Home Range and Habitat Use of Florida Box Turtles (*Terrapene bauri*) in the Ten Thousand Islands, Florida

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ABSTRACT.—For taxa with dispersal limitations, such as freshwater turtles, an understanding of their habitat and spatial needs can elucidate their risk to expected environmental and climatic changes. Florida Box Turtles (*Terrapene bauri*), a species of greatest conservation need, occurs in a diverse range of subtropical habitats on the Florida peninsula, including low-lying coastal areas subject to threats from climate change and sea level rise. We used radiotelemetry to assess the home range size and habitat use of Florida Box Turtles on a 37-ha anthropogenic, shell work island in southwestern Florida at the margin of its climatic niche. Home range calculated as 100% minimum convex polygons ranged from 0.29–1.52 ha with an average of 0.81 ha, which is consistent with, but smaller than, other parts of their range, and annual survivorship was estimated to be 0.875 (95% confidence interval = 0.67–1). Florida Box Turtles were most commonly located in tropical hardwood hammock forests (50.9%); other habitat use included shrub-scrub-cactus (29.6%), mangrove forest (13.4%) and shell barren (6.0%). Additional information on reproductive output, growth, temporal variation in survival, and response to disturbance such as hurricanes, storm overwash, and sea level rise is necessary to assess the long-term persistence of this population in the face of anticipated transitions of Florida's habitats because of global climate change.

Climate change presents many threats to natural ecosystems and may influence their functionality and stability (Intergovernmental Panel on Climate Change [IPCC], 2014). Coastal systems are particularly likely to be strongly affected because of shifting climate regimes, extreme weather events, and inundation from sea level rise associated with global warming (Noss, 2011; Wetzel et al., 2013; Williams, 2013). Terrestrial and freshwater reptile species that occupy low-lying coastal areas are expected to experience increasing pressures from climate change, especially those living at the margins of their environmental tolerances (McCallum et al., 2009; Pearlstine et al., 2010; Woodland et al., 2017). Reduced habitat quality, exposure to lethal thermal limits, and increased sex bias of offspring from warming temperatures are all potential climate-related stressors that may lead to population decline (Winter et al., 2016; Mothes et al., 2020). Turtles, a severely threatened vertebrate group, respond negatively to the compounding effects of fragmented habitat, unsustainable harvesting for human use, and now a rapidly changing climate (Lovich et al., 2018; Rhodin et al., 2018; Butler, 2019). Many nonmarine turtle species are relatively poor dispersers that are unequipped for accelerated habitat change (Gibbons et al., 2000; Butler, 2019), but some have been shown to move on short spatial scales in response to disturbance (Dodd et al., 2006; O'Dell et al., 2021). Given that dispersal is context dependent and relies on habitat availability, research on turtle space use and movement behavior (e.g., home range) are useful to determine their vulnerabilities and coping mechanisms in response to rapid climate change and to inform management actions (Woodland et al., 2017; Mothes et al., 2020, O'Dell et al., 2021).

North American box turtles (*Terrapene* spp.) have an extensive geographic range spanning the length of the eastern seaboard of the United States from New England south to the Florida Keys, west into the Great Plains, and with isolated lineages in Mexico. Box turtles are known to exhibit home range fidelity and have been documented in association with a high diversity of habitats and spatial configurations of resources (Stickel, 1950; Nieuwolt, 1996; Dodd, 2001; Kiester and Willey, 2015). Habitat quality can differ regionally and may influence the scale of movements in box turtle populations (Donaldson and Echternacht, 2005; Iglay et al., 2007; Refsnider et al., 2012; Kapfer et al., 2013). Therefore, evaluating home ranges of North American box turtles within different geographic regions can inform their management and conservation (Stickel, 1989; Greenspan et al., 2015). At the southernmost range limit in the United States, Florida Box Turtles (*Terrapene bauri*) provide an opportunity to study movement and habitat use in the context of ongoing natural and anthropogenic changes of the coastal Florida landscape. Conservation needs of the species in Florida are considerable (Florida Fish and Wildlife Conservation Commission [FWC], 2019), and quantitative ecological research is needed for robust management decisions of their populations in this region (Dodd and Franz, 1993; Verdon and Donnelly, 2005; Farrell et al., 2006).

The development of requisite management plans and species protections, however, are often directed at the species level (Alacs et al., 2007). The Eastern Box Turtle (*Terrapene carolina*, sensu lato) presents with a challenging phylogenetic history, complicated by intergradation and introgression of its subspecies, especially where lineages introgress in the Florida Panhandle (Farrell et al., 2006; Butler et al., 2011; Kiester and Willey, 2015; Seidel and Ernst, 2017). Though the taxonomic delineation of the genus remains unresolved, recent genetic studies on the *Terrapene carolina* complex acknowledge *Terrapene bauri* as unique, with an estimated divergence of millions of years ago from *T. carolina* (Butler et al., 2011; Martin et al., 2013). The Turtle Taxonomy Working Group also permits the use of *T. bauri* in their assessment of modern turtle species (Rhodin et al., 2017). With allocation of protection being contingent upon biological classification (Alacs et al., 2007), the distinction of *T.*

bauri at the species level may be an important element to their conservation.

Terrapene bauri is endemic to peninsular Florida and nearshore islands as well as the Florida Keys (Ernst and Lovich, 2009), which further contributes to their uniqueness as a species. Various Florida studies on these terrestrial turtles have reported population size, activity, diet, survival, and response to disturbance (Langtimm et al., 1996; Dodd, 1998; Jennings, 2007; Platt et al., 2009; Dodd et al. 2012). Previous habitat studies have primarily occurred within palm-pepper forests on Egmont Key in Hillsborough County (Dodd et al., 1994), the pine rockland habitats of Big Pine Key in Monroe County (Verdon and Donnelly, 2005; Platt et al., 2010), and mesic hammocks in Volusia County (Pilgrim et al., 1997). However, few data are available for the movement and home range size of *T. bauri* in Florida, which is essential information for understanding its natural history. Even less frequent are accounts of their association with subtropical mangrove and tropical hardwood hammock ecosystems (Verdon, 2004; Farrell et al., 2006; Jones et al., 2016). South Florida's Everglade's coastline is projected to experience adverse changes including severe habitat loss or complete submersion from 1 m of climate-related sea level rise (Pearlstine et al., 2010; Benscoter et al., 2013). As a dispersal-limited species isolated by island geography, *T. bauri* here may be especially vulnerable to habitat loss, which underscores an additional need for data on their behavioral ecology.

Here, we studied *Terrapene bauri* in southwestern Florida within the Ten Thousand Islands National Wildlife Refuge (TTINWR) and Rookery Bay National Estuarine Research Reserve (RBNERR) in Collier County, a region defined by an extensive formation of mangrove islands. We used radiotelemetry to describe the survival rates and home range size of adult *T. bauri* and to assess habitat use in subtropical mangrove-dominated island environments. Given that the genus *Terrapene* is generally associated with temperate regions, its spatial ecology and habitat requirements at the southern extent of its range are both interesting and relevant to any management strategy that may be developed for the conservation of representative, resilient, and persistent populations.

MATERIALS AND METHODS

Study Site.—The TTINWR, which encompassed most of our primary study site, comprises approximately 14,664 ha of expansive estuaries, mangroves, and marshes located within Collier County, Florida (Fig. 1). The RBNERR is composed of approximately 44,515 ha of coastal scrub, barrier islands, mangroves, and submerged lands. The protected TTINWR and RBNERR areas, along with adjacent conservation lands (e.g., Fakahatchee Strand State Preserve State Park, Collier Seminole State Park, Picayune Strand State Forest, Big Cypress National Preserve, and Everglades National Park), provide vital habitat for numerous species of flora and fauna and offer a wide variety of public recreational activities. Our study was conducted on a shell work island located within the boundaries of TTINWR. The exact site location has been withheld because of poaching and conservation concerns.

