



Traveling to thermal refuges during stressful temperatures leads to foraging constraints in a central-place forager

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Central-place foragers can be constrained by the distance between habitats. When an organism relies on a central place for thermal refuge, the distance to food resources can potentially constrain foraging behavior. We investigated the effect of distance between thermal refuges and forage patches of the cold-intolerant marine mammal, the Florida manatee (*Trichechus manatus latirostris*), on foraging duration. We tested the alternative hypotheses of time minimization and energy maximization as a response to distance between habitats. We also determined if manatees mitigate foraging constraints with increased visits to closer thermal refuges. We used hidden Markov models to assign discrete behaviors from movement parameters as a function of water temperature and assessed the influence of distance on foraging duration in water temperatures above ($> 20^{\circ}\text{C}$) and below ($\leq 20^{\circ}\text{C}$) the lower critical limit of the thermoneutral zone of manatees. We found that with increased distance, manatees decreased foraging duration in cold water temperature and increased foraging duration in warmer temperatures. We also found that manatees returned to closer thermal refuges more often. Our results suggest that the spatial relationship of thermal and forage habitats can impact behavioral decisions regarding foraging. Addressing foraging behavior questions while considering thermoregulatory behavior implicates the importance of understanding changing environments on animal behavior, particularly in the face of current global change.

Key words: behavioral thermoregulation, central-place foraging, Florida manatee, foraging theory, hidden Markov model, thermal refuge, *Trichechus manatus latirostris*

A common assumption in foraging ecology is that foragers maximize energetic gains while minimizing costs (Stephens and Krebs 1987). Central-place foragers are a particular example where foraging theory predicts aspects of behavioral costs associated with traveling back and forth between forage locations and a central place (e.g., nest site, cover—Orians and Pearson 1979). In central-place foraging, costs can include predation risk (Kie 1999), missed opportunities of prey items or mates in other forage patches (Shochat et al. 2004; Olsson and Bolin 2014), and the cost of travel to forage patches (Chapman et al. 1989). The cost of travel influences time-energy budgets; greater distances require more movement and therefore have higher energetic costs. Greater distances can also increase exposure to predation or stressful abiotic conditions and reduce the amount of time available for obtaining food (Chapman et al. 1989). Thus, central-place foragers tend to maximize energy

gains in farther forage patches to offset the greater cost of travel (Kacelnik 1984).

Though the effects of predation risk on foraging behavior in central-place foragers are well known (Martindale 1982; Vásquez 1994; Kie 1999; Bakker et al. 2005), the effects of energetic constraints associated with abiotic factors, such as temperature, are less understood. It is possible that thermoregulatory costs may outweigh foraging needs when environmental temperatures are outside the thermoneutral zone (the range of temperatures that allow for homeostasis—Scholander et al. 1950) of an animal. In these instances, the central place may act as a thermal refuge if the habitat can maintain a microclimate within the thermoneutral zone (McArthur 1987; Huey 1991). Short-term use of thermal refuges may lead to decreased energy expenditure compared to other thermoregulatory strategies, such as panting (Bustamante et al. 2002; Bacigalupi et al.

2003). However, long-term use may constrain foraging and decrease fitness if thermal refuges lack abundant or quality forage resources (Bozinovic and Vásquez 1999; Kenagy et al. 2002a; du Plessis et al. 2012). Thermal refuges limit foraging duration in central-place foragers such as degus (*Octodon degus*—Melcher et al. 1990; Kenagy et al. 2002a, 2002b), but none of these analyses considered the effect of distance to foraging resources on foraging behavior. In large mammals, such as wild boar (*Sus scrofa*—Choquenot and Ruscoe 2003) and the Florida manatee (*Trichechus manatus latirostris*—Haase et al. 2017), distance dictated forage patch selection, but these studies did not determine the effect of distance on foraging duration (i.e., patch residence time) within these habitats. Greater distances result in greater energetic costs, and must be balanced against energetic gains, such as time spent foraging within patches of food resources.

The Florida manatee is a species that can be used to test hypotheses regarding the constraints thermoregulation may impose on foraging behavior. Florida manatees are limited during the winter to the southern area of their distribution due to their high sensitivity to cold water temperature (Irvine 1983). On account of their low metabolic rate (measured rates are 25–30% of expected rates predicted by body size), manatees are intolerant to water temperatures below 20°C (Irvine 1983). Manatees become central-place foragers in the winter, and make repeated trips between their primary food resource (i.e., seagrass) and warm-water thermal refuges found in inland natural spring systems or the outflows of power plants (Laist and Reynolds 2005; Laist et al. 2013). These warm-water thermal refuges usually lack sufficient forage resources, and thus manatees often travel as far as 50 km to forage habitats (Barton 2006; Deutsch et al. 2006).

