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Author(s): Michael T. Jones , Lisabeth L. Willey , and Noah D. Charney
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Box Turtles (*Terrapene carolina bauri*) on Ancient, Anthropogenic Shell Work Islands in the Ten Thousand Islands Mangrove Estuary, Florida, USA

MICHAEL T. JONES,[1,2] LISABETH L. WILLEY,[1,3] AND NOAH D. CHARNEY[4]

[1]*Organismic and Evolutionary Biology, University of Massachusetts, Amherst, Massachusetts 01003 USA*
[4]*Hampshire College, Amherst, Massachusetts 01003 USA*

ABSTRACT.—**We investigated the ecology, distribution, and density of Florida Box Turtle (*Terrapene carolina bauri* Taylor, 1895) populations in the Ten Thousand Islands (TTI), an estuarine mangrove ecosystem in southwestern Florida. The distribution and ecology of Box Turtles in this region and this habitat type have not been previously investigated. The study area encompassed 18 islands and included five natural islands, 13 man-made shell islands, and adjacent mangrove environments. Two hundred and twenty-nine live Box Turtles and 95 Box Turtle shells were detected a total of 409 times on seven of the 18 islands. The seven islands where Box Turtles were detected ranged in size from 7.3 to 31.0 ha and were ancient shell work sites, apparently constructed by the Calusa or other Prehistoric Indians approximately 1,900 to 900 years before present (ybp). Box Turtles were not detected on natural islands. We detected Box Turtles primarily in subtropical hardwood hammock forests, but we detected 10% of turtles in mangrove or mangrove ecotones. Males were larger than females across all sites. We detected a significant difference in body size between living and dead adults. We estimated population size on four shell work islands to range from 43 (SE = 3.5) turtles to 270 (SE = 244) turtles and estimated densities ranging from 2.7–12.2 turtles/ha. Box Turtles on the shell work islands of the TTI are a unique example of populations living on ancient, manmade islands. However, known populations are small and isolated and may be susceptible to increased human recreational use, mechanized vegetation management, or predation by raccoons.**

The Florida Box Turtle (*Terrapene carolina bauri* Taylor, 1985) occurs in mesophytic hardwood hammocks and palmetto forests throughout peninsular Florida, United States (Dodd et al., 1994; Dodd, 2001; Ernst and Lovich, 2009). In the xeric Lower Florida Keys, *T. c. bauri* occurs in pine rockland, pine forests, and scrubland habitats (Verdon and Donnelly, 2005). In addition to the Keys and islands in Florida Bay, Box Turtles are known from several barrier islands along the west coast (Dodd, 2001; Krysko et al., 2011; Appendix 1). The ecology and behavior of Florida Box Turtles have been examined closely at Egmont Key, a barrier island in Hillsborough County (Franz et al., 1992; Dodd, 1994; Dodd et al., 1994; Langtimm et al., 1996; Dodd, 1997; Dodd et al., 1997; Dodd, 1998; Dodd, 2001; Jennings, 2003, 2007; Dodd et al., 2012) and Big Pine Key, an oolitic limestone island in the Florida Keys, Monroe County (Liu et al, 2004; Verdon and Donnelly, 2005; Platt et al., 2009, 2010), as well as at other sites on the mainland (Pilgrim et al., 1997). Museum specimens of this turtle have also been explored systematically (Ernst et al., 1995, 1998). However, the ecology, distribution, and abundance of Florida Box Turtles in the extensive, subtropical mangrove ecosystems of southwestern Florida has not been investigated (Dodd, 2001; Ernst and Lovich, 2009). From 2006 to 2014 we surveyed for Florida Box Turtles in the northern Ten Thousand Islands (TTI), a mangrove-dominated estuarine ecosystem encompassing more than 160 km^2 of mangrove forests between Marco Island and Chatham River.

