Avian Behavior, Ecology, and Evolution

Interannual colony exchange among breeding Eastern Brown Pelicans

Intercambio interanual de colonias entre individuos reproductivos de Pelecanus occidentalis carolinensis

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ABSTRACT. Colonial seabirds often display high rates of interannual site fidelity to breeding locations, especially as adults. Species using more nearshore or coastal systems, however, may display comparatively less fidelity than highly pelagic species. We used long-term GPS tracking data to assess the frequency of interannual colony switching in Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) in the South Atlantic Bight, a species about which adult site fidelity is poorly understood. By using recursive behavioral patterns to identify nest locations, we report 36% of reproductive attempts occurred at colonies that were different from the colony used in a prior year. Colony switching was especially prevalent in female pelicans, and distances between switched colonies ranged from 56 to 592 km. We suggest that long-term telemetry may be a reliable tool for assessing interannual breeding site fidelity, especially when compared to more traditional band resighting efforts.

RESUMEN. Las aves marinas coloniales con frecuencia muestra una alta fidelidad interanual en la ubicación de la reproducción, especialmente como adultos. Las especies que usan sistemas cerca de la costa o costales, sin embargo, pueden mostrar comparativamente menor fidelidad que las especies pelágicas. Utilizamos datos de largo plazo de rastreadores GPS para determinar la frecuencia de cambio interanual de colonias por *Pelecanus occidentalis carolinensis* en la bahía del sur del atlántico, una especie sobre la cual la fidelidad de los adultos es poco entendida. Por medio del uso de patrones comportamentales recursivos, para identificar la ubicación de los nidos, reportamos que el 36% de los intentos de reproducción ocurrieron en colonias diferentes a las colonias utilizadas el año anterior. El intercambio de colonias fue especialmente prevalente en pelicanos hembra y las distancias entre las colonias tuvieron un rango entre 56 y 592 km. Sugerimos que la telemetría a largo plazo puede ser una herramienta confiable para determinar la fidelidad de sitios de reproducción interanual, especialmente cuando es comparada con métodos más tradicionales de anillamiento y reavistamiento.

Key Words: *colony fidelity; metapopulation; seabird; South Atlantic Bight; tracking*

INTRODUCTION
Fidelity to a breeding site, or the interannual return to the same general location by a reproductive individual, has traditionally been cited as one of the defining natural history characteristics of seabirds globally (Coulson 2001). Indeed, despite highly vagile capabilities seabirds tend to display limited inter-colony exchange of reproductive adults and this subsequently results in low rates of dispersal, i.e., the seabird paradox (Milot et al. 2008). Movement of breeding adults among colonies has been reported, however, especially among species that are more coastal or nearshore in nature, e.g., terns and gulls, as opposed to more pelagic species, e.g., albatrosses and shearwaters. For example, Fernández-Chacón et al. (2013) documented adult dispersal from one colony to another by reproductive-age Audouin's Gulls (*Ichthyaetus audouinii*) over a period of 10 years following a cumulative decline in habitat quality. Established breeders also relocate from older colonies to newer colonies in Black-legged Kittiwakes (*Rissa tridactyla*), despite site fidelity being generally high in this species (Kildaw et al. 2005). Spendelow et al. (1995) describe the presence of regular inter-colony movements among a metapopulation of adult Roseate Terns (*Sterna dougallii*) in the Northwest Atlantic, possibly as a result of active habitat selection during the pre-breeding period. Similarly, Breton et al. (2014) documented movements of adult Common Terns (*Sterna*

hirundo) between colonies in the same region. Unexpectedly, colony-level dispersal increased with age in this metapopulation, with the odds of a tern changing breeding colonies between reproductive attempts increasing with age (Breton et al. 2014). Although the mechanisms behind colony switching remain unclear, resource tracking precipitated by limitations in foraging range or the relative instability of nearshore habitats have been hypothesized to contribute to the presence of switching in species using coastal habitats (Spendelow et al. 1995).

