

Factors influencing Brown Pelican (*Pelecanus occidentalis*) foraging movement patterns during the breeding season

S.T. Walter, P.L. Leberg, J.J. Dindo, and J.K. Karubian

Abstract: During the breeding season, seabird foraging behaviors are driven by a combination of individual- and external-based factors. This study evaluated how two individual-based factors (body condition and sex) and two external factors (nest stage and colony size), and their interactions, were related to movement. To do so, we used movement data obtained from 22 GPS-tagged Brown Pelicans (*Pelecanus occidentalis* L., 1766) breeding in the northern Gulf of Mexico. In Brown Pelicans, the post-egg-hatching phase imposes increased foraging demands on breeding adults relative to the prehatching phase. This study demonstrates that the progression of the breeding period affects the nature and intensity of the relationship between individual-based factors and movement patterns. In particular, birds in relatively lower condition traveled greater distances during foraging trips during the energetically demanding posthatching phase, but not during the incubation stage. Contrary to many seabird species studied to date, neither colony size nor sex appeared to affect Brown Pelican movement patterns. Our results suggest that nest stage is the most important factor influencing foraging movements, and that it may modulate relationships between condition and movement. More refined measures of body condition and foraging behavior will allow further insights into the movement ecology of this seabird.

Key words: animal tracking, barrier islands, Brown Pelican, coastal ecology, foraging movement, Gulf of Mexico, *Pelecanus occidentalis*.

Résumé : Pendant la saison des amours, une combinaison de facteurs individuels et externes influence les comportements d'alimentation des oiseaux de mer. L'étude évalue le lien entre deux facteurs individuels (l'embonpoint et le sexe) et deux facteurs externes (le stade de nidification et la taille de la colonie) et leurs interactions, d'une part, et les déplacements, d'autre part. Pour ce faire, des données sur les déplacements de 22 pélicans bruns (*Pelecanus occidentalis* L., 1766) reproducteurs dotés d'étiquettes GPS dans le nord du golfe du Mexique ont été utilisées. Chez les pélicans bruns, la demande alimentaire augmente chez les adultes reproducteurs au stade suivant l'éclosion des œufs par rapport au stade précédant l'éclosion. L'étude démontre que le moment durant la période de reproduction a une incidence sur la nature et l'intensité de la relation entre les facteurs individuels et les motifs de déplacement. Plus particulièrement, les oiseaux dont l'embonpoint est relativement faible se déplacent sur de plus grandes distances pour s'alimenter durant le stade post-éclosion où la demande énergétique est élevée, mais non durant le stade d'incubation. Contrairement à de nombreuses espèces d'oiseaux marins étudiées à ce jour, ni la taille de la colonie, ni le sexe ne semblent avoir une incidence sur les motifs de déplacement des pélicans bruns. Nos résultats donnent à penser que le stade de nidification est le facteur qui exerce la plus grande influence sur les déplacements d'alimentation et qu'il pourrait moduler les relations entre l'embonpoint et les déplacements. Des mesures plus fines de l'embonpoint et du comportement d'alimentation permettront de jeter un meilleur éclairage sur l'écologie des déplacements de cet oiseau de mer. [Traduit par la Rédaction]

Mots-clés : pistage d'animaux, îles barrières, pélican brun, écologie côtière, déplacement d'alimentation, golfe du Mexique, *Pelecanus occidentalis*.

Introduction

During nesting and chick-rearing periods, foraging patterns of avian species commonly shift to reflect reproductive requirements and constraints (McNamara and Houston 1996; Barbraud and Chastel 1999; Weimerskirch et al. 2001). Movements of breeding seabirds during this time are primarily associated with foraging to provision young and themselves (Weimerskirch et al. 1993; Lormée et al. 2005; Ochi et al. 2010). These movements may be modulated by individual factors (e.g., age, physiological body condition, body size, sex) and external conditions such as nest stage or colony size (Ricklefs 1990; Roff 1992, 2002; Stearns 1992). However, the nature and relative importance of interactions between

these factors in regard to movement during reproduction remain unclear and it may be only under the most demanding circumstances when individual trait differences actually influence movement (Ballard et al. 2010; Lescroël et al. 2010). Characterizing seabird interactions between individual- and external-based factors in regard to movement during reproduction remains an area of active research among behavioral ecologists.