Our shell work island study site has unique historical origins as a major shell work site constructed by the indigenous Calusa between about 1,900 to 900 years before present (YBP) (Schwadron, 2010). The nonagricultural Calusa utilized the rich coastal food resources in south Florida and

constructed settlements from molluscan by-products such as Oyster (*Crassostrea* spp.), Crown Conch (*Melongena* sp.), and Whelk (*Busycon* sp.) shells (Moore, 1921; Marquardt, 2004, 2010; Schwadron, 2010; Hutchinson et al., 2016; Thompson et al., 2016). The prehistoric shell work site has an area just over 30 ha and was constructed gradually in phases for both human occupation and societal functions (Schwadron, 2010). Areas of exposed shell substrate or shell barren habitat are still currently present with sparse vegetation. Coastal hardwood hammock dominates the upland areas of the island as closed canopy habitat composed primarily of tropical hardwood species such as gumbo limbo (*Bursera simaruba*), strangler fig (*Ficus aurea*), white stopper (*Eugenia axillaris*), Florida swamp-privet (*Forestiera segregata*), saffron plum (*Sideroxylon celastrinum*), and soapberry (*Sapindus saponaria*). Shrub-scrub-cacti habitat occurs throughout the island with dense thickets of barb-wire cacti (*Acanthocereus tetragonus*), prickly-pear cacti (*Opuntia stricta*), and agave (*Agave decipiens*) as well as white indigoberry (*Randia aculeata*), Florida swampprivet, and gumbo limbo. The shrub-scrub-cacti habitat is relatively sunny, dry, and differs from the hammock in having an open canopy and overall shorter tree and shrub size. In addition, mangrove forests dominated by red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), and buttonwood (*Conocarpus erectus*) encompass the perimeter of the island and are present within the recessed inland areas. Climate in south Florida is characterized as subtropical, with seasonal precipitation differences that distinguish a wet season from May to October and a dry season from November to April (Verdon and Donnelly, 2005). Average annual precipitation ranges from 119–157 cm with 60% of total rainfall occurring in the wet season (Obeysekera et al., 1999).

Radiotelemetry.—Individual *Terrapene bauri* were opportunistically captured by hand through visual surveys during a long-term population assessment from 2010–2016 to determine species distribution and ecology (Jones et al., 2016; Jones and Willey, 2017). The abundance estimate for the study island is approximately 261.5 turtles (Jones et al. 2016). In March 2016, we outfitted a subset of 10 turtles with a 12-g R2020 radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota) on their posterior carapace using water weld plumbing epoxy. Transmitters weighed <5% of the turtle's body mass. We assigned each turtle a unique number according to the system of Ernst et al. (1974) that was notched into their marginal shell scutes with a triangular file (Cagle, 1939) for future identification. During initial capture, we determined sex (males were identified by a more pronounced plastron concavity and longer/thicker tail), and measured body mass (nearest g) using a 2,500-g spring-loaded scale (Medio Line, Pesola, Switzerland). Body size measurements (millimeters) were taken using dial calipers (straight carapace length, straight plastron length, plastron width at the hinge, carapace width at the eighth marginal scute, and carapace height at the highest point; Jones and Willey 2017). We handled the turtles for no more than 15 min and released them in the location they were captured. We located each turtle using a 148–174 MHz R1000 telemetry receiver (Communications Specialists Inc., Orange, California) approximately 1 day per week from March 2016 through October 2016 and once in March 2017 prior to removal of the radiotransmitters. Tracking was limited by US Fish and Wildlife personnel availability. We collected turtle radio locations using either a handheld Garmin Etrex Global Positioning System (GPS) unit (Garmin International Inc., Olathe,
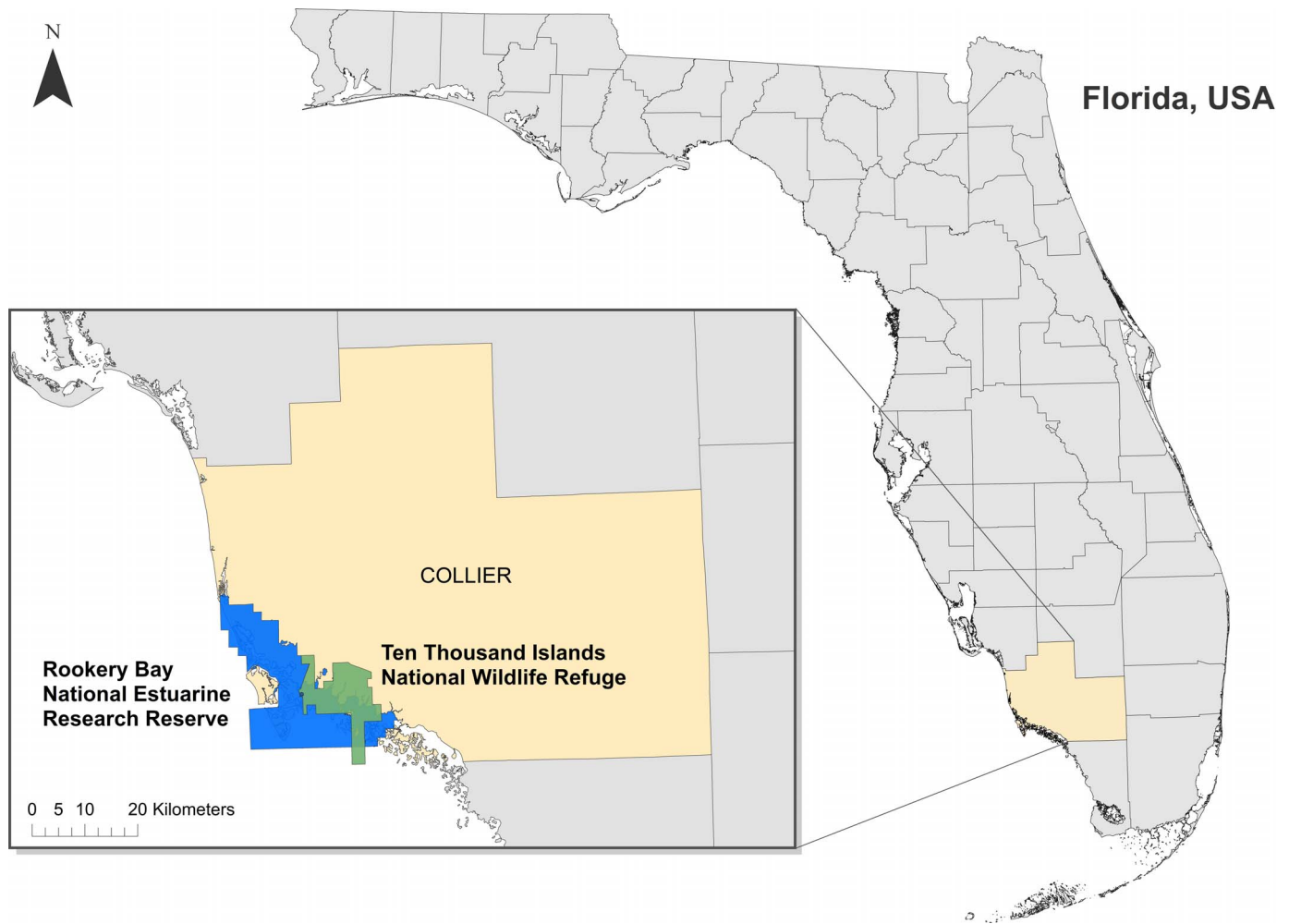
FIG. 1.   Study site for the 2016–2017 *Terrapene bauri* home range assessment located in southwestern Florida within the Ten Thousand Island National Wildlife Refuge (TTINWR) and Rookery Bay National Estuarine Research Reserve (RBNERR), Collier County, Florida, USA. TTINWR boundaries are delineated in green and RBNERR are delineated in blue.

Kansas) with ±5-m accuracy or a hand held Trimble Juno GPS unit (Trimble Navigation Limited, Westminster, Colorado) with ±2-m accuracy. Because of transmitter detachments, we did not track two of the turtles (F1052, M193) after 10 August 2016 and 23 August 2016, respectively. A single study animal (F1057) died of unknown causes during the study and therefore was not tracked after 6 September 2016, leaving a total of seven turtles tracked for the entire time period. Using the length of time tracked for each animal, we estimated annual survival based on the Kaplan-Meier estimator with the survival package (Therneau, 2015) in R (R Core Team, 2018).

