use a wider range of resources and may be more resilient to environmental disturbances that are geographically narrow. During the non-breeding season, tricolored herons were considerably more habitat-specialized than white ibis, with colony-level variation in land cover use but an overall reliance on emergent herbaceous wetlands and a small number of high-quality protected or privately-owned sites. In contrast, while wetlands still represented the dominant land cover for white ibis, woody wetlands were proportionately more common, and they used a broader array of habitats, including developed areas and uplands, to a much greater extent.

White ibis tended to remain within the southeastern United States year-round but ranged widely within this region. In contrast, tricolored herons traveled to multiple countries during the non-breeding season but used a more limited suite of sites within the U.S. From a management perspective, interjurisdictional coordination would likely be important for conserving both species, but international coordination is likely to be far more relevant for tricolored herons than for white ibis. Survival estimates also suggest different levels of confidence in interpreting population status between the two species. For tricolored herons, annual survival estimates were extremely low irrespective of age, and if taken at face value, this is indicative of a precipitous population decline. However, the apparent survival estimates for tricolored herons should be interpreted with caution given that weather-related events (e.g., hurricane frequency) during the study period likely contributed to lower apparent survival. In contrast, survival estimates for our

sample of marked white ibis appeared more consistent with known life-history patterns, suggesting a higher degree of confidence in estimates we obtained during this study.

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APPENDIX A

Bird identifier, capture age, tracking history, and sample sizes for tricolored herons captured at breeding colonies in coastal Alabama 2020-2022*.

ID	Capture Age	Track Start	Track End	Breeding Season	Migration Strategy	Migration Timing	Non-breeding Season	Survival
T23089	juvenile	6/21/20	9/22/20	N	Y	N	Y	Y
T23091	juvenile	6/21/20	11/18/21	N	Y	Y	Y	Y
T23092	juvenile	6/22/20	5/18/21	N	Y	N	Y	Y
T23096	juvenile	7/6/20	9/26/20	N	Y	Y	Y	Y
T23289	juvenile	6/11/20	11/27/20	N	Y	Y	Y	Y
T23291	juvenile	6/12/20	8/23/20	N	Y	Y	Y	Y
T23292	juvenile	6/20/20	8/24/20	N	Y	Y	Y	Y
T23293	juvenile	6/13/20	7/31/20	N	N	N	N	Y
T23295	juvenile	6/13/20	10/26/20	N	Y	Y	Y	Y
T23296	juvenile	6/14/20	11/12/20	N	Y	Y	Y	Y
T23297	juvenile	6/21/20	9/23/20	N	Y	Y	Y	Y
T23298	juvenile	6/18/20	12/11/20	N	Y	Y	Y	Y
T23300	juvenile	6/20/20	10/8/20	N	Y	Y	Y	Y
T23392	juvenile	5/30/20	6/5/20	N	N	N	N	N
T23394	juvenile	5/31/20	9/19/20	N	N	N	N	Y
T23395	juvenile	5/31/20	9/21/20	N	Y	N	Y	Y
T23400	juvenile	6/5/20	10/28/20	N	Y	Y	Y	Y
T23099	juvenile	6/10/21	9/14/22	Y	Y	N	Y	Y
T06552	juvenile	6/14/21	9/6/21	N	Y	Y	Y	Y
T23100	juvenile	6/14/21	10/19/21	N	Y	Y	Y	Y
T06554	juvenile	6/15/21	6/18/21	N	N	N	N	N
T06555	juvenile	6/15/21	6/17/21	N	N	N	N	N
T06553	juvenile	6/15/21	8/8/22	Y	Y	N	Y	Y
T06556	juvenile	6/16/21	5/4/22	N	Y	Y	Y	Y
T06559	juvenile	6/17/21	6/20/21	N	N	N	N	N
T06562	juvenile	6/23/21	3/28/22	N	Y	Y	Y	Y
T06561	juvenile	6/23/21	12/9/21	N	Y	Y	Y	Y
T06572	juvenile	6/25/21	11/20/21	Y	Y	Y	Y	Y
T06573	juvenile	6/26/21	6/29/21	N	N	N	N	N
T23094	adult	6/27/20	12/14/20	N	Y	N	Y	Y
T23098	adult	6/9/21	7/16/21	N	N	N	N	Y
T06551	adult	6/14/21	2/20/24	Y	Y	N	Y	Y
T06557	adult	6/17/21	11/20/21	N	Y	Y	Y	Y
T06560	adult	6/17/21	7/10/24	Y	Y	N	Y	Y
T06566	adult	6/24/21	8/30/22	N	Y	Y	Y	Y
T06567	adult	6/24/21	10/20/21	N	Y	Y	Y	Y
T06571	adult	6/25/21	1/14/22	N	Y	Y	Y	Y
T06576	adult	6/30/21	5/1/22	N	Y	Y	Y	Y
T06577	adult	6/30/21	4/12/22	N	Y	Y	Y	Y
T06583	adult	7/7/21	2/11/22	Y	Y	Y	Y	Y
T06585	adult	5/29/22	4/16/23	Y	Y	Y	Y	Y
T06589	adult	6/3/22	10/9/22	Y	Y	Y	Y	Y
T06592	adult	6/7/22	1/18/24	Y	Y	N	Y	Y
T06591	adult	6/7/22	7/10/24	Y	Y	N	Y	Y
T06596	adult	6/11/22	11/12/22	Y	Y	Y	Y	Y
T34232	adult	6/14/22	10/4/22	Y	Y	Y	Y	Y
T34233	adult	6/14/22	11/15/22	Y	Y	Y	Y	Y
T34237	adult	6/18/22	10/20/22	N	Y	Y	Y	Y
T34240	adult	6/20/22	12/23/22	Y	Y	Y	Y	Y
T34242	adult	6/21/22	7/10/24	Y	Y	N	Y	Y
Total				15	42	31	42	45

