



Quality of thermal refuges influences use by the cold-intolerant Florida manatee

Catherine G. Haase^{1,2,4,*}, Robert J. Fletcher Jr.³, Daniel H. Slone¹,
James P. Reid¹, Susan M. Butler¹

¹US Geological Survey Wetland and Aquatic Research Center, Gainesville, FL 32653, USA

²School of Natural Resources and Environment, University of Florida, Gainesville, FL 32603, USA

³Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32603, USA

⁴Present address: Department of Biology, Austin Peay State University, Clarksville, TN 37044, USA

ABSTRACT: Thermal refuges are habitats used by species for behavioral thermoregulation. These habitats can be highly dynamic and are often influenced by fluctuations in local climate. When protected species require thermal refuges, it is necessary to identify stable and high-quality areas by evaluating species use in response to variation in thermal refuge quality. Here, we assessed behavioral thermoregulation in the Florida manatee *Trichechus manatus latirostris*, a cold-intolerant marine mammal. Using metrics from ectotherm physiology, we evaluated thermal quality of 2 refuge types (passive thermal basins, natural springs) in 2 areas of their distribution. Thermal refuge quality was assessed with respect to the lower critical threshold of the manatee (20°C) and the surrounding ambient temperatures and compared between refuge types. We used GPS locations of manatees to quantify visits to refuges and calculated total visit duration in each refuge by individual manatees. At natural springs, we found a negative correlation between visit duration and ambient temperature during cold weather; visit duration also increased with the temperature differential between the spring and the lower critical thermal threshold. Visit duration at passive thermal basins was negatively correlated with the thermal differential between the refuge and the lower critical thermal threshold. The relationship between thermal refuge quality and time-use metrics sheds light on the potential implications of habitat degradation on animal energetics and behavior. Given these results, focusing on potential key refuges in each system may inform targeted management and habitat restoration efforts to maintain adequate thermal refuge environments for this listed species.

KEY WORDS: Cold stress · Florida manatee · Mammal conservation · Thermal refuges · *Trichechus manatus latirostris*

1. INTRODUCTION

The importance of understanding the interaction between an organism and its thermal environment is being increasingly emphasized due to the accumulating evidence of the effects of contemporary climate change (Walther et al. 2002, Parmesan & Yohe 2003, Deutsch et al. 2008, Velásquez-Tibatá et al. 2013). Thermoregulatory strategies evolve to prevent negative consequences of stressful environmental

temperatures and allow many organisms to withstand extreme temperature fluctuations (Gilman et al. 2006, Kearney et al. 2009). However, the increasing magnitude and frequency of extreme temperatures can have negative impacts on a species' ability to maintain heat balance over the long term, on the maintenance of energy reserves necessary for growth and reproduction, and eventually on population persistence (Oswald & Arnold 2012, Huey et al. 2012, Conradie et al. 2019, O'Connor et al. 2021).

*Corresponding author: haasec@apsu.edu

Behavioral thermoregulation through the use of thermal refuges can potentially buffer species from the detrimental impacts of unsuitable environmental temperatures (Kearney et al. 2009). Thermal refuges are habitats that maintain microclimates, namely temperature and humidity, which are within the thermal limits of the organism (Huey 1991). Thermal refuges occur due to some physical property of the habitat, such as cover from solar radiation or source of warmer temperatures; however, these resources can be still influenced by daily or seasonal fluctuations in local climate (Dugdale et al. 2013). Thus, thermal refuge quality can potentially change over time and across a species' distribution depending on habitat structure and surrounding environments (Keppel et al. 2012, Dugdale et al. 2013, 2015, Brewitt & Danner 2014).

Variability in the quality of a thermal refuge can directly impact animal energetics and ultimately affect animal survival and reproductive potential (Hudson 1985, McNamara & Houston 1986, Caraco et al. 1990). As ectothermic species rely on external temperature to regulate body temperature, most research on the impacts of thermal refuge quality has focused on amphibians, reptiles, and fishes (Ebersole 2002, Humphries & Umbanhowar 2007, Sutton et al. 2007, Thompson et al. 2018). However, many endothermic species also rely on thermal refuges to combat stressful temperatures (Schwab & Pitt 1991, Godvik et al. 2009, Oswald & Arnold 2012, van Beest et al. 2012), yet this area of research is underexplored in mammals and birds. In order to truly identify habitats necessary for species' survival in the face of changing climates, we must be able to describe how thermal refuge fluctuations can alter behavioral thermoregulation (Elmore et al. 2017).

We can quantify the quality of a thermal refuge by describing basic thermal characteristics, namely average temperature, temperature variability, or observed extreme temperatures over a period of time (Beauregard et al. 2013, Camacho et al. 2015). Additional metrics include calculating the temperature differential between thermal refuges and the surrounding environment, as this can indicate the refuge's ability to be more suitable compared to non-refuge environments (Hertz et al. 1993). However, all current metrics do not relate refuge conditions to the thermal biology of the study species, which is necessary to determine if a refuge is providing the means for thermoregulation in reference to a species' physiology.

Herbivorous mammals are often the focus of research studies on behavioral thermoregulation

(Rettie & Messier 2000, Fernández et al. 2002, Baciagalupe et al. 2003, Dussault et al. 2004, Haase et al. 2020). For example, the Florida manatee *Trichechus manatus latirostris* is an herbivorous aquatic mammal of conservation concern that thermoregulates by using thermal refuges. Due to their herbivorous diet and low metabolic rate, manatees become cold-stressed at water temperatures below 20°C and seek thermal refuges in the form of inland natural springs, warm-water outflows from power plants, or passive thermal basins (Laist et al. 2013). Often, habitats used for thermal refuge lack adequate forage resources (Rettie & Messier 2000), resulting in clear, directed movements between thermal and forage habitats when transitioning between thermoregulatory and foraging behaviors (Terrien et al. 2011, Mabilille et al. 2012). In these instances, we can explicitly assess how a species uses thermal refuges without confounding use with other requirements (e.g. foraging). Additionally, the quality of each thermal refuge type used by manatees can vary: freshwater springs usually maintain constant water temperatures of 22°C while passive thermal basins may often fall below the 20°C threshold (Flamm et al. 2013). Therefore, the Florida manatee is a suitable study species to address questions regarding the use of thermal refuges in response to thermal refuge quality across their distribution.

Using GPS location data from tagged and tracked manatees in 2 different habitat systems (one containing natural springs as thermal refuges, one containing passive thermal basins), we assessed how variation in thermal refuge quality can influence behavioral thermoregulation. We first quantified thermal refuge quality using 3 metrics pulled from the ectotherm physiology literature (Hertz et al. 1993): (1) the mean deviation between the refuge and the environment, (2) the mean deviation between the refuge and the lower temperature threshold of manatees (20°C; defined by an increase in metabolic rate to maintain body temperatures), and (3) the proportion of time the temperature in the refuge is above the lower threshold. We examined differences in these metrics between refuge types and variation within individual refuges within a winter season. Given the consistent outflow of warm water in natural springs, we predicted that springs would be higher in thermal refuge quality (i.e. larger deviations above ambient and critical temperatures) and less variable (i.e. less variation in deviation from the lower temperature threshold; d_{lct}) than passive thermal basins. We also expected that passive thermal basins would have less variation in deviation

from ambient conditions (d_e) as they may align with ambient temperatures more closely than springs that have constant temperatures. We then hypothesized that manatees, as cold-intolerant mammals, manage use of thermal refuges based on thermal quality. Thus, we predicted that manatees would spend more time per visit in thermal refuges that maintain thermal quality during the winter when manatees must tradeoff foraging with behavioral thermoregulation.