Home Range and Movement.—To estimate home range size, we calculated minimum convex polygons (MCP; Fig. 2) and fixed kernel density estimators (KDE; Fig. 3) for each radio-tagged turtle based on its telemetry points. One complication associated with KDE is user choice in selecting the appropriate bandwidth smoothing factor (h). The value h can considerably impact KDE estimates (Seaman et al., 1998; Laver and Kelly, 2008), creating the potential for inconsistencies that affect the accuracy of determining home range in reptiles (Row and Blouin-Demers, 2006). In addition, deficient reporting of methods by authors (Laver and Kelly, 2008) and the use of outdated home range software extensions for Geographic Information Systems (GIS) (e.g., Animal Movements for ArcView extension, Hooge and

Eichenlaub, 1997; Hawth's Tools, Beyer, 2004; Home Range Tools, Rodgers et al., 2015), challenge the possibility of reproducible standards. Though most recent studies use 95% MCP, we used 100% MCP to estimate each turtle's total home range and assumed any movements to be biologically significant. However, we also reported 95% MCP and KDE at the 95% and 50% contours in efforts to offer comparability with other studies that may use similar estimators and methods. Prior to analysis, we converted turtle locations from decimal degrees to the projected coordinate system NAD 1983 UTM Zone 17N in ArcMap 10.5.1 (ESRI, Redlands, California). We estimated home ranges using the functions mcp and kernelUD in the adehabitatHR package (Calenge, 2006) in R (R Core Team, 2018). We calculated the smoothing parameter (h) for kernel estimations using both the reference default (href) and also a specified h value of 46.15 m (the mean distance since last location), which represented a biologically relevant value for the turtles at our study site. We did not utilize Least Squares Cross Validation (LSCV) because of its sensitivity to sample size and recommendation of ≥50 observations per individual (Seaman et al., 1999). We also used location data to measure movement distances of each individual turtle during the study period. We calculated the straight line distance between two successive turtle relocations in Excel (version 15.0.5485, Microsoft, Redmond, Washington) to determine the
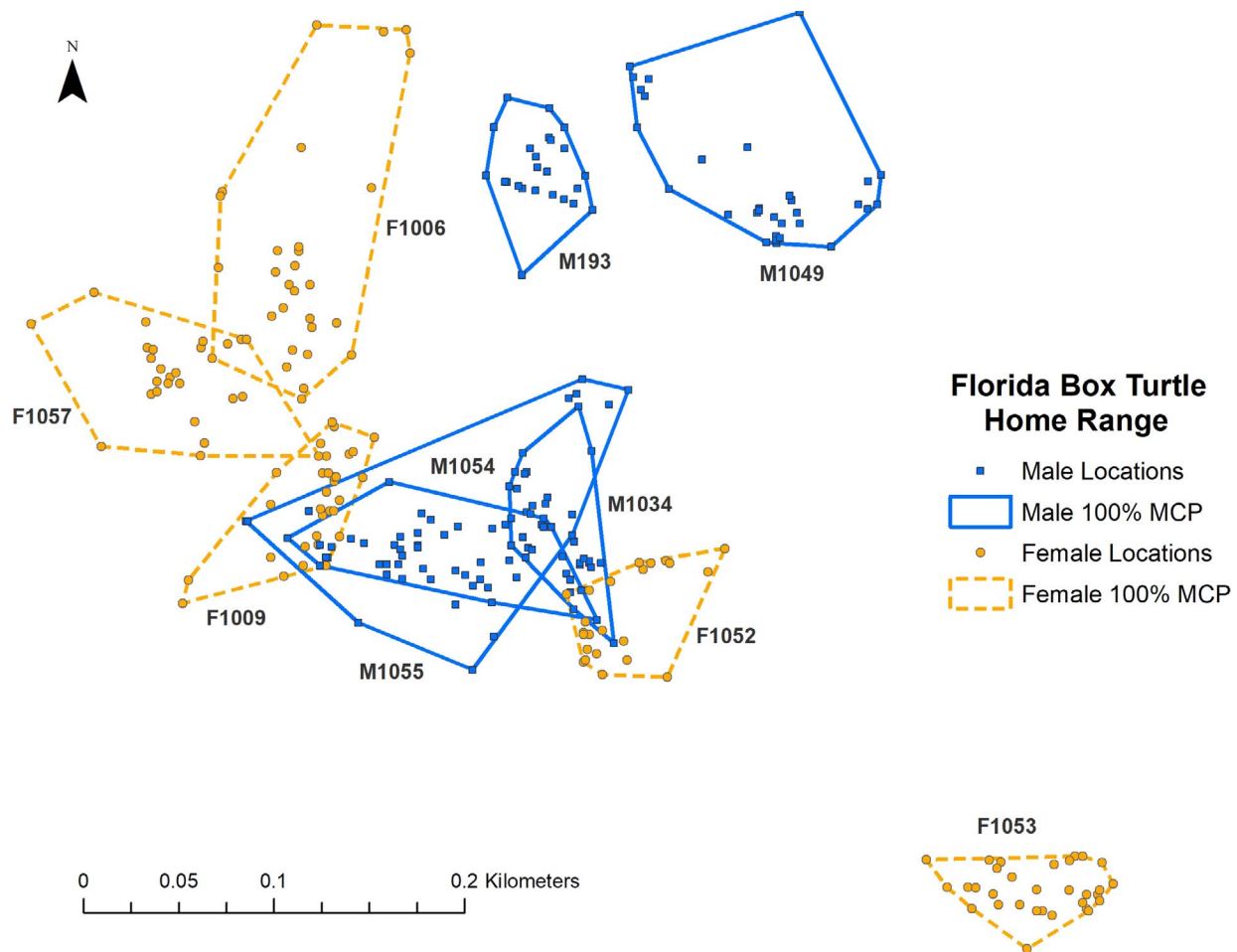
FIG. 2. Map of home ranges using 100% minimum convex polygons (MCP) for radio-tracked turtles at the study site in the Ten Thousand Islands National Wildlife Refuge and Rookery Bay National Estuarine Research Reserve, Florida, USA.

distance since last location in meters. We calculated daily movement distances by dividing the distance since last location by the number of days between relocations. We averaged movement distances by individual, sex, and across all turtles to identify patterns.

Habitat Use.—At each turtle location, we recorded habitat parameters such as dominant species for canopy, shrub, and herbaceous layers within 5 m of the telemetry location to assess habitat associations. We classified dominant cover type as tropical hardwood hammock forest, mangrove forest, shrub-scrub-cactus, or exposed shell barren. We determined average habitat use by calculating the percentage of each turtle's locations that occurred in each dominant cover type before averaging across all turtles.

Data Analysis.—We conducted all statistical analyses using RStudio (version 1.1.447) and Program R (version 3.4.4) (R Core Team, 2018). We set the level of significance for all tests to $\alpha = 0.05$. We visually assessed home range and movement data, which met assumptions for normality. We used Welch's two sample *t*-test (function t.test; stats package) to compare male and female MCP sizes and movements. We ran a correlation test (function cor.test; stats package) to evaluate the relationship between MCP size and body size using straight carapace length measurements. We conducted a Fisher's Exact test (function fisher.test; stats package) to determine if habitat associations

between males and females were significantly different from each other.

RESULTS

We tracked 10 adult *T. bauri* (five males and five females) for a total of 287 relocations. Radios were deployed from March 2016 to March 2017. Carapace length ranged in size from 121–149 mm. Based on the single observed death and the total number of days tracked, annual survivorship was estimated to be 0.875 (95% CI = 0.67–1) using the Kaplan-Meier estimator, which accounts for censored data.

