



Original Article

Condition-dependent foraging strategies in a coastal seabird: evidence for the rich get richer hypothesis

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The degree to which foraging individuals are able to appropriately modify their behaviors in response to dynamic environmental conditions and associated resource availability can have important fitness consequences. Despite an increasingly refined understanding of differences in foraging behavior between individuals, we still lack detailed characterizations of within-individual variation over space and time, and what factors may drive this variability. From 2014 to 2017, we used GPS transmitters and accelerometers to document foraging movements by breeding adult Brown Pelicans (*Pelecanus occidentalis*) in the northern Gulf of Mexico, where the prey landscape is patchy and dynamic at various scales. Assessments of traditional foraging metrics such as trip distance, linearity, or duration did not yield significant relationships between individuals. However, we did observe lower site fidelity and less variation in energy expenditure in birds of higher body condition, despite a population-level trend of increased fidelity as the breeding season progressed. These findings suggest that high-quality individuals are both more variable and more efficient in their foraging behaviors during a period of high energetic demand, consistent with a “rich get richer” scenario in which individuals in better condition are able to invest in more costly behaviors that provide higher returns. This work highlights the importance of considering behavioral variation at multiple scales, with particular reference to within-individual variation, to improve our understanding of foraging ecology in wild populations.

Key words: behavioral flexibility, central place foraging, foraging ecology, individual variation, seabird, telemetry

INTRODUCTION

An animal's movement decisions and associated rates of energy expenditure have important implications for its survival and fitness, which in turn scale up to shape broader population dynamics. In idealized models of optimal foraging behavior, individuals are assumed to move through environments, in which resources may be patchily distributed, in a manner that maximizes net energy gain (Schoener 1971; Pyke 1984) and abandon patches when they fall below a certain threshold of quality (marginal value theorem; Charnov 1976). In reality, however, social and ecological factors including competition, environmental disturbance, and imperfect knowledge about the distribution of patches may affect resource access over space and time, leading to deviations from behaviors predicted by optimality models. To characterize these behavioral

changes, researchers often focus on between-individual differences in foraging metrics, primarily with regard to individual attributes such as age, sex, or personality (Marchetti and Price 1989; Desrochers 1992; Clarke et al. 1998; Ruckstuhl 1998; Bolnick et al. 2003), and responses to external factors such as density-dependent competition (Sih 1984; Rita et al. 1996) or environmental heterogeneity (Wiens 1976; Kotler and Brown 1988; Patrick et al. 2013; Patrick et al. 2014). This body of work has advanced our understanding of foraging ecology by revealing how endogenous and exogenous factors may interact to shape consistent foraging differences within populations.

Because exogenous factors may change dynamically and affect resource availability at various spatial and temporal scales, we might also expect to observe substantial within-individual variation, or behavioral flexibility, in foraging behaviors in addition to between-individual variation (Dingemanse 2002; Morand-Ferron et al. 2007; Biro and Adriaenssens 2013; Stamps 2016). This is particularly true during periods of intense energetic demand (Parrish

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1997), pronounced change in environmental conditions (Bonte et al. 2007), or predation risk (Briffa et al. 2013), when not all individuals may adjust behaviors in the same way or to the same degree. If certain individuals exhibit greater variation over time than others, ecologically important patterns may go unrecognized if only differences among individual means or personalities are considered (Dingemanse et al. 2010; Royauté and Dochtermann 2017), thus limiting the accuracy of population-level inferences and assessment of the degree to which those populations may be affected by environmental change.

The relationship between an individual's quality and its behavioral flexibility is of particular interest, since the energetic costs and rewards of variability remain poorly resolved (Weimerskirch 1998; Piersma and van Gils 2011). On one hand, individuals in better condition may exhibit reduced flexibility, for example by achieving social dominance and monopolizing resources in high-quality patches while others are forced to travel elsewhere (Weimerskirch 1998; Thums et al. 2013). Alternatively, individuals in better condition may travel more, due to a superior ability to track changing resources and bear increased travel costs (van Gils et al. 2007; Lescroël et al. 2010). Both of these scenarios have been observed in experimental settings (David et al. 2012; Dosmann et al. 2015), but field-based tests of behavioral flexibility in foraging movements in relation to body condition are rare. Lescroël et al. (2010) found that individuals in better condition were able to access foraging locations that were costlier to reach but returned higher energetic rewards, whereas individuals in poorer condition were not able to do so. This pattern could be described as a "rich get richer" scenario, in which only individuals above a certain physiological threshold are able to access relatively inaccessible but higher quality food sources. The degree to which this framework of seabird foraging in relation to indicators of individual quality, and the degree to which behavioral flexibility may be mediated by individual characteristics, applies to other systems is currently unclear, and longer-term observations of individual movements are still needed to fully understand the ecological effects of patchy resource distributions in this context.

The relationship between condition and variation in foraging movements is likely to be of particular importance for central-place foraging species, in which individuals return to a home location between trips rather than moving continuously or randomly through an environment (Orians and Pearson 1979). Although widespread, this strategy presents obvious challenges for resource acquisition, including high competition close to the colony and a reduced awareness of changes in patch availability throughout the landscape over time (Manly et al. 2002; Matthiopoulos 2003). As frequent top predators and colonial nesters, seabirds are ecologically important central-place foragers that are especially sensitive to local environmental change (Cairns 1988; Piatt et al. 2007; Piatt and Sydeman 2007), making them appropriate subjects for examination of flexible foraging tactics in response to dynamic resource availability.