*****To avoid excessively long column names, shorter names are used in the Appendix to correspond to the full topic titles in the report. Each row represents information for one bird individual, and the "Total" row indicates the number of birds included in each analysis. "Track Start" and "Track End" indicate the beginning and end of data transmission by the platform terminal transmitters (PTT). "Y" indicates that the bird was included in the analysis, while "N" indicates it was not. Specifically, Breeding Season corresponds to Daily Movements and Habitat Use During the Breeding Season; Migration Strategy corresponds to Seasonal Movements from Breeding Colonies to Wintering Areas; Migration Timing corresponds to the Migration Timeline Figures; Non-breeding Season corresponds to Daily Movements and Habitat Use During the Non-Breeding Season; and Survival corresponds to Annual Survival Estimates.

APPENDIX B

Bird identifier, capture age, tracking history, and sample sizes for white ibis captured at breeding colonies in coastal Alabama 2020-2022*.

ID	Capture Age	Track Start	Track End	BD	HR	JJ	JS	JA	SA	LB	LN	ED	NB	S
W22301	juvenile	5/25/20	9/19/23	Y	N	Y	Y	Y	N	Y	Y	Y	Y	Y
W22304	juvenile	6/1/20	8/26/20	N	N	Y	N	N	N	Y	Y	Y	Y	Y
W22305	juvenile	6/1/20	10/4/20	N	N	Y	N	N	N	Y	Y	Y	Y	Y
W22307	juvenile	6/4/20	11/13/20	N	N	Y	N	N	N	Y	Y	Y	Y	Y
W22308	juvenile	6/4/20	7/16/20	N	N	Y	N	N	N	Y	N	N	N	Y
W22310	juvenile	6/4/20	11/13/20	N	N	Y	N	N	N	Y	Y	Y	Y	Y
W22311	juvenile	6/5/20	8/21/20	N	N	N	N	N	N	N	N	N	N	Y
W22313	juvenile	6/11/20	7/7/20	Y	N	Y	N	N	N	Y	N	Y	N	Y
W22314	juvenile	6/11/20	4/3/21	N	N	Y	N	N	N	Y	Y	Y	Y	Y
W22315	juvenile	6/12/20	12/12/20	N	N	Y	N	N	N	N	Y	Y	Y	Y
W22316	juvenile	6/14/20	8/16/20	N	N	Y	N	N	N	Y	Y	Y	N	Y
W22317	juvenile	6/18/20	12/24/23	N	Y	Y	Y	Y	N	Y	Y	Y	Y	Y
W22318	juvenile	6/18/20	7/30/24	N	N	Y	Y	Y	N	Y	Y	Y	Y	Y
W22319	juvenile	6/19/20	8/16/20	N	N	N	N	N	N	N	N	N	N	N
W22320	juvenile	6/19/20	12/23/20	N	N	Y	N	N	N	N	Y	Y	Y	Y
W22321	juvenile	6/19/20	7/28/24	N	N	N	N	N	N	N	N	N	Y	Y
W22347	juvenile	6/4/21	7/30/24	N	N	Y	Y	Y	N	Y	Y	Y	Y	Y
W08101	juvenile	6/10/21	12/9/21	Y	N	Y	N	N	N	N	Y	Y	Y	Y
W08103	juvenile	6/10/21	10/23/23	Y	N	Y	Y	Y	N	Y	Y	Y	Y	Y
W08104	juvenile	6/15/21	12/20/21	N	N	Y	N	N	N	N	Y	Y	Y	Y
W08105	juvenile	6/17/21	12/13/21	Y	N	Y	N	N	N	Y	Y	Y	Y	Y
W08107	juvenile	6/17/21	12/21/21	N	N	Y	N	N	N	N	Y	Y	Y	Y
W08108	juvenile	6/20/21	6/19/22	N	N	Y	Y	N	N	Y	Y	Y	Y	Y
W08109	juvenile	6/24/21	9/30/23	Y	Y	Y	Y	Y	N	Y	Y	Y	Y	Y
W08114	juvenile	6/29/21	2/16/23	N	N	N	N	N	N	N	N	N	N	N
W08147	juvenile	7/6/22	1/1/23	Y	N	Y	N	N	N	N	Y	Y	Y	Y
W08146	juvenile	7/6/22	7/9/22	N	N	N	N	N	N	N	N	N	N	N
W08148	juvenile	7/6/22	8/8/22	N	N	N	N	N	N	N	N	Y	N	Y
W08150	juvenile	7/6/22	11/19/22	Y	N	Y	N	N	N	Y	Y	Y	Y	Y
W22332	sub-adult	7/6/20	10/26/20	N	N	N	N	N	N	N	N	N	Y	N