Prolonged or repeated exposure to water temperatures < 20°C makes it difficult for manatees to regulate their body temperature and can initiate cold stress syndrome (CSS—Bossart 2001; Bossart et al. 2002). Manatees suffering from CSS become lethargic, which results in dehydration and depletion of fat stores as foraging intake is reduced or even completely ceases (Bossart 2001). Immune function is also compromised with the onset of CSS and increases the chance of infection from disease or pathogens (Bossart et al. 2002). Although the Florida manatee was recently reclassified to “threatened” from the previous designation of “endangered” under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2017), continued protection of this species requires understanding the relationship between behavior and the spatial distribution of habitats.

The energetic trade-offs between foraging and maintaining thermal balance likely impose strong selective pressures on manatee behavior and habitat use. We therefore evaluated the effect of distance between forage patches (seagrass beds) and their central place (warm-water refuges) on the foraging behavior of the Florida manatee. The cost of travel associated with greater distances should result in increased foraging duration in farther seagrass beds to offset the energetic cost (i.e., energy maximization—Belovsky 1984). However, because of

the thermoregulatory cost of traveling and foraging in water temperatures below their lower critical threshold, manatees may alternatively reduce foraging duration in farther seagrass habitats to minimize exposure to thermal stress (i.e., time minimization—Belovsky and Slade 1986). We therefore predicted different effects in regard to water temperature: when water temperature is > 20°C, manatees would maximize energy and forage longer in farther seagrass beds, while temperatures < 20°C would constrain foraging to shorter bouts in farther habitats. Furthermore, if foraging duration is limited by travel distance, then we also predicted that manatees would mitigate these constraints by visiting closer seagrass beds more often than farther seagrass beds.

MATERIALS AND METHODS

Study area.—The study area encompassed the coastal system of southwestern Florida along the Gulf of Mexico, including Everglades National Park, Big Cypress National Preserve, the Ten Thousand Islands National Wildlife Refuge, and the Fakahatchee Strand State Preserve (Fig. 1). Mangrove forests are the major habitat type within the system, with the dominant species being the red mangrove (*Rhizophora mangle*). Inland shallow bays and riverine systems break up the forests, providing soft and hard bottom substrate for numerous seagrass species and macroalgae (Hartman 1979; Slone et al. 2013). Access to vegetation inshore often is limited, as most of the study area is too deep and too dark to support submerged aquatic vegetation (Packard and Wetterqvist 1986). Manatees can feed on overhanging vegetation along banks, such as leaves from red mangroves (Allen et al. 2018); however, these forage resources are not preferred and are only foraged upon when temperatures are too cold for manatees to travel (Spiegelberger and Ganslosser 2005). To escape cold water in our study area, manatees rely on passive thermal basins (Laist and Reynolds 2005), which are small pockets of warm water found inland and within bays. The warmth from passive thermal basins is generated and maintained in various ways: by shallow areas with muddy bottoms that absorb solar heat throughout the day, deep depressions that hold warm water, or inverted haloclines formed by the trapping of warm saltwater under a layer of cold freshwater from rivers or man-made weirs (Stith et al. 2011).

Data collection.—Forty free-ranging manatees were captured according to the methods outlined in Weigle et al. (2001), tagged, and tracked (Marmontel et al. 2012) in the study area from 2002 to 2008. All manatees were captured and released within the same day to limit the effect of captivity on behavior. We also did not use any data from manatees that were captured for rehabilitation purposes. The tag apparatus consisted of a floating, satellite-linked Argos—GPS tag (TMT-460 or TMT-462; Telonics, Inc., Mesa, Arizona) that was attached to a belt around the caudal peduncle of the animal by a nylon tether (Slone et al. 2017). The tag was required to be at the water surface to receive a GPS signal. There was a single release point on the tether that would allow the

