ARTICLE

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Support for the fasting endurance hypothesis of partial migration in a nearshore seabird

Bradley P. Wilkinson[1] ![ORCID] | **Patrick G. R. Jodice**[2]

[1]Department of Forestry and Environmental Conservation, South Carolina Cooperative Fish and Wildlife Research Unit, Clemson University, Clemson, South Carolina, USA

[2]U.S. Geological Survey South Carolina Cooperative Fish and Wildlife Research Unit, Department of Forestry and Environmental Conservation, Clemson University, Clemson, South Carolina, USA

Correspondence
Bradley P. Wilkinson
Email: bradley.wilkinson@duke.edu

Present address
Bradley P. Wilkinson, Department of Biology, Duke University, Durham, North Carolina, USA.

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Abstract

Partial migration occurs when only a fraction of a population migrates instead of all individuals. Considered an evolutionary precursor to full migration, understanding why some individuals choose to undertake migration while others do not may serve to inform general migratory theory. While several hypotheses currently exist for explaining the maintenance of partial migration, empirical support for many is limited. To address this gap, we analyzed GPS data acquired from brown pelicans (*Pelecanus occidentalis*; $n = 74$), a partially migratory seabird, nesting on six colonies in the South Atlantic Bight over the course of four autumn migrations. We estimated that approximately 74% of pelicans nesting within the study area may be migratory on an annual basis, with the remainder staying within the surrounding marine ecoregion year-round. Mean date of migration initiation was 9 November, although movements occurred from September to December. Results from Cox's proportional hazards modeling indicated significant positive and negative effects of sea surface temperatures and body condition on migration rate, respectively. We suggest that the ontogenetic migration of the primary forage species of brown pelicans from estuarine to pelagic environments causes a seasonal reduction in prey and that pelicans in poor body condition are unable to meet the energetic demands potentially associated with this decrease in prey availability (i.e., the fasting endurance hypothesis of partial migration). Although we did not find evidence for a density-dependent migratory response, the effects of intraspecific competition on migration in pelicans also appear to warrant consideration.

KEYWORDS
body condition, movement behavior, resource abundance, seabird, telemetry

INTRODUCTION

Seasonal migrations are a common adaptive behavior of vagile organisms resulting in increased growth, survival, or reproduction across space and time (Shaw, 2016). Migration allows individuals to avoid unfavorable conditions (Bartel et al., 2011; Poulin et al., 2012; Xu & Si, 2019), access habitats advantageous for reproduction distinct from primary foraging areas (Semlitsch, 2008; Stewart & DeLong, 1995; Weimerskirch et al., 2017), or track specific resources such

as seasonal vegetation growth or prey (Furey et al., 2018; Sergeant et al., 2015). Both internal and external factors may cause individuals to initiate migration (Jachowski & Singh, 2015). For example, physiological condition may act as one of several internal drivers (Hegemann et al., 2019), while environmental cues such as seasonal changes in light or temperature may act as external drivers, especially when these signals indicate resource availability either locally or at the migratory destination (Ramenofsky et al., 2012; Winkler et al., 2014).

At the population level, seasonal migration may be undertaken by all or some fraction of individuals (obligate and partial migration, respectively; Dingle & Drake, 2007; Terrill & Able, 1988). Although the evolutionary drivers of each form are poorly understood, partial migration is more common, especially among avian taxa, and is thought to be a precursor to obligate migration (Berthold, 1999; Hegemann et al., 2019; Pulido, 2011). Several hypotheses exist explaining the mechanisms underlying the maintenance of partial migration and, by extension, the development of obligate migration (Chapman et al., 2011). For example, the competitive release hypothesis posits that dominant individuals will tend to be sedentary while subordinate individuals will tend to migrate to alleviate the effects of intraspecific competition (Bai et al., 2012; Chapman et al., 2011; Gauthreaux, 1978), often characterized by a positive density-dependent response (Lamb et al., 2017a). Alternatively, the fasting endurance hypothesis posits that a seasonal reduction in foraging opportunities or food availability triggers migratory behaviors for those individuals unable to meet energetic demands (e.g., in poorer body condition and/or with limited food resources; Chapman et al., 2011; Gow & Wiebe, 2014). The thermal tolerance hypothesis suggests that individuals unable to incur the cost of enduring thermal extremes at the nesting area will migrate (Belthoff & Gauthreaux, 1991; Chapman et al., 2011; Palacín et al., 2009). Under this hypothesis, individuals of either small or large body size (depending on their thermal intolerance to cold or hot, respectively) or those experiencing more extreme ambient conditions (e.g., at the edges of geographic ranges) will tend to migrate to areas that are less likely to have conditions that exceed an intrinsic thermal tolerance threshold.

The respective portions of resident and migratory individuals within a population may vary on an interannual basis based on prevailing environmental conditions, especially if the individuals that make up the population possess varying genetic liabilities for migratory decision-making (i.e., the threshold model of migration; Pulido, 2011). Within a partially migratory population, migratory decisions made by individuals can also have direct fitness consequences resulting from the spatial and temporal stochasticity of the extrinsic factors that influence the decision-making process (Fieberg et al., 2008; Pratt et al., 2017; Reid et al., 2020). For example, there may be weak or neutral selective pressure to remain resident during typical nonbreeding conditions but a strong survival benefit associated with migration during extreme conditions (Acker et al., 2021). This interannual variation in selective pressures may contribute to the maintenance of multiple strategies within a population.

Our understanding of drivers of avian migration has been derived disproportionately from studies focused on (1) clearly defined migrations between relatively sessile breeding and nonbreeding periods (e.g., neotropical migratory passerines or Arctic-nesting shorebirds), (2) spring migration (i.e., the return to breeding grounds; Gallinat et al., 2015; Haest et al., 2019), (3) Arctic and temperate systems (Sekercioglu, 2010), and (4) mainland and/or terrestrial systems (Shaw, 2016). Our goal was to examine drivers of migration in a partial migrant from a coastal, lower latitude system. Whereas higher latitude systems have relatively predictable peaks and troughs of resource abundance, lower latitude systems may have much more subtle, unpredictable, or heterogeneously distributed resources across space and time, accompanying less-defined boundaries of seasonality (Lisovski et al., 2017).