2. MATERIALS AND METHODS

2.1. Study area and available thermal refuges

The study area encompassed 2 distinct habitat systems of the Florida manatee (Fig. 1): northwestern Florida, with the primary focus on Crystal River National Wildlife Refuge located in the Kings Bay Manatee Protection Area, and southwestern Florida,

with a primary focus on the Ten Thousand Islands National Wildlife Refuge and Everglades National Park. The northwestern habitat system reached south to Chassahowitzka National Wildlife Refuge and north along the Florida panhandle. This area included Crystal River National Wildlife Refuge, Kings Bay Manatee Protection Area, and Homosassa Springs State Park (Fig. 1, top inset) and contained over 15 first-order magnitude springs (i.e. discharges $>2.8 \text{ m}^3 \text{ s}^{-1}$) (Laist & Reynolds 2005b). The southwestern habitat system reached from Marco Island in the north to the southern tip of the Everglades in the south and consisted of Everglades National Park, Big Cypress National Preserve, Collier Seminole State Park, Fakahatchee Strand Preserve State Park, and Ten Thousand Islands National Wildlife Refuge (Fig. 1, bottom inset). Unlike northern Florida, the southern region lacks natural springs. Manatees instead rely on passive thermal basins, which are small pockets of warm water that remain warmer than surrounding condi-

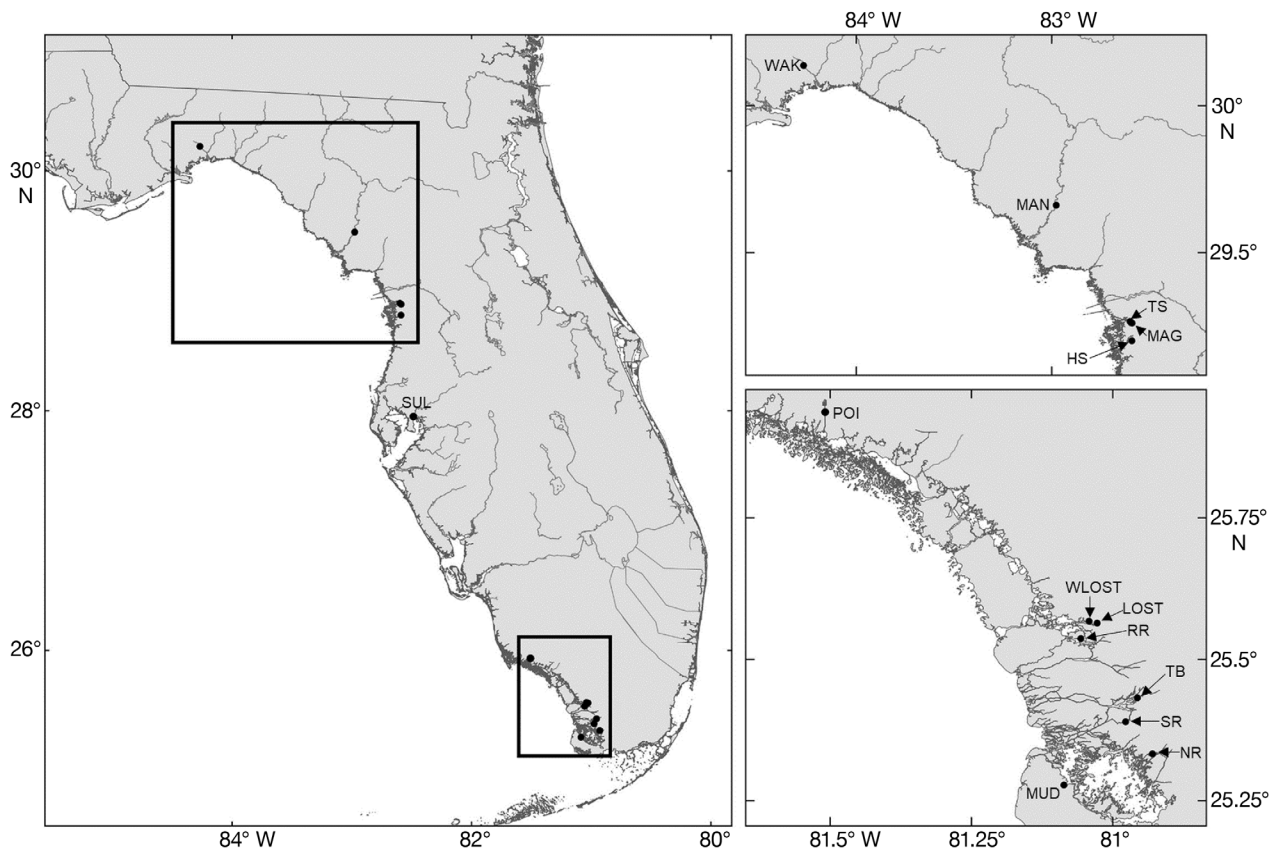


Fig. 1. Left: instrumented thermal refuge sites used by tagged Florida manatees *Trichechus manatus latirostris* in the analyses (SUL: Sulphur Springs). Top inset: the instrumented springs used by tagged manatees in the northwestern region during the winter (WAK: Wakulla Springs, MAN: Manatee Springs, TS: Three Sisters Spring; MAG: Magnolia Springs, HS: Homosassa Springs). Bottom inset: instrumented passive thermal basins used by manatees in the southwestern region during the winter (POI: Port of the Islands, WLOST: West Lostman River, LOST: Lostman River, RR: Rodgers River, TB: Tarpon Bay, SR: Shark River, NR: North River, MUD: Mud Bay)

tions due to various physical characteristics of the microhabitat (Stith et al. 2012). Many passive thermal basins in the region are caused by deep depressions in the bottom substrate that trap warm water as it cools slower than surrounding areas or by shallow basins with muddy bottoms that absorb solar radiation throughout the day. These passive thermal basins are often affected by tidal cycles and air temperature (Stith et al. 2011). Other passive thermal basins are produced by temperature-inverted haloclines, where warm saltwater is trapped under a layer of colder freshwater discharged by rivers or man-made weirs; the salinity stratification prevents water turn-over and allows these pockets of warm water to remain consistently warmer than the surface (Stith et al. 2011). The quality and reliability of inverted thermal haloclines vary in response to tidal cycles, freshwater flows, and manatee abundance (due to high densities disrupting weak haloclines disrupting temperature inversion) within the refuge.

2.2. Determining thermal refuge quality

Locations of natural springs were defined using GIS shapefiles mapped from aerial photography and validated by field measurements by the Florida Fish and Wildlife Conservation Commission (last updated in 2010; resolution: 1:12000). Locations of passive thermal basins were previously determined by Slone et al. (2017, 2018) 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⁻¹ in speed. To deal with possible location errors associated with GPS data, we added a 5 m buffer around all thermal refuge shapefiles.

We gathered water temperature data from 6 natural springs from the US Geological Survey (USGS) National Water Information System (NWIS) and measured water temperature in 8 passive thermal basins with HOBO water temperature sensors (Onset Computer Corp.) over the course of the study (natural springs: mean no. of years = 1.67, minimum = 1.0, maximum = 3.0; passive thermal basins: mean no. of years = 2.25, minimum = 1.0, maximum = 6.0; Fig. 1). All temperatures were logged every 15 min. Ambient water temperatures, used to represent conditions outside of the thermal refuge, were retrieved from weather stations managed by the USGS NWIS. We calculated the distance from each thermal refuge to each weather station and used water temperature from the closest weather station. If there was no USGS weather station within the local area (<10 km), a sec-

ond temperature sensor was placed near the thermal refuge to record the surrounding temperature.

We quantified thermal quality based on the ability of a refuge to stay above the lower critical temperature threshold of Florida manatees and above surrounding water temperatures. Hertz et al. (1993) defined the quality of a thermal refuge for ectotherms as the mean deviation between the environmental temperature and the selected or preferred temperature (i.e. d_e). We modified this equation to calculate the mean deviation between the environment, in this case, the thermal refuge (T_r), and the surrounding ambient water conditions (T_a):

$$d_e = \frac{\sum(T_r - T_a)}{n} \quad (1)$$

summed across all temperature measurements, represented by n . If d_e is positive, then the refuge is, on average, warmer than the surrounding environment. However, this equation does not take into consideration the lower critical temperature threshold of manatees. Therefore, we also defined the thermal quality based on the ability of the thermal refuge to maintain temperatures above the lower critical temperature defined from previous lab experiments (20°C; Irvine 1983). We modified Eq. (1) to calculate the mean deviation between the thermal refuge and the lower critical temperature of manatees (i.e. T_{lct}):

$$d_{lct} = \frac{\sum(T_r - T_{lct})}{n} \quad (2)$$

If d_{lct} is positive, then the thermal refuge, on average, maintains temperatures that reduce the metabolism requirements of manatees. To compare general trends in thermal refuge quality when water temperatures were below 20°C, we filtered to only thermal refuge temperatures when ambient temperatures were equal to or below 20°C and calculated d_e and d_{lct} for each month of a winter season for each thermal refuge. As a single winter encompasses 2 numeric years (November–March), we classified data collected in January–March as the previous year for our analyses (noted as ‘winter year’). We also calculated a third metric of refuge quality as the percent of time (over the month) the refuge was above the 20°C threshold.