Home Range and Movement.—The number of locations per turtle ranged from 23 to 31 (mean = 28.6). The individuals with <30 locations (loss of transmitter $n = 2$, death $n = 1$) were excluded from mean home range calculations. Average 100% MCP for *T. bauri* on the island was estimated as 0.81 ha (range: 0.29–1.52 ha, $n = 7$; Table 1). Home range sizes of males (MCP: 0.39–1.52 ha, $n = 4$) were similar to females (MCP: 0.29–1.35 ha, $n = 3$). There were no significant differences between the sexes ($t = -0.52$, df = 4, $P = 0.625$) and no significant correlations between body size and home range size ($t = -0.16$, df = 5, $P = 0.878$). The smallest and largest 95% KDE from all calculations was 0.78 ha and 7.31 ha, respectively ($n = 7$; Table 1). The 50% KDE ranged from 0.22–1.83 ha. The average distance that *T. bauri* traveled per day across all seven individuals was 6.3 m (range = 4.3–9.3 m). There were
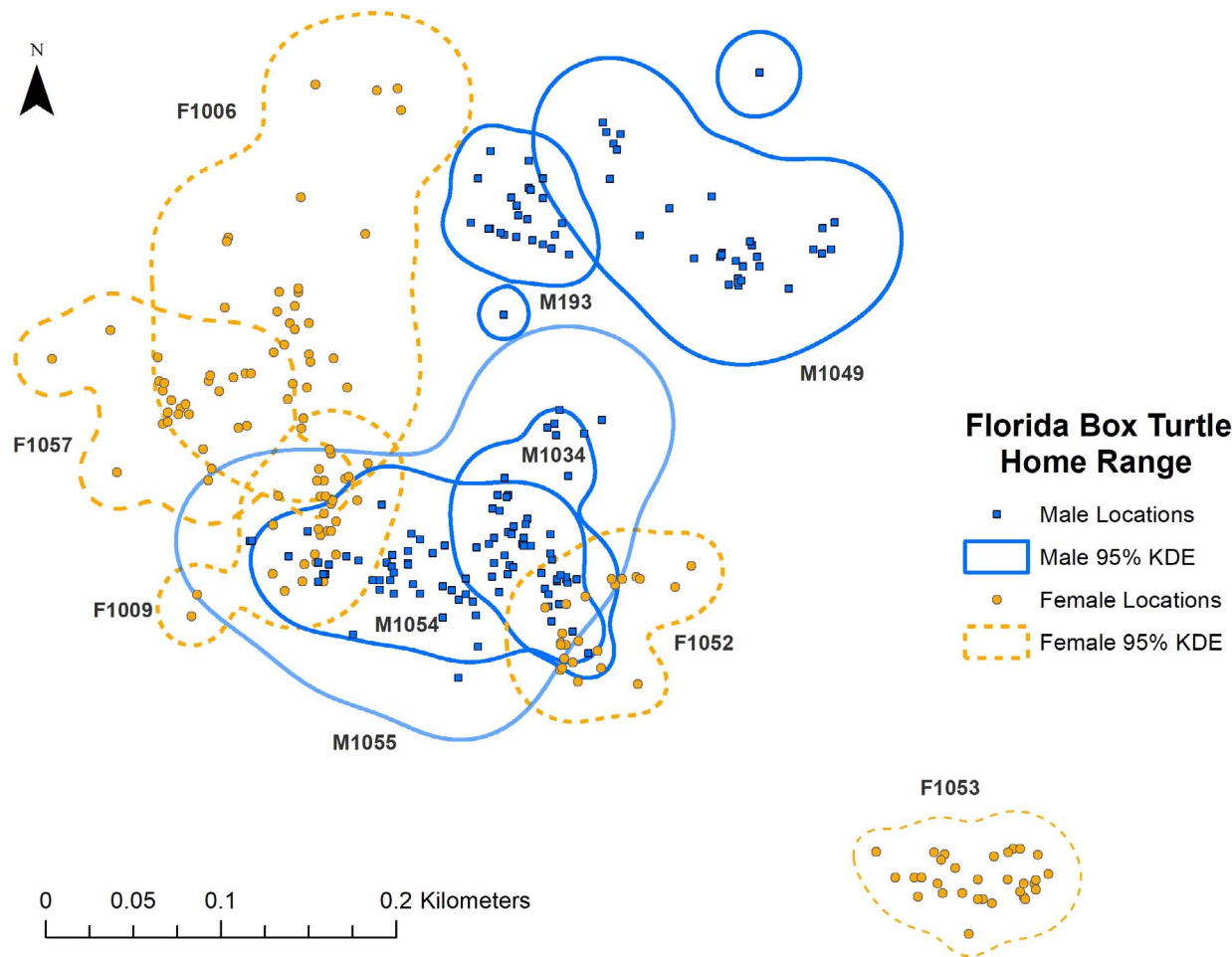
FIG. 3.   Map of home ranges using 95% kernel density estimates (KDE-href) for radio-tracked turtles at the study site in the Ten Thousand Islands National Wildlife Refuge and Rookery Bay National Estuarine Research Reserve, Florida, USA.

no significant differences in daily movement distances ($t = -0.16$, df = 4.04, $P = 0.879$) between the sexes (males $n = 4$, females $n = 3$).

Habitat Use.—Based on field observations of the 287 relocations from 10 turtles, an average of 50.9% of telemetry locations were associated with hardwood hammock (SE = 9.4, Table 2) and 29.6% (SE = 6.1) with shrub-scrub-cactus. Mangrove forest (13.4%, SE = 5.7) and shell barren habitat (6.0%, SE = 2.4) were also utilized. Habitat use did not differ significantly between the sexes ($\chi^2 = 2.78$, df = 3, $P = 0.426$).

TABLE 1.   Body mass (g), movement (m), and home range size (ha) for 10 radio-tracked *Terrapene bauri* (Florida Box Turtles) on a shell work island in the Ten Thousand Islands National Wildlife Refuge and Rookery Bay National Estuarine Research Reserve, Florida, USA. Radios were deployed March 2016–March 2017. Movement is represented by average distance per day (DPD). Home range was estimated using minimum convex polygons (95% and 100%) and kernel density estimators (KDE, 95% and 50% core range). *N* is the total number of individual turtle locations. Due to transmitter detachments (193, 1052) and a death (1057), those three turtles were not included in the mean calculations.

Turtle no.	Sex	N	Mass	DPD	Minimum convex polygon		KDE (href)		KDE (specified h value)	
					95%	100%	95%	50%	95%	50%
1006	F	30	452	8.88	1.32	1.35	3.50	0.71	6.91	1.53
1009	F	31	441	4.87	0.28	0.43	1.05	0.23	5.02	1.14
1052	F	23	433	4.38	0.26	0.35	0.96	0.24	4.86	1.14
1053	F	31	376	4.63	0.25	0.29	0.78	0.22	4.74	1.11
1057	F	26	383	4.55	0.51	0.81	1.57	0.28	5.26	1.18
193	M	24	413	2.52	0.18	0.33	0.70	0.17	4.58	1.06
1034	M	30	546.5	4.32	0.30	0.39	0.98	0.23	4.89	1.14
1049	M	31	497	5.88	0.62	1.09	2.45	0.54	6.15	1.45
1054	M	31	486.5	6.16	0.46	0.64	1.69	0.43	5.49	1.30
1055	M	30	429	9.27	1.42	1.52	4.04	1.08	7.31	1.83
Mean										
Females				6.13	0.62	0.69	1.78	0.39	5.56	1.26
Males				6.41	0.70	0.91	2.29	0.57	5.96	1.43
Total				6.29	0.66	0.81	2.32	0.49	5.79	1.36

TABLE 2. Average habitat use for 10 radio-tracked *Terrapene bauri* (Florida Box Turtles) on a shell work island in the Ten Thousand Islands National Wildlife Refuge and Rookery Bay National Estuarine Research Reserve, Florida, USA.