Furthermore, coastal and nearshore systems are characterized by highly dynamic and variable resource abundances (Knip et al., 2010) and estuarine-influenced habitats within coastal ecosystems are some of the most productive and complex environments globally (Kennish, 2002). This is in part due to the wide variety of input variables determining productivity within estuaries, including freshwater discharge and nutrient load, sunlight availability, wind regimes, tidal action, and oceanic factors such as sea surface temperature (SST), sea surface salinity, and sea surface height (Boyer et al., 1993; Janzen & Wong, 2002; Morris et al., 1990; Torregroza-Espinosa et al., 2021). Estuarine systems provide critical breeding and early life-stage habitat for many species of marine fish that subsequently are key components of complex food webs. These forage fish often time their own ontogenetic or seasonal movements with localized shifts in primary productivity. It may, therefore, be adaptive for upper-trophic-level predators, especially those with mobile capabilities, to be responsive to the same or similar environmental cues as their primary prey, even when the predator is not directly affected by the environmental change (e.g., tracking interannual changes in ocean temperature as a measure of prey abundance; Szesciorka et al., 2020).

The Eastern brown pelican (*Pelecanus occidentalis carolinensis*) is an apex predator in nearshore systems that is distributed widely from tropical to temperate waters of the western North Atlantic. The breeding range

for this species extends throughout the US coast of the Gulf of Mexico and on the Atlantic coast from southern Florida to the Chesapeake Bay. This range spans approximately 21° of longitude and 14° of latitude and encompasses a diversity of nearshore ecosystems. While early investigations using band recoveries suggested an annual movement of adults away from breeding colonies (Schreiber & Mock, 1988), the advent of bird-borne satellite tracking technology confirmed a partial migration strategy for breeding populations both in the northern Gulf of Mexico and in the South Atlantic Bight (SAB) (King et al., 2013; Lamb et al., 2017a; Poli, 2015). While several studies exist examining drivers of brown pelican movement within the breeding season (Geary et al., 2019, 2020; Walter et al., 2014), relatively little attention has been paid to factors causing large-scale movements outside of the reproductive period. An exception is Lamb et al. (2017a), which documented a significant and positive density-dependent effect on both autumn migration strategy and migration distance for pelicans in the northern Gulf of Mexico, consistent with the competitive release hypothesis. Drivers of partial migration are complex, however, and may not be homogenous among populations for species with expansive ranges, such as the brown pelican. Hypotheses of partial migration are also not mutually exclusive, and several mechanisms could be operating simultaneously. The aim of the current study is, therefore, to leverage tracking data collected from pelicans breeding in the SAB, a more latitudinally expansive system compared to the northern Gulf of Mexico, to examine drivers of partial migration during the postbreeding season.

METHODS

Study area and focal species

The SAB is generally defined as the extent of Atlantic coastal North America from the Cape Fear River Basin to Cape Canaveral (~34°–28° latitude). It is characterized by a complex geomorphology dominated by estuarine systems, salt marshes, and barrier islands. There are ca. 15 pelican colonies active in any given year within the SAB, as not every colony is active every year (Jodice et al., 2013). Colony sizes range from <100 to nearly 4000 pairs, with the largest colonies located near Charleston, SC, USA (32.8° N, Figure 1). Brown pelicans in this region typically cease nesting activity by late August, after which a portion of individuals from any given colony may undertake movements away from the breeding area that may manifest as short-range relocations or long-distance migrations.

Encompassing the SAB and approximating its borders is the Carolinian marine ecoregion (Spalding et al., 2007; Figure 1). Dominated by the interaction of the Gulf Stream with the relatively broad continental shelf, which determines much of the large-scale oceanography of the area, the Carolinian ecoregion is subject to seasonal shifts in productivity in both nearshore and pelagic waters (Voulgaris, 2013). Together with the Northern Gulf of Mexico marine ecoregion, this area forms the Warm Temperate Northwest Atlantic marine province (Spalding et al., 2007). To the south exists the Floridian marine ecoregion, encompassing much of southern Florida and the Keys (Spalding et al., 2007). Part of the Tropical Northwestern Atlantic marine province, the Floridian ecoregion exhibits markedly less seasonal fluctuations in oceanography and is more closely aligned with the Caribbean (Longhurst, 2007).

Data collection

This study was performed under the auspices of the Clemson University Animal Care and Use Committee (#2017-008). We deployed 65-g solar GPS Platform Terminal transmitters (GeoTrak Inc., North Carolina, USA) on brown pelicans ($n = 86$) during the reproductive periods of 2017–2020 at six colonies within the SAB. Briefly (see Lamb et al., 2017 for details), adult pelicans were captured on the nest while chick-rearing (May–August) via either a neck or leg lasso. Transmitters ($10 \times 3.5 \times 3$ cm) were attached dorsally via a backpack-style harness constructed using Teflon ribbon and weighed ≤3% of the body mass of instrumented birds (range = 2475–4350 g). Transmitters were programmed to record locations at 90-min intervals between 11:30 and 01:00 GMT (i.e., 10 locations/day) from September to November, and to record locations at 120-min intervals between 12:00 and 02:00 GMT (i.e., 8 locations/day) from November to March to conserve battery power during seasons with lower sunlight availability. Unit error was assumed to be similar to that of Lamb et al. (2017a), that is, 4.03 ± 2.79 m.

We measured the tarsus, culmen, and mass during capture, and collected 3–4 body feathers from the dorsal side of the pelican above the uropygial gland. DNA from feathers was then extracted and developed via PCR for sex determination (Animal Genetics Inc., Florida, USA). Total handling time averaged 15 (±3 min).