2.3. Animal location data

A total of 36 free-ranging manatees were captured, tagged, and tracked in the study areas (see Weigle et al. 2001 for capture methodology and Marmontel et al. 2012 for tracking methodology); 26 manatees were tagged over the years 2002–2009 and tracked

in the southwestern network and 10 individuals were tagged over the years 2007–2015 and tracked in the northwestern network. The tag apparatus consisted of a floating satellite-linked (www.argos-system.com) GPS tag (www.telonics.com) that was attached to a belt around the peduncle of the animal by a nylon tether (Slone et al. 2017), with 2 release points that would allow the animal to break free if it became entangled. Tags remained on the manatee until they broke off and were located or until the animal was retagged. Some of the tags had temperature sensors (Tidbit, Onset Computer Corp.; accuracy $\pm 0.2^\circ\text{C}$) on the peduncle band that recorded the water conditions experienced by the animal; these temperature values were used to fill in gaps in thermal refuge temperatures. GPS locations were recorded with <5 m accuracy every 15–30 min (Adrados et al. 2002, Tomkiewicz et al. 2010). We limited analyses to GPS data from each winter season (November–March) since winter is when manatees are susceptible to cold stress and use thermal refuges. We only used manatees that were tracked for at least 14 d to ensure we did not constrain the representation of visit duration over the time tracked.

We defined use of thermal refuges if GPS locations fell within the borders of the thermal refuge shapefiles. We used the time stamp of each GPS location to calculate the total duration manatees spent within each thermal refuge (h) before leaving that refuge. If a manatee left a refuge but returned to the same refuge within 1 h, we considered it the same bout. If the manatee left a refuge and moved to a new refuge, we considered these separate bouts. We filtered out any bouts that were less than 1 h. We removed visits that had a corresponding mean ambient temperature $>20^\circ\text{C}$ over the visit duration, as we assumed manatees were not using the thermal refuge for behavioral thermoregulation. Finally, we calculated the mean visit duration per refuge per month for each winter season. To calculate thermal refuge quality at the time-scale relevant for manatee behavior, we calculated the 3 thermal refuge metrics (d_e , d_{lct} , and percent time $>20^\circ\text{C}$) over 14 d prior to a manatee leaving a refuge after a visit. As 14 d is one standard deviation above the mean visit duration, we assumed this duration would encompass the thermal refuge metrics a manatee would experience during each visit.

2.4. Statistical analysis

After confirming normality of the data with a Shapiro-Wilk normality test, we used a linear mixed-

effects model framework to determine differences between refuge types (natural springs and passive thermal basins) in the 3 monthly metrics of thermal quality (d_e , d_{lct} , and percent time $>20^\circ\text{C}$) within a winter season. Our models included monthly d_e , d_{lct} , or percent time $>20^\circ\text{C}$ for each refuge as a response variable, refuge type as a fixed effect, and refuge as a random effect. We used an arcsine transformation commonly used with percentages to transform the response variable of percent time $>20^\circ\text{C}$. Finally, we assessed differences in variability between the 2 thermal refuge types by performing a Fisher's F -test for equal variances for all 3 monthly metrics. We then developed a second suite of linear mixed-effects models to assess if any significant differences in thermal quality occurred within individual refuges during the winter season. Three models were created for each refuge type as we separated the data to determine differences independent of type. These models included the 3 metrics (monthly d_e , d_{lct} , or percent time $>20^\circ\text{C}$) for each refuge as the response variable, the interaction between refuge and month as fixed effects, and winter year as a random effect.

To test our second hypothesis that manatees manage use of thermal refuges based on thermal quality, we examined differences in tagged manatee use between refuge types. Our metric of manatee use was the continuous number of hours spent within a refuge during a visit with the sampling unit as each individual visit. After confirming data were not normal, we used a generalized linear mixed-effects model (family Gamma with a log-link) to determine differences in visit duration per manatee as a response to thermal refuge type depending on the month of the year. We included thermal refuge type, month, and their interaction as fixed effects and each individual manatee identification number as a random effect.

Finally, we assessed the effects of thermal refuge quality on visit duration to determine the best predictor of thermal refuge use. To test our hypothesis, we created a suite of generalized linear mixed-effects models (Gamma distribution with a log-link) with the response variable as the duration of each individual visit and either ambient temperature, one of the 3 thermal quality metrics (d_e , d_{lct} , or percent $>20^\circ\text{C}$ for each refuge), or ambient temperature plus one of the metrics as the predictor variables. All temperature/thermal quality metrics were calculated over the 14 d period prior to a manatee leaving the refuge after a visit. All models included month as a fixed effect and manatee identification as a random effect. We split the data by thermal refuge type and created the suite

of models for both springs and passive thermal basins to allow the top model to vary between types. We calculated the conditional R^2 values associated with generalized linear mixed models with the methodology described by Nakagawa & Schielzeth (2013) for the top model given conditional Akaike's information criterion for small sample sizes (AICc) for each of the suite of models (Burnham & Anderson 2002). All analyses used a significance level of $\alpha = 0.05$ and were completed using R v.3.6.3 (R Core Team 2020).

3. RESULTS

We calculated the thermal refuge quality metrics (d_e , d_{lct} , and percent time $>20^\circ\text{C}$) in 6 natural springs and 8 passive thermal basins across the 2 study regions (Table 1 & Table S1 in the Supplement at www.int-res.com/articles/suppl/n051p089_supp.pdf). Most of the refuges of both types maintained water temperatures above ambient temperatures, while only natural springs maintained water temperatures above the lower critical temperature for manatees over all winters (Table 1, Fig. 2). Our prediction that natural springs have higher thermal quality compared to passive thermal basins was supported for all metrics (Table 1, Fig. 3). Springs had higher d_e (passive ther-

mal basins as baseline: mean \pm SE: $\beta = 2.75 \pm 0.98$, $p = 0.020$; Fig. 4A), d_{lct} ($\beta = 2.47 \pm 0.79$, $p = 0.008$; Fig. 4B), and percent time $>20^\circ\text{C}$ ($\beta = 52.50 \pm 14.95$, $p = 0.004$; Fig. 4C) metrics. We also expected that there would be differences in metric variances between refuge types, with natural springs having higher variance in d_e compared to passive thermal basins, but lower variance in d_{lct} and percent time $>20^\circ\text{C}$. These predictions were supported in part by our analyses, as passive thermal basins had significantly larger variances in all 3 metrics (d_e : $F_{69} = 2.56$, $p = 0.001$; d_{lct} : $F_{69} = 3.24$, $p < 0.001$; $>20^\circ\text{C}$: $F_{69} = 6.63$, $p < 0.001$).