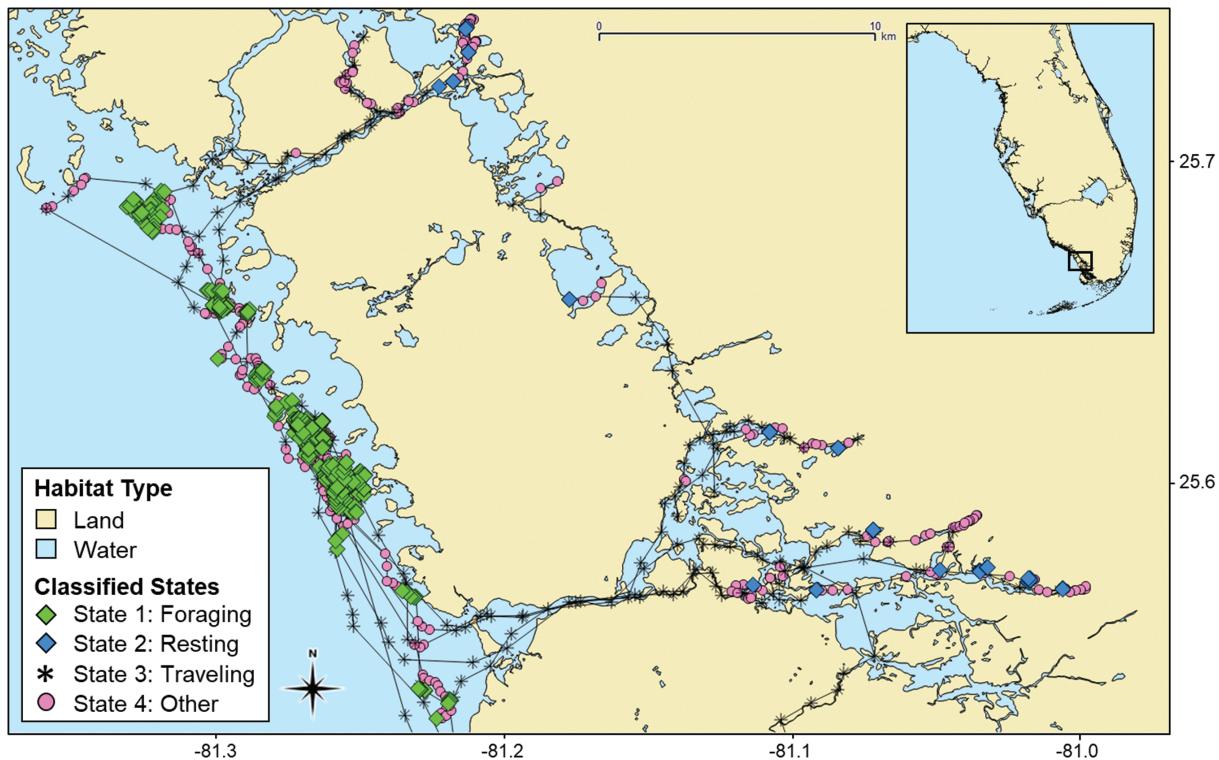


Fig. 1.—An example movement track of a Florida manatee (*Trichechus manatus latirostris*) and the predicted behaviors for each GPS location. Box indicates highlighted region.

animal to break free if the tag became entangled (Reid et al. 1995). Tags remained on the manatee until they broke off, were replaced in water by researchers, or until the animal was recaptured and retagged. Devices were set to record GPS locations every 30–60 min. GPS location data were obtained by download from recovered tags or by relay through the Argos link (<http://www.argos-system.org>). Ninety-five percentage of locations were recorded with < 5-m accuracy (S lone et al. 2013). We filtered telemetry data to remove fixes before and after the tag was on the animal.

Thermal refuge locations were previously mapped from repeated observations of manatee use during the winter by the USGS (J. P. Reid and D. H. S lone, pers. obs.) using methods described by S lone et al. (2018). More specifically, S lone and colleagues determined thermal refuge use areas by quantifying the top 10% of a kernel density analysis of movement paths during cold temperatures (< 20°C) < 200 m in length and < 0.2 km/h in speed (S lone et al. 2018). We calculated the distance from each GPS location to weather stations managed by the USGS National Water Information System (<https://waterdata.usgs.gov/nwis>) or the South Florida Water Management District (<http://my.sfwmd.gov/dbhydrosql>) in ArcGIS 10.3 (ESRI 2011) and linked water temperature (°C) from the closest weather station (< 10 km) at the date and time of each location to represent ambient conditions.

Data analysis.—We used a hidden Markov model (HMM), a form of a state-space model that can be used to classify discrete “hidden” or latent behavioral states that cannot be directly observed (Patterson et al. 2009). HMMs use observed

variables (e.g., animal movement data), with the assumption that those observed variables are a representation of the hidden state (Langrock et al. 2012b). Typically, HMMs applied in animal movement analyses utilize step lengths and relative turning angles between successive GPS points (i.e., time step) to classify states (Patterson et al. 2009). For each time step, the HMM can estimate the probability of each hidden behavioral state given the observed movement variable distributions for that state (Michelot et al. 2016). In a mixture model framework, the hidden states assume a first-order Markov process and thus the probability of each state is dependent on the previous hidden state. HMMs therefore consist of the initial transition probabilities from state i to state j at time t , γ_{ijt} , defined by

$$\gamma_{ijt} = \Pr(S_{t+1} = j | S_t = i), i, j = 1, \dots, N \quad (1)$$

where S_{t+1} is the unobserved state at time $t + 1$, S_t is the observed state at time t , and N is the total number of states (Langrock et al. 2012a).