To estimate adult physical condition, we developed a body condition index (BCI) following Lamb et al. (2017a). Assuming a linear relationship between culmen length (a proxy for skeletal size) and body mass, a best-fit regression equation was calculated to generate predicted body
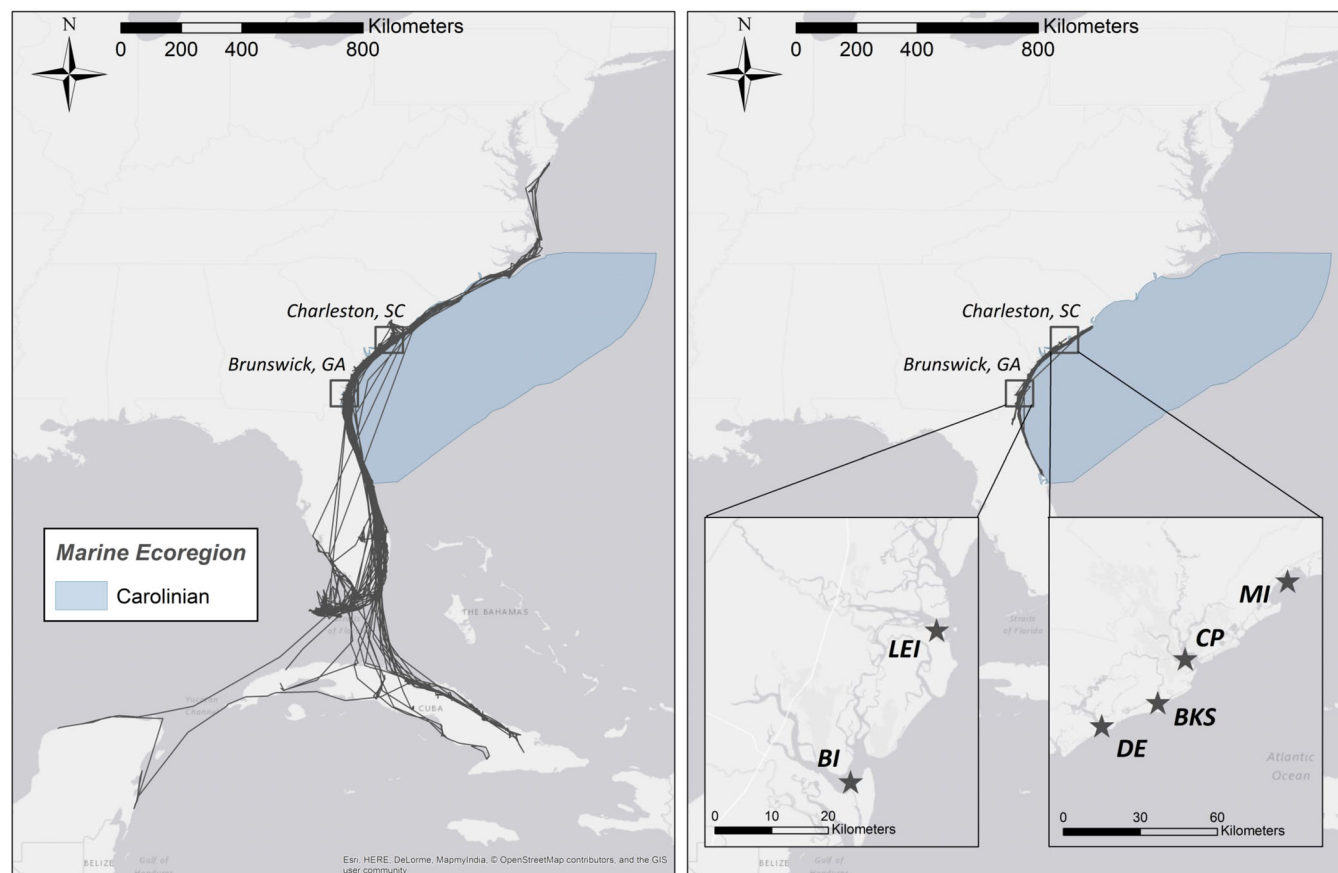
FIGURE 1 Movements of migratory (left) and resident (right) eastern brown pelicans tagged with GPS-Platform Terminal transmitters satellite transmitters in the South Atlantic Bight, USA. The shaded blue region represents the borders of the Carolinian marine ecoregion used to delimit migratory behaviors. Inset maps depict the locations of breeding colonies near Brunswick, GA, and Charleston, SC, respectively. BI, Bird Island; BKS, Bird Key Stono; CP, Castle Pinckney; DE, Deveaux Bank; LEI, Little Egg Island; MI, Marsh Island.

mass based on culmen length. BCI was then defined as the difference between measured body mass and predicted body mass, with negative values indicating an individual in a relatively poorer condition and positive values indicating an individual in a relatively better condition. Regression equations were calculated separately for each sex to account for inherent sexual dimorphism in the species (Shields, 2020). We also tested whether BCI was correlated with date of capture, as condition was only measured once at deployment and may vary with phenology. Finally, colony-specific estimates of the number of breeding pairs of pelicans were obtained following counts of colonial waterbirds in each state (Table 1) as a measure of conspecific density.

Data processing

Erroneous GPS locations were removed via a combination of visual inspection and speed filtering at ≥65 km/h (Schnell & Hellack, 1978). Because we were interested in regional-scale movements, GPS data were reduced to a single location per day by taking the daily mean of all recorded fixes for each individual. As the latest date of initial transmitter deployment during the study was 10 August, and no individuals had yet exhibited prior migratory behavior, we removed all locations preceding that date. This allowed for the movement track of each individual to commence on the same date regardless of year, ensuring that, in subsequent modeling, the observation period for each individual would begin simultaneously.

To distinguish between migratory and resident behaviors at the individual level, we examined daily locations of pelicans from the beginning of the observation period as defined above until either the track ended or 1 March of the subsequent year, whichever occurred first. In rare instances ($n = 7$), GPS locations were transmitted after the unit had become detached from the bird or the individual had perished. In these cases, the end of the track was determined via visual inspection for the cessation of movement. We used the spatial boundary of the Carolinian marine ecoregion for categorizing migratory and resident pelicans. Migratory individuals were defined

TABLE 1 Characteristics and sample sizes of GPS-tracked eastern brown pelicans from six breeding colonies in the South Atlantic Bight, USA.