Our primary objectives were to 1) assess the broad-scale distribution of Box Turtles throughout the northern TTI including potentially suitable upland habitats on both naturally formed islands and shell work islands, 2) estimate the size and density of the Box Turtle population at four selected sites, and 3) evaluate population status and threats to population persistence through standardized, long-term monitoring. We present population size estimates from four islands where we conducted repeated surveys at intervals between 2010 and 2014 and also analyze and compare morphometric data from seven islands where Box Turtles were detected. Our assessment may inform future efforts to manage Box Turtles in coastal mangrove ecosystems and provides some insight into the ecology of terrestrial turtles on small, manmade, offshore, subtropical islands.

MATERIALS AND METHODS

Study Area.—The TTI extend from Marco Island and Cape Romano in Collier County as far south and east as Cape Sable, Monroe County (Fig. 1). The structure of the archipelago changes dramatically in the vicinity of Pavilion Key and the Chatham River where, to the north, the islands are smaller and far-more numerous. The northern TTI encompass a vast archipelago of several hundred small islands and islets associated with the estuaries of the Pumpkin, Fakahatchee, East, Ferguson, Barron, Turner, and Chatham rivers, primarily within Collier County, while the southern TTI are composed of more-contiguous mangrove areas. Parkinson (1989) identified three types of islands in the northern TTI region; 1) seaward (barrier) mangrove islands, 2) interior mangrove islands, and 3) shell work islands constructed by the Calusa and possibly other Prehistoric Indians prior to Spanish contact in the early 16th Century (Schwadron, 2010).

Both seaward and interior mangrove islands are dominated by forests of red mangrove (*Rhizophora mangle* L.) and black mangrove (*Avicennia germinans* (L.) L.). In addition to extensive sand beaches, the larger seaward mangrove islands support coastal hardwood hammock habitats dominated by hardwood species such as gumbo limbo (*Bursera simaruba* [L.] Sarg.) (Garmestani et al., 2000). The prehistoric shell work islands also

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[3] Present address: Antioch University New England, 40 Avon St., Keene, New Hampshire 03431 USA

[2] Corresponding Author. Present address: Department of Environmental Conservation, Holdsworth Building, University of Massachusetts, Amherst, Massachusetts 01003 USA; E-mail: mtjones@bio.umass.edu

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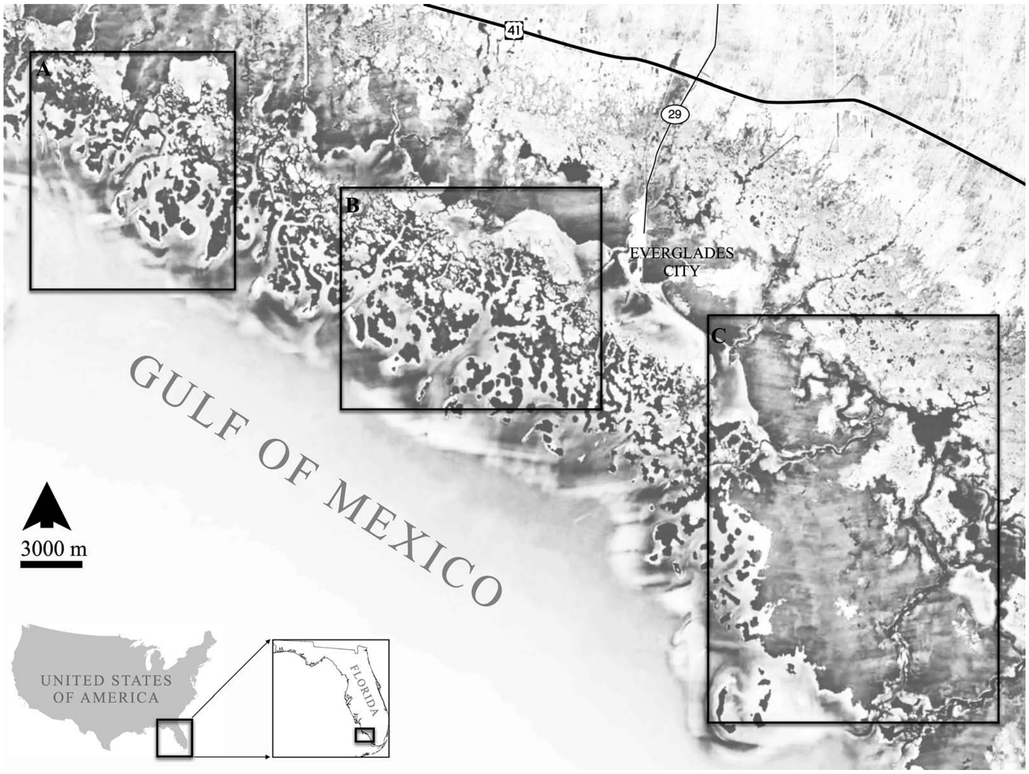