In this study, we utilize 4 years of breeding season tracking data on a population of nesting brown pelicans (*Pelecanus occidentalis*) in the northern Gulf of Mexico to investigate both within- and between-individual variations in foraging movements. Based on previous findings, body condition is an important predictor of average daily movement rates in this population (Walter et al. 2014). Therefore, our over-arching hypothesis was that body condition should be associated with an individual's ability to vary its foraging behaviors in a variety of ways over time, presumably to

track shifting prey resources, with this pattern becoming more pronounced as chick growth imposes greater demands on provisioning adults. More specifically, we predicted that individuals in better body condition would exhibit reduced foraging site fidelity (i.e., higher variation in space use) and lower variation in energy expenditure as they presumably discovered more high-quality foraging patches and thus improved foraging efficiency. As low site fidelity in this scenario is presumably associated with a more exploratory nature involving travel throughout the region, we also predicted that on average, individuals in better condition would take less linear trips of longer distance and duration.

METHODS

Ethics statement

All field work was approved by the Tulane Institutional Care and Use Committee (IACUC) Permit #0395R2. Bird marking was approved by Bird Banding Laboratory Permit #06669 and Louisiana Department of Wildlife and Fisheries (LDWF) Scientific Collecting Permit nos. LNHP-14-034, LNHP-15-034, LNHP-16-028, and LNHP-17-042. Island access was also granted annually by LDWF.

Study system and data collection

The focal area of this study was Raccoon Island, located in Terrebonne Bay, LA in the northern Gulf of Mexico (29.0519°N, -90.9336°W). Raccoon is the largest seabird colony in Terrebonne Bay, with 3000–5000 brown pelican nests commonly initiated each year (Selman et al. 2016). The island is approximately 2.3 km long, and its interior is dominated by several grass and shrub species, all of which serve as nesting sites for several bird species. In this region, brown pelicans primarily prey on Gulf menhaden (*Brevoortia patronus*) (Shields 2014; Lamb et al. 2017), which are patchily distributed in schools over time and space, as well as heavily fished during the pelican breeding season (Ahrenholz 1991; Langseth et al. 2014). Tracking work began in synchrony with the hatching dates of the first cohort of eggs, typically in late April or early May of each year, from 2014 to 2017.

We selected nesting adults to track that were in the posthatching phase of nesting, with nests only in black mangrove (*Avicennia germinans*) 1–1.5 m in height to control for potential differences in behaviors related to ability to acquire high-quality nesting sites (Walter et al. 2013). We captured individuals either by hand or using leg snares and attached e-Obs© tracking units (e-Obs Digital Telemetry, Gruenwald, Germany). Units recorded and stored GPS locations every 15 min, as well as acceleration values in 3 dimensions at a rate of ~5 unitless values per second (5 Hz). These values are subsequently converted to units of *g* using calibrated values derived before unit deployment. We attached units using a backpack-style harness made of Teflon ribbon (Bally Ribbon Mills, Bally, PA) and copper clasps. The full tracking apparatus weighed approximately 110 g, less than 5% of any bird's body mass (range: 2600–4330 g). We took blood samples for lab-based determination of sex (Fridolfsson and Ellegren 1999), marked individuals with metal and color leg bands, and used morphological measurements to calculate indices of body condition (standardized residuals of linear regressions of log-transformed body mass on $3 * \log(\text{tarsus length})$ for each sex (Andersson et al. 2002). We revisited the island every 7–10 days after deployment, remotely downloaded tracking data to a handheld base station, and checked nests of tracked individuals to document nest fate and ensure that collected data

represented behavior of birds that were continuing to provision young.

Data processing and analysis

We used Microsoft Excel and custom scripts in R version 3.4.0 (R Core Team 2016) to remove duplicate locations and prepare data for analysis. We isolated “complete” foraging trips that began and ended on the colony within the same day using the “adehabitatLT” package in R (Calenge 2015), removed locations on the nest or beach of the colony, and rediscritized them to recover the entire trajectory of the foraging bout. Once individual trips were isolated, we calculated the following 5 descriptive foraging metrics: the total duration, total distance traveled, maximum distance traveled (as the furthest recorded point from the individual’s nest), linearity (0–1, where 1 represents a completely straight line; Batschelet 1981; Benhamou 2004), and departure angle (as the mean absolute angle of the first 10 points in the trajectory). Using accelerometer data, we also calculated overall dynamic body acceleration (ODBA), in which the static component of acceleration is subtracted from each recorded axis, and the remaining dynamic components of each axis are then summed (Wilson et al. 2006). ODBA has been demonstrated to be an accurate correlate of energy expenditure across a variety of taxa (Wilson et al. 2006; Halsey et al. 2009; Halsey et al. 2011; Watanabe et al. 2013), making it a useful metric by which energy expenditure of individual movement patterns may be assessed. For this study, we calculated a proxy for total energy expenditure for a foraging trip by multiplying its ODBA by its duration.