Characteristic	Bird Island	Little Egg Island	Deveaux Bank	Bird Key Stono	Castle Pinckney	Marsh Island
Coordinates	31°07′ N 81°26′ W	31°18′ N 81°16′ W	32°32′ N 80°10′ W	32°37′ N 79°59′ W	32°46′ N 79°54′ W	32°59′ N 79°33′ W
No. tracked adults	6	5	19	22	16	6
Percentage males	33	20	37	59	38	83
Years	2020	2020	2017–2020	2017–2018, 2020	2017–2020	2017
Mean colony size (pairs)	396	421	1107	3019	566	713

as those that departed the marine ecoregion at some point during the observation period, while resident individuals were defined as those remaining within the boundary of the ecoregion throughout the duration of the observation period (maximum distance to boundary = 510 km). We chose to use the marine ecoregion boundary as a migratory threshold because, unlike purely distance-based metrics, the boundaries of the marine ecoregion are ecologically meaningful. Pelicans may depart the area surrounding the breeding colony, for example, yet remain within an ecologically similar environment throughout the annual cycle.

For those individuals that migrated (i.e., departed the ecoregion), we used the package migrateR in the R statistical framework to determine the day on which migratory behavior commenced (Spitz, 2019). As tracks did not include return movements in the spring, each track was fitted to a "disperal" movement model, which functionally represents one half of a full "migration" model (i.e., only an outbound segment). Models are based on net-squared displacement, with the "dispersal" model showing an increase in displacement over time with a distinct movement period (see Spitz et al., 2017 for details). An estimation of the starting date of migratory movements was extracted based on percent of net distance traveled, where the start date was defined as the day on which 5% of the modeled migratory distance was achieved (Spitz, 2019).

Environmental covariates

We selected environmental variables that both matched the hypotheses of partial migration outlined in Chapman et al. (2011) and that were also comparable to Lamb et al. (2017a). For example, the thermal tolerance hypothesis suggests that individuals unable to incur the cost of enduring thermal extremes at the nesting area will migrate. We, therefore, downloaded ambient air temperatures (2 m above surface level; ERA5 reanalysis) from the Movebank

Environmental Data Automated Track Annotation System (Env-DATA) for each daily averaged pelican location. Air temperature data (2 m above surface level) was provided at a resolution of 0.25° and recorded at 12:00 EST for each day. To approximate the fasting endurance hypothesis, which states that seasonal reductions in foraging opportunities drive the need to migrate for those individuals unable to meet energetic demands, we included environmental variables that influence the abundance and distribution of Atlantic menhaden (*Brevoortia tyrannus*), the primary prey of pelicans in the SAB (Shields, 2020). While we were unable to directly measure menhaden abundance, SST and chlorophyll *a* (chl *a*) concentrations may serve as local proxies for relative menhaden availability in the environment (Geary et al., 2020). We also chose to include a daily index of the North Atlantic Oscillation (NAO), which can modulate menhaden abundance in the SAB on larger climatic scales (Roberts et al., 2019). Spatially and temporally explicit measures of SST and chl *a* were obtained using the R package rerddapXtracto. Daily Multi-scale Ultra-high Resolution SST was provided by the NASA Jet Propulsion Laboratory GHRSST at 0.01° resolution. Chl *a* concentrations were downloaded from the Aqua MODIS satellite as an 8-day composite at 4-km resolution, as daily and 3-day composites contained too many cells of missing data to successfully incorporate into subsequent time-to-event modeling. Daily NAO indices were downloaded from the NOAA Climate Prediction Center (https://www.cpc.ncep.noaa.gov, accessed 18 March 2021). Finally, we also downloaded estimated measures of the meridional (north–south) wind component at 10 m above ground level (ERA5 reanalysis) from the Env-DATA system at a spatial granularity of 0.25° and recorded them at 12:00 EST for each day. As the migratory movements of pelicans in the SAB are largely latitudinal, we hypothesized that individuals may choose to depart under favorable (tailwind) conditions. Data were organized such that increasingly positive values corresponded to increased wind velocities flowing from south to north (i.e., a strong headwind), whereas

increasingly negative values corresponded to increased wind velocities flowing from north to south (i.e., a strong tailwind).

Statistical analysis

We used time-to-event modeling to investigate the influence of intrinsic and extrinsic factors on the migratory decisions of brown pelicans. Specifically, covariates were fitted using Cox's proportional hazards model (CPHM), a form of survival modeling that can be applied to specific biological events that are single occurrences (Rivrud et al., 2016; Sherrill-Mix et al., 2008). Underlying the CPHM is the hazard function, which is the modeled rate of occurrence of the specific event through time. As hazards are rates, not probabilities, in the current application, the hazard represents the instantaneous potential for migration to occur at time t per unit time (e.g., the rate of daily migration decreases by a factor of x for every unit increase in variable y).

Several advantages exist for applying CPHMs to animal telemetry data. Often, tracking data contain incomplete information for individuals who experience tag failure or mortality before the event of interest occurs. Nonoptimal strategies for handling censored individuals include discarding collected data or inferring nonobserved behavior (Sherrill-Mix et al., 2008). CPHMs instead allow the user to incorporate all the collected data from the observation period into the model. This is both methodologically and ethically preferable, especially when considered in the context of animal-borne telemetry. CPHMs also allow for time-dependent covariates without requiring an underlying distribution function of the hazard. The CPHM does assume that a baseline hazard exists and that the effects of the covariates on the hazard are proportional (i.e., a given covariate influences the risk of migration in each individual equally over time and is additive on one scale). A CPHM then estimates the multiplicative effect of the covariates on the baseline hazard.

Model selection was undertaken using an information theoretic approach. We first fit a global model containing the singularly measured variables of sex, BCI, culmen length, and colony size and the time-dependent variables of NAO, SST, chl a, ambient air temperature, and meridional wind component. Variables were then removed via stepwise selection using Akaike information criterion (AIC), with those not improving the AIC being iteratively discarded. The subsequent model with the lowest AIC value was, therefore, selected as the most appropriate. Interactions between variables selected in the best-performing model were also examined for subsequent improvement of fit. We also investigated potential lag

effects by calculating 7-, 10-, and 13-day rolling averages of SST and iteratively adding them to the best-supported model. It should be noted that inclusion of both singularly measured and time-dependent variables within the model theoretically allows for the detection of factors that may influence whether or not an individual will migrate, as well as when that migration may take place.