Across months within the winter season, all 6 natural springs had considerable variation in d_e (all $p < 0.050$; Fig. 3A), but only Wakulla Springs varied across months in d_{lct} ($p = 0.030$; Fig. 3B). Almost all springs maintained refuge temperatures $>20^\circ\text{C}$ for most of the winter (all $p > 0.050$; Fig. 3C), except for Wakulla Springs, which varied considerably throughout the winter season ($p = 0.004$). Passive thermal basins fell into 2 general groups: those sites that tracked ambient temperatures and therefore had little differences in d_e across the winter season (Lostman River, West Lostman River, Rodgers River, Shark River, and Tarpon Bay; all $p > 0.050$) and those that varied considerably in d_e (Mud Bay, Port of the Islands, and North River; all $p < 0.050$; Fig. 3A). Pas-

Table 1. Summary of thermal refuge quality between 2 refuge types (natural springs, passive thermal basins) during cold ambient temperatures ($<20^\circ\text{C}$) in Florida. Thermal refuge quality was calculated as the mean deviation between each refuge and the surrounding environment (d_e) or the lower critical temperature of the Florida manatee, *Trichechus manatus latirostris* (20°C ; d_{lct}), and the percent of time the refuge maintained temperatures above this threshold ($\% >20^\circ\text{C}$) over the study period. Positive values indicate that the refuge, on average, maintains temperatures above the surrounding environment or the critical threshold, respectively. Metrics were calculated across winter months (November–March) for each refuge

Thermal refuges	d_e			d_{lct}			% >20°C			No. of winters
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	
Passive thermal basin										
Lostman River	1.09	0.72	0.04 to 1.67	-0.13	0.79	-1.30 to 0.46	50.76	32.85	8.94 to 89.16	1
Mud Bay	4.38	2.53	1.29 to 8.59	1.09	3.70	-7.98 to 4.94	73.06	30.82	19.64 to 100	3
North River	3.59	1.94	1.38 to 6.83	0.26	3.25	-8.10 to 2.71	59.67	32.55	3.57 to 100	3
Port of the Islands	5.79	2.51	0.63 to 11.82	2.95	1.99	-1.16 to 6.06	86.54	24.88	17.24 to 100	6
Rodgers River	2.51	5.46	0.16 to 16.95	-0.78	1.46	-2.40 to 2.75	30.81	28.58	4.23 to 100	2
Shark River	0.90	0.74	0.38 to 1.43	-0.27	2.13	-1.77 to 1.24	56.82	61.07	13.64 to 100	1
Tarpon Bay	2.33	0.09	2.21 to 2.40	-0.17	1.02	-1.40 to 1.04	53.59	25.76	34.85 to 91.67	1
West Lostman River	0.94	1.11	0.27 to 2.60	-1.63	0.72	-2.40 to -0.94	19.69	17.22	4.23 to 44.12	1
Natural springs										
Homosassa Springs	5.40	1.05	3.62 to 7.02	3.11	0.17	2.73 to 3.22	100	0.00	100 to 100	2
Magnolia Springs	5.28	0.66	4.53 to 6.21	2.47	0.24	2.30 to 2.87	97.87	3.85	91.13 to 100	1
Manatee Springs	6.14	1.67	3.79 to 7.99	2.62	0.28	2.31 to 2.90	100	0.00	100 to 100	1
Sulphur Springs ^a	7.88	1.08	5.96 to 9.84	4.70	0.29	4.27 to 5.13	100	0.00	100 to 100	3
Three Sisters	6.13	1.27	4.29 to 7.68	2.32	0.65	1.33 to 3.15	90.27	8.06	77.45 to 99.76	1
Wakulla Springs	3.19	2.08	1.20 to 6.80	1.16	2.38	0.06 to 5.99	67.42	19.52	50.46 to 100	2
^a Note: USGS gauge at Sulphur Springs vent (Station 2306000) is not in waters accessible by manatees, which have access to spring water mixed with river water										

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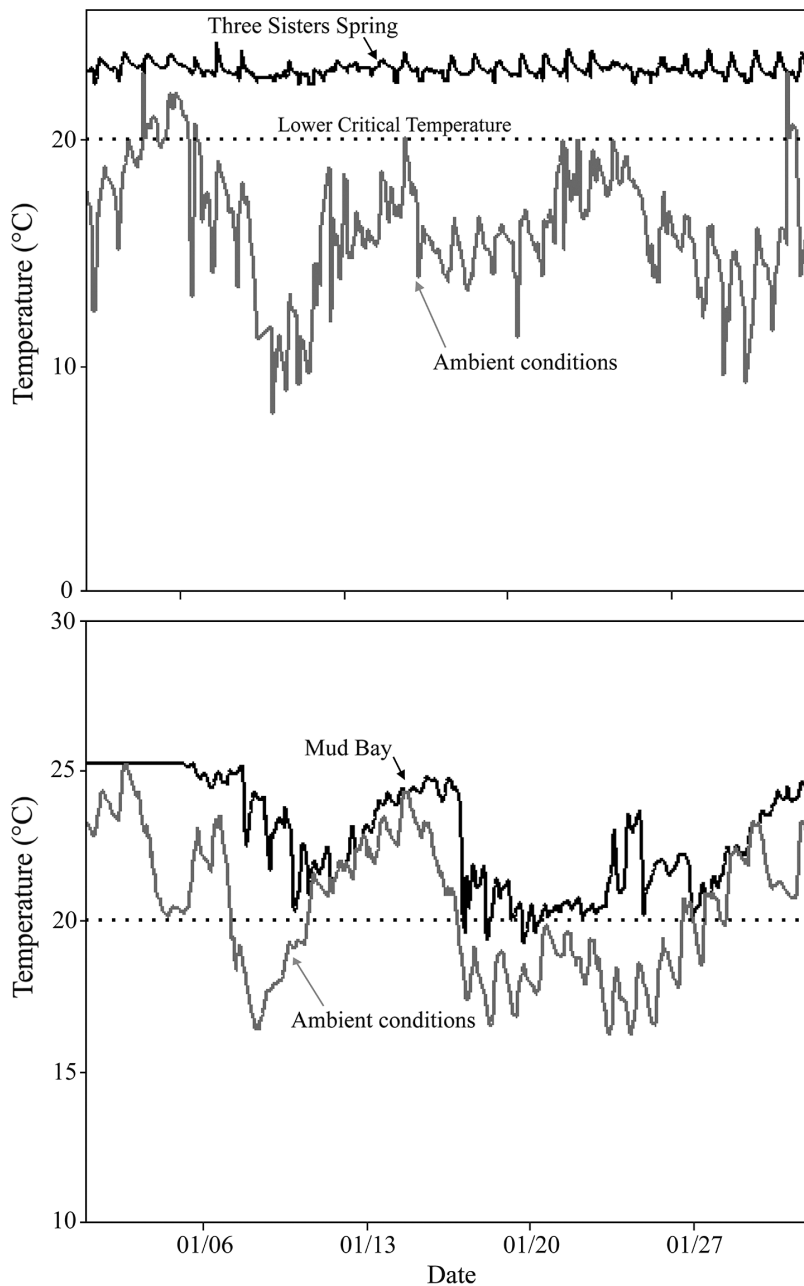


Fig. 2. Variation in water temperature during January 2015 at Three Sisters Spring (top) in northwest Florida and Mud Bay (bottom), a passive thermal basin in southwest Florida. Water temperatures represent the thermal refuge conditions (black lines), ambient conditions outside of the refuges (grey lines), and the lower critical temperature of the Florida manatee *Trichechus manatus latirostris* (dashed lines)

sive thermal basins differed little in d_{lct} over the winter season (all $p > 0.050$; Fig. 3B); Port of the Islands and Mud Bay did not have significant impacts of month, but potentially could with more data given the p-values reported (Port of the Islands: $p = 0.050$; Mud Bay: $p = 0.050$). Finally, all passive thermal

basins had significant differences between months in the percent time the refuge temperatures were above 20°C (all $p < 0.050$; Fig. 3C).

Out of the 36 manatees tracked, 21 were tracked for at least 14 d over the winter (12 in the southwestern network and 9 in the northwestern network) and were included in the analyses. Manatees were tracked for an average (\pm SD) of 75.54 ± 74.43 d (minimum: 17 d; maximum: 322 d) over the winter months. The number of successful GPS fixes per animal averaged 1697.08 ± 1636.10 (minimum: 72 fixes; maximum: 6654 fixes), with a total of 44 124 fixes used in the analysis. The number of visits to thermal refuges when ambient water temperatures were $<20^{\circ}\text{C}$ ranged from 4 to 89 per animal over the study period (median = 12.5, 1Q = 10, 3Q = 30.25) with, on average, 4.30 ± 2.78 manatees visiting a single thermal refuge (Table 2). The visit duration within a thermal refuge ranged from a mean of 19.08 ± 34.36 h in passive thermal basins (minimum: 1.02 h; maximum: 395.32 h, $n = 192$ visits) to 32.83 ± 51.57 h in natural springs (minimum: 1.00 h; maximum: 440.50 h; $n = 415$ visits). Manatees spent more time in springs per visit than passive thermal basins (with passive thermal basins as baseline [\pm SE]: $\beta = 0.95 \pm 0.29$, $p = 0.001$), an effect that was impacted by month ($\beta = 0.06 \pm 0.02$, $p = 0.010$; Fig. 4D).