Body condition may influence movement of breeding seabirds. Animals are thought to modulate breeding effort by balancing investment in self-maintenance against investment in their young such that body reserves at the onset of breeding influence foraging behavior (Charlesworth 1980; Drent and Daan 1980). Although

Received 26 February 2014. Accepted 23 July 2014.

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the direction and magnitude of this relationship varies across systems (Takahashi et al. 2003), among long-lived seabirds low body reserves are often associated with reduced investment in reproduction (Monaghan et al. 1992; Wendeln and Becker 1999; Ballard et al. 2010). In some cases, however, individuals in lower condition may increase foraging activity to successfully reproduce (i.e., Lescroël et al. 2010). Within a single season and population, however, variation among individuals in body reserves may be associated with differences in foraging behavior at the individual level (McNamara and Houston 1996).

Sex-related differences in foraging movements among seabirds also occur (for a review see Lewis et al. 2002). Sex-biased foraging traits are commonly attributed to sexual size dimorphism, whether males are the larger sex (González-Solís et al. 2000; Lecomte et al. 2010; Ochi et al. 2010; Weimerskirch et al. 2012), or females (Guerra and Drummond 1995; Lormée et al. 2005; Weimerskirch et al. 2006, 2009). When sexual size differences result in ecological segregation in seabirds, the smaller sex commonly travels greater distances during foraging and engages in more active foraging behaviors.

Seabird foraging patterns can also shift over the course of the reproductive period to reflect changes in nest stage. Relative to the incubation period, the chick-rearing period requires increased food acquisition to provision chicks, which can thereby result in increased foraging activity (Weimerskirch et al. 2003; Ochi et al. 2010; Welcker et al. 2012). Furthermore, seabird colony size can affect prey densities within the surrounding region (Hunt et al. 1986). As the number of nesting pairs at an island increases, increased near-colony intraspecific foraging competition may require some individuals to fly farther distances from nest sites to acquire adequate prey (Weimerskirch 1998; Lescroël et al. 2010).

While recognizing that multiple environmental factors can regulate seabird foraging patterns (e.g., weather, sea conditions, and prey density), this study focuses on what the individual and external factors described above can tell us about the movement of seabirds during the breeding season. In the northern Gulf of Mexico, Brown Pelicans (*Pelecanus occidentalis* L., 1766) breed on coastal islands during spring and summer, form monogamous pair bonds, and are central-place foragers (Shields 2002). Like many seabird species, the Brown Pelican is sexually dimorphic; males are 15%–20% heavier than females (Shields 2002). Despite conservation interest in the species since the 1950s (Nesbitt et al. 1978; McNease et al. 1984), the species remains relatively poorly known. Recently, however, research has revealed basic ecological information regarding nesting and habitat relationships (Visser et al. 2005; Robinson and Dindo 2011; Walter et al. 2013a), colony persistence and initiation (Visser and Peterson 1994; Walter et al. 2013b), and coarse-scale movement patterns in the northern Gulf of Mexico (Walter et al. 2013c).

In this study high-resolution movement data, acquired from GPS tracking devices, were used to evaluate movement patterns of 22 breeding Brown Pelicans in the northern Gulf of Mexico. We assessed how body condition, sex, nest stage, and colony size were associated with our two response metrics: “total distance moved per day”, which reflects distances traveled between nest and foraging sites, and “nonlinear distance moved per day”, which is representative of foraging activity. We predicted that birds with high body condition would travel greater distances away from the nest early in the breeding season, before young are hatched. Second, we expected that females, the smaller sex, would move greater distances than would males. Third, we predicted that during the posthatching period, movement associated with foraging would increase compared with the prehatching period, particularly for individuals at large colony sites because of increased intraspecific prey competition. Each of these predictions is related to our over-arching expectations for Brown Pelicans, that (i) individual-based factors (i.e., body condition or sex) will modulate movement behaviors associated with foraging activity and

(ii) effects will be most pronounced under the most challenging circumstances, such as those related to nest stage or colony size.