Turtle no.	Hardwood hammock	Mangrove forest	Shell barren	Shrub-scrub-cactus
193	45.83	0.00	16.67	37.50
1006	76.67	6.67	3.33	13.33
1009	90.32	0.00	3.23	6.45
1034	30.00	0.00	3.33	66.67
1049	19.35	54.84	3.23	22.58
1052	8.70	30.43	4.35	56.52
1053	54.84	19.35	3.23	22.58
1054	83.87	0.00	0.00	16.13
1055	76.67	3.33	0.00	20.00
1057	23.08	19.23	23.08	34.62
Average (SE)	50.93 (9.43)	13.38 (5.72)	6.04 (2.40)	29.63 (6.11)

DISCUSSION

The average home range size we observed for *T. bauri* on the island (0.81 ha) is smaller than what is generally observed for adult box turtle populations in the southeastern United States (Habeck et al., 2019). Home range studies for *T. carolina* have reported MCPs of 1.88 ha in Tennessee (Donaldson and Echternacht, 2005); 6.45 ha, 2.68 ha, and 4.9–17.3 ha in North Carolina (Hester et al., 2008; Kapfer et al., 2013; Roe et al., 2020); and 10.33 ha in Georgia (Greenspan et al., 2015). However, comparing home range studies among *Terrapene* spp. is difficult given the many calculation methods for home range and movement (Dodd, 2001; Ernst and Lovich, 2009; Kiester and Willey, 2015; Habeck et al., 2019). Even when consistent metrics are used (e.g., MCPs), home range sizes can also differ from factors such as sample size, number of relocations, and length of time tracked (Marchand et al., 2002; Donaldson and Echternacht, 2005; Boyle et al., 2009). The short-term duration of our study with limited sample size may contribute to our smaller findings when compared with averages reported by Habeck et al. (2019). However, *Terrapene* populations at the extreme southern extent of the range, such as *T. bauri* in Florida, have received limited attention with regard to home range and movement and may be underrepresented in current average estimates. While Pilgrim et al. (1997) and Farrell et al. (2006) report movement observations of Florida Box Turtles using radiotelemetry in Volusia County, and thread trailing was used on juvenile box turtles to study movement at Egmont Key (Jennings, 2003), the only study to report home range and movement estimates in southern Florida for *T. bauri* from radio-tracked animals is Verdon (2004) in the Lower Keys, Monroe County. Verdon (2004) found an average MCP of 1.4 ha (range 0.26–3.57 ha) and movements of 13.1 m per day in the dry season and 30.0 m in the wet season (*n* = 11 turtles, 426 captures). Our results were similar, though smaller with *T. bauri* MCPs (*n* = 7), ranging from 0.29–1.52 ha and average movement distances of 6.3 m per day (Table 1). Verdon (2004) tracked Florida Box Turtles for a full year of wet and dry seasonal variation and had an average of 38.7 relocations per turtle compared to our study with 28.6 relocations per turtle, which may partially account for the smaller home range sizes we observed. There is also a substantial disparity in the size of both islands. Although Big Pine Key contains fragmented habitat because of urban development, the 2,400-ha island is markedly larger than our 30-ha study island, potentially allowing larger home ranges (Verdon, 2004). Yet, habitat quality and spatial configuration of resources can also affect home range size (Nieuwolt, 1996; Dodd, 2001; Kiester and Willey,

2015; Roe et al., 2020). The hardwood hammock, scrub, and mangrove habitats at our study site may possibly offer more diverse and favorable conditions for *T. bauri* than the xeric pine rocklands at Big Pine Key, decreasing both the necessity for movement to locate resources and the home range sizes.

In their meta-analysis assessing variation in home range, Habeck et al. (2019) found that habitat structure at the ecoregional scale influences the home range size of Ornate Box Turtles (*Terrapene ornata*), but not for *T. carolina*. Because the Everglades ecoregion was not represented in the Habeck et al. (2019) study, nor were any Florida populations of *T. bauri*, additional *T. bauri* populations should be examined to ask whether home range size varies by habitat type for this species. Though not assessed by Habeck et al. (2019), finer scale habitat differences between our Florida Box Turtle study population and others in Florida are also important because locality and area resources may also affect home range behavior (Pilgrim et al. 1997; Dodd, 2001; Farrell et al., 2006).

Our annual survival estimate of 0.875 (95% CI = 0.67−1) is consistent with mark–recapture-based estimates of this same population (0.83, Jones et al., 2016), as well as of *Terrapene carolina* (sensu lato), in the literature (0.83−0.98 in Delaware [Nazdrowicz et al., 2008], 0.96 in Indiana [Currylow et al., 2011], 0.86−0.91 [Roe et al., 2019] and 0.91−0.97 in North Carolina [Roe et al., 2021]) and in Florida specifically (0.56−0.67 [Verdon and Donnelly, 2005], 0.87−0.89 [Dodd et al., 2006]). However, our data represent only a short time period (1 yr), and therefore do not include stochastic disturbance events or long-term changes in suitability because of climate change or sea level rise. Future studies examining reproductive output for our *T. bauri* population would allow an assessment of its long-term viability and susceptibility to climate change. At this thermally extreme southern range, global warming has the capacity to not only skew sex ratios toward female-only populations but may also warm nest incubation temperatures too high for survival (Gibbons et al., 2000; Hawkes et al., 2007; Wyneken and Lolavar, 2015), both of which could lead to drastic decline and inability to maintain future populations.

During the course of our study, individual variation occurred in the use of habitat types, as described in other box turtle studies (Dodd, 2001; Farrell et al., 2006; Frederickson, 2014; Roe et al., 2018). Although all *T. bauri* at our study site used transitional zones between habitat types on the island, some turtles were predominantly observed in hardwood hammock, some in shrub-scrub-cactus and, most notably, some individuals used mangrove forests. Given that mangrove habitat use appears to be uncharacteristic for *T. bauri* (Farrell et al., 2006),

the use of mangrove forest by *T. bauri* is unique to our study area and for the broader species complex. Although mangroves may be more prevalent in our study area, or more proximal to typical upland habitats, Verdon (2004) recorded only a single *T. bauri* observation in mangrove habitat out of 1,884 captures that were primarily in pine rocklands (86.9%). The association of *T. bauri* with tropical hardwood hammock is also distinctive, as it is a community type rare to the United States but endemic to south Florida (Loope and Urban, 1980; Olmstead et al., 1980) and, therefore, an uncommon occurrence in *Terrapene* habitat use. Rare cacti and agave vegetation are another uncommon habitat type present on the island and used by our radio-tagged turtles.

The Ten Thousand Island region of southwestern Florida is dominated by mangrove habitats, and relatively few islands contain upland hardwood hammock. Therefore, understanding how much area of this habitat type is necessary to support a *T. bauri* home range and population can be useful information for their management. *Terrapene* spp. commonly occupy mesic woodlands (Dodd, 2001), making the availability of hardwood hammock for *T. bauri* in our study region important. Hardwood hammock occurs on slightly elevated uplands and therefore rarely floods, yet it remains moist and cool because of the closed forest canopy structure (US Fish and Wildlife Service [USFWS], 2011). The semideciduous vegetation also generates an ample layer of leaf litter and soil humus (USFWS, 2011). Compared to the other habitat types on the island, the dense understory and leaf litter layer of the hammock is where box turtles were often found partially buried. Several tree species in this habitat type produce fruit as well (Karim and Main, 2004). The characteristics of hardwood hammocks support life history requirements for *T. bauri*. Turtles can take refuge from desiccating winds and extreme subtropical temperatures within the microenvironment of tropical hardwood hammocks while also maintaining access to food resources. Therefore, the expected changes and loss of upland forest habitat in southern Florida because of global climate change are of concern for the survival of this population. Pearlstine et al. (2010) summarizes the ramifications of climate change in southwestern Florida, including the Ten Thousand Islands, which could incur reduction or complete loss of habitats because of sea level rise, drought, and increased storm activity as well as the conversion of plant communities from temperature increases, salinity changes, and invasion of exotic vegetation.