Manatees increased time in thermal refuges, specifically natural springs, in response to ambient temperature and the ability of refuges to remain above the lower critical threshold of 20°C (d_{lct} ; AICc = 10463.10, log-likelihood [LL] = -5225.55, no. of parameters [K] = 6, AIC weights [w_i] = 0.98, $R^2 = 0.30$; Table 3). Visit duration had a negative relationship with ambient water temperature, with manatees spending

more time per visit as temperatures decreased ($\beta = -0.24 \pm 0.07$, $p < 0.001$). Manatees also increased visit duration in springs that were higher than the lower critical threshold, with a greater d_{lct} ($\beta = 0.27 \pm 0.07$, $p < 0.001$). Visit duration in springs was not impacted by time of year, as month was not a sig-

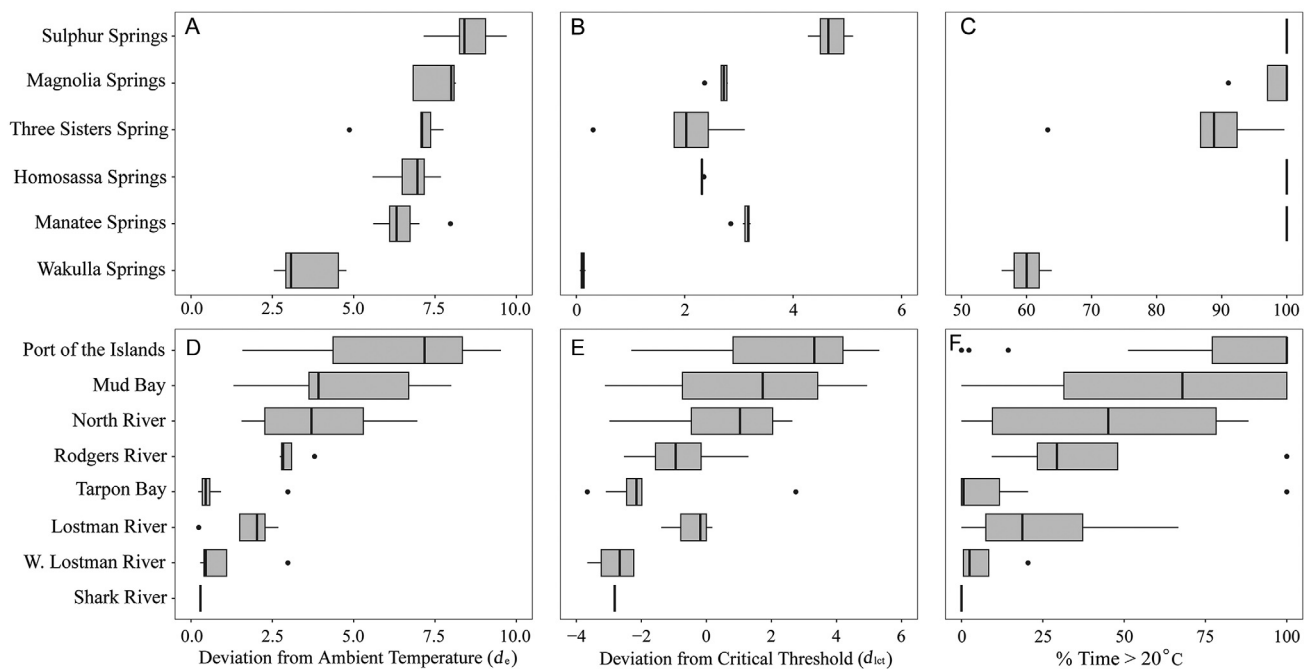


Fig. 3. Thermal refuge quality metrics that influence visit duration by Florida manatees *Trichechus manatus latirostris* in (A–C) natural springs in northwestern Florida and (D–F) passive thermal basins in southwestern Florida in winter (November–March). (A,D) Mean monthly deviation between refuge water temperature ($^{\circ}\text{C}$) and ambient temperature; (B,E) mean monthly deviation between refuge water temperature and the lower critical threshold of the manatee (20°C); and (C,F) the percent time a thermal refuge was above the lower critical threshold. Boxes: 25th and 75th percentiles; whiskers extend to the smallest/largest value from $1.5 \times$ the interquartile range, respectively; points: outliers. Metrics based on data filtered to periods when mean daily ambient water temperature was less than 20°C .

Table 2. Summary of use of natural springs and passive thermal basins by Florida manatees *Trichechus manatus latirostris* for thermal refuges. Use was defined by consecutive GPS locations within a single thermal refuge during winter months (November–March) when ambient temperatures were $<20^{\circ}\text{C}$. Identification numbers of water temperature stations from the US Geological Survey (USGS) National Water Information System (NWIS) are also reported for natural springs; (–) no stations were located in the passive thermal basins

Refuge	USGS NWIS Station ID	No. of manatees visited	No. of visits per manatee		Visit duration (h)	
			Mean	SD	Mean	SD
Passive thermal basins						
Lostman River	–	3	15.00	10.44	7.47	5.51
Mud Bay	–	4	12.00	6.50	49.94	42.06
North River	–	1	8.00	0.00	8.01	2.13
Port of the Islands	–	8	11.25	5.23	27.38	47.12
Rodgers River	–	4	4.50	2.89	8.47	4.87
Shark River	–	4	10.50	10.08	7.99	6.75
Tarpon Bay	–	2	4.50	4.95	7.94	6.65
West Lostman River	–	1	20.00	0.00	7.56	5.31
Natural springs						
Homosassa Springs	2310688	4	16.25	14.97	26.92	30.87
Magnolia Springs	2310743	2	21.00	28.28	22.37	33.26
Manatee Springs	2323566	5	8.00	13.47	65.49	47.84
Sulphur Springs	2306000	1	2.00	0.00	15.99	12.71
Three Sisters	2310735	9	42.44	42.15	26.10	24.55
Wakulla Springs	3014070	8	32.38	49.70	84.76	95.48

nificant variable ($p = 0.15$). Visit duration in passive thermal basins, however, was impacted only by d_{ict} ($\text{AICc} = 4566.07$, $\text{LL} = -2278.03$, $K = 5$, $w_i = 0.45$, $R^2 = 0.45$), though this top model was within $2 \Delta\text{AICc}$ values of the model containing ambient temperature and d_{ict} (Table 3), which was the top model for natural springs. Visit duration decreased with d_{ict} ($\beta = -0.54 \pm 0.01$, $p < 0.001$), which was opposite of what we expected. It is also worth noting that the second-best model for passive thermal basins (the top model for natural springs) also had a negative relationship between d_{ict} and visit duration ($\beta = -0.56 \pm 0.15$, $p = 0.001$).

4. DISCUSSION

Variation in the thermal environment of thermal refuges can be a critical factor influencing animal behavior, particularly during periods when an