Materials and methods

Study system and field data

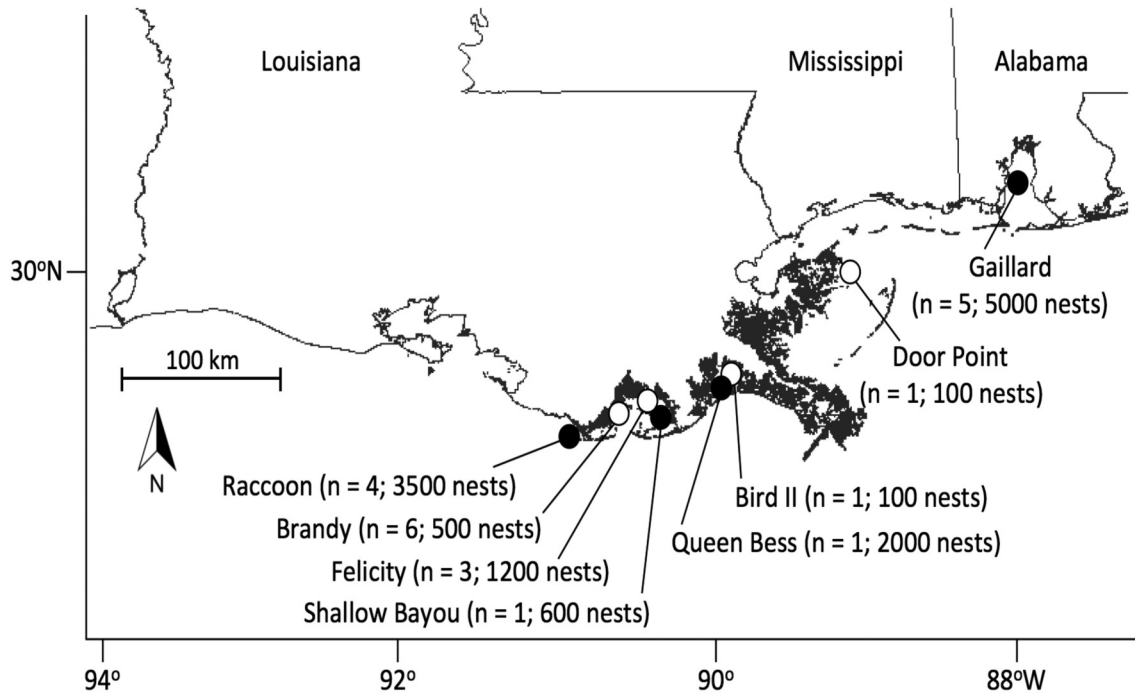
We deployed GPS tracking devices on eight Brown Pelicans from each of the following island breeding colonies: Raccoon, Shallow Bayou, and Queen Bess Islands, Louisiana, and Gaillard Island, Alabama ($N = 32$ total individuals; Fig. 1). We captured incubating adults on the nest using leg nooses and attached an E-Obs© tracking device to each bird with a backpack harness constructed of Teflon ribbon and copper hardware (tag and harness weighed 110 g, <4% of the bird’s body mass, on average). We weighed individuals to the nearest 5 g (minus the tag and harness masses), measured tarsus length to the nearest 0.05 cm, collected a blood sample, and released the birds in good condition <45 min after capture.

We obtained movement data from 1 April to 19 July 2012, by downloading location data from the tracking devices to a hand-held “base station” in the field. In practice, this meant bringing the base station within 200 m of a tagged bird for reliable download, which we accomplished during biweekly trips to known colonies and resting areas in the study region. Tags were programmed to record location data between the hours of 0400 and 2000 at 15 min intervals each day.

This study focuses on 22 individuals (17 from Louisiana; 5 from Alabama) for which we were able to download data following release and for which we recorded body-mass data. We excluded one individual from Alabama for which mass was not recorded, as well as nine tagged individuals for which we were not able to collect location data. For these nine individuals, we are uncertain if transmitters failed, if the birds immediately departed in study area following tagging, or if the birds remained in the area with functioning units but never came within data download range. Sixteen of the 22 relocated individuals abandoned their nests following capture and later re-nested. Of individuals for which we have location data, there was pronounced regional variation in patterns of abandonment, with a high rate (16 of 17 birds) in Louisiana and a low rate (0 of 5 birds) in Alabama. The degree to which abandonment occurred as a result of capturing the parent at the nest site is not clear; while 7 of 16 birds that abandoned their nests did so within 48 h of capture, the remaining 9 birds returned to their nests and then abandoned 4–37 days after capture (overall time to abandon = 7 ± 10 days (mean \pm SD)). All 16 of these individuals re-nested on either the same or another island within the same state that they were initially captured.