W22335	sub-adult	5/30/21	7/30/24	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
W22336	sub-adult	5/30/21	6/18/22	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
W22337	sub-adult	5/30/21	6/17/21	N	N	N	N	N	N	N	N	N	N	N
W22339	sub-adult	5/31/21	8/8/21	N	N	N	N	N	Y	Y	Y	N	N	Y
W22341	sub-adult	5/31/21	6/1/23	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
W22349	sub-adult	6/7/21	8/30/21	N	N	N	N	N	Y	Y	Y	N	Y	Y
W08111	sub-adult	6/29/21	9/20/23	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
W08112	sub-adult	6/29/21	10/6/23	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
W08139	sub-adult	6/25/22	6/27/22	N	N	N	N	N	N	N	N	N	Y	N
W22326	adult	6/29/20	3/30/23	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
W22327	adult	6/29/20	7/30/24	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
W22331	adult	7/6/20	8/12/22	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
W22334	adult	5/28/21	1/5/24	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
W08113	adult	6/29/21	7/31/24	Y	Y	N	N	N	Y	Y	Y	Y	N	Y
W08115	adult	6/29/21	7/31/24	Y	N	N	N	N	Y	Y	Y	Y	Y	Y
W08130	adult	6/3/22	7/31/24	N	N	N	N	N	Y	Y	Y	Y	Y	Y
W08135	adult	6/13/22	7/31/24	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
W08136	adult	6/16/22	7/31/24	N	N	N	N	N	Y	Y	Y	Y	Y	Y
W08144	adult	6/30/22	11/12/23	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
W08145	adult	7/2/22	12/17/23	Y	Y	N	N	N	Y	Y	Y	Y	Y	Y
Total				22	15	23	7	6	18	35	39	39	39	44

*****To avoid excessively long column names, abbreviations are used in the appendix to match the full topic titles in the report. Each row represents information for one bird individual, and the "Total" row indicates the number of birds included in each analysis. "Track Start" and "Track End" indicate the beginning and end of data transmission by the platform terminal transmitters (PTT). "Y" indicates that the bird was included in the analysis, while "N" indicates it was not. In this table, BD refers to breeding season daily movement plots; HR to philopatric home ranges; JJ, JS, and JA to plots showing locations of white ibis tagged as juveniles during their first, second, and third year after capture; SA to plots of locations for birds tagged after their hatch year (including subadults and adults); LB to breeding season location plots; LN to seasonal movement plots of non-breeding season locations; ED to the model explaining Euclidean displacement from coastal Alabama breeding colonies; NB to non-breeding season daily movement and habitat use analyses; and S to annual survival estimates.

APPENDIX C

Products Associated with this Study

Dissertations

Gulick, Christopher. 2025. Dispersal, survival, and regional habitat use of the American white ibis. Ph.D. Dissertation, University of Florida, Gainesville, FL.