We performed all statistical analysis in R. We first ascribed individual characteristics (sex, condition, day, and year) in addition to the previously described trip characteristics (Supplementary Tables 1 and 2). To determine whether there was a relationship between individual characteristics and distributions of colony departure directions, we separated birds by sex ($n = 14$ females and 16 males) and used natural breaks in the distribution of birds’ body condition to separate birds into 3 groups representing low, medium, and high body condition ($n = 10$ in each group; see Supplementary Table 1). We then calculated the mean and variance in trip direction for each group, used Rayleigh’s test of uniformity to determine deviation from circular normal angle distributions, and performed a Watson–Wheeler test to determine whether the 3 groups’ distributions differed significantly from one another, using the R package “circular” (Agostinelli and Lund 2017).

We next examined changes in explicit space use, within and between individuals over time, during complete foraging trips. We used 2 approaches to characterize foraging site fidelity as the degree of overlap between sequential pairs of foraging trips (i.e., starting with the second trip, comparing overlap between that trip and the one preceding it). We first converted each trip into presence/absence rasters to simply identify where birds were located on the landscape, using a grid with 2×2 km cells. Since the scale at which pelicans perceive or navigate the environment when making various movement decisions is not known, we generated these rasters at a variety of resolutions; grids of comparable resolutions (0.9–6 km cells) yielded qualitatively similar results. Secondly, we generated 2 movement-based kernel home ranges for each trip: a 50% range which roughly corresponds to areas where most foraging is assumed to take place, and a 95% range that reflects the majority of the area traversed during a trip, including potential landmarks used in navigating the environment. Home ranges were constructed using

the biased random bridge method in the “adehabitatHR” package (Benhamou and Cornélis 2010; Calenge 2015), using the BRB.D function to calculate diffusion parameters for each home range, h_{\min} value of 450 m, minimum step length of 5 m, on a grid of extent 20 and size 2000 to generate high-resolution images. For the rasters, we calculated overlap as the percentage of cell overlap between each pair of trips (Bradshaw et al. 2004). For home ranges, we calculated Bhattacharyya’s affinity, which measures the probability of 2 ranges representing identical utilization of space (Bhattacharyya 1943; Fieberg and Kochanny 2005). Each of these measures of overlap was used as the response variable in separate analyses. As our measurement of site fidelity could be confounded by changing home range size, with large home ranges eventually having greater overlap when birds forage in the same general region (i.e., a bay), we also calculated the area of each home range as a response variable for a separate analysis. These space use characteristics were all analyzed using mixed-effect models, with sex, body condition, year and Julian day as fixed effects and bird identity as a random effect. To control for the fact that consecutive foraging trips in the data set were not always equally spaced in time (due to incomplete recorded trips in the telemetry data), we included the time between each pair of trips as an additional predictor in the site fidelity models. Finally, to determine whether these patterns changed over time at different rates based on condition, we included a day \times condition interaction term in each model, which we retained when found to be significant. For raster and home range overlap models, we utilized beta-inflated regression with the “gamlss” package in R (Rigby and Stasinopoulos 2005) to account for the presence of zeroes in the 2 overlap response variables. To examine within-individual variation in energy expenditure, we also used a multiple linear regression to test for correlates of coefficients of variation for individuals’ trip energy expenditure, using sex and condition as predictors.

Finally, we analyzed variation in more traditional foraging trip metrics. To measure among-individual variation, we constructed separate linear mixed effects models, all of which used sex, body condition, year, and Julian day as predictors, for each of our response foraging metrics (total distance, maximum distance, duration, linearity, and energy expenditure), again with bird identity as a random effect. We also assessed behavioral flexibility by calculating repeatability within individuals using the R package “rptR” (Nakagawa and Schielzeth 2010). In all relevant cases, we made appropriate variable transformations to meet basic model assumptions: total distance, maximum distance, and duration were all square-root transformed, whereas linearity was arcsine-transformed.

RESULTS

Raw data collection from birds included in analysis yielded 55 316 GPS points from 30 birds (mean = 1843.87 ± 884.20 [SD] pts/bird) (Geary et al. 2018). We received usable round-trip data from 13 birds in 2014, 4 birds in 2015, 7 birds in 2016, and 6 birds in 2017 ($n = 30$ total birds). We removed 1288 movement segments from the data set due to insufficient GPS fixes to accurately describe entire foraging bouts, resulting in 678 isolated, complete foraging trips (mean = 22.60 ± 20.78 trips/bird; see Supplementary Table 1).

All 3 condition classes significantly departed from a uniform distribution of departure angles when leaving the colony on foraging trips ($P < 0.001$), with all birds exhibiting a consistent bias toward traveling east–west toward the neighboring bays (means: 68–125°,

where 0° is due north). However, there was significant variation between the 3 condition classes in degree of variance in departure angles ($W = 26.425$, $df = 4$, $P \leq 0.001$), with birds in higher condition exhibiting higher variance in these angles 0.762 versus 0.691 and 0.664 for low and medium conditions, respectively, on a 0–1 scale; **Figure 1**. This was not the case in a similar comparison between sexes, for which no differences in departure angle were noted ($W = 4.990$, $df = 2$, $P = 0.082$).