RESULTS

Movement data ($n = 7717$ daily observations) were collected for 74 brown pelicans within the defined observation period (Table 1). Each pelican was represented in the CPHM by a single year of tracking, although six pelicans were tracked for >1 year (five individuals for 2 years; one individual for 3 years). Only a single year per individual was used to avoid biasing the model toward an individual strategy. We chose to use tracking data in the model from the first observation period that ended in either residency or migration (i.e., to eliminate censored data when complete data were available). None of the six pelicans tracked for >1 year switched strategies between years when a strategy was evident (i.e., excluding years of censored data).

We classified 47 individuals as migratory (Figure 2), with an average migration initiation date of 9 November $\pm$ 24 days (range = 2 September–28 December). A total of 10 individuals were confirmed as residents of the SAB throughout the observation period. The remaining 17 individuals provided censored data, with end dates ranging from 20 August to 19 February (median = 20 October). On average, pelicans that were labeled as migratory traveled a maximum distance of 977 $\pm$ 301 km from their colony of origin, which is approximately five times the average maximum distance traveled by pelicans labeled as resident (196 $\pm$ 137 km). As colonies of origin averaged 422 $\pm$ 87 km from the border of the ecoregion, migratory pelicans tended to continue traveling an additional ~550 km once exiting, underscoring the large-scale movements undertaken by these individuals (Figure 1). Sex ratios for migratory pelicans (43%:57% male to female) and resident pelicans (50%:50% male to female) were similar.

In order to approximate the percentage of pelicans that may be migratory from the SAB in any given year, we compared the number of confirmed migrants to confirmed residents (i.e., individuals with censored data were not included). Because a GPS transmitter would need to remain functional for a longer period of time to confirm residency (i.e., transmit from 10 August to 1 March, $n = 203$ days) versus indicate migration (i.e., latest initiation of migration was 28 December, $n = 140$ days), we chose to compare the number of individuals that both
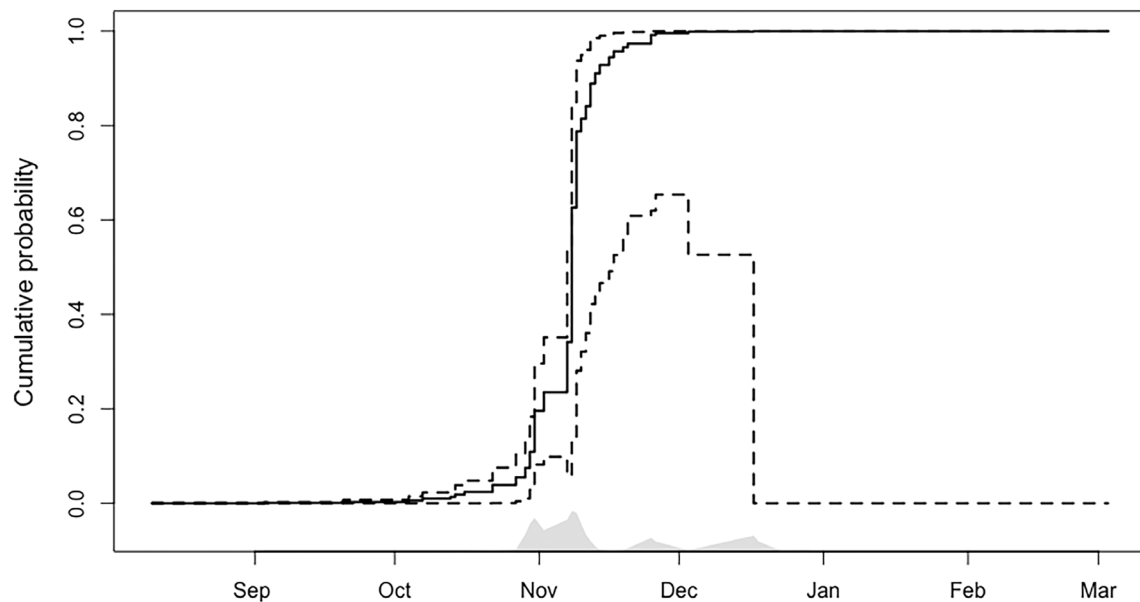
FIGURE 2 Cumulative migration probability (solid line) with 95% CI (dashed line) throughout the observation period for eastern brown pelicans in the South Atlantic Bight derived from the final Cox's proportional hazards model. Shaded gray region represents the temporal distribution of migration events ($n = 47$). Note the broad CI near the end of the observation period, which reflects the occurrence of individuals remaining resident (i.e., within the ecoregion) for the entire observation period.

migrated and had transmitters that were operational for the full observation period ($n = 29$) to the number of confirmed residents ($n = 10$). Using this approximation, we, therefore, estimate that ~74% of pelicans breeding within the SAB may migrate out of the ecoregion on an annual basis. This estimate remains unchanged if instead the total number of migrants ($n = 47$) is compared to the number of birds (both resident and censored) that did not migrate by the latest recorded migratory date (28 December; $n = 16$).

Tracks from migratory individuals indicated a variety of destinations upon exiting the Carolinian marine ecoregion (Figure 1). Frequently used areas included the southern Florida peninsula, the Florida Keys, and the northern coast of Cuba. The southern coast of Cuba and the Yucatan Peninsula of Mexico were also used, although less commonly. Northward movements were comparatively rare. Two individuals exited the Carolinian marine ecoregion to the north, reaching the Chesapeake Bay; because both movements were followed by a return to the SAB before 1 March, they were not considered to represent migratory events for the purposes of this study. One individual returned south after its northward trip and exited the Carolinian marine ecoregion to overwinter in southern Florida (treated as a migratory individual). The transmitter of the second individual ceased to operate soon after his arrival back in the SAB and was, therefore, treated as censored data. Pelicans that remained within the SAB primarily used

the coasts of Georgia and southern South Carolina, rarely moving north of Charleston.