Assessing breeding site fidelity typically has been undertaken using long-term banding records and/or capture-mark-recapture methodologies (e.g., Breton et al. 2014). Determining rates of inter-colony movement using band resighting techniques, however, requires adequate observer coverage at all potential colony locations (Spendelow et al. 1995, Selman et al. 2012). For seabirds that may have widely-dispersed breeding colonies spanning large ranges, or where the nesting habitat is highly dynamic or difficult to visually survey for bands, e.g., barrier or estuarine islands with low topographic relief and high vegetation, this may serve to be a significant logistical challenge (Spendelow et al. 1995). With the advancement of satellite tracking technology, however, it is now possible to monitor individual birds over the course of multiple breeding seasons with high spatial and

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Table 1. Colony locations within the South Atlantic Bight and sample sizes for adult Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) tracked with GPS satellite transmitters in South Carolina (SC) and Georgia (GA), USA.

Colony	Marsh Island, SC	Castle Pinckney, SC	Bird Key Stono, SC	Deveaux Bank, SC	Little Egg Bar, GA	Bird Island, GA
Latitude	32.9894	32.7742	32.6326	32.5461	31.3074	31.1132
Longitude	-79.5534	-79.9107	-79.9827	-80.1933	-81.2709	-81.4356
Colony Area (ha)	15	9	11	81	78	6
No. of GPS Deployments	7	20	25	23	5	6
No. of Birds Tracked > 1 Year	4	2	5	5	2	2
Males / Females	4 / 0	0 / 2	2 / 3	0 / 5	0 / 2	0 / 2
No. of Colony Switches	0	1	3	2	2	0

temporal precision, eliminating issues of observer effort underpinning band resighting approaches (e.g., Selman et al. 2012). Uncovering basic life-history traits, such as breeding site fidelity, is critical for establishing ecological baselines and subsequently assessing how potential threats, e.g., tropical storms, human disturbance, oil spills, etc., affect nearshore seabirds.

The Eastern Brown Pelican (*Pelecanus occidentalis carolinensis*) is a large nearshore seabird inhabiting a geographically expansive breeding range from tropical to temperate coasts of the western North Atlantic (Shields 2020). Core breeding areas include the northern Gulf of Mexico and the mid- and southern-portion of the Atlantic coast of the United States (Shields 2020). Despite relatively extensive banding efforts in both regions, especially of chicks, significant data gaps remain concerning colony dynamics and interannual movements of both juveniles and adults (Schreiber and Mock 1988, Jodice et al. 2007). The goal of the current study was to leverage long-term telemetry data of adult pelicans tagged in the U.S. South Atlantic Bight (the coastal area approximately between the Cape Fear River and Cape Canaveral; Michel 2013) to inform breeding site fidelity in the species. To do so we used daily movements collected across multiple breeding seasons to identify likely nest locations based on patterns of recursive behavior, and matched these locations to known pelican colony sites. Determining the prevalence of colony-level exchange of breeding adults has important implications for the management and conservation of Brown Pelicans because it is difficult to place colony-specific trends of abundance into a broader regional context without key demographic parameters (Jodice et al. 2007).

METHODS
Field research was undertaken with permission from the Clemson University Animal Care and Use Committee (#2017-008). Permitting for data collection was provided by the U.S. Geological Survey Bird Banding Lab (#22408), South Carolina Department of Natural Resources (BB-18-22), and Georgia Department of Natural Resources (#1001056923).

Adult Brown Pelicans (n = 86) were outfitted with solar-powered GPS-PTT transmitters (GeoTrak Inc., North Carolina, USA) during the reproductive periods (May–August) of 2017–2020 on six breeding colonies in the South Atlantic Bight (Table 1). Transmitters (65 g; 10 x 3.5 x 3 cm) were attached dorsally to adult pelicans during either late incubation or early chick-rearing using a backpack-style harness system constructed of Teflon ribbon. Adults were captured during early morning hours at the nest via

either a neck or leg lasso, fit with a transmitter, and had morphological measurements taken before being released approximately 50 m from the nest site (handling time ≤ 20 mins). Transmitters constituted 3% body mass of outfitted adults (range = 2475–4350 g), and were programmed to record 12 GPS positional fixes per day at 90 min intervals between the hours of 10:00 and 02:30 GMT during the breeding season. For additional details on specific deployment methodology see Lamb et al. (2017a). Unit error was assumed to approximate that of Lamb et al. (2017b), i.e., 4.03 ± 2.79 m. During capture, 3–4 body feathers were also collected dorsally above the uropygial gland for individual sexing. DNA was extracted from feathers and developed via PCR (Animal Genetics Inc., Florida, USA).