Spatially explicit analyses of foraging locations corroborated the idea that condition and individual-level variability may be related. Specifically, we observed a negative correlation between raster-generated metrics of overlap and body condition, with an approximately 12% decrease per unit increase in condition ($t = -2.224$, $P = 0.026$, condition range: -2.11 – 1.72 , **Figure 2a**), even as population-wide measures of raster overlap increased over time (0.9% per day) as nestlings matured and their energetic costs increased ($t = 3.706$, $P < 0.001$, **Figure 2b**). Similarly, within-individual overlap in 95% home ranges also decreased approximately 15% per unit increase in condition ($t = -2.096$, $P = 0.036$), despite population-wide increases of 0.9% per day ($t = 2.934$, $P = 0.003$). In contrast, 50% core usage area overlap also increased with time ($t = 3.201$, $P = 0.001$) but was not correlated with condition ($t = -0.757$, $P = 0.449$). Overall 50% and 95% home range sizes became smaller with time ($P < 0.001$ in both cases), suggesting that the increase we observed in site fidelity

over time is not attributable to growing home ranges. These 2 models also had a significant day \times condition interaction term ($t = 2.144$, $P = 0.032$ and $t = 2.354$, $P = 0.019$, respectively) with positive coefficients (0.003 in both cases) indicating that despite the decrease in home range sizes at the population level, high-condition birds' home ranges remained relatively larger.

Variation in total ODBA—our proxy of energy expenditure—was negatively correlated with condition ($t = -2.354$, $P = 0.026$; **Figure 3**). In other words, despite being more variable in terms of where they foraged, individuals in better condition expended a more consistent amount of energy per foraging trip relative to individuals in poorer condition.

Analyses examining variation in total distance, maximum distance, duration, linearity, and energy expenditure found significant but low within-individual repeatability in all cases ($r = 0.046$ – 0.153 , $SE = 0.024$ – 0.047 , $P < 0.01$ for all metrics), indicating low overall consistency in these basic metrics. Although significant predictors emerged in our comparisons of the same metrics across individuals and time, we believe that they lacked biological relevance as the sizes of effects were small (**Supplementary Table 3**). For example, although males had significantly shorter durations of foraging bouts than females ($P < 0.0015$), it is unlikely that an average difference of about 3 min in duration would have any effect on pelican energetics or foraging success.

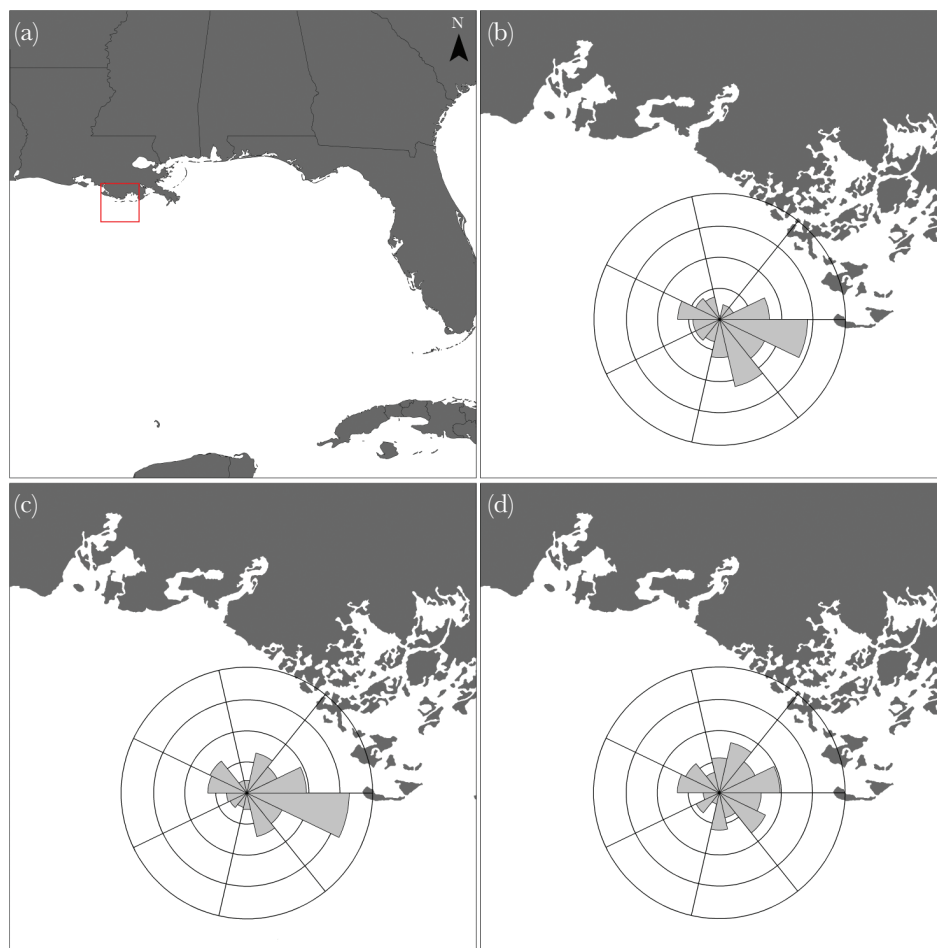


Figure 1

Visualization of departure angles by brown pelicans in the Gulf of Mexico after separating individuals into 3 classes of body condition. (a) Location of the study site in relation to the rest of the northeastern Gulf of Mexico; (b–d) variance in departure angles of low (b), medium (c), and high (d) conditions.