Island forests rely heavily on precipitation as a freshwater source (Langston et al., 2017), which is then stored in the soil vadose zone (see Sternberg et al., 2007 and Saha et al., 2011 for process descriptions). As sea level rises, soils and groundwater become flooded with sea water and the fresh vadose water decreases. The accumulation of salt and anoxic conditions result in physiological stresses too extreme for tree regeneration and survival (Ross et al., 1994; Williams et al., 1999; Desantis et al., 2007; Saha et al., 2011; Jones and Koptur, 2017). Additionally, the rise in temperature and decrease in rainfall predicted for southern Florida may intensify these effects for vegetation by contributing to soil dryness (Desantis et al., 2007; Pearlstine et al., 2010; Saha et al., 2011). Further, the expected increase of storm intensity may also cause more-frequent forest damage by uprooting canopy trees and exposing young undergrowth to storm-surged saltwater (Michener et al., 1997; Langston et al., 2017). In general, the low-lying elevation of Florida increases its susceptibility to the average expected sea level rise (Ross et al., 2016). The risk of full inundation for the lowest shell work

islands in our study region is plausible, and larger islands could experience a reduction in the size of upland habitat (Jones et al., 2016).

Though geographic shifts to suitable habitat may occur with climate-related changes at the edge of a species range (Parmesan, 2006), rapid change over short time scales can challenge terrestrial reptiles such as box turtles that have limited long-distance dispersal abilities (McCallum et al., 2009). As an island population, *T. bauri* at our study site are further restricted by sea water and are even more limited in their ability to disperse than are other reptiles on the mainland. Additionally, they may be functioning close to their physiological tolerances in the subtropical conditions of this extreme southerly range (Demetrio, 2019). Therefore, the loss of hardwood hammock habitat, combined with accelerated temperature increases from changing climatic conditions, may be particularly consequential for *T. bauri*. Individuals on our island study site would need to persist in smaller areas with limited resources and less access to hammock microenvironments needed for thermoregulation. Studies on *T. bauri* by Dodd et al. (2012) at Egmont Key over a 16-yr period showed some resilience to large-scale habitat disturbances such as overwash from tropical storms and extensive canopy loss from exotic plant removal. On the larger 180-ha island of Egmont Key, *T. bauri* that were relocated to unaffected areas maintained stable populations, provided that initial mortality was avoided. However, substantial loss of land from sea level rise would most likely create difficulties for terrestrial turtles to find new habitat and recover from storms. Continued erosion from storm disturbances and lack of sand deposition from human coastal development has already resulted in a loss of nearly one half of Egmont Key since the early 1900s (Dodd et al., 2006).

The role of mangrove forests as a driver of structural change in plant communities also poses a question for our study system. Mangroves have the ability to capitalize on sea level rise and warming temperatures. At the northern extent of their range with higher salinity tolerances, mangroves can outcompete other species to expand their distribution, which has led to changes in the habitat composition of several coastal Florida areas (Ross et al., 1994; Krauss et al., 2011; Saha et al., 2011; Langston et al., 2017). Though six of the turtles tracked in our study used mangrove forest within their home ranges, mangrove use averaged only 13.4% across all 10 turtles. Noninundated habitat is also needed for turtle nesting. Therefore, it is questionable whether *T. bauri* could solely exist in this habitat type. Furthermore, mangrove forests are sensitive to climate change, and they succumb to rapid submersion and harsh storm disturbances if canopy damage is extensive and soil surface elevation is not able to be rebuilt (Michener et al., 1997; Smith et al., 2009; Krauss et al., 2014). Due to uncertainties in climate projections, only long-term studies documenting the landscape changes of south Florida and subsequent habitat use by *T. bauri* can assist in answering questions about the future of this unique ecosystem and how populations will respond.

To our knowledge, aside from Verdon's (2004) research at Big Pine Key, our study represents the only other assessment of *T. bauri* using radiotelemetry in the subtropical habitats of southern Florida. Our results are therefore particularly informative with regard to their home range and habitat use in a subtropical region. Given the considerable effects that a changing climate could have on our *T. bauri* population and on others in Florida, continued monitoring of movement and field mapping to assess habitat selection and availability across

the islands is recommended. Sustained, long-term research could have a meaningful impact for *T. bauri* conservation and would not only provide land managers and researchers with improved knowledge of its ecological requirements, but also provide critical information necessary for evaluating *T. bauri*'s level of adaptation or extinction risk to environmental and climatic change.

Literature Cited

Alacs, E., F. Janzen, and K. Scribner. 2007. Genetic issues in freshwater turtle and tortoise conservation. Chelonian Research Monographs 4:107–123.

Benscoter, A. M., J. S. Reece, R. F. Noss, L.A. Brandt, F. J. Mazzotti, S. S. Romanach, and J. I. Watling. 2013. Threatened and endangered subspecies with vulnerable ecological traits also have high susceptibility to sea level rise and habitat fragmentation. PLoS One 8:e70647.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. Available from: https://helpdesk.forestry.oregonstate.edu/software/geospatial-modelling-environment.

Boyle, S. A., W. C. Lourenco, L. R. da Silva, and A. T. Smith. 2009. Home range estimates vary with sample size and methods. Folia Primatologica 80:33–42.

Butler, C. J. 2019. A review of the effects of climate change on chelonians. Diversity 11:138.

Butler, J. M., C. K. Dodd, M. Aresco Jr., and J. D. Austin. 2011. Morphological and molecular evidence indicates that the Gulf Coast box turtle (*Terrapene carolina major*) is not a distinct evolutionary lineage in the Florida Panhandle. Biological Journal of the Linnean Society 102:889–901.

Cagle, F. R. 1939. A system of marking turtles for future recognition. Copeia 1939:170–173.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Currylow, A. F., P. A. Zollner, B. J. MacGowen, and R. N. Williams. 2011. A survival estimate of midwestern adult eastern box turtles using radiotelemetry. American Midland Naturalist 165:143–149.

Demetrio, C. 2019. Home range, habitat use and thermal ecology of the Florida box turtle (*Terrapene bauri*) on an anthropogenic island in southwestern Florida. M.S. thesis, Antioch University New England, USA.

Desantis, L. R. G., S. Bhotika, K. Williams, and F. E. Putz. 2007. Sea-level rise and drought interactions accelerate forest decline on the Gulf Coast of Florida, USA. Global Change Biology 13:2349–2360.

Dodd, C. K. Jr. 1998. Biomass of an island population of Florida box turtles (*Terrapene carolina bauri*). Journal of Herpetology 32:150–152.

———. 2001. North American Box Turtles: A Natural History. University of Oklahoma Press, USA.

Dodd, C. K. Jr., and R. Franz. 1993. The need for status information on common herpetofaunal species. Herpetological Review 24:47–50.

Dodd, C. K. Jr., R. F. Franz, and L. L. Smith. 1994. Activity patterns and habitat use of box turtles (*Terrapene carolina bauri*) on a Florida island, with recommendations for management. Chelonian Conservation and Biology 1:97–106.

Dodd, C. K. Jr., A. Ozgul, and M. K. Oli. 2006. The influence of disturbance events on survival and dispersal rates of Florida box turtles. Ecological Applications 16:1936–1944.

Dodd, C. K. Jr., N. L. Hyslop, and M. K. Oli. 2012. The effects of disturbance events on abundance and sex ratios of a terrestrial turtle, *Terrapene bauri*. Chelonian Conservation and Biology 11:44–49.

Donaldson, B. M., and A. C. Echternacht. 2005. Aquatic habitat use relative to home range and seasonal movement of eastern box turtles (*Terrapene carolina*: Emydidae) in eastern Tennessee. Journal of Herpetology 39:278–284.

Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. Johns Hopkins University Press, USA.

Ernst, C. H., M. F. Hershey, and R. W. Barbour. 1974. A new coding system for hard-shelled turtles. Kentucky Academy of Sciences 35:27–28.

Farrell, T., C. K. Dodd Jr., and P. May. 2006. *Terrapene carolina*—eastern box turtle. Chelonian Research Monographs 3:235–248.

Frederickson, T. S. 2014. Thermoregulation and habitat use of the eastern box turtle in southwestern Virginia. Northeastern Naturalist 21:554–564.

(FWC) Florida Fish and Wildlife Conservation Commission. 2019. Florida's Wildlife Legacy Initiative: Florida's state wildlife action plan. Tallahassee, Florida. Available from: https://myfwc.com/media/22767/2019-action-plan.pdf.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, et al. 2000. The global decline of reptiles, déjà vu amphibians. BioScience 50:653–666.