Zhang, Ke. 2025. Movement ecology of white ibises and tricolored herons in the Gulf of America and associated relationships with haemosporidian parasites. Ph.D. Dissertation, University of Florida, Gainesville, FL.

Presentations

Gulick, C. K., K. Zhang, and A. N. Powell. 2025. How important are rare irruptive breeding events for a population of nomadic wading birds? The Waterbird Society Annual Meeting, Traverse City, Michigan.

Zhang, K., C. Gulick, and A. N. Powell. 2025. Movement ecology of Tricolored Herons shows mixed migration strategies. The Waterbird Society Annual Conference, Traverse City, Michigan.

Zhang, K., C. K. Gulick, and A. N. Powell. 2025. Roosting and foraging dynamics of wading birds during the non-breeding season. American Ornithological Society, St. Louis, Missouri.

Zhang, K., C. K. Gulick, and A. N. Powell. 2025. Nomadic vs. Central Place Foraging: divergent movement strategies in White Ibis and Tricolored Heron across wetland habitats. Waterbirds Society Meeting, San Jose, Costa Rica.

Gulick, Christopher K., K. Zhang, and A. N. Powell. 2025. Sexually-selected traits drive dispersal in a purportedly nomadic wading bird. Waterbird Society Annual Meeting, San Jose, Costa Rica.

Powell, A. N., C. K. Gulick, and K. Zhang. 2024. Colonial wading bird tracking and habitat use assessment. DOI Internal Restoration Weekly Meeting Presentation (Virtual).

Gulick, C. K. and A. N. Powell. 2024. On the trail of a wetland wanderer: what we have learned from tracking white ibises across the Southeastern United States. Invited Talk: Alachua County Audubon, Gainesville, Florida.

Gulick, C. K. and A. N. Powell. 2024. Tracking a wetland wanderer: What can we learn from wading bird movements in the Southeastern US? Invited Talk: University of Miami Integrative Waterbird Biology Lab, Miami, Florida.

Gulick, C. K. and A. N. Powell. 2024. What can we learn from wading bird movements in the Southeastern US? Invited Talk: Angelo State University Bio Lunch, San Angelo, Texas.

Gulick, C. K. and A. N. Powell. 2024. Tracking waterbird movements and habitat use throughout Louisiana. Invited Talk: Louisiana Cooperative Fish and Wildlife Research Unit, Baton Rouge, Louisiana.

Gulick, C. K., K. Zhang, and A. N. Powell. 2023. Breeding season selection of anthropogenic resources varies across pre-breeding movement modes in the white ibis. American Ornithological Society Annual Meeting, London, Ontario.

Gulick, C. K., K. Zhang, and A. N. Powell. 2023. Breeding season selection of anthropogenic resources varies across age and pre-breeding movement modes in the American white ibis. Florida TWS, Jacksonville, Florida.

Gulick, C. K., K. Zhang, and A. N. Powell. 2023. What can spatial networks tell us about wading birds in the coastal Gulf of Mexico? Annual Meeting of The Waterbird Society, Ft. Lauderdale, Florida.

Zhang, Ke, C. K. Gulick, and A. N. Powell. 2023. Infection rates of avian malaria in white ibis and tricolored herons in the southeastern US. Annual Conference of the Waterbirds Society, Fort Lauderdale, Florida.

Zhang, K., C. K. Gulick, Z. S. White, K. Wilson, S. M. Wisely, and A. N. Powell. 2023. Haemosporidian parasites wading birds captured from breeding colonies in coastal Alabama. Annual Meeting, American Ornithological Society, London, Ontario.

Zhang, K., C. K. Gulick, Z. S. White, K. Wilson, S. M. Wisely, and A. N. Powell. 2023. Haemosporidian parasites on wading birds captured from breeding colonies in coastal Alabama. Wildlife Disease Association Annual Meeting, Athens, Georgia.

Zhang, K., C. K. Gulick, and A. N. Powell. 2023. Haemosporidian parasites in wading birds captured from breeding colonies in coastal Alabama. Florida TWS Meeting, Jacksonville, Florida.

Zhang, K., C. K. Gulick, and A. N. Powell. 2022. American white ibis and tricolored heron non-breeding utilization ranges in the Gulf of Mexico. 46th Annual meeting of the Waterbird Society, Corpus Christi, Texas.

Gulick, C. K., K. Zhang, and A. N. Powell. 2022. Breeding season selection of anthropogenic resources varies with age and movement modes in the American white ibis. 46th Annual meeting of the Waterbird Society, Corpus Christi, Texas.