To assess colony fidelity on an interannual basis, only pelicans that were tracked for > 1 reproductive period were included in the analysis (n = 20). We further restricted data analysis to those movements that occurred from 1 May–31 July, corresponding to the approximate periods of incubation and chick-rearing in this population (Sachs and Jodice 2009). Tracks were visually assessed for erroneous locations, i.e., implausible relocations rapidly occurring hundreds of km away, using the Movebank system (Kranstauber et al. 2011).

Individual nesting sites were identified during each reproductive period, i.e., year, using the "find_nests" function in the R package *nestR* (Picardi et al. 2021). This function uses quantifiable patterns of recursive behavior found in bird-bourne telemetry data, together with user-provided ecological knowledge of the study species, to identify likely nest locations (Fig. 1; Picardi et al. 2020). Specifically, input parameters are chosen based on the known nesting ecology of the species for which potential nests are to be located. For Brown Pelicans, we constrained the nesting period to begin 1 May and terminate 31 July during each year of the study. We chose a nesting period of 90 days, matching the approximate length of incubation and chick-rearing in this species (Shields 2020). The function was set to search for return points within a 250 m buffer around each relocation, i.e., all points within the buffer surrounding a given location would count as recursive movements to that original point. We chose a relatively wide buffer compared to the assumed spatial error of the GPS unit to account for the potential movement of pelican chicks away from the exact nest site as they aged and roamed the colony. Beginning at approximately 21 days of age, young pelicans begin to form creches that may be > 10 m away from the nest of any individual chick (Sachs and Jodice 2009). As such, provisioning adults may not return to the nest per se, but instead deliver meals to the chick