FIG. 1. Map of the northern Ten Thousand Islands mangrove estuary in Collier County, Florida, United States. The three rectangles designated A, B, and C represent clusters of survey sites. Six survey locations are located within Area A; nine survey locations are located in Area B; and three survey locations are located in Area C.

support coastal hardwood hammock habitats, and the larger of these islands also encompass "insolated terrain" or open shell barrens with sparse vegetation including clumps of exotic Brazilian pepper (*Schinus terebinthifolius* Raddi). Mangrove forest occurs around the periphery of most shell work islands, forming a buffer between upland terrestrial habitats and the open water of the Gulf of Mexico and its tidal tributaries. Mangrove forest occasionally exists as landlocked occurrences within the coastal hardwood hammock or insolated terrain of large shell work islands. Thorny shrubs and cacti (*Acanthocereus tetragonus* L. Hummelinck and *Opuntia stricta* Haw.) occur locally throughout the hammock forests, in open barrens, and in some places form dense thickets (Schwadron, 2010; Wilder and Barry, 2012). Citrus species (e.g., *Citrus aurantifolia* [Christm.] Swingle) and tamarind (*Tamarindus indica* L.) currently growing on larger islands likely date from the agricultural era of the 20th Century where the larger shell work islands were farmed (Wilder and Barry, 2012). Gopher Tortoise (*Gopherus polyphemus* Daudin, 1802) occurs on at least two of the larger shell mounds (Jones et al., 2011).

The shell work islands are of varying age but were constructed mostly between about 1,900 to 900 ybp (Schwadron, 2010; Wilder and Barry, 2012), with portions of some sites dating to 3,000 to 4,000 ybp. Although their exact function and use probably varied within and across islands, they appear to have served as long-term living sites. The prehistoric shell work islands were constructed primarily from the shells of Eastern Oyster (*Crassostrea virginica* Gmelin), other bivalves, and gastropods such as Horse Conch (*Pleuroploca gigantea* Kiener) and True Tulip (*Fasciolaria tulipa* Linnaeus; Simpson, 1920; Schwadron 2010) and are structurally composed of raised crescents, high mounds, and canal and ditch systems (Schwadron, 2010). Numerous shell works islands occur throughout the northern TTI region. The largest of the shell work islands (up to 31 ha) were inhabited during the early 20th Century but are currently uninhabited. Cisterns, foundations, pilings, and other evidence of more-recent occupation are scattered widely throughout the larger shell work islands. By the beginning of the 21st Century, most of the major shell work sites between Goodland and Chokoloskee had been abandoned completely, with the exception of a developed walking trail at one site (Site K, see Table 1). Based on carbon-14 (^{14}C) estimates of rates of sea level-rise (Parkinson, 1989), the largest shell work islands have likely been isolated from the mainland for 1,500 to 2,000 yr, or most of their estimated existence (Schwadron, 2010).