We estimated nest locations of all 22 focal individuals via analysis of tracking data and confirmed actual coordinates with a hand-held GPS unit at nine total nests that we were able to access (three in Louisiana, five in Alabama). To assess the precision of our location estimates for the remaining nests identified by tracking data alone, we compared ground-truthed vs. estimated locations of our nine known nests (difference = 5 ± 2 m (mean \pm SD); range = 2–7 m). Based on this level of accuracy, in combination with movement data consistent with nesting behavior at these locations, we did not distinguish between estimated vs. ground-truthed nest-site locations during further analyses. For individuals that abandoned their nest where captured, and we were not able to visit their new nests, we carefully reviewed location data of the tagged adult, which clearly demonstrated the individuals returned to one very particular site on a daily basis, remained at that site when not foraging, and remained there for the duration of our data collection (aside from foraging trips, thus indicating that these are not birds that died on an island). From our previous and intensive research efforts, we recognize this behavior as that of a nesting Brown Pelican. Our data for each of our 22 focal individuals corresponds to a single nesting attempt (for birds that abandoned

Fig. 1. Nesting islands in the northern Gulf of Mexico where we tagged 22 Brown Pelicans (*Pelecanus occidentalis*) that we tracked for foraging movement in 2012. Solid circles indicate where individuals were both tagged and nested, while open circles are nesting relocation sites. Numbers of tracked nesting pelicans per island and approximate number of total nests per island are provided in parentheses following the island name. Shaded areas along the shoreline indicate marsh and swamp habitats.



their nests following capture, we only present movement data collected during the active period at the new nest).

Response and explanatory variables

During Brown Pelican nesting, movements away from the nest most likely represent some form of activity related to foraging (e.g., direct travel to specific foraging grounds, exploratory searching, and repeated prey capture attempts within an area). Movements extraneous to foraging may include assessment of other colonies and searching for extra-pair mates, yet these behaviors are unlikely to be frequent while the birds are actively nesting (Shields 2002). Consequently, we generally refer to any movement away from the nest as “foraging behavior or effort”. To tease apart different aspects of movement as they relate to foraging, we developed the three complementary movement metrics of (1) total distance moved per day, (2) maximum linear distance moved per day, and (3) nonlinear distance moved per day. We log-transformed ($\log(\text{value} + 1.0)$) measures to meet the assumptions of our statistical models, and back-transformed values for presentation. Total distance moved per day was calculated by summing all distances between consecutive data points during which movement occurred and reflects distances traveled between nest and foraging sites over the course of a day. Maximum linear distance moved per day was calculated as the greatest straight-line distance between any two locations during a day and provides a measure of the range covered during foraging. This measure was typically, but not always, the distance between the nest site and the most distant location visited during the day. Because these first two metrics were highly correlated ($r = 0.94$, $P < 0.001$), we only present results for total distance moved per day because it likely provides better insight to the degree of foraging effort within a day, as opposed to maximum linear distance, which represents long-distance movement that may not require considerable effort for Brown Pelicans that can use dynamic soaring. We developed our third metric of movement, nonlinear distance moved per day, by obtaining the residuals from a regression of total distance moved

per day on maximum linear distance per day. This allowed us to factor out movement associated with straight-line flight during a day, which yields the relative degree to which birds varied their flight course. Although these nonlinear movements only account for 12% of the variation in pelican movements, these deviations from straight-line movement can offer insights to other flight activities such as foraging. Positive residuals indicate that birds were engaged in frequent changes in direction, which is often indicative of active prey searching and capture activity (Wood et al. 2000; Jonsen et al. 2005, 2007). Negative residuals suggest movement with relatively little deviation from the straight-line course, suggesting more time passively traveling from location to location without the immediate intent of prey capture.

We identified four candidate explanatory variables that we expected might affect movement: body condition, sex, nest stage, and colony size. Body condition (i.e., size-adjusted mass) was calculated using the standardized residuals of linear regression (SAS Institute Inc. 2008; PROC REG) on the log-transformed body mass against three times the log-transformed tarsus length (Andersson et al. 2002). This measure was taken at the time of capture, and thus reflects condition early in the breeding season. Sex was determined in the laboratory via polymerase chain reaction (PCR) of blood samples, following methods in Fridolfsson and Ellegren (1999). For each pelican, its colony size was the approximate number of nesting pairs on the island (S.T. Walter, unpublished data; T.J. Hess and the Louisiana Department of Wildlife and Fisheries, unpublished data). For nest stage, we classified each data point as belonging to the pre-egg-hatching period (1–45 days since nest initiation) or the posthatching period (46–102 days). Movement data allowed us to determine the first day of renesting for individuals that renested; for birds that did not renest, we back-calculated nest start dates based on egg hatch date and (or) chick development (Shields 2002; S.T. Walter, unpublished data). For our tracking data, the first nest-stage day for birds that remained at their original nests was 42 ± 8 days (mean \pm SD) (range 37–54 days).