Fig. 1. Example tracks of individual Eastern Brown Pelicans (*Pelecanus occidentalis carolinensis*) displaying likely breeding movements at two colonies in the South Atlantic Bight. (A) illustrates likely breeding movements of an individual at Little Egg Bar, Georgia, USA, which was outfitted with a GPS transmitter the prior year while on a nest at Bird Key Stono, South Carolina, USA. (B) illustrates likely breeding movements of an individual at Castle Pinckney, South Carolina, USA, which was outfitted with a GPS transmitter the prior year while on a nest at Little Egg Bar, Georgia, USA. (C) and (D) depict the relative locations of Little Egg Bar and Castle Pinckney, respectively.
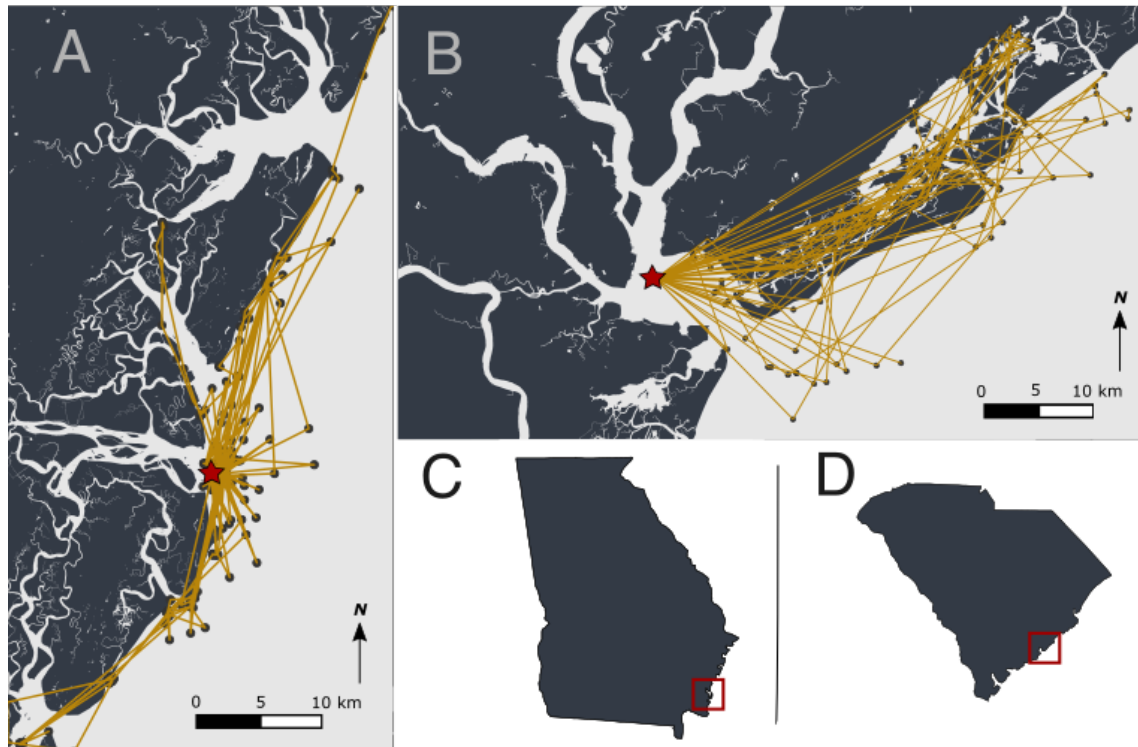
within the formed creche, which may also be mobile in nature. In addition, we chose a buffer of 250 m to more appropriately match the aims of the study, i.e., to determine fidelity to colony location, not nest site. The minimum number of relocations required to occur within the 250 m buffer to be identified as a possible nest location was set to 10, and a possible nest location had to be visited for at least five consecutive days to be further considered. If an individual had ≤ 5 relocations on a day, e.g., because of equipment failures, and none of the recorded points occurred within the buffer of a possible nest location, that day would not count as a break in consecutive visitation days as the odds of the bird visiting the nest but the visit not being recorded were significantly increased. Finally, at least 50% of relocations had to occur within the buffer on the day with the most number of visits to the possible nest location, and at least 25% of days had to include at least one visit to the possible nest location between the first and last day of use. Overall, parameter selection was based on an informal assessment of attendance patterns with the goal of reducing the likelihood of incorrectly identifying a location as a nesting site when in fact a pelican may have only been using the site transiently, e.g., a pelican visiting a site but not nesting. We then applied these parameters to the tracks of each individual pelican occurring within each reproductive period for which spatial data were collected.

Because pelicans are strictly colonial nesters, the spatial output of the nest finding function was compared to known pelican colony locations using the Seabird Colony Registry and Atlas for the Southeastern United States (Ferguson et al. 2018) and the Florida Fish and Wildlife Conservation Commission Historic Waterbird Colony Locator (Florida Fish and Wildlife Research Institute 2021). Possible nest locations identified from the "find_nests" function that were not spatially matched to a known pelican breeding colony were not considered to represent nest attempts in further analyses. In addition to nesting colonially, post-breeding pelicans tend to loaf and roost colonially on favored islands, which may themselves be breeding colonies (Schreiber and Schreiber 1982). Particularly if a reproductive attempt fails early, adult pelicans may disperse to another colony for the remainder of the breeding season. Despite these movements, there is scant evidence that pelicans will attempt to breed again on another colony within the same year following dispersal under normal conditions (Shields 2020). However, Walter et al. (2014) documented adult pelicans re-nesting at different colonies following initial nest abandonment associated with capture and GPS tagging, i.e., possible researcher disturbance. As such, we considered the first possible nest location that occurred at a known pelican colony per breeding season to represent a known breeding attempt; possible nest locations

occurring at known pelican colony locations later in the season, e.g., late June or July, were not considered to represent reproductive dispersal events although it is possible pelicans did attempt to breed. In addition, although we cannot conclusively reject the possibility that nest locations identified using the aforementioned methods did not result instead from an adult pelican socially attending a known colony for the duration of the reproductive period without breeding, as may occur in prospecting immatures (Shields 2020), we assume this behavior is rare in adult individuals and that identified nest locations corresponded to genuine reproductive attempts. If there were no possible nests identified in a given season for an individual pelican, or all possible nest locations identified did not correspond to a known colony location during a given season, we did not assign a nest location for that reproductive attempt.