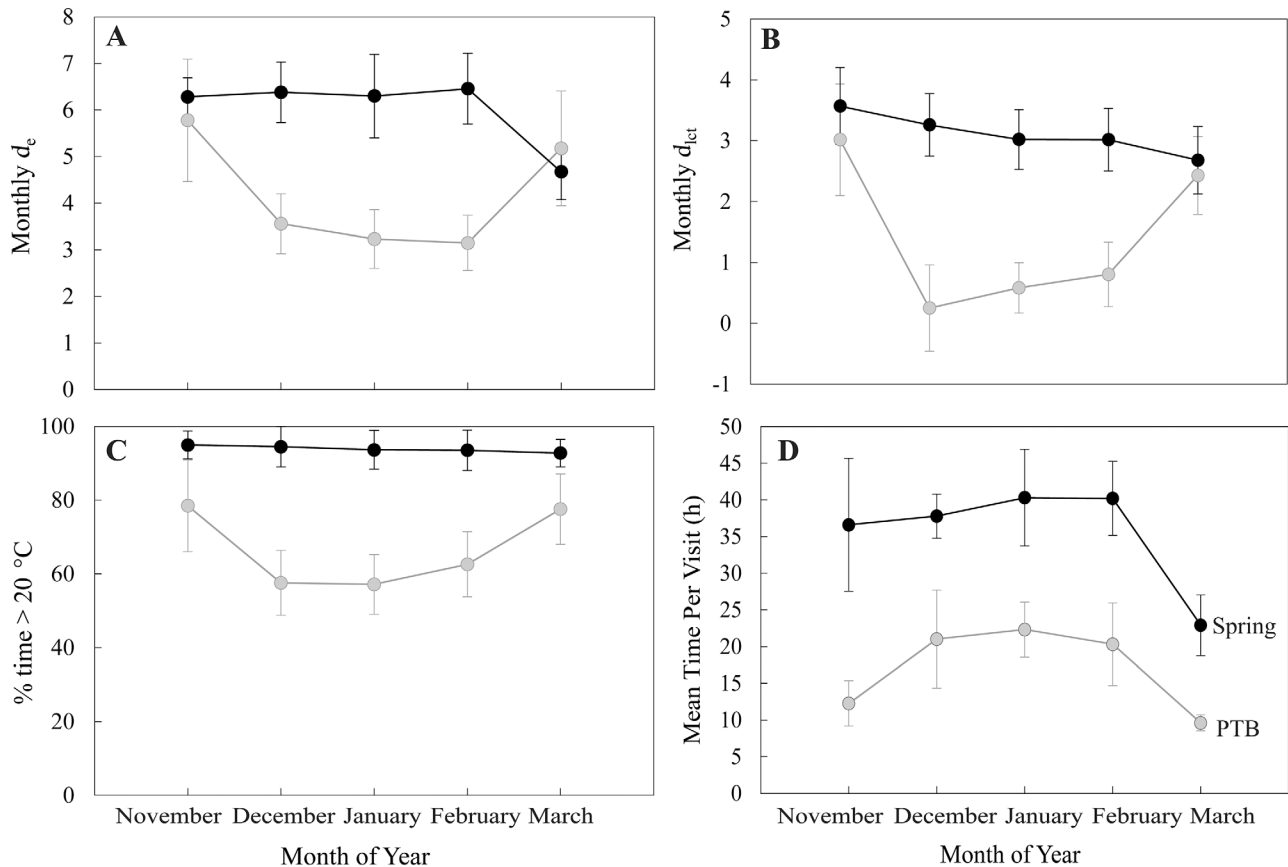


Fig. 4. Thermal refuge quality metrics that influence visit duration by Florida manatees *Trichechus manatus latirostris* in natural springs in northwestern Florida and passive thermal basins (PTB) in southwestern Florida in winter (November–March). (A) Mean monthly deviation between refuge water temperature ($^{\circ}\text{C}$) and ambient temperature (d_e); (B) mean monthly deviation between refuge water temperature and the lower critical threshold of the manatee (20°C) (d_{lct}); (C) the percent time a thermal refuge was above the lower critical threshold; and (D) the mean duration per visit to a thermal refuge over the winter.

Metrics based on data filtered to periods when mean daily ambient water temperature was less than 20°C

animal is susceptible to temperature stress (Aublet et al. 2009, van Beest et al. 2012). We found that the ability of a thermal refuge to maintain water temperatures above 20°C , the temperature at which Florida manatees begin to experience cold stress, can explain manatees' use of some thermal refuges. Our hypothesis was that manatees would respond to exposure to cold water temperatures by increasing the duration of visits to thermal refuges that maintained warmer temperatures than the surrounding environment and the lower critical threshold. Our results present contrasting conclusions for the 2 types of refuges: manatees in natural spring systems spent a longer duration per visit in springs that were above 20°C in response to colder conditions but were found to decrease visit duration in passive thermal basins. These findings may shed light on the implications of thermal stress on animal behavior and the trade-offs associated with behavioral thermoregulation (Bacigalupe et al. 2003, Deutsch et al. 2022a).

We suspect this contrasting relationship between visit duration in different thermal refuge types was due to weak and/or variable sources of warm water that quickly mix with the surrounding cooler waters in passive thermal basins. Given that passive thermal basins are not a steady source of warm water like springs but rather are caused by a variety of inconsistent factors (groundwater seeps, solar-radiation-heated basin, temperature-inverted halocline), we suspect refuge temperature and ambient water temperature have a tight relationship. This relationship could explain why manatees seemed to decrease visit duration to passive thermal basins as the differential between water temperature and the lower critical threshold increased. Ambient temperature was included in the second highest-ranked model, but this relationship was not positive as expected. The difficulty in interpreting these results may lie in the fact that the models include both inter-site variation and temporal variation (within sites). It is quite possi-

Table 3. Differences in conditional Akaike information criterion from the top model (ΔAICc), log-likelihood (LL), number of parameters (K), AIC weights (w_i), and conditional R^2 for generalized linear mixed-effect models describing the effect of thermal refuge quality on mean duration spent in refuges per visit by the Florida manatee *Trichechus manatus latirostris*. Thermal refuge quality was calculated by 4 metrics for 2 wk prior to the manatee ending its visit. Refuge quality was represented as the mean deviation between each refuge temperature and the surrounding environment (d_e), the mean deviation between the refuge temperature and the lower critical temperature (20°C ; d_{ict}), and the percent time the refuge was above the critical temperature ($>20^\circ\text{C}$). All models also included month as a fixed effect and manatee ID as a random effect and used a Gamma distribution with a log-link

Model	ΔAICc	LL	K	w_i	R^2
Passive thermal basins					
d_{ict}	0.00	-2278.03	5	0.45	0.45
Mean ambient temperature + d_{ict}	1.09	-2277.58	6	0.26	0.44
Mean ambient temperature + d_e	2.16	-2278.11	6	0.15	0.39
% time $>20^\circ\text{C}$	3.51	-2279.79	5	0.08	0.37
d_e	5.40	-2280.73	5	0.03	0.36
Mean ambient temp. + % time $>20^\circ\text{C}$	5.64	-2279.85	6	0.03	0.37
Manatee ID only	8.44	-2283.25	4	0.01	0.41
Mean ambient temperature	9.85	-2282.96	5	<0.01	0.38
Natural springs					
Mean ambient temperature + d_{ict}	0.00	-5225.55	6	0.99	0.30
d_{ict}	10.39	-5231.74	5	0.01	0.31
d_e	11.45	-5232.28	5	<0.01	0.26
Mean ambient temperature	12.65	-5232.88	5	<0.01	0.25
% time $>20^\circ\text{C}$	12.86	-5232.98	5	<0.01	0.26
Mean ambient temperature + d_e	13.42	-5232.26	6	<0.01	0.26
Mean ambient temp. + % time $>20^\circ\text{C}$	13.76	-5232.43	6	<0.01	0.25
Manatee ID only	14.24	-5234.67	4	<0.01	0.27

ble that the relationship is positive across sites and manatees spend more time at warmer sites, but negative within sites when manatees spend more time at the passive thermal basin in mid-winter when the difference is lower compared to early/late winter months because the animals do not have better options. Ultimately, we can conclude that the variety of passive thermal basins causes manatees to use these thermal refuges in different ways, depending on temperature conditions.

There was a relationship between ambient water temperature and visit duration at natural springs that may be related to the northerly locations of natural springs, where manatees are more exposed to cold ambient temperatures for extended periods of time. Extremely cold ambient temperatures can be lethal to manatees, so it is not surprising that northern populations, where water temperatures are more likely to reach lethal limits, are more sensitive to ambient conditions compared to the southern population. The fact that there were significant differences in both manatee use and thermal quality between the 2 different refuge types has implications for refuge con-

servation. Our results may help to identify potential key refuges in each system and inform targeted management and habitat restoration efforts to maintain adequate thermal refuge environments.

Thermal refuges face an uncertain future in Florida with the combination of increased use of fresh groundwater reducing spring flows and loss of power plant discharges that manatees depend on, in addition to global climate change. With an increasing human population in the state, increased withdrawals from groundwater for personal and agricultural use can result in decreased flows to spring systems and a reduction in the plume of spring vents (Sucsy et al. 1998, Laist & Reynolds 2005a). Drastic reduction in warm water availability in these areas could alter manatee use and potentially lead to higher mortality events if manatees are not able to find other thermal refuges. Given the importance to manatee behavior of maintaining steady temperatures above ambient temperatures and the 20°C threshold, permanent reductions of warm water refuges within an ecosys-

tem may impact species survival rates. To date, little research has considered the effects of the permanent removal of refuges. Future studies could help to assess the effects of the removal of refuges on manatee behavior and inform resource management options to prevent cold-stress-related deaths.