BCI was not significantly correlated with date of capture ($r(72) = 0.03$, $p = 0.77$). AIC stepwise selection indicated the proportional hazards model with the best fit included BCI and time-dependent terms SST, NAO, and chl *a*. The remaining variables (sex, culmen length, colony size, chl *a*, ambient air temperature, and meridional wind component) did not improve model fit and were excluded. Interactions between BCI and the selected time-dependent terms also did not improve model fit. Additionally, model performance decreased with an increasingly lagged average SST. Model diagnostics based on scaled Schoenfeld residuals indicated that assumptions of proportionality were met for each variable. Model concordance (0.735 ± 0.04 SE) indicated good predictive ability of the model, with likelihood ratio and Wald tests achieving high significance ($p < 0.001$). SST had a significant positive effect on the hazard, with a 79% (95% CI: 56%–120%) increase in the daily departure rate for every 1°C increase in temperature (Table 2), despite an overall cooling trend within the season. BCI had a significant negative effect on the hazard, with a 0.23% (95% CI: 0.07%–0.40%) decrease in the daily departure rate for every unit increase in condition (Table 2). NAO and chl *a*, while included in the final model, did not reach statistical significance (i.e., CI of the hazard overlapped 1). Data generated during this study are available as a USGS data release (Wilkinson & Jodice, 2022).

TABLE 2 Output from the top-ranked Cox's proportional hazards model as applied to migratory pelicans in the South Atlantic Bight, USA.

Variable	Coefficient	SE	Hazard	z	p
BCI	−0.002	0.001	0.998	−2.768	0.006
NAO	−0.449	0.253	0.638	−1.776	0.076
SST	0.585	0.103	1.794	5.658	<0.001
Chl a	0.084	0.080	1.087	1.046	0.295

Note: Hazard values >1 indicate a positive effect, <1 indicate a negative effect, and =1 indicate no effect.
Abbreviations: BCI, body condition index; Chl a, chlorophyll concentration; NAO, North Atlantic oscillation index; SST, sea surface temperature.

DISCUSSION

Animal migration is both one of the most ubiquitous behaviors in ecology and also one of the most difficult to study and, consequently, least understood (Wilcove & Wikelski, 2008). Particularly vexing is partial migration, whereby some individuals from a population may undertake energetically expensive and potentially risky long-distance movements while others will remain within the same explicit area over time. Here, we suggest that both intrinsic (body condition) and extrinsic (resource abundance) factors contributed to the migratory strategies of brown pelicans in a subtropical marine system. Instead of evaluating preexisting and competing hypotheses a priori and subsequently fitting models to them, we followed a hypothetico-deductive approach, which resulted in a model aligned most closely with the fasting endurance hypothesis of partial migration (Chapman et al., 2011). Given the relative scarcity of literature empirically supporting this hypothesis, we posit that continued tracking of partially migratory species may be a key opportunity for testing the evolution of migratory behavior generally (Lundblad & Conway, 2020).

Resource abundance (e.g., prey availability) is the primary extrinsic factor underlying partial migration under the fasting endurance hypothesis. For brown pelicans in the SAB, diet is largely composed of a single species, the Atlantic menhaden (Blus, 1982; Sprunt, 1925). Studies during the breeding season indicate that up to 95% of chick forage can be composed of menhaden (Baldwin, 1946; Fogarty, 1981) and that adults and chicks tend to share similar diets (Shields, 2020). Although diet has not been well documented during the nonbreeding season, we can assume that postbreeding pelicans would not undergo a seasonal shift in diet if menhaden remained available given the foraging efficiency this item provides (Lamb et al., 2017b). If so, then menhaden likely represent a critical resource for both migratory and resident pelicans while in the SAB. We, therefore, posit that pelican migration is linked to the availability of a specific, preferred size class of menhaden and that this availability interacts with

intrinsic factors (i.e., factors represented by our measure of BCI) to influence the probability of migration among individuals. Here, we review diet preference, how this interacts with availability via menhaden ontogeny, and ultimately how these factors may then influence migration-related decisions.

Pelicans preferentially consume smaller, juvenile (0–1 year old) menhaden compared to larger, adult fish when available (Lamb et al., 2017b). This age-related bias may be driven in part by ontogenetic habitat associations in developing menhaden (Lamb et al., 2017b). Adult menhaden spawn offshore in the mid-shelf region (20–60 m depth) primarily during the winter, and in the SAB typically in association with the western boundary of the Gulf Stream, beyond the expected foraging range of pelicans (Checkley et al., 1988, 1999). Larvae then become dependent upon ocean circulation mechanisms to deliver them into estuarine complexes for development in the late winter or early spring (Hare et al., 1999; Lozano et al., 2012) where larval menhaden proceed to juvenile stages over the course of the summer months, taking advantage of the abundant resources available during this time and transitioning from capturing live zooplankton to planktonic filter feeding (Friedland et al., 1996). Finally, each menhaden cohort will exit the estuaries in the autumn to join the offshore adult population, which is itself at least partially migratory in nature, exhibiting a net southward movement during the winter months from the Northeast and Mid-Atlantic Bight to the SAB (Liljestrand et al., 2019).

Tracking of brown pelicans in the SAB has indicated that foraging adults rarely occur in waters further than 5–10 km offshore, instead relying on estuarine and nearshore environments rather than on pelagic systems for prey acquisition (Poli, 2015; Wilkinson et al., 2019). These habitats are heavily favored by developing menhaden as nurseries, and within these systems, menhaden appear to serve as a locally abundant resource for pelicans while they are present (Glass & Watts, 2009; Hartman & Brandt, 1995). However, the availability of juvenile menhaden as a resource may decrease suddenly

and rapidly during the seasonal transitions from summer to autumn due to their ontogeny. Therefore, the autumn migration of juvenile Atlantic menhaden from inshore, estuarine habitats to offshore, pelagic environments may represent a key change in resource availability for brown pelicans that subsequently acts as an extrinsic driver for their own migration from the SAB.