Table 1. Top ranking models that evaluated the effect of body condition (Cond), sex, colony size (CS), and nest stage (NS) variables on (a) total distance moved per day and (b) nonlinear distance moved per day for 22 Brown Pelicans (*Pelecanus occidentalis*) breeding in the northern Gulf of Mexico, 2012.

Model	K	ΔAIC_c^*	w_i
(a) Response variable: total distance moved per day			
Cond + NS + Cond \times NS	4	0.0	0.59
Cond + Sex + NS + Cond \times NS	5	2.0	0.22
NS	2	3.4	0.11
Null	1	4.9	0.05
Cond + NS	3	7.3	0.02
Sex	2	7.5	0.01
Cond	2	8.6	0.01
Cond + CS + NS + Cond \times NS	5	18.6	0.00
CS	2	19.8	0.00
Cond + CS + Sex + NS + Cond \times NS	6	20.6	0.00
(b) Response variable: nonlinear distance moved per day			
NS	2	0.0	0.85
Sex + NS	3	5.2	0.06
Cond + NS	3	6.4	0.03
Sex + NS + Sex \times NS	3	6.8	0.03
Null	1	7.3	0.02
Sex	2	12.2	0.00
Cond	2	13.2	0.00
Cond + Sex	3	17.8	0.00
CS + Sex + NS	4	26.5	0.00
Cond + CS + NS	4	27.6	0.00

Note: Number of parameters (K), difference in Akaike's information criterion adjusted for small sample size (ΔAIC_c), and Akaike weights (w_i) are presented in the table.

* AIC_c of the top model in *a* was 847.7. The AIC_c of the top model in *b* was 363.1.

Finally, we blocked our analyses by region (east or west of the Mississippi River) to determine if space accounted for variation in movement. This geographic nesting classification might help us account for different prey availability or behaviors (such as those from reneesting) that may have influenced our analyses. However, in none of our preliminary analyses did this variable explain any variation in movement once other terms were included in our statistical models, thus we removed the term "nest region" from our analyses.

Statistical analyses

To evaluate how the four explanatory variables (body condition, sex, nest stage, and colony size) influenced movement, we performed separate Akaike's information criterion (AIC) analyses for our two response variables of total distance moved per day and nonlinear distance moved per day. Nest stage was evaluated as a within-plot factor, while sex, body condition, and colony size were evaluated as between-plot factors. "Individual" was used as a random effect and the error degrees of freedom were estimated with the Satterthwaite procedure. Each of the two AIC analyses included 37 biologically plausible models that included different combinations of main effects (i.e., nest stage, parental condition, sex, and colony size) and main effects with two-way interaction models; insufficient data precluded examination of higher order interactions. We also ran the fully saturated global model and null intercept models for comparison. To obtain AIC values adjusted for small sample size (AIC_c ; Burnham and Anderson 2002), we used mixed-model ANOVAs (SAS Institute Inc. 2008; PROC MIXED). Models with $\Delta AIC_c < 2$ units from the model with the smallest AIC_c value were considered to provide reasonable support for the data (Burnham and Anderson 2002). Model weights (w_i) were calculated to provide an additional measure of model support; models with larger weights provide more support for the data (Burnham and Anderson 2002). Finally, Tukey-Kramer tests for multiple comparisons were used to assess differences among least-squares means that were adjusted by other significant factors within models.