Currently, plans to restore sheet flow to Everglades National Park aim to remove artificial canals to allow freshwater to naturally flow from the eastern half to the west (Comprehensive Everglades Restoration Plan; www.evergladesrestoration.gov/). The current restoration efforts have resulted in the imminent elimination of a high-quality, yet artificial, warm-water refuge used by manatees in the area. This primary warm water site for manatees in the Ten Thousand Islands region occurs within the canal system of the Port of the Islands residential area (Stith et al. 2006, 2011). Mitigation efforts include creating a warm-water refuge by dredging deep pools that tap into warm, saline groundwater (Edwards et al. 2021). Our results describe water quality preferences of manatees in 2 areas of the state, highlighting the importance of water temperature within refuges.

Understanding linkages between specific hydrological variables and thermal refuge quality can help to properly assess how changes to the hydrology of the Everglades may impact manatee thermal refuge use.

The relationship between thermal refuge quality and time-use metrics sheds light on the potential implications of habitat degradation on animal energetics and behavior (Brewitt & Danner 2014). Manatees, like many other species, require 2 distinct and often spatially separated habitats for thermoregulation and foraging (Haase et al. 2017). Our results indicate the importance of thermal quality for the use of thermal refuges and thus we can ascertain that spatiotemporal variability in refuge quality can shape manatee behavior. For species with similar requirements, the relative time spent within different habitat types can indicate the potential for energy intake via foraging or energy conservation via thermoregulation (Belovsky 1984, 1986, Bacigalupe et al. 2003). As energy budgets can be limited by time and visit duration within thermal refuges was correlated with refuge quality, any changes in quality may result in restrictions to acquiring energetic resources. The need to forage to maintain the high energetic demands of endothermic body temperatures in cold water temperatures could be potentially offset by the use of quality thermal refuges. For example, manatees often remain in thermal refuges for extended visits when temperatures drop far below 20°C, selecting to conserve energy and fast than to risk hypothermia (Laist & Reynolds 2005b, Deutsch et al. 2022a,b). Therefore, thermal refuges that remain above the threshold may be important during periods of thermal stress. Additional research highlights the need to gain more information on trade-offs between foraging and thermoregulation and the impacts of factors such as climate change that may alter these trade-offs can help to inform conservation efforts.

Although our results suggest manatees may manage thermal stress by using refuges, there are a few limitations that need to be considered in the application of our study. This work compared 2 different regions that vary in mean ambient conditions, overall thermal quality, and potential disturbance. As manatees in each region did not have access to both refuge types, we are unable to explicitly address which refuge would be selected over the other. Visit duration may also be influenced by the number of warm-water refuges in proximity to the site of interest. Manatees visiting springs in Crystal River can leave and swim a short distance to another spring in that system; likewise, manatees visiting Sulphur Springs have 3 power plant thermal discharges nearby to

select from, whereas manatees using Wakulla Spring have fewer options at much greater distances. Therefore, visit duration is unlikely to be influenced solely by the temperature metrics examined in this study, but also by the spatial configuration of habitats (Haase et al. 2020). Additionally, distance between forage and thermal habitats can directly alter the duration of each behavior (Haase et al. 2020); this variable could potentially also drive time spent in the thermal refuge. However, adequate mapping of all available seagrass beds across our study area was not as extensive as needed to perform this analysis. Finally, as the northwest region is more developed while the southwest region is more secluded, human influence on thermal refuge use could also impact use.

Thermal refuges have the potential to buffer the effects of climate change by providing relief from thermal stress (Keppel et al. 2012). Shifts in habitat use and activity times have already been observed in species when exposed to temperatures outside their critical limits for periods greater than average (Bozinovic 2002). The presence of thermal refuges has also been shown to highly influence species distributions, suggesting that the quality of thermal habitats may become even more critical in times of thermal stress (Keppel et al. 2012, Brewitt & Danner 2014). The effects of refuge quality on time in refuges indicated by our results suggest that high-quality resources provide physiological relief and allow species to conserve energy because of time budgets in addition to the physiological buffering resulting from time spent in the refuge. In the face of a changing climate and alterations to habitat, understanding the complex relationships between variations in microclimate, the quality of microhabitat relative to the thermal limits of a species, and animals' responses to stressful temperatures can help to inform resource management and conservation considerations.

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Data archive. Manatee GPS locations and thermal refuge temperature data are available in Slone et al. (2022, 2023a,b).

LITERATURE CITED

- ✦ Adrados C, Girard I, Gendner JP, Janeau G (2002) Global positioning system (GPS) location accuracy improvement due to selective availability removal. *C R Biol* 325: 165–170
- ✦ Aublet JF, Festa-Bianchet M, Bergero D, Bassano B (2009) Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. *Oecologia* 159: 237–247
- ✦ Bacigalupe LD, Rezende EL, Kenagy GJ, Bozinovic F (2003) Activity and space use by degus: a trade-off between thermal conditions and food availability? *J Mammal* 84: 311–318
- ✦ Beauregard D, Enders E, Boisclair D (2013) Consequences of circadian fluctuations in water temperature on the standard metabolic rate of Atlantic salmon parr (*Salmo salar*). *Can J Fish Aquat Sci* 70:1072–1081
- ✦ Belovsky GE (1984) Herbivore optimal foraging: a comparative test of three models. *Am Nat* 124:97–115
- ✦ Belovsky GE (1986) Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. *Oecologia* 70:35–52
- Bozinovic F (2002) Physiological ecology and evolution. Theory and study cases in vertebrates. Ediciones Universidad Catolica de Chile, Santiago
- ✦ Brewitt KS, Danner EM (2014) Spatio-temporal temperature variation influences juvenile steelhead (*Oncorhynchus mykiss*) use of thermal refuges. *Ecosphere* 5:art92
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York, NY
- ✦ Camacho A, Trefaut Rodrigues M, Navas C (2015) Extreme operative temperatures are better descriptors of the thermal environment than mean temperatures. *J Therm Biol* 49–50:106–111
- ✦ Caraco T, Blanckenhorn WU, Gregory GM, Newman JA, Recer GM, Zwicker SM (1990) Risk-sensitivity: ambient temperature affects foraging choice. *Anim Behav* 39: 338–345
- ✦ Conradie SR, Woodborne SM, Cunningham SJ, McKechnie AE (2019) Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. *Proc Natl Acad Sci USA* 116:14065–14070
- ✦ Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci USA* 105:6668–6672
- Deutsch CJ, Castelblanco-Martínez DN, Cleguer C, Groom R (2022a) Movement behavior of manatees and dugongs. II. Small-scale movements reflect adaptations to dynamic aquatic environments. In: Marsh H (ed) *Ethology and behavioral ecology of Sirenia*. Ethology and behavioral ecology of marine mammals. Springer International Publishing, Cham, p 233–298
- Deutsch CJ, Castelblanco-Martínez DN, Groom R, Cleguer C (2022b) Movement behavior of manatees and dugongs. I. Environmental challenges drive diversity in migratory patterns and other large-scale movements. In: Marsh H (ed) *Ethology and behavioral ecology of Sirenia*. Ethology and behavioral ecology of marine mammals. Springer International Publishing, Cham, p 155–231
- ✦ Dugdale SJ, Bergeron NE, St-Hilaire A (2013) Temporal variability of thermal refuges and water temperature patterns in an Atlantic salmon river. *Remote Sens Environ* 136:358–373
- ✦ Dugdale SJ, Bergeron NE, St-Hilaire A (2015) Spatial distribution of thermal refuges analysed in relation to river-scape hydromorphology using airborne thermal infrared imagery. *Remote Sens Environ* 160:43–55
- ✦ Dussault C, Ouellet JP, Courtois R, Pettorelli J, Breton L, Larochelle J (2004) Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience* 11: 321–328
- Ebersole JL (2002) Heterogeneous thermal habitat for north-east Oregon stream fishes. PhD dissertation, Oregon State University, Corvallis, OR
- ✦ Edwards HH, Hostetler JA, Stith BM, Martin J (2021) Monitoring abundance of aggregated animals (Florida manatees) using an unmanned aerial system (UAS). *Sci Rep* 11:12920
- ✦ Elmore RD, Carroll JM, Tanner EP, Hovick TJ, Grisham BA, Fuhlendorf SD, Windels SK (2017) Implications of the thermal environment for terrestrial wildlife management. *Wildl Soc Bull* 41:183–193
- ✦ Fernández MJ, López-Calleja MV, Bozinovic F (2002) Interplay between the energetics of foraging and thermoregulatory costs in the green-backed firecrown hummingbird *Sephanoides sephanioides*. *J Zool (Lond)* 258:319–326
- ✦ Flamm RO, Reynolds JE, Harmak C (2013) Improving conservation of Florida manatees (*Trichechus manatus latirostris*): conceptualization and contributions toward a regional warm-water network management strategy for sustainable winter habitat. *Environ Manage* 51:154–166
- ✦ Gilman SE, Wetthey DS, Helmuth B (2006) Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. *Proc Natl Acad Sci USA* 103:9560–9565
- ✦ Godvik IMR, Loe LE, Vik JO, Veiberg V, Langvatn R, Mysterud A (2009) Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* 90:699–710
- ✦ Haase CG, Fletcher RJ, Slone DH, Reid JP, Butler SM (2017) Landscape complementation revealed through bipartite networks: an example with the Florida manatee. *Landsc Ecol* 32:1999–2014
- ✦ Haase CG, Fletcher RJ, Slone DH, Reid JP, Butler SM (2020) Traveling to thermal refuges during stressful temperatures leads to foraging constraints in a central-place forager. *J Mammal* 101:271–280
- ✦ Hertz PE, Huey RB, Stevenson RD (1993) Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am Nat* 142:796–818
- Hudson RJ (1985) *Bioenergetics of wild herbivores*, 1st edn. CRC Press, Boca Raton, FL
- ✦ Huey RB (1991) Physiological consequences of habitat selection. *Am Nat* 137:S91–S115
- ✦ Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philos Trans R Soc B* 367:1665–1679
- Humphries MM, Umbanhowar J (2007) Filtering environmental variability: activity optimization, thermal refuges, and the energetic responses of endotherms to temperature. In: Vasseur DA, McCann KS (eds) *The impact of*