Greenspan, S. E., E. P. Condon, and L. L. Smith. 2015. Home range and habitat selection in the eastern box turtle (*Terrapene carolina carolina*) in a longleaf pine (*Pinus palustris*) reserve. Herpetological Conservation and Biology 10:99–111.

Habeck, C., M. Figueras, J. Deo, and R. Burke. 2019. A surfeit of studies: what have we learned from all the box turtle (*Terrapene carolina* and *T. ornata*) home range studies? Diversity 11:68.

Hawkes, L. A., Broderick, A. C., Godfrey, M. H., and B. J. Godley. 2007. Investigating the potential impacts of climate change on a marine turtle population. Global Change Biology 13:923–932.

Hester, J., S. Price, and M. Dorcas. 2008. Effects of relocation on movements and home ranges of eastern box turtles. Journal of Wildlife Management 72:772–777.

Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to ArcView, Version 1.1. Alaska Science Center Biological Science Office. US Geological Survey, USA.

Hutchinson, D. L., L. Norr, T. Schober, W. H. Marquardt, K. J. Walker, L. A. Newsom, and C. M. Scarry. 2016. The Calusa and prehistoric subsistence in central and south Gulf Coast Florida. Journal of Anthropological Archaeology 41:55–73.

Iglay, R. B., J. L. Bowman, and N. H. Nazdrowicz. 2007. Eastern box turtle (*Terrapene carolina carolina*) movements in a fragmented landscape. Journal of Herpetology 41:102–106.

(IPCC) Intergovernmental Panel on Climate Change. 2014. Climate Change 2014: Synthesis Report. Pp. 151 in R. K. Pachauri and L. A. Meyer (eds.), Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Switzerland.

Jennings, A. H. 2003. Daily and seasonal activity patterns and movements of juvenile box turtles (*Terrapene carolina bauri*) on Egmont Key, Florida. Chelonian Conservation and Biology 4:578–587.

———. 2007. Use of habitats and microenvironments by juvenile Florida box turtles, *Terrapene carolina bauri*, on Egmont Key. Herpetologica 63:1–10.

Jones, I. M., and S. Koptur. 2017. Dead land walking: the value of continued conservation efforts in south Florida's imperiled pine rocklands. Biodiversity Conservation 26:3241–3253.

Jones, M. T., and L. L. Willey. 2017. Distribution, population structure, and movement patterns of Florida box turtles (*Terrapene carolina bauri*) in the northern Ten Thousand Islands, Florida Summary Report 2010–2016. American Turtle Observatory, USA.

Jones, M. T., L. L. Willey, and N. D. Charney. 2016. Box turtles (*Terrapene carolina bauri*) on ancient, anthropogenic shell work islands in the Ten Thousand Islands Mangrove Estuary, Florida, USA. Journal of Herpetology 50:94–101.

Karim, A., and M. B. Main. 2004. Tropical hardwood hammocks in Florida. University of Florida IFAS Extension. Available from: http://edis.ifas.ufl.edu/UW206.

KAPFER, J. M., D. J. MUNOZ, J. D. GROVES, AND R. W. KIRK. 2013. Home range and habitat preferences of eastern box turtles (*Terrapene carolina* Linnaeus, 1758) in the Piedmont Ecological Province of North Carolina (USA). Herpetology Notes 6:251–260.

KIESTER, A. R., AND L. L. WILLEY. 2015. *Terrapene carolina* (Linnaeus 1758)—Eastern box turtle, common box turtle. Chelonian Research Monographs–Conservation Biology of Freshwater Turtles and Tortoises 5:1–25.

KRAUSS, K. W., A. S. FROM, T. W. DOYLE, T. J. DOYLE, AND M. J. BARRY. 2011. Sea level rise and landscape change influence mangrove encroachment onto marsh in the Ten Thousand Islands region of Florida, USA. Journal of Coastal Conservation 15:629–638.

KRAUSS, K. W., K. L. MCKEE, C. E. LOVELOCK, D. R. CAHOON, N. SAINTILAN, R. REEF, AND L. CHEN. 2014. How mangrove forests adjust to rising sea level. The New Phytologist 202:19–34.

LANGTIMM, C. A., C. K. DODD JR., AND R. Z. FRANZ. 1996. Estimates of abundance of box turtles (*Terrapene carolina bauri*) on a Florida island. Herpetologica 52:496–504.

LAVER, P. N., AND M. J. KELLY. 2008. A critical review of home range studies. Journal of Wildlife Management 72:290–298.

LANGSTON, A. K., D. A. KAPLAN, AND F. E. PUTZ. 2017. A casualty of climate change? Loss of freshwater forest islands on Florida's Gulf Coast. Global Change Biology 23:5383–5397.

LOOPE, L. L., AND N. H. URBAN. 1980. A Survey of Fire History and Impact in Tropical Hardwood Hammocks in the East Everglades and Adjacent Portions of Everglades National Park. Report T-592. Publication of Archival Library and Museum Materials. Available from: https://palmm.digital.flvc.org/islandora/object/fiu%3A14435#page/FI05928732_cover1/mode/2up.

LOVICH, J. E., J. R. ENNEN, M. AGHA, AND J. W. GIBBONS. 2018. Where have all the turtles gone, and why does it matter? BioScience 68:771–781.

MARCHAND, M., M. M. QUINLAN, AND C.W. SWARTH. 2002. Movement patterns and habitat use of eastern box turtles at the Jug Bay Wetlands Sanctuary, Maryland. Pp. 55–61 in C. W. Swarth, W. M. Roosenburg, and E. Kiviat (eds.), Conservation and Ecology of Turtles of the Mid-Atlantic Region. Bibliomania, USA.

MARQUARDT, W. H. 2004. Calusa. Pp. 204–212 in R. D. Fogelson (ed.), Handbook of North American Indians. Volume 14: Southeast. Smithsonian Institution, USA.

———. 2010. Shell mounds in the southeast: middens, monuments, temple mounds, rings, or works? American Antiquity 75:551–570.

MARTIN, B. T., N. P. BERNSTEIN, R. D. BIRKHEAD, J. F. KOUKL, S. M. MUSSMANN, AND J. S. PLACYK. 2013. Sequence-based molecular phylogenetics and phylogeography of American box turtles (*Terrapene* spp.) with support from DNA barcoding. Molecular Phylogenetics and Evolution 68:199–134.

MCCALLUM, M. L., J. L. MCCALLUM, AND S. E. TRAUTH. 2009. Predicted climate change may spark box turtle declines. Amphibia-Reptilia 30:259–264.

MICHENER, W. K., E. R. BLOOD, K. L. BILDSTEIN, M. M. BRINSON, AND L. R. GARDNER. 1997. Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. Ecological Applications 7:770–801.

MOORE, C. B. 1921. Notes on shell implements from Florida. American Anthropologist, New Series 23:12–18.

MOTHES, C., H. HOWELL, AND C. SEARCY. 2020. Habitat suitability models for the imperiled wood turtle (*Glyptemys insculpta*) raise concerns for the species' persistence under future climate change. Global Ecology and Conservation 24:e01247.

NAZDROWICZ, N. H., J. L. BOWMAN, AND R. R. ROTH. 2008. Population ecology of the eastern box turtle in a fragmented landscape. Journal of Wildlife Management 72:745–753.

NIEUWOLT, P. M. 1996. Movement, activity, and microhabitat selection in the western box turtle, *Terrapene ornate luteola*, in New Mexico. Herpetologica 52:487–495.

NOSS, R. F. 2011. Between the devil and the deep blue sea: Florida's unenviable position with respect to sea level rise. Climate Change 107:1–16.

OBEYSEKERA, J., J. A. BROWDER, L. HORNUNG, AND M. A. HARWELL. 1999. The natural south Florida system I: climate, geology, and hydrology. Urban Ecosystems 3:223–244.

O'DELL, D. I., J. M. KARBERG, K. C. BEATTIE, K. A. OMAND, AND E. C. BUCK. 2021. Changes to spotted turtle (*Clemmys guttata*) habitat selection in response to a salt marsh restoration. Wetlands Ecology and Management 29:301–313.