The probability of transitioning from one state to another can often be a function of time-varying covariates (Michelot et al. 2016), in which the estimation of covariate parameters can be incorporated via the multinomial logit link in calculating transition probabilities. With N states,

$$\gamma_{ijt} = \Pr(S_{t+1} = j | S_t = i) = \frac{\exp(n_{ij})}{\sum_{k=1}^N \exp(n_{ik})} \quad (2)$$

Where

$$n_{ij} = \begin{cases} \beta_0^{(ij)} + \sum_{l=1}^p \beta_1^{(ij)} \omega_{lt} & \text{if } i \neq j, \\ 0 & \text{otherwise.} \end{cases} \quad (3)$$

Here ω_{lt} is the l -th covariate at time t and p is the number of covariates considered (Michelot et al. 2016). The HMM estimates parameters using a recursive algorithm, which maximizes the expected log-likelihood of the state given the observed variables (Langrock et al. 2012a; Michelot et al. 2016). In a four-state model, there are 32 parameters estimated: the initial probabilities of each state, the transition probabilities between each state, and the parameters describing the movement tracks (step length and turning angles). These parameters are then used to assign the most probable state at each time step given the transition probabilities using the Viterbi algorithm (Viterbi 1967; Michelot et al. 2016).

We used package *moveHMM* (Michelot et al. 2016) in R version 3.5.2 (R Core Team 2019) to fit a four-state model given previous assumptions on manatee behavior, with states representing “traveling,” “foraging,” “resting” (assuming thermoregulation), and “other” behaviors (Castelblanco-Martínez et al. 2015). Due to the unequal fix intervals associated with GPS tagging of diving marine mammals (Slone et al. 2013), there are often missing data. We first used package *amt* to predict missing locations based on a continuous-time correlated random walk (Johnson et al. 2008) and resampled the data to 1-h intervals within a 15-min window. Correlated random walks assume autocorrelation in animal movement and predict the next location based on the previous step distance and turning angles. We assumed missing locations would occur in water and not land. If a significant period of time was missing between steps (> 6 h), we split the movement track into separate “bursts” to be analyzed as two different movement paths. We then calculated the step distance and turning angles between successive GPS points within each time step. We filtered erroneous data by removing locations that were greater than 10 km from the previous location (akin to maximum manatee traveling speeds). We treated these instances as separate bouts. We filtered the data to only include November–March, as we were only interested in responses to cold water during winter months (Stith et al. 2011). We fit the HMMs with *fitHMM* using a Gamma distribution to describe step length and a von Mises distribution to describe turning angles (Supplementary Data SD1; McClintock and Michelot 2018). Though Gamma distributions do not account for zeroes, there were no zero step lengths because even if a manatee did not move, subsequent GPS locations would not be the exact same location due to tag movement. We determined priors for both distributions (Supplementary Data SD1) for each behavior given assumptions of manatee movement during behaviors observed in previous studies (Slone et al. 2013, 2018; Castelblanco-Martínez et al. 2015).

We included covariates that potentially described the probability of transitioning between different behavioral states in four candidate HMMs. Our null model included a factor distinguishing between cold ($\leq 20^\circ\text{C}$) and warm ($> 20^\circ\text{C}$) water

temperatures, as we assumed behavior would differ below or above the lower critical temperature. We created three additional HMMs with this factorial effect and other covariates: 1) continuous water temperature, 2) distance between thermal and forage habitats, and 3) interaction between continuous water temperature and distance between habitats (Supplementary Data SD1). We used Akaike’s information criteria (AIC) to evaluate the strength of support for each HMM (Burnham and Anderson 2002) and selected the HMM with the lowest AIC score.

Each time step was designated the state with the highest probability given the Viterbi algorithm (Viterbi 1967; Michelot et al. 2016) from the top HMM. We classified each state as a specific behavior by summarizing the mean step length and turning angle of each state and compared our classifications to previous analyses classifying manatee behavior based on step lengths (Slone et al. 2013; Castelblanco-Martínez et al. 2015). We validated the behavioral classifications by comparing opportunistic observations of tagged manatees that coincided with the time and date of GPS locations of a predicted behavior ($n = 53$ observations). Every time a tagged manatee was observed during other field sampling, the date, time, and behavior was recorded. The observed behaviors were grouped into foraging, resting in a thermal refuge (assumed thermoregulation), traveling, or other behaviors. Other behaviors included milling, cavorting, or searching. We then compared the observed behaviors to the behavior predicted for the successive GPS locations at the time of observation.