RESULTS

We tracked $n = 18$ adult pelicans for two breeding seasons and $n = 2$ adult pelicans for three breeding seasons, representing 42 possible reproductive periods (Table 1). Because the colony location of the first breeding season was known, i.e., the location that the bird was captured, we evaluated the efficacy of the nest-finding algorithm using these data. Using the parameters stated, the "find_nests" function was able to correctly identify the breeding colony for 90% of known locations. The two cases for which the function failed to correctly identify a known colony location occurred as a result of insufficient data, as individuals either abandoned the nest or experienced nest failure within 7 days of tag deployment, or had a transmitter deployed comparatively late in the breeding season, e.g., mid-July.

Of the 20 individuals tracked across multiple reproductive periods, seven pelicans (35%) switched colonies during the year after capture. Ten adult pelicans (50%) returned to breed at the same colony where they were captured the previous year. Two pelicans were tracked for three breeding seasons. One nested at the original colony of capture in the third year of deployment after skipping reproduction in the second, i.e., it returned to the same colony of capture following a skipped breeding season, while the other relocated to a different colony during the second year before returning to the original colony of capture in the third, i.e., it returned to the colony of capture following a breeding season spent on a different colony. The remaining individual pelican was tracked for two seasons, but appeared to skip breeding in the second year, i.e., no possible nest locations were identified. In total, 55% of possible reproductive attempts occurred at the same colony of capture, 36% were at a different colony, and 9% were skipped completely.

For the eight pelicans that exhibited a relocation to a different breeding colony, the median distance moved was 191 km (range = 56–592 km). Correspondingly, six movements were between colonies located in different states, while the remaining two movements were between colonies located within the same state (Fig. 2). Although colony switching occurred in both sexes, more females switched colonies than did males (75% of switches were female). Females were also the only sex to skip a reproductive attempt entirely ($n = 2$).

Fig. 2. Map of Eastern Brown Pelican (*Pelecanus occidentalis carolinensis*) colonies within the South Atlantic Bight, USA. Arrows indicate the movement of adult pelicans from the colony of capture to a different colony in a subsequent reproductive season. Arrow thickness represents number of colony exchange (thin = 1, thick = 2). Inset map depicts the movement of an individual pelican from Deveaux Bank to Bird Island Florida outside of the South Atlantic Bight in the following breeding season. Colony marker size indicates approximate number of breeding pairs per season. Letters indicate colony name (MI = Marsh Island, CP = Castle Pinckney, BKS = Bird Key Stono, DB = Deveaux Bank, LEB = Little Egg Bar, BIG = Bird Island Georgia, BIF = Bird Island Florida).
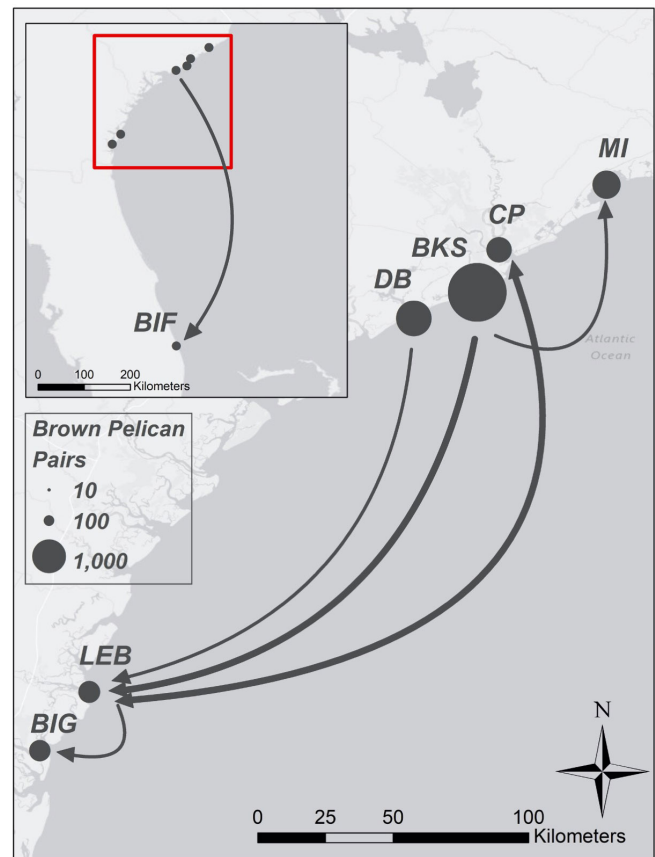
DISCUSSION