Results

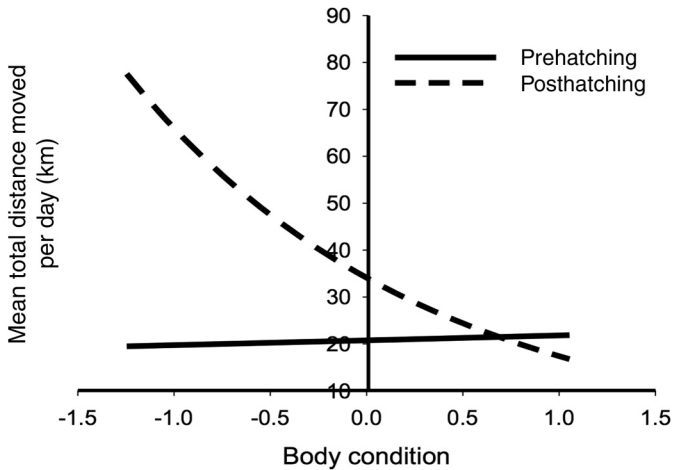
We tracked movement of 22 Brown Pelicans (10 males and 12 females) over 560 tracking days and 35 727 data-point locations. Individuals were tracked for 25.5 ± 16.3 days (range 5–74 days), with 1624 ± 1037 locations obtained per individual. Tracking occurred between nest-days 1 and 102; 72% of days occurred during the pre-hatch period and 28% occurred during the post-hatch period. Birds exhibited a leptokurtic distribution of distances moved from the nest, with no evidence of a bimodal distribution of distances moved overall (i.e., dual foraging strategy; Weimerskirch 1998; Congdon et al. 2005; Ochi et al. 2010), nor in relation to sex or nesting stage.

When considering the factors influencing total distance, the model with the most information included nest stage, body condition, and their interaction (Table 1). The model with the second highest model weight included these same terms as well as individual sex. The only other model that contained marginally more information than the null model was a model that contained only nest stage. Before eggs hatched, body condition did not affect total distance, yet during the nestling provisioning period, birds in better condition flew shorter total distances from the nest (Fig. 2).

There was no support for an interaction between nest stage and body condition when modeling nonlinear distance. The only model with measurably more support than the null model was the model that contained nest stage (Table 1). Birds made substantially more movements than would be expected for their maximum daily movement between two points in the post-hatch stage than during incubation. We take this to represent an increase in foraging activity associated with feeding nestlings.

In spite of a large range in colony size (Fig. 1), this variable provided little information regarding either of our movement metrics, either as a main effect or as part of an interaction with other factors. We also observed sexual dimorphism among birds that we tracked; males were heavier than females (3.26 ± 0.17 vs. 2.40 ± 0.19 kg; Satterthwaite's t test, $t_{[20]} = -11.08$, $P < 0.001$). However, there was little evidence that sex affected movement. As

Fig. 2. The relationship between body condition and mean total distance moved per day in Brown Pelicans (*Pelecanus occidentalis*) breeding in the northern Gulf of Mexico. Body condition did not affect total distance moved per day in the prehatch period, yet during the nestling provisioning (posthatch) period, pelicans that were in better condition flew shorter mean total distances per day.



previously noted, sex was a term in a model of total distance that provided marginal support for the data (Table 1). However, the sex effect was negligible because its confidence intervals overlapped zero; body condition, nest stage, and their interaction accounted for the majority of variation in the model.

Discussion

The nestling provisioning period during seabird reproduction necessitates greater foraging activity, relative to the incubation period, primarily to acquire prey for the brood beyond the adults' own nourishment requirements (e.g., Weimerskirch et al. 2003; Watanuki et al. 2004; Ballard et al. 2010). Our findings suggest that, as in many other species, this is the case for Brown Pelicans breeding in the northern Gulf of Mexico. Interestingly, inter-individual differences in body condition influenced total distances moved per day by breeding Brown Pelicans during the posthatch stage, but not during the prehatch stage. These results suggest that more demanding circumstances, such as rearing young, may reveal important relationships that are absent or minimal during other phases of the reproductive cycle (e.g., Grant and Grant 1993; Lesacroël et al. 2010). For Brown Pelicans, this consideration is likely to be relevant to studies of individual and population-level responses to naturally occurring and anthropogenically induced challenges.

In general, seabird individuals in the best condition often invest more in reproduction, in the form of increased foraging activities to better nourish nestlings, relative to individuals in poor condition (Stearns 1992; Roff 1992, 2002; Wendeln and Becker 1999). However, other research has indicated that foraging effort during reproduction may not be related to body condition (Takahashi et al. 2003). In our study, Brown Pelicans in low condition traveled greater distances during the posthatching phase. Individuals with better condition may have had an early physiological advantage that allowed them to forage more efficiently and, consequently, traveled less distance per day during foraging trips. A similar trend was reported for the Adélie Penguin (*Pygoscelis adeliae* Hombron and Jacquinot, 1841) in that individuals in better condition during the reproduction season remained in better condition throughout breeding, while better providing for their young (Ballard et al. 2010; Lesacroël et al. 2010). These findings suggest that at least in some species, a positive feedback loop may exist between foraging efficiency and condition such that "the rich get richer" by obtaining more resources per unit of energy expended