To test our competing foraging duration hypotheses, we aggregated the behavioral tracks into “bouts” of continuous periods of time where the manatee remained within a single behavior (Bennison et al. 2018). As we were interested in how distance between forage and thermal habitats played a role on foraging behavior, we limited our analysis to those foraging bouts that were succeeded by travel to a thermal refuge (classified as “resting” behavior). We also collapsed foraging bouts with short travel in between (< 1 h) into a single foraging bout. We calculated the mean ambient temperature for each of these aggregated bouts. We used the *gdistance* package to calculate the distance from the last foraging bout location to the thermal refuge used for the successive resting behavior; distances were calculated by water route around land to consider the appropriate travel path of the manatee (Haase et al. 2017). We fit generalized linear mixed models in R package *lme4* (Bates et al. 2010) to contrast the effects of travel distance from thermal refuges on foraging duration during cold ($\leq 20^\circ\text{C}$) and warm ($> 20^\circ\text{C}$) water temperatures. We fit the models with a Gamma distribution for the response variable of foraging duration to determine the influence of distance to thermal refuges.

To test our foraging visitation prediction, we calculated the number of visits per forage patch by counting the number of continuous foraging bouts per seagrass habitat patch. We then fit a generalized linear mixed model to those visits that were preceded by resting behaviors as described above. We used a Poisson distribution for the response variable to determine the effect of travel distance on the number of visits to forage habitats. We included manatee ID as a random effect on the

intercept to control for the effect of individual characteristics on behavior and centered travel distance on the mean and scaled by standard deviation in all models. We calculated the marginal R^2 values associated with generalized linear mixed models with methodology described by Nakagawa and Schielzeth (2013).

RESULTS

We tracked each manatee for a mean of 141 ($\pm 117\text{ SD}$) days; two individuals that were tracked < 14 days were removed and therefore reduced our sample size from 40 to 38 individuals. The mean number of successful GPS locations per animal was 5,516 ($\pm 5,339$) locations, with a total of 209,582 locations used in the analyses. The number of missing locations varied among individuals (range: 1–222 locations) and were dependent on the duration of time each manatee was tracked. Missing locations made up 1.10% of all fix attempts, and also varied by individual (range: 0.15–4.95%). We treated tracks with more than four consecutive missing locations (i.e., 6 h) as separate bursts, with the number of bursts per individual also dependent on the tracking duration (1–57 bursts).

The four-state HMM included what we refer to as “traveling” (mean step length across all individuals: $1.21 \pm 0.90\text{ SD km}$; 25% quantile: 0.67 km, 75% quantile: 1.41 km), “foraging” (step length: $0.15 \pm 0.08\text{ km}$; 25% quantile: 0.08 km, 75% quantile: 0.20 km), “resting” (step length: $0.10 \pm 0.16\text{ km}$; 25% quantile: 0.01 km, 75% quantile: 0.40 km), and “other” (step length: $0.82 \pm 0.92\text{ km}$; 25% quantile: 0.48 km, 75% quantile: 0.95 km) behaviors (Figs. 1 and 2). The approximate threshold of step length that separated traveling behavior from other activity was approximately 1 km; both resting and foraging states never had step lengths above 1 km, and the “other” state was below 1 km 78.00% of the time. The top HMM model included the covariate of water temperature factored into “low” and “warm” levels (Supplementary Data SD1). This HMM resulted in manatees resting $36.73 \pm 10.25\%$ of the time, foraging $50.64 \pm 9.00\%$, traveling $11.87 \pm 5.20\%$, and spent $0.80 \pm 0.63\%$ of the time in other behaviors. During cold temperatures ($\leq 20^\circ\text{C}$), manatees were resting $52.05 \pm 19.02\%$ of the time, foraging $33.98 \pm 19.29\%$, traveling $13.52 \pm 7.85\%$, and spent $0.46 \pm 0.76\%$ of the time in other behaviors. During warm temperatures ($> 20^\circ\text{C}$), manatees were resting $36.23 \pm 10.37\%$ of the time, foraging $50.01 \pm 9.24\%$, traveling $12.01 \pm 5.37\%$, and spent $1.66 \pm 0.63\%$ of the time in other behaviors. Most foraging behaviors occurred outside of the inland riverine channels; there were some instances where inland states were classified as foraging behavior (3.20%). We removed these fixes from the analysis ($n = 6,706$) as we were unable to determine if these were foraging events or misclassified resting behaviors. All resting behaviors occurred inland and travel and other behaviors occurred all over the study area (Fig. 1). We observed behaviors of tagged manatee on 53 occasions. Our visual validation protocol suggested that 84.91% of the behavior states were classified correctly by the HMM (Table 1). The behavior that was misclassified the most was foraging behavior (16.5% incorrectly classified as traveling); the model often classified foraging behavior as traveling when