Multi-annual telemetry offers the capacity to follow individuals through multiple reproductive attempts. We leveraged this capacity to examine the occurrence of breeding site fidelity in the Eastern Brown Pelican, a species with unknown rates of intercolony exchange among reproductively active adults and one of high conservation interest in the southeastern United States (Jodice et al. 2007, 2019). Although a relatively small sample size, we provide evidence that adult pelicans may not return to the same colony to breed on an interannual basis, instead attempting

reproduction at colonies up to 600 km from the previous location. Our data also suggest that adult pelicans may skip reproduction during some years. This behavior was only detected in females in this study, which for long-lived seabirds may bear increased costs of reproduction compared to males (Cruz-Flores et al. 2021). If colony switching in consecutive years occurs regularly, in the absence of a strong population-level driver such as habitat degradation, e.g., island erosion, increased predation, or disturbance, then our concept of population structure for Eastern Brown Pelicans may need to focus more on meta-population dynamics than on individual colonies, and subsequently may warrant consideration of management actions at the regional as well as the local level.

Efforts to determine site fidelity in Brown Pelicans have historically focused on band resighting efforts of pre-breeding individuals to determine natal philopatry (Anderson 1983, Walter et al. 2013). In the northern Gulf of Mexico and along the Atlantic coast, resighting of young birds on natal islands in subsequent years seemed to indicate a high rate of natal philopatry in this species, and by extension the possibility of strong breeding site fidelity in adulthood (Walter et al. 2013). However, studies of natal philopatry typically included either low resighting rates, incomplete observer coverage, or both (Walter et al. 2013), none of which are surprising given the challenging logistics of resighting birds in these complex coastal systems. In contrast, Anderson (1983) noted the frequent dispersal and exchange of young pelicans in the Sea of Cortez among breeding colonies in the region. Importantly, the movement of adult populations were not examined in these earlier studies.

Selman et al. (2016) suggested the large-scale movement of breeding pelicans in coastal Louisiana from a given colony to another following dynamic coastal processes such as erosion. During our study, however, there were no substantial geomorphological changes to the islands that supported the colonies, i.e., island-wide subsidence, erosion, vegetation loss, or flooding as can occur to these islands (Jodice et al. 2007, Eggert 2012). Our findings instead suggest that there may be an active exchange of adult Brown Pelicans between colonies in the southeastern United States, especially within the South Atlantic Bight.

The decision to switch colonies could be influenced by many factors acting at levels below that of the colony, e.g., individual variation in tolerance to local disturbance, parasite loads, or predation. Another possible ecological driver may be density dependence. During this study, both Deveaux Bank and Bird Key Stono variously hosted the largest pelican colonies on the U.S. Atlantic coast (~2500–3000 pairs; Sanders et al. 2021, Wilkinson 2021). In contrast, frequent destinations for colony-switching pelicans (e.g., Little Egg Bar; $n = 3$) are considerably smaller (~400 pairs; Wilkinson 2021). We posit that the switching of adults away from large colonies may serve to limit colony size once the carrying capacity of the surrounding marine environment has been reached (sensu Lamb et al. 2017b), as neither island appears limited in nesting space, i.e., there appears to be adequate nesting habitat remaining on both islands despite the large number of pairs. Notably, we did not track any individuals switching to a colony of larger size; all colony switches were to colonies with either fewer or approximately equivalent numbers of breeding pairs.