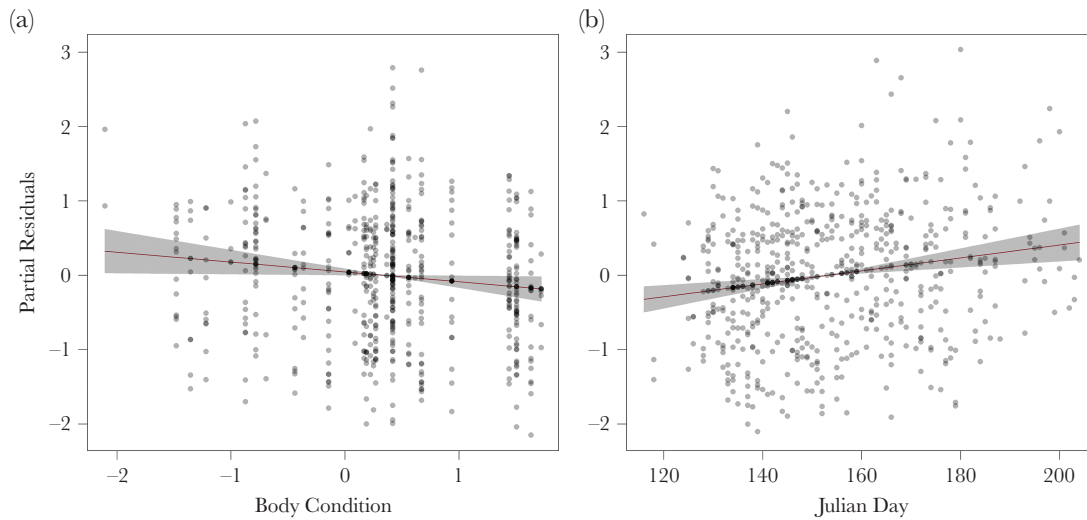


Figure 2

Partial residual plots demonstrating brown pelican foraging site fidelity for each trip (as calculated by presence/absence rasters) in relation to (a) body condition and (b) Julian day. Analysis of 95% home ranges yielded qualitatively similar results.

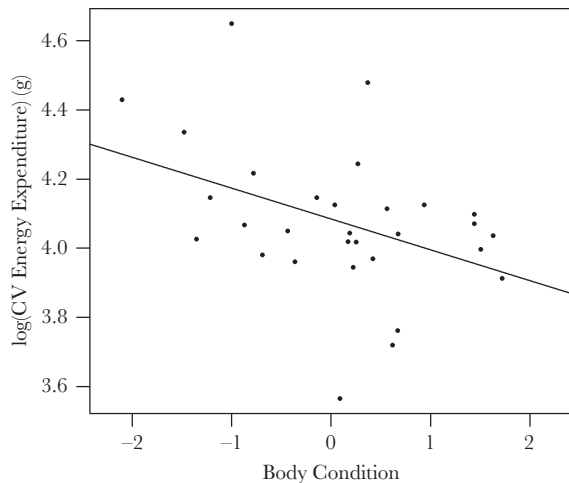


Figure 3

Relationship between body condition and coefficients of variation in energy expenditure in breeding brown pelicans. Birds in better condition exhibited lower overall variation in energy expenditure, possibly associated with higher foraging efficiency.

DISCUSSION

Studies of foraging ecology have traditionally focused on differences between individuals, yet there are good reasons to believe that substantial variation exists within individuals over time, and that this variation may have important consequences both for individuals' fitness and subsequent demographic processes. Yet the nature of this variation, and the degree to which it may be shaped by endogenous factors (e.g., condition and sex) and exogenous factors (e.g., shifting distributions of resources and increasing energetic demands associated with reproduction) remain poorly understood. We found that basic foraging metrics of brown pelicans in the northern Gulf of Mexico did not vary meaningfully across tracked cohorts when average values for an individual were assessed. In contrast, behavioral flexibility in foraging behaviors differed considerably between individuals across multiple metrics.

First, although the population exhibited a gradual increase in site fidelity during tracking periods, we found that individuals in better condition exhibited increased variability in the areas in which they foraged. This suggests that higher-condition individuals may be able to maintain dynamic foraging strategies, despite increasing physiological challenges associated with provisioning growing chicks. These patterns cannot be explained by changes in home range size, which decreased as chicks increased in age, further emphasizing the importance of spatially explicit considerations in characterizations of foraging behavior. Condition-based differences in foraging site fidelity suggest that this population does not follow an ideal-free distribution (Fretwell and Lucas 1969), in which individuals settle into areas proportionally to their resource availability, nor do inferior competitors appear to be excluded from resource-rich patches. Rather, a more exploratory strategy may decrease within-patch competition from other pelicans and improve foraging efficiency, but may not be energetically feasible for lower-condition individuals without risking mortality or nest failure. As such, this may represent another example of a "rich get richer" scenario, where individuals continually reap the rewards afforded them by better condition, perhaps beginning with and maintaining high foraging efficiency by continually locating new patches as others are depleted (Lescroël et al. 2010).