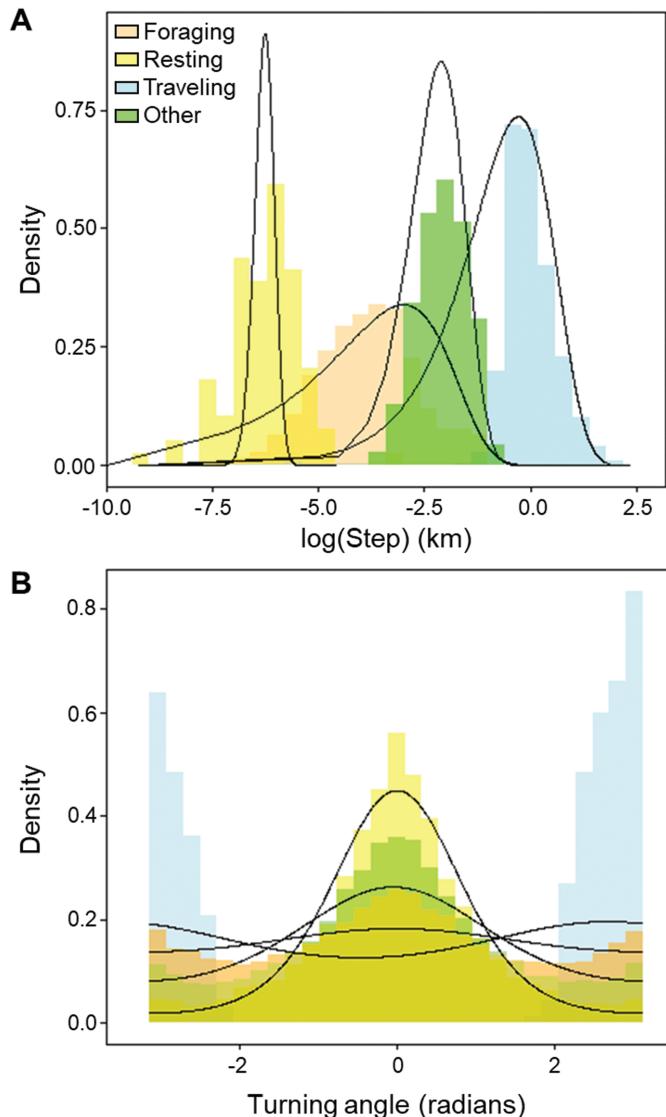


Fig. 2.—Density histograms and fitted distributions for (A) step length (km) and (B) turning angle (radians) for each state of the top four-state model fitted to movement parameters of the Florida manatee (*Trichechus manatus latirostris*). Step velocities were fitted using a Gamma distribution and turning angles were fitted using a von Mises distribution. Step lengths were natural logged for visualization.

manatees foraged while moving at fast speeds. We collapsed the classified GPS locations into 5,799 total foraging bouts across the study period, with 2,278 bouts used in the cold water analysis and 3,521 bouts in the warm water analysis.

As expected by foraging theory, manatees increased foraging duration within seagrass beds farther from thermal refuges when water temperature was greater than the 20°C critical threshold ($\beta = 0.25 \pm 0.03$, $P < 0.001$, $R^2_{GLMM(m)} = 0.24$; Fig. 3A). The mean distance traveled to foraging locations during warm temperature was $19.34 \pm 14.50\text{ km}$. In water temperature $\leq 20^\circ\text{C}$, manatees decreased the amount of time spent foraging in seagrass patches at farther distances from thermal refuges ($\beta = -0.18 \pm 0.08$, $P < 0.01$, $R^2_{GLMM(m)} = 0.27$; Fig. 3B). The mean distance traveled to foraging locations during cold temperature was $11.71 \pm 10.60\text{ km}$. Manatees also increased the

Table 1.—The percentage (%) of 53 behavioral observations classified by the hidden Markov model determining behavior of the Florida manatee (*Trichechus manatus latirostris*). Values with asterisks indicate incorrect classifications.

Classified behavior	Observed behavior			
	Foraging (n = 24)	Resting (n = 19)	Traveling (n = 8)	Other (n = 2)
Foraging	83.5	4.8*		
Resting		90.5		
Traveling	16.5*		87.5	50.0*
Other		4.8*	12.5*	50.0

number of visits to seagrass patches that were closer to thermal refuges ($\beta = -0.21 \pm 0.02$, $P < 0.001$, $R^2_{GLMM(m)} = 0.45$; Fig. 3C), as expected.

DISCUSSION

Reliance on thermal refuges that lack foraging resources results in central-place foraging behaviors that are driven by travel distance between habitats. In the case of the Florida manatee, individuals balance energy acquisition (foraging in seagrass beds) with conserving energy (resting in thermal refuges). In water temperatures above the critical threshold of 20°C, foraging duration is driven by the distance between seagrass beds and thermal refuges, as predicted by foraging theory. When water temperatures are less than the threshold, however, foraging duration is constrained by distance, and decreases the farther seagrass beds are from thermal refuges. Finally, manatees mitigate these constraints by visiting closer beds more often than farther beds.