While we were unable to monitor menhaden abundance directly, we included environmental variables that influence menhaden distribution and abundance in our models of pelican migration (SST, chl *a*, NAO; Geary et al., 2020; Roberts et al., 2019). The final model included each of these proxy variables for menhaden abundance, to the exclusion of other environmental variables such as ambient temperature or meridional wind component that might influence pelicans more directly (e.g., via thermal tolerance or flight energetics). Of these, SST was a highly significant and positive predictor of the rate of pelican migration. Pelicans that migrated

appeared to have experienced a relative increase in SST that was preceded first by a variable period of depressed SSTs (Figure 3). Juvenile menhaden are triggered to leave estuarine systems for the pelagic environment by periods of sustained, cool SSTs that occur seasonally during autumn. For example, Friedland and Haas (1988) documented consistent initiation of menhaden emigration from an estuarine complex in Virginia 5 days after the onset of SSTs below 24°C. Records from June and Chamberlin (1959) indicated that emigration in Delaware commenced once temperatures in the estuarine environment fell below those of the adjacent ocean. While it may be beneficial for pelicans to remain in the area during such menhaden emigration events, as the relative availability of juvenile menhaden may be temporarily enhanced through the movement of many individuals, following emigration there may be a significant decrease in menhaden abundance in the nearshore habitats that pelicans use for foraging. As SSTs undergo local
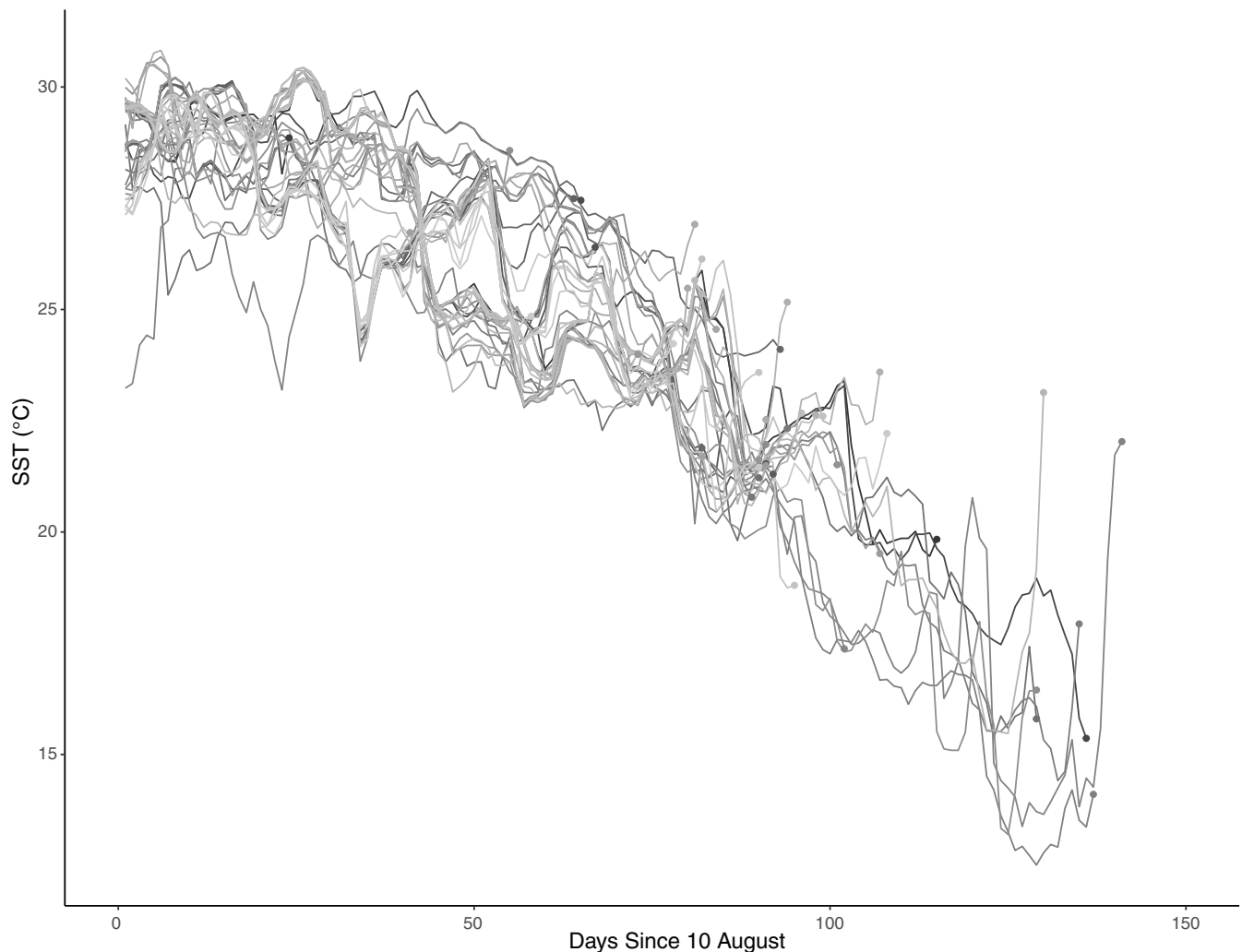
FIGURE 3 Sea surface temperatures (SST, in degrees Celsius) experienced by migratory ($n = 47$) GPS-tracked pelicans in the South Atlantic Bight over the study period, beginning 10 August. Lines are shaded by individual, with solid circles indicating the migration event.

rewarming, pelicans may then choose to migrate as menhaden movement ceases and abundances are depressed. The association of pelicans with cooler relative SSTs during the nonbreeding season is further supported by Lamb et al. (2020), which documented a rangewide selection for low SSTs relative to availability during the winter based on a habitat suitability analysis of tracked individuals. In addition, the relationship between elevated SST and migration rate in our study did not change even when SST was calculated using rolling averages, suggesting that pelicans that are experiencing warmer temperatures on a broader temporal scale will tend to migrate compared to those experiencing cooler temperatures. However, it should be noted that models using lagged SST performed significantly worse than the nonlagged model, indicating that short-term SST fluctuations remain a better overall predictor of migration rate in this system.