Increased variability may be associated with various foraging skills, such as landscape-level knowledge of patches (Irons 1998), interpretation and use of social information at the colony (Ward and Zahavi 1973) or on foraging grounds (Thiebault et al. 2014; Tremblay et al. 2014), use of distant fishing vessels to locate large schools (Votier et al. 2010), or exploitation of regional weather patterns or environmental characteristics that improve efficiency of movement over long distances (Wilson et al. 2012; Shepard et al. 2013). In keeping with this scenario, individuals in better condition appeared to expend energy at more consistent rates across trips, as measured by ODBA, a proxy of energy expenditure, further lending support to the interpretation that these individuals could be accessing better patches that improve their rates of prey capture and therefore offset travel costs. The opposite scenario for lower-condition individuals could also explain

their more variable energetic returns as they potentially remain in lower-quality foraging areas. However, the overall increase in site fidelity we observed in these cohorts suggests that in general, the population may gradually locate and revisit more reliable foraging grounds, somewhat mitigating the costs associated with reduced exploration. Although our findings are consistent with a “rich get richer” scenario, additional work is required to better understand this system, including continuous measures of condition and direct measures of the energetic returns from different foraging patches.

Although our results provide insights into how body condition might mediate foraging behavior, several components remain unexplored and warrant future investigation. It may be that foraging behaviors may carry different energetic costs for different individuals (e.g., less agile dives and greater stability in flight for heavier birds), but these assumptions would also suggest that ODBA and the resultant proxy measure of energy expenditure might be lower overall for heavier birds, which we did not detect (Supplementary Table 3). We also find it unlikely that a bird in better condition (i.e., relatively well-fed) would be less agile, given the tactics necessary for this species to successfully target and capture fish. More broadly, given the importance of the dynamic resource landscape in the northern Gulf of Mexico, variable foraging strategies may result in individuals experiencing differential marine conditions between years, which may affect rates at which menhaden schools are discovered. Direct measures of energy expenditure and intake would also enhance our understanding of relationships between foraging site fidelity and condition-based strategies. Finer-grained behavioral data, both on foraging grounds (Thiebault et al. 2014; Tremblay et al. 2014) and on the colony, would help us to resolve the degree to which social information use and alternative foraging tactics shape brown pelican foraging strategies and their outcomes. In tandem with continued collection of acceleration data, this information would allow us to more intimately link strategies to their respective energetic efficiencies.

Previous work on the same study population in a single season of tracking by Walter et al. (2014) found that body condition was an important predictor of movement between individuals—a pattern that we did not recover in the current, multiyear study. This earlier study was conducted on birds that renested after transmitter attachment on different barrier islands, limiting our ability to make direct comparisons between the 2 studies. We consider it possible that the differences between the 2 studies may be explained in part by the data used for analysis (round-trip foraging bouts in this study vs. all movement data), potentially decreased movement ability of lower-condition birds after incurring the cost of initiating a second nest, different regional marine conditions during the 2012 study period, the fact that the 2012 birds nested on a wider range of barrier islands, or some combination thereof. Taken together, these 2 tracking studies reveal ways in which condition may influence brown pelican movement capabilities, with evidence for both a population-wide effect from the earlier study and within-individual effects in the current study. Better resolving the ways in which individual-level variance may scale up to population-level trends represents an important goal for this and other study systems moving forward.

Our findings underscore the importance of considering within-individual variability in behavior, as it may reveal important differences between individuals that may not be apparent when only between-individual averages are compared (Buss and Greiling 1999; Royauté and Dochtermann 2017). This variability may be of particular importance when environments are highly dynamic at a variety

of spatiotemporal scales, where the capacity for flexible foraging strategies could carry important fitness consequences, especially as anthropogenic disturbances continually alter ecosystems worldwide (Balmford et al. 2003). Our results also corroborate earlier findings that body condition, even if measured at a single time point, is a robust predictor of many behavioral attributes (Ballard et al. 2010; Walter et al. 2014). We propose that the use of condition, in tandem with other indicators of individual quality (Patrick and Weimerskirch 2014), has great potential to explain individual-level variation in future studies of animal movements. As these and other metrics of animal movement are gathered in increasing detail, they will continue to broaden our understanding of relationships between the behaviors of individuals and consequent population and ecosystem-level processes.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Geary et al. (2018, 2019).

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REFERENCES

- Agostinelli C, Lund U. 2017. R package circular: circular statistics (version 0.4–93). <https://r-forge.r-project.org/projects/circular/>. Accessed December 5, 2018.
- Ahrenholz DW. 1991. Population biology and life history of the North American menhadens, *Brevoortia* spp. *Mar Fish Rev*. 53:3–19.
- Andersson S, Pryke SR, Ornborg J, Lawes MJ, Andersson M. 2002. Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *Am Nat*. 160:683–691.
- Ballard G, Dugger K, Nur N, Ainley DG. 2010. Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Mar Ecol Prog Ser*. 405:287–302.
- Balmford A, Green RE, Jenkins M. 2003. Measuring the changing state of nature. *Trends Ecol Evol*. 18:326–330.
- Batschelet E. 1981. *Circular statistics in biology*. New York: Academic Press.
- Benhamou S. 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *J Theor Biol*. 229:209–220.
- Benhamou S, Cornélis D. 2010. Incorporating movement behavior and barriers to improve kernel home range space use estimates. *J Wildl Manage*. 74:1353–1360.
- Bhattacharyya A. 1943. On a measure of divergence between two statistical populations defined by their probability distribution. *Bull Calcutta Math Soc*. 35:99–109.