Including the response to temperature in analyses of foraging behavior allowed us to parse apart differences in behavior between nonstressful and stressful environmental situations. As predicted by foraging theory, manatees increased foraging duration in seagrass beds that were farther from thermal refuges during nonstressful conditions ($> 20^\circ\text{C}$; Fig. 3A). Manatees often are observed to forage 2.5–8.2 h/day when not required to use thermal refuges (Bengston 1981, 1983). Longer foraging bouts can potentially sustain manatee metabolism during periods of extended refuge use due to the digestion of forage (Hudson 1985; Rosen et al. 2007). However, when foraging in water temperatures below their critical threshold ($\leq 20^\circ\text{C}$), manatees reduced foraging efforts when they were required to travel greater distances between resources (Fig. 3B). These different effects between cold ($\leq 20^\circ\text{C}$) and warm ($> 20^\circ\text{C}$) water may be attributed to the low metabolic rate of the manatee compared to other marine mammals of similar body size (Irvine 1983)—suggesting that manatees can only maintain thermal balance within a cold environment for a short period of time before returning back to thermal refuges. These effects would then derive shorter foraging bouts in seagrass beds that are farther from thermal refuges.

Farther travel distances between habitats may result in greater thermoregulatory costs due to increased exposure to cold water temperature during the time it would take for travel. Manatees increased visitation to closer seagrass beds, perhaps to make up for foraging constraints. Similar responses to stressful environmental temperatures have been observed in other mammalian species, including antelope ground squirrels (*Ammospermophilus leucurus*—Chappell and Bartholomew

1981), moose (*Alces alces*—Belovsky and Slade 1986), and wild boar (*S. scrofa*—Choquenot and Ruscoe 2003). In these species, less time is spent outside thermal refuges during times of peak thermal stress (Bozinovic and Vásquez 1999; Bacigalupo et al. 2003) but it is unknown if the distance between forage and thermal resources would also impact activity budgets in these species as the models were not spatially explicit.

We can quantify the effects of thermal heterogeneity on foraging behavior through a combination of biophysical, spatial, and behavioral methods (Karasov 1986; Krebs et al. 1993; Bacigalupo and Bozinovic 2002; Aublet et al. 2009). Statistical models such as HMMs have been extensively used to classify behavior based on characterization of movement data (Jonsen et al. 2005; Patterson et al. 2009; Langrock et al. 2012b). Though these methodologies have been vetted extensively (Nathan et al. 2008; Schick et al. 2008), there could still potentially be error in the model due to other behaviors of manatees that are difficult to classify based on movement data alone, such as mating, drinking, and cavorting with conspecifics (Castelblanco-Martínez et al. 2015). We make the assumption that foraging bouts only occurred offshore, and that all resting behaviors occurred in warm-water refuges inland.

We did not consider the effect of forage quality or intake quantity on behavior within our analyses. We assumed manatees were foraging the entire duration of each foraging bout, which may not always be the case. Inclusion of caloric content of consumed forage species could provide a better means to explicitly quantify a time-energy budget for manatees and allow for the variation in forage species to alter our predictions. Likewise, manatees may forage in areas outside of seagrass beds, such as on algae or overhanging bank vegetation (Spiegelberger and Ganslosser 2005; Allen et al. 2018) as observed in related manatee species. Our model did classify foraging events inland, which may or may not be true foraging events. We constrained our analyses to foraging on in seagrass beds, though manatees may alter their thermoregulatory behavior if they can find forage near or within thermal refuges. Further research into describing explicit foraging behavior and species-specific energy content would strengthen our predictions.

Behavioral responses to stressful environmental conditions are complex and therefore resource selection studies should consider the effects of abiotic factors when managing for thermally intolerant species. The incorporation of thermal ecology into foraging theory allowed us to assess how a patchy seascape of foraging and thermal habitats can influence foraging behaviors. Given the current threatened status of manatees in the southeastern United States, evaluating the relationship