OLMSTEAD, I. C., L. L. LOOPE, AND C. E. HILSENBECK. 1980. Tropical Hardwood Hammocks of the Interior of Everglades National Park

and Big Cypress National Reserve. Report T-604. Publication of Archival Library and Museum Materials. Available from: https://palmm.digital.flvc.org/islandora/object/fiu%3A16738#page/FI06041905_cover1/mode/2up.

PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

PEARLSTINE, L. G., E. V. PEARLSTINE, AND N. G. AUMEN. 2010. A review of the ecological consequences and management implications of climate change for the everglades. Journal of North American Benthological Society 29:1510–1526.

PILGRIM, M. A., T. M. FARRELL, AND P. G. MAY. 1997. Population structure, activity, and sexual dimorphism in a central Florida population of box turtles, *Terrapene carolina bauri*. Chelonian Conservation and Biology 2:483–488.

PLATT, S. G., C. HALL, H. LIU, AND C. K. BORG. 2009. Wet-season food habits and intersexual dietary overlap of Florida box turtles (*Terrapene carolina bauri*) on National Key Deer Wildlife Refuge, Florida. Southeastern Naturalist 8:335–346.

PLATT, S. G., H. LIU, AND C. K. BORG. 2010. Fire ecology of the Florida box turtle (*Terrapene carolina bauri* Taylor) in pine rockland forests of the lower Florida Keys. Natural Areas Journal 30:254–260.

R CORE TEAM. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: https://www.R-project.org/.

REFSNIDER, J. M., J. STRICKLAND, AND F. J. JANZEN. 2012. Home range and site fidelity of imperiled ornate box turtles (*Terrapene ornata*) in northwestern Illinois. Chelonian Conservation and Biology 11:78–83.

RHODIN, A. G. J., J. B. IVERSON, R. BOUR, U. FRITZ, A. GEORGES, H. B. SHAFFER, AND P. P. VAN DIJK. 2017. Turtles of the world: annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status. 8th ed. Chelonian Research Monographs 7:1–292.

RHODIN, A. G., C. B. STANFORD, P. P. VAN DIJK, C. EISEMBERG, L. LUISELLI, R. A. MITTERMEIER, R. HUDSON, B. D. HORNE, E. V. GOODE, G. KUCHLING, ET AL. 2018. Global conservation status of turtles and tortoises (Order Testudines). Chelonian Conservation and Biology 17:135–161.

RODGERS, A. R., J. G. KIE, D. WRIGHT, H. L. BEYER, AND A. P. CARR. 2015. HRT: home range tools for ArcGIS. Version 2.0. Ontario Ministry of Natural Resources and Forestry. Centre for Northern Forest Ecosystem Research, Canada.

ROE, J. H., K. H. WILD, AND Z. R. LUNN. 2018. Inter- and intra-population variation in habitat selection for a forest-dwelling terrestrial turtle, *Terrapene carolina*. Herpetological Conservation and Biology 13:711–725.

ROE, J. H., K. H. WILD, AND M. S. CHAVEZ. 2019. Responses of a forest-dwelling terrestrial turtle, *Terrapene carolina*, to prescribed fire in a Longleaf Pine ecosystem. Forest Ecology and Management 432:949–956.

ROE, J. H., A. L. KISH, AND J. P. NACY. 2020. Variation and repeatability of home range in a forest-dwelling terrestrial turtle: implications for prescribed fire in forest management. Journal of Zoology 310:71–82.

ROE, J. H., G. J. GRAETER, A. A. LAVERE, AND A. B. SOMERS. 2021. State-wide population characteristics and long-term trends for eastern box turtles in North Carolina. Ecosphere 12:e03378.

ROSS, M. S., J. J. O'BRIEN, AND L. DA SILVEIRA LOBO STERNBERG. 1994. Sea-level rise and the reduction in pine forests in the Florida Keys. Ecological Applications 4:144–156.

ROSS, M. S., J. P. SAH, P. L. RUIZ, A. A. SPITZIG, AND S. C. SUBEDI. 2016. Inferring implications of climate change in south Florida hardwood hammocks through analysis of metacommunity structure. Diversity and Distributions 22:783–796.

ROW, J. R., AND G. BLOUIN-DEMERS. 2006. Kernels are not accurate estimators of home range size for herpetofauna. Copeia 2006:797–802.

SAHA, A. K., S. SAHA, J. SADLE, J. JIANG, M. S. ROSS, R. M. PRICE, L. STERNBERG, AND K. S. WENDELBERGER. 2011. Sea level rise and south Florida coastal forests. Climatic Change 107:81–108.

SCHWADRON, M. 2010. Landscapes of maritime complexity: prehistoric shell work sites of the Ten Thousand Islands, Florida. Ph.D. diss., University of Leicester, UK.

SEAMAN, D. E., B. GRIFFITH, AND R. A. POWELL. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26:95–100.

SEAMAN, D. E., J. MILLSPAUGH, B. KERNOHAN, G. BRUNDIGE, K. RAEDEKE, AND R. GITZEN. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Seidel, M. E., and C. H. Ernst. 2017. A systematic review of the turtle family Emydidae. Vertebrate Zoology 67:1–122.

Smith, T. J., G. H. Anderson, K. Balentine, G. Tiling, G. A. Ward, and K. R. T. Whelan. 2009. Cumulative impacts of hurricanes on Florida mangrove ecosystems: sediment deposition, storm surges, and vegetation. Wetlands 29:24–34.

Sternberg, L., S. Y. Tey, S. M. L. Ewe, F. Miralles-Wilhelm, and D. L. DeAngelis. 2007. Competition between hardwood hammocks and mangroves. Ecosystems 10:648–660.

Stickel, L. F. 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). Ecological Monographs 20: 351–378.

———. 1989. Home range behavior among box turtles (*Terrapene c. carolina*) of a bottomland forest in Maryland. Journal of Herpetology 23:40–44.

Therneau, T. 2015. A package for survival analysis in R. Version 2.38. Available from: https://CRAN.R-project.org/package=survival.

Thompson, V. D., W. H. Marquardt, A. Cherkinsky, A. D. Roberts Thompson, K. J. Walker, L. A. Newsom, and M. Savarese. 2016. From shell midden to midden-mound: the geoarchaeology of Mound Key, an anthropogenic island in southwest Florida, USA. PLoS One 11: e0154611.

(USFWS) United States Fish and Wildlife Service. 2011. South Florida Multi-Species Recovery Plan: Tropical Hardwood Hammock. USFWS Southwest Region.

Verdon, E. 2004. Activity patterns, habitat use, and movements of the Florida box turtle (*Terrapene carolina bauri*) in the Florida Keys. M.S. thesis, Florida International University, USA.

Verdon, E., and M. A. Donnelly. 2005. Population structure of Florida box turtles (*Terrapene carolina bauri*) at the southernmost limit of their range. Journal of Herpetology 39:572–577.

Wetzel, F. T., H. Beissmann, D. J. Penn, and W. Jetz. 2013. Vulnerability of terrestrial island vertebrates to projected sea-level rise. Global Change Biology 19:2058–2070.

Williams, S. J. 2013. Sea-level rise implications for coastal regions. Journal of Coastal Research 63:184–196.

Williams, K., K. C. Ewel, R. P. Stumpf, F. E. Putz, and T. W. Workman. 1999. Sea-level rise and coastal forest retreat on the west coast of Florida, USA. Ecology 80:2045–2063.

Winter, M., W. Fiedler, W. M. Hochachka, A. Koehncke, S. Meiri, and I. De la Riva. 2016. Patterns and biases in climate change research on amphibians and reptiles: a systematic review. Royal Society Open Science 3:160158.

Woodland, R. J., C. L. Rowe, and P. Henry. 2017. Changes in habitat availability for multiple life stages of diamondback terrapins (*Malaclemys terrapin*) in Chesapeake Bay in response to sea level rise. Estuaries and Coasts 40:1502–1515.

Wyneken, J., and A. Lolavar. 2015. Loggerhead sea turtle environmental sex determination: implications of moisture and temperature for climate change based predictions for species survival. Journal of Experimental Zoology B (Molecular and Developmental Evolution) 324:295–314.