Kildaw et al. (2005) describe colony-switching among established breeders of Black-legged Kittiwakes, and concluded that habitat quality was a larger driver of movement to new colonies than individual quality. Although the authors did not measure habitat quality directly, many of their proposed mechanisms involved density-dependent responses, e.g., prey abundance and accessibility, nest site suitability and availability, parasite loads, and disease transmission (Kildaw et al. 2005). We suggest that many of the same mechanisms may be operating in our study system as well. Importantly, Kildaw et al. (2005) note that for established breeders to relocate to a new colony, the realized habitat quality of the current colony should be lower than the apparent quality of the new location.

Researcher disturbance is another mechanism that may have driven some events of colony switching, particularly the capture and handling event and subsequent outfitting of the bird with a backpack transmitter. For example, Walter et al. (2014) found that a significant number of pelicans captured for GPS telemetry in Louisiana later abandoned their nest, and either re-nested on the same colony or relocated to a different colony within the same year. During our study, however, handling time was relatively brief (< 20 min compared to ~45 min in other reported studies) and all GPS units were below the recommended 3% body mass guideline for mitigating impacts to large seabirds. Using identical capture and handling techniques as well as identical transmitters and harnesses, Lamb et al. (2017a) found that most outfitted pelicans continued normal nesting behavior post-capture. For example, only 4% of instrumented pelicans renested on a different colony than the colony of capture during the same breeding season, while 88% continued to attend their original nest (Lamb et al. 2017a). The aforementioned study did not, however, assess capture and handling impacts across subsequent breeding seasons. Additionally, because unbiased rates of interannual colony fidelity in adults have yet to be assessed for this species, there does not exist a control group with which to estimate transmitter effects. Our data suggest that most individuals returned to the same colony of capture the following year to nest, indicating that if researcher disturbance occurred it was not systemic. We suggest that the colony switching we observed reflects genuine ecological decisions made by adult pelicans in colony choice while also acknowledging the possible contributions of capture and handling effects.

Our findings have important implications for how pelican populations are structured within this area. For example, Jodice et al. (2007) suggested immigration/emigration processes at both the state and regional levels as possible mechanisms explaining trends of Brown Pelican abundance in South Carolina. However, evidence for this was based on decreasing nest counts in South Carolina with concomitant increases in nest counts in places such as Georgia, not on documented movements of individuals. We detected frequent movement between these two states, with the highest number of movements involving birds either recruiting to or departing from Little Egg Bar in coastal Georgia from/to one of the four South Carolina colonies (Fig. 2). This study also further lends support for the management of pelicans, and possibly other coastal seabirds in the region, at scales larger than individual colonies or states. Such regional-scale management may be increasingly important as the effects of climate change have the potential to alter the structure of current pelican colonies and shift population dynamics.

Results presented here suggest that future studies of Brown Pelican demography in the South Atlantic Bight might benefit from the consideration of including the possibility of adult exchange between colonies in model parameters. In addition, when considered as samplers of the marine environment, adult pelicans may not reflect a lifetime spent breeding in the same location. This has important implications in ecological research as well, for example, in contaminant studies, and may help explain why contaminant loads are frequently homogenous among individuals sampled on different colonies within the same region (Newtoff and Emslie 2017, Lamb et al. 2020, Wilkinson et al. 2022). For large avian species, the use of multi-annual tracking may represent a robust method for assessing site fidelity and dispersal when undertaken responsibly.

Responses to this article can be read online at:
https://journal.afonet.org/issues/responses.php/74

Data Availability:

Data generated during this study are available as a USGS data release (Wilkinson and Jodice 2022; https://doi.org/10.5066/P9BZ5TL9).

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