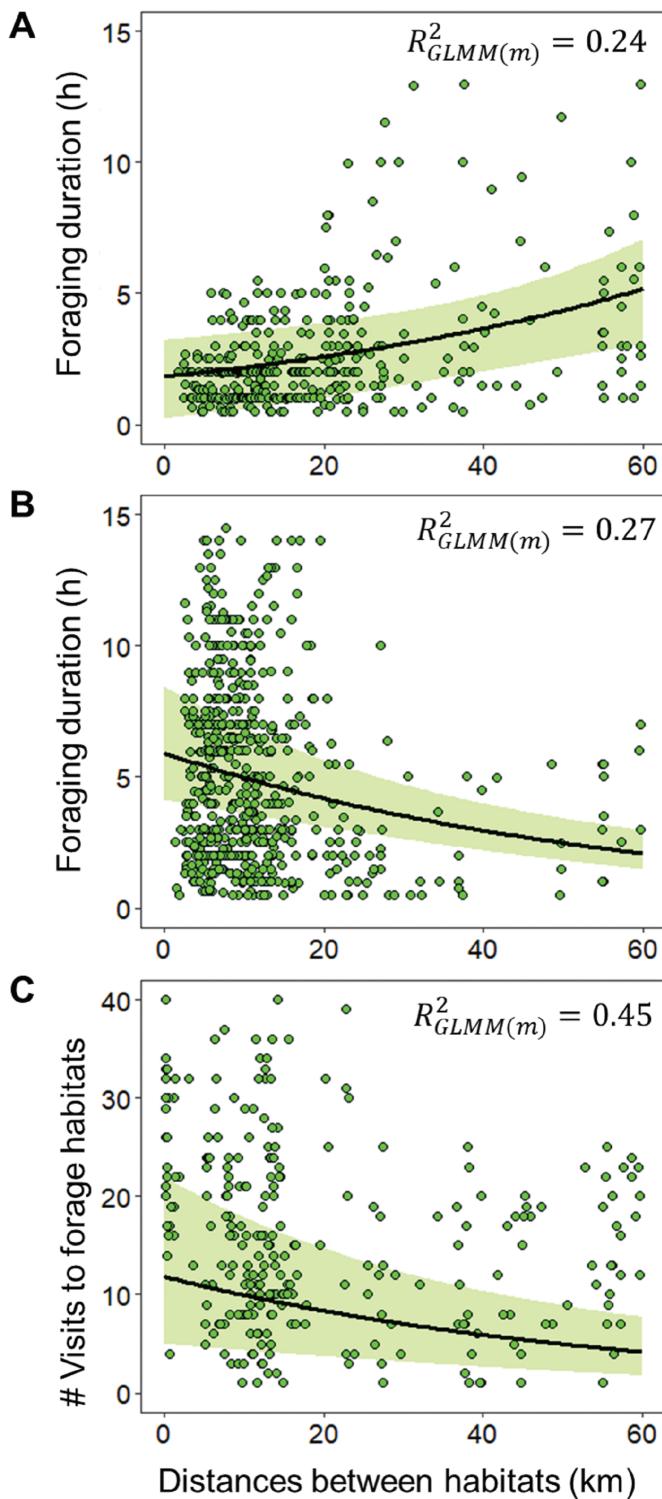


Fig. 3.—Foraging duration (h) of the Florida manatee (*Trichechus manatus latirostris*) as a function of the distance to thermal refuge (km) in water temperature (A) above and (B) below the 20°C critical threshold, and (C) the number of visits to foraging patches as a function of distance to thermal refuge (km) when water temperature was below the 20°C critical threshold. Distances were measured with respect to land and represent waterway distance. Black lines represent predicted duration and shading represents 95% confidence intervals. All predictions are from models contained manatee ID as a random effect on the intercept. Marginal R^2 values are reported (s).

between foraging behavior, the spatial distribution of habitats, and critical temperature thresholds is imperative to properly managing their habitats. Currently, highly used warm-water refuges located from the outflows of coastal power plants are under threat of potential closures (Laist and Reynolds 2005). The uncertainty of the future availability of these critical habitats is of management concern for manatee populations that rely on these areas for thermal refuge. As our results emphasize that manatees can be constrained in foraging efforts due to the distance between thermal refuges and seagrass beds, any change in the availability of warm water may seriously affect the population (Laist et al. 2013; Haase 2016).

The importance of spatial variation in temperature at a micro-climate scale is becoming more apparent as animals respond to changes in local climates across the planet (Sears et al. 2011). Decisions to allocate time and energy toward different behaviors are dictated by the balance of energy expenditure with energy procurement (Belovsky 1986; McNamara and Houston 1986). When species rely on two different resources that are spatially separated, incorporating this spatial relationship into behavior models may more appropriately explain variation in activity times and habitat use (Haase et al. 2017). Integrating thermal ecology into our understanding of animal behavior can therefore shed light on the impacts of global change (Walther et al. 2002; Parmesan and Yohe 2003). With the onset of shifting climatic regimes, quantifying the relationship between environmental temperature and behavioral decisions is critical to understand the effects of climate change on animal processes and population dynamics (Walther et al. 2002).

DATA ACCESSIBILITY

The data are not available for archiving because they are sensitive locality data for threatened species.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Supplementary tables and figures associated with the hidden Markov models.

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