- environmental variability on ecological systems. The Peter Yodzis Fundamental Ecology Series, Springer Netherlands, Dordrecht, p 61–87
- ✦ Irvine AB (1983) Manatee metabolism and its influence on distribution in Florida. *Biol Conserv* 25:315–334
- ✦ Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proc Natl Acad Sci USA* 106:3835–3840
- ✦ Keppel G, Niel KPV, Wardell-Johnson GW, Yates CJ and others (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob Ecol Biogeogr* 21:393–404
- ✦ Laist DW, Reynolds J (2005a) Florida manatees, warm-water refuges, and an uncertain future. *Coast Manage* 33: 279–295
- ✦ Laist DW, Reynolds JE (2005b) Influence of power plants and other warm-water refuges on Florida manatees. *Mar Mamm Sci* 21:739–764
- ✦ Laist DW, Taylor C, Reynolds JE (2013) Winter habitat preferences for Florida manatees and vulnerability to cold. *PLOS ONE* 8:e58978
- ✦ Mabile G, Dussault C, Ouellet JP, Laurian C (2012) Linking trade-offs in habitat selection with the occurrence of functional responses for moose living in two nearby study areas. *Oecologia* 170:965–977
- Marmontel M, Reid J, Sheppard JK, Morales-Vela B (2012) Tagging and movement of sirenians. In: Hines E, Reynolds JE, Aragonés L, Mignucci-Giaonni AA, Marmontel M (eds) *Sirenian conservation: issues and strategies in developing countries*. University Press of Florida, Gainesville, FL, p 116–125
- ✦ McNamara JM, Houston AI (1986) The common currency for behavioral decisions. *Am Nat* 127:358–378
- ✦ Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142
- ✦ O'Connor RS, Le Pogam A, Young KG, Robitaille F and others (2021) Limited heat tolerance in an Arctic passerine: thermoregulatory implications for cold-specialized birds in a rapidly warming world. *Ecol Evol* 11:1609–1619
- ✦ Oswald SA, Arnold JM (2012) Direct impacts of climatic warming on heat stress in endothermic species: seabirds as bioindicators of changing thermoregulatory constraints. *Integr Zool* 7:121–136
- ✦ Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/
- ✦ Rettie WJ, Messier F (2000) Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466–478
- ✦ Schwab FE, Pitt MD (1991) Moose selection of canopy cover types related to operative temperature, forage, and snow depth. *Can J Zool* 69:3071–3077
- Slone DH, Butler SM, Reid JP, Haase CG (2017) Timing of warm water refuge use in Crystal River National Wildlife Refuge by manatee—results and insights from global positioning system telemetry data. US Geological Survey, Wetland and Aquatic Research Center, Gainesville, FL
- Slone DH, Butler SM, Reid JP (2018) Movements and habitat use locations of manatees within Kings Bay Florida during the Crystal River National Wildlife Refuge winter season (November 15–March 31). Open-File Report 2018–1051. US Geological Survey, Reston, VA
- ✦ Slone DH, Reid JP, Butler S, Haase CG, Fletcher RJ Jr (2022) GPS telemetry of Florida manatees and riverine water temperatures from southwest Florida 2002–2015: U.S. Geological Survey data release. <https://doi.org/10.5066/P9QT5VC1>
- ✦ Slone DH, Butler SM, Reid JP (2023a) Manatee tracking, sighting and environmental data from the Northern Gulf of Mexico, 2013–2019: U.S. Geological Survey data release. <https://doi.org/10.5066/P98C25SK>
- ✦ Slone DH, Butler S, Reid JP, Kleen J, Palmer J (2023b) GPS telemetry and other data sets of Florida manatees from Crystal River, FL 2006–2018: U.S. Geological Survey data release. <https://doi.org/10.5066/P9A6YY9G>
- Stith BM, Slone DH, Reid JP (2006) Review and synthesis of manatee data in Everglades National Park. US Geological Survey, Gainesville, FL
- ✦ Stith BM, Reid JP, Langtimm CA, Swain ED and others (2011) Temperature inverted haloclines provide winter warm-water refugia for manatees in southwest Florida. *Estuar Coast* 34:106–119
- ✦ Stith BM, Slone DH, de Wit M, Edwards HH and others (2012) Passive thermal refugia provided warm water for Florida manatees during the severe winter of 2009–2010. *Mar Ecol Prog Ser* 462:287–301
- Sucsy P, Hupalo R, Freeman B (1998) Minimum flow determination for Blue Spring, Volusia County: the relationship between ground water discharge and winter refuge for manatees. Department of Water Resources, St. Johns River Water Management District, Palatka, FL
- ✦ Sutton RJ, Deas ML, Tanaka SK, Soto T, Corum RA (2007) Salmonid observations at a Klamath River thermal refuge under various hydrological and meteorological conditions. *River Res Appl* 23:775–785
- ✦ Terrien J, Perret M, Aujard F (2011) Behavioral thermoregulation in mammals: a review. *Front Biosci (Landmark Ed)* 16:1428–1444
- ✦ Thompson ME, Halstead BJ, Donnelly MA (2018) Thermal quality influences habitat use of two anole species. *J Therm Biol* 75:54–61
- ✦ Tomkiewicz SM, Fuller MR, Kie JG, Bats KK (2010) Global positioning system and associated technologies in animal behaviour and ecological research. *Philos Trans R Soc B* 365:2163–2176
- ✦ van Beest FM, Van Moorter B, Milner JM (2012) Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Anim Behav* 84:723–735
- ✦ Velásquez-Tibatá J, Salaman P, Graham CH (2013) Effects of climate change on species distribution, community structure, and conservation of birds in protected areas in Colombia. *Reg Environ Change* 13:235–248
- ✦ Walther GR, Post E, Convey P, Menzel A and others (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Weigle BL, Wright IE, Ross M, Flamm R (2001) Movements of radio-tagged manatees in Tampa Bay and along Florida's west coast, 1991–1996. FMRI Tech Rep TR-7. Florida Marine Research Institute, St. Petersburg, FL