- Biro PA, Adriaenssens B. 2013. Predictability as a personality trait: consistent differences in intraindividual behavioral variation. *Am Nat.* 182:621–629.
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The ecology of individuals: incidence and implications of individual specialization. *Am Nat.* 161:1–28.
- Bonte D, Bossuyt B, Lens L. 2007. Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider. *Behav Ecol.* 18:438–443.
- Bradshaw CJA, Hindell MA, Sumner MD, Michael KJ. 2004. Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Anim Behav.* 68:1349–1360.
- Briffa M, Bell A, Hankison S, Laskowski K, Dall S, Houston A, McNamara J, Wolf M, Doorn G van, Leimar O, et al. 2013. Plastic pre-empt: reduced predictability in the face of predation risk in hermit crabs. *Biol Lett.* 9:20130592.
- Buss DM, Greiling H. 1999. Adaptive individual differences. *J Pers.* 67:209–243.
- Cairns DK. 1988. Seabirds as indicators of marine food supplies. *Biol Oceanogr.* 5:261–271.
- Calenge C. 2015. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.* 197:516–519.
- Charnov E. 1976. Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* 9:129–136.
- Clarke J, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S. 1998. Sex differences in Adélie penguin foraging strategies. *Polar Biol.* 20:248–258.
- David M, Auclair Y, Giraldeau L-A, Cézilly F. 2012. Personality and body condition have additive effects on motivation to feed in Zebra Finches *Taeniopygia guttata*. *Ibis (Lond. 1859).* 154:372–378.
- Desrochers A. 1992. Age and foraging success in European blackbirds: variation between and within individuals. *Anim Behav.* 43:885–894.
- Dingemanse N. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim Behav.* 64:929–938.
- Dingemanse NJ, Kazem AJ, Réale D, Wright J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol Evol.* 25:81–89.
- Dosmann AJ, Brooks KC, Mateo JM. 2015. Within-individual correlations reveal link between a behavioral syndrome, condition and cortisol in free-ranging Belding's ground squirrels. *Ethology.* 121:125–134.
- Fieberg J, Kochanny CO. 2005. Quantifying home-range overlap: the importance of the utilization distribution. *J Wildl Manage.* 69:1346–1359.
- Fretwell SD, Lucas HLJ. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.* 19:16–36.
- Fridolfsson A-K, Ellegren H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *J Avian Biol.* 30:116.
- Geary B, Walter ST, Leberg PL, Karubian J. 2018. Data from: condition-dependent foraging strategies in a coastal seabird: evidence for the rich get richer hypothesis. *Behav Ecol.* doi:10.5441/001/1.212g53s7
- Geary B, Walter ST, Leberg PL, Karubian J. 2019. Data from: condition-dependent foraging strategies in a coastal seabird: evidence for the rich get richer hypothesis. Dryad Digital Repository. doi:10.5061/dryad.5tb3312
- van Gils JA, Munster VJ, Radersma R, Liefhebber D, Fouchier RA, Klaassen M. 2007. Hampered foraging and migratory performance in swans infected with low-pathogenic avian influenza A virus. *PLoS One.* 2:e184.
- Halsey LG, Shepard EL, Quintana F, Gomez Laich A, Green JA, Wilson RP. 2009. The relationship between oxygen consumption and body acceleration in a range of species. *Comp Biochem Physiol A Mol Integr Physiol.* 152:197–202.
- Halsey LG, Shepard EL, Wilson RP. 2011. Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comp Biochem Physiol A Mol Integr Physiol.* 158:305–314.
- Irons DB. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology.* 79:647–655.
- Kotler BP, Brown JS. 1988. Environmental heterogeneity and the coexistence of desert rodents. *Annu Rev Ecol Syst.* 19:281–307.
- Lamb J, Satgé Y, Jodice P. 2017. Diet composition and provisioning rates of nestlings determine reproductive success in a subtropical seabird. *Mar Ecol Prog Ser.* 581:149–164.
- Langseth BJ, Purcell KM, Craig JK, Schueller AM, Smith JW, Shertzer KW, Creekmore S, Rose KA, Fennel K. 2014. Effect of changes in dissolved oxygen concentrations on the spatial dynamics of the Gulf menhaden fishery in the northern Gulf of Mexico. *Mar Coast Fish.* 6:223–234.
- Lescroël A, Ballard G, Toniolo V, Barton KJ, Wilson PR, Lyver PO, Ainley DG. 2010. Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology.* 91:2044–2055.
- Manly BJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002. Resource selection by animals: statistical design and analysis for field studies. *Technology.* 221. doi:10.1007/0-306-48151-0
- Marchetti K, Price T. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biol Rev.* 64:51–70.
- Matthiopoulos J. 2003. The use of space by animals as a function of accessibility and preference. *Ecol Modell.* 159:239–268.
- Morand-Ferron J, Giraldeau LA, Lefebvre L. 2007. Wild Carib grackles play a producer-scrouter game. *Behav Ecol.* 18:916–921.
- Nakagawa S, Schielzeth H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol Rev Camb Philos Soc.* 85:935–956.
- Orians GH, Pearson NE. 1979. On the theory of central place foraging. *Columbus: Anal. Ecol. Syst. Ohio State Univ. Press:*155–177.
- Parrish JD. 1997. Patterns of frugivory and energetic condition in Nearctic landbirds during autumn migration. *Condor.* 99:681–697.
- Patrick SC, Bearhop S, Grémillet D, Lescroël A, Grecian WJ, Bodey TW, Hamer KC, Wakefield E, Le Nuz M, Votier SC. 2014. Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *OIKOS.* 123:33–40.
- Patrick SC, Charmantier A, Weimerskirch H. 2013. Differences in boldness are repeatable and heritable in a long-lived marine predator. *Ecol Evol.* 3:4291–4299.
- Patrick SC, Weimerskirch H. 2014. Personality, foraging and fitness consequences in a long lived seabird. *PLoS One.* 9:e87269.
- Piatt J, Harding A, Shultz M, Speckman S, van Pelt T, Drew G, Kettle A. 2007. Seabirds as indicators of marine food supplies: cairns revisited. *Mar Ecol Prog Ser.* 352:221–234.
- Piatt J, Sydeman W. 2007. Seabirds as indicators of marine ecosystems. *Mar Ecol Prog Ser.* 352:199–204.
- Piersma T, van Gils JA. 2011. The flexible phenotype: a body-centred integration of ecology, physiology, and behaviour. *Oxford: Oxford University Press.*
- Pyke G. 1984. Optimal foraging theory: a critical review. *Annu Rev Ecol Syst.* 15:523–575.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed December 5, 2018.
- Rigby RA, Stasinopoulos DM. 2005. Generalized additive models for location, scale and shape (with discussion). *Appl Stat.* 54:507–554.
- Rita H, Ranta E, Peuhkuri N. 1996. Competition in foraging groups. *OIKOS.* 76:583–586.
- Royauté R, Dochtermann NA. 2017. When the mean no longer matters: developmental diet affects behavioral variation but not population averages in the house cricket (*Acheta domestica*). *Behav Ecol.* 28:337–345.
- Ruckstuhl KE. 1998. Foraging behaviour and sexual segregation in bighorn sheep. *Anim Behav.* 56:99–106.
- Schoener TW. 1971. Theory of feeding strategies. *Annu Rev Ecol Syst.* 2:369–404.
- Selman W, Hess TJ, Linscombe J. 2016. Long-term population and colony dynamics of brown pelicans (*Pelecanus occidentalis*) in rapidly changing coastal Louisiana, USA. *Waterbirds.* 39:45–57.
- Shepard EL, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB. 2013. Energy landscapes shape animal movement ecology. *Am Nat.* 182:298–312.
- Shields M. 2014. Brown Pelican: *pelecanus occidentalis*. In: Poole A, Gill F, editors. *The birds of North America*. Ithaca (NY): Cornell Lab of Ornithology.
- Sih A. 1984. Optimal behavior and density-dependent predation. *Am. Nat.* 123:314–326.
- Stamps JA. 2016. Individual differences in behavioural plasticities. *Biol Rev Camb Philos Soc.* 91:534–567.
- Thiebault A, Mullers R, Pistorius P, Meza-Torres MA, Dubroca L, Green D, Tremblay Y. 2014. From colony to first patch: processes of prey searching and social information in Cape Gannets. *Auk.* 131:595–609.
- Thiebault A, Mullers RHE, Pistorius PA, Tremblay Y. 2014. Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. *Behav Ecol.* 25:1302–1310.
- Thums M, Bradshaw CJ, Sumner MD, Horsburgh JM, Hindell MA. 2013. Depletion of deep marine food patches forces divers to give up early. *J Anim Ecol.* 82:72–83.