(Lesacroël et al. 2010). The fact that a measure of Brown Pelican body condition obtained early in the breeding season during this study predicted subsequent total movement distance per day suggests that differences in condition early in breeding may reflect future, interindividual differences in foraging behaviors. Future work might clarify these issues by directly characterizing foraging "efficiency" per se in the Brown Pelican by measuring individual dive events, by obtaining repeated and more refined measures of body condition throughout the breeding season (LaBocha and Hayes 2012), and by making detailed measures of parental provisioning. Furthermore, as we noted a trend for increased distances traveled from the nest, but not increased number of foraging trips per day, for low-condition individuals in the posthatching phase, assessment of regional prey availability may also help explain movement patterns as has been demonstrated in other seabird research (Watanuki et al. 2004).

Reduced distances moved for high-condition pelicans may have also been in part due to adequate body reserves that allowed increased investment to chick survival by means of increased nest guarding. For instance, adult Snow Petrel (*Pagodroma nivea* (G. Forster, 1777)) individuals with relatively greater body condition spent more time at the nest, which resulted in higher chick survival (Tveraa and Christensen 2002). As Brown Pelican nestlings are susceptible to mortality from weather and attack by other pelicans or predators (Shields 2002), adults in better condition in this study may have forgone foraging trips directed towards self-nourishment (as opposed to gathering prey for young; Weimerskirch et al. 2003; Guilford et al. 2009; Welcker et al. 2012) to the benefit of investing greater attention to nest guarding duties. This trend has been reported for Adélie Penguins (Ballard et al. 2010). However, we were unable to determine the number of chicks fledged for our tracked pelicans and do not know if decreased adult movement was associated with increased reproductive success. Given that adult body condition during breeding can influence reproductive output (Chastel et al. 1995), we recommend additional research that investigates relationships between body condition and foraging trends.

Sex, particularly among sexually dimorphic seabirds, commonly influences foraging movement patterns (González-Solís et al. 2000; Lewis et al. 2002; Weimerskirch et al. 2006), but we found no strong evidence for disparate movement patterns between males and females in our study. Although the Brown Pelican's dominate prey item, the Gulf menhaden (*Brevoortia patronus* Goode, 1878) (Shields 2002), is prevalent within our study region (Deegan 1990; Vaughan et al. 2007), we unfortunately lack data on specific abundances and distributions during our study. Given the ability of prey to influence seabird movement patterns (Lewis et al. 2002; Guilford et al. 2009), we suggest future studies incorporate this variable. Not only could these data help elucidate how males and females respond to shifts in prey distribution, but they could also provide insight on pelican colony size that may influence movement patterns based on varying levels of intraspecific foraging competition near breeding sites.

In conclusion, changes in parental care requirements during the breeding period appear to modulate the nature and intensity of the relationship between individual-based factors and movement: birds in relatively lower condition traveled greater distances during foraging trips during the energetically demanding post-egg-hatching phase. Although our metric of total distance moved per day provides one representation of foraging movement behavior, assessing actual energy expenditure by adults during foraging might provide additional insight to factors that affect movement. Incubation and brooding, especially in systems with high or low ambient temperatures, have been shown to be energetically demanding in other seabirds (e.g., Hand et al. 1981; Oswald et al. 2008; Mallory et al. 2009). Future work that directly measures energy expenditure, during both foraging and incubation or brooding, may be helpful in explaining why Brown Pelican

movement patterns during the nesting period are influenced by interactions of individual and temporal-based factors. Larger sample sizes of tracked individuals may also increase statistical power to assess interactions. Finally, although no large environmental disturbances occurred during our research (oil spills, hurricanes, etc.), factors such as these and others that may affect prey density (e.g., the hypoxic zone that forms each summer off the Louisiana coast) could provide further insight into pelican behavior during the breeding season.

Acknowledgements

Sincere thanks go to B. Olinger for field assistance, B. Geary for map creation, and J.K. Karubian and P.L. Leberg laboratory members for assistance with pelican capture. We also thank two anonymous reviewers that provided constructive feedback on our original manuscript. Research was conducted with appropriate permissions from the states of Louisiana (LNHP-12-024) and Alabama (MB182448-0), as well as Tulane University (IACUC No. 395). This research was supported by the National Science Foundation (grant No. 1139962 to J.K.K. and P.L.L.).

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