A decrease in resource abundance, as may occur with menhaden emigration, may subsequently lead to a concomitant increase in intraspecific competition among pelicans (Duijns & Piersma, 2014). Increased intraspecific competition could lead to changes in intrinsic factors that might also affect migration strategy. We found that BCI was significantly related to the migration hazard. For every unit increase in BCI, the hazard was decreased by 0.23%, indicating that those individuals in worse condition were more likely to exit the SAB given equal environmental conditions (Table 2). We posit that the annual emigration of juvenile menhaden out of estuarine systems drives local resource scarcity, thereby increasing competition among pelicans. Individuals in better body condition may be more competitive than individuals in poorer condition at acquiring limited resources, or they may be better able to withstand periods of resource shortages. For example, Geary et al. (2019) found that during the breeding period, higher quality pelicans in better body condition were also more efficient in foraging and took more variable risks with higher energetic returns than individuals in poorer conditions, which tended to show a reduced capacity for risk-taking in their foraging behavior (i.e., the rich get richer hypothesis). This suggests that individuals in good condition are more likely to be strong competitors or have the capacity to withstand food shortages compared to individuals who are in poor condition. However, individuals in poor condition may also choose to migrate regardless of prey availability, given the lack of a significant interacting term between BCI and SST within our selected model. It is important to note that skeletal body size was not supported in the final model of pelican migration, indicating that the decision to migrate was dependent more on the relative condition of the individual and less on absolute size. Interspecific competition for juvenile menhaden is likely to be of comparatively reduced importance, given the relatively low contributions of this species to the diets of other estuarine predators in the region (e.g., terns, gulls, dolphins; Aygen & Emslie, 2006; McGinnis & Emslie, 2001; Pate & McFee, 2012).

In contrast to the fasting endurance hypothesis, where the primary driver of migration is individual physiology (i.e., the inability of individuals to withstand resource scarcity), density dependence is the main factor influencing migration under the competitive release hypothesis. However, Chapman et al. (2011) note that resource availability is typically density dependent, and untangling the nuances of physiology versus competition is likely difficult. For example, Lamb et al. (2017a) found evidence for density-dependent drivers of both migration strategy and migratory distance in pelicans nesting along the northern Gulf of Mexico. In that study, migratory behavior was positively related to colony size, with individuals from larger colonies being more likely to migrate and to migrate a longer distance than individuals from smaller colonies. In addition, there was also a significant effect of skeletal body size, with larger individuals more likely to remain near the colony as residents. The conclusion reached was that intraspecific competition, driven by density-dependent factors, was the primary driver of partial migration for that population, which closely matches the competitive release hypothesis.

In contrast to Lamb et al. (2017a), we were unable to find evidence for colony size or skeletal body size as a predictor of pelican migration in the SAB. While we cannot exclude the possibility that mechanisms associated with competitive release are operational in our study system, our modeling results are more closely aligned with the physiological mechanisms underpinning fasting endurance. In addition to the inherent ecological difference between the Gulf of Mexico and the SAB, there also exist significant differences in colony structure between the two studies. For example, study sites in the Gulf of Mexico included a larger range of colony sizes than in the SAB (~40–4500 pairs vs. 400–3000 pairs, respectively; Lamb et al., 2017a). Pelican colonies in Lamb et al. (2017a) were also widely spaced along the entire US coastline of the Gulf, generally separated by ≥100 km. Colonies in the current study were much more closely spaced, especially when considered within South Carolina and Georgia (~25 km, respectively). Given that colonies in each state were within the daily foraging range of individual pelicans, for the purposes of intraspecific density dependence they may better be considered as two clustered subpopulations rather than exclusive colonies (Ainley et al., 2003). For example, our estimate of the proportion of the total pelican population within the SAB likely to be migratory in any given year is within

the bounds estimated by Lamb et al. (2017a) for only the largest colonies in the Gulf of Mexico. De facto individual colony size may, therefore, be less important as a driver of competition in this system than overall subpopulation size, unlike in the northern Gulf.

Finally, differences in methodologies between the two studies may also have contributed to differences in outcomes. For example, we used (1) the borders of an ecologically meaningful habitat (i.e., marine ecoregion) to classify migratory behaviors, while Lamb et al. chose a distance-based metric better suited to the Gulf of Mexico, (2) time-to-event models in place of generalized linear models, and (3) individual variables for potential extrinsic drivers instead of a single indexed score for all environmental variables. These differences represent the tailoring of approaches chosen to theoretically match the characteristics of these two study systems. While the conclusions from the two studies are not mutually exclusive, further study is warranted to make clear the role of intraspecific competition as a contributor to partial migration in this species (i.e., as a result of resource scarcity, density dependence, or both). Brown pelicans may represent a model species on which to test hypotheses related to partial migration, given the relatively broad range of the species and the variety of marine ecosystems they inhabit (Bowlin et al., 2010).

CONCLUSION

Despite recent increases in animal-borne tracking capabilities, the fundamental ecology of migration for many species remains unclear. Particularly unresolved are the mechanisms underpinning the maintenance of partial migration (Chapman et al., 2011). We provide support for the fasting endurance hypothesis of partial migration using telemetry data from postbreeding brown pelicans in the SAB. Time-to-event models indicated significant positive and negative effects of SST and BCI, respectively, on the migration rates of pelicans, and we suggest that pelicans in poor condition are more likely to migrate and that migration may be driven in part by seasonal reductions in prey availability. Further work could focus on resolving the importance of intraspecific competition on migratory behavior for this population, determining if there is a relationship between migratory strategy and future fitness, and assessing how climate change may impact pelican migration via the potential alteration of menhaden development and emigration.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the USGS ScienceBase-Catalog: https://doi.org/10.5066/P9YH2U8D.

ORCID

Bradley P. Wilkinson https://orcid.org/0000-0003-1447-4429

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