- Tremblay Y, Thiebault A, Mullers R, Pistorius P. 2014. Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. *PLoS One*. 9:e88424.
- Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J. 2010. Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *J Appl Ecol*. 47:487–497.
- Walter ST, Carloss MR, Hess TJ, Leberg PL. 2013. Hurricane, habitat degradation, and land loss effects on brown pelican nesting colonies. *J Coast Res*. 29:187–195.
- Walter ST, Karubian JK, Dindo JJ. 2014. Factors influencing brown pelican (*Pelecanus occidentalis*) foraging movement patterns during the breeding season. *Can J Zool*. 92:885–891.
- Ward P, Zahavi A. 1973. The importance of certain assemblages of birds as “information-centres” for food-finding. *Ibis (Lond)*. 115:517–534.
- Watanabe Y, Reyier E, Lowers R, Imhoff JI, Papastamatiou YP. 2013. Behavior of American alligators monitored by multi-sensor data loggers. *Aquat Biol*. 18:1–8.
- Weimerskirch H. 1998. How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. *J Anim Ecol*. 67:99–109.
- Wiens JA. 1976. Population responses to patchy environments. *Annu Rev Ecol Syst*. 7:81–120.
- Wilson RP, Quintana F, Hobson VJ. 2012. Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc Biol Sci*. 279:975–980.
- Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ. 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J Anim Ecol*. 75:1081–1090.