Our study area included 18 islands in the northern TTI distributed approximately from immediately east of Goodland (25.92°N, 81.65°W) to the Chatham River (25.68°N, 81.29°W), a linear distance of about 42 km (Fig. 1). Portions of this study area were located within Everglades National Park (ENP), Ten Thousand Islands National Wildlife Refuge (TTINWR), and Rookery Bay National Estuarine Research Reserve (RBNERR). Five study islands are seaward mangrove islands ranging in size from 4.1 to 16.4 ha. Thirteen islands, ranging in size of upland area from 2.0 to 31.0 ha, are shell work islands, most of which were apparently constructed by Prehistoric Indians over more than a 1,000-yr period during Pre-Columbian times (Moore, 1919, 1921; Simpson, 1920; Widmer, 1988; Schwadron, 2010). Study sites were accessed by canoe or motorboat from Goodland, Everglades City, or Chokoloskee based on proximity to the target island. Our exact survey locations are withheld as one method to minimize the risk of poaching.

Field Methods.—Our surveys consisted of 1) exploratory surveys on one island (Site K) conducted between 2006 and

TABLE 1. Results of surveys for Florida Box Turtle, *Terrapene carolina bauri* in the Ten Thousand Islands, Collier County, Florida, United States.

Site code	Island type	Area (ha)	Total survey hours	Dead turtles	Live turtles	Unique live turtles encountered	Total turtle encounters	Live turtles/ survey hours	Population estimate	Standard error	Density estimate (turtles/ha)
A	Shell (Calusa)	3.95	2.10	0	0	0	0	0.00			
B	Shell (Calusa)	27.93	113.92	60	130	106	190	1.14	261.50	64.7	9.36
C	Shell (Calusa)	31.02	62.48	12	47	41	59	0.75	270.40	244	8.72
D	Shell (Calusa)	4.88	3.50	0	0	0	0	0.00			
E	Shell (Calusa)	3.81	3.60	0	0	0	0	0.00			
F	Natural	8.95	8.60	0	0	0	0	0.00			
G	Natural	7.47	1.13	0	0	0	0	0.00			
H	Natural	5.69	3.33	0	0	0	0	0.00			
I	Natural	4.09	2.60	0	0	0	0	0.00			
J	Shell (Calusa)	17.80	78.05	11	58	53	69	0.74	217.60	128.6	12.23
K	Shell (Calusa)	16.13	110.80	4	76	26	80	0.69	43.50	3.5	2.70
L	Shell (Unknown)	2.65	2.00	0	0	0	0	0.00			
M	Shell (Calusa)	7.26	7.40	2	3	3	5	0.41			
N	Shell (Calusa)	11.84	8.07	5	0	0	5	0.00			
O	Shell (Unknown)	2.00	1.10	0	0	0	0	0.00			
P	Shell (Calusa)	11.91	5.83	1	0	0	1	0.00			
Q	Shell (Calusa)	2.03	2.50	0	0	0	0	0.00			
R	Natural	16.44	5.18	0	0	0	0	0.00			

2009, 2) searching for new populations from 2010–2014, and 3) timed surveys within known populations from 2010–2014. Islands on which turtles were detected by 2010 became "reference islands," and we intensified search efforts there to obtain estimates of population densities and to estimate detection rates. The end result of this protocol is that many islands were subject to relatively low search effort while a few reference islands were subject to relatively high search effort. Only the nonexploratory surveys conducted at the 18 study islands between February 2010 and March 2014 (modes 2 and 3) were included in population analyses, although morphological characteristics of animals observed during exploratory surveys from 2006–2009 were included in morphological analyses.

Two to eight surveyors conducted diurnal visual surveys between sunrise and sunset to locate individual turtles (Stickel, 1950). The number of surveyors on each island also varied, resulting in different levels of effort for each of the reference sites (Table 1) and reflecting personnel availability within partnering agencies that owned the individual sites. Surveys were conducted during January, February, March, August, and October, and we attempted to survey representative portions of the total upland area of each island as well as adjacent and insolated mangrove habitats. Our search image consisted of looking for turtles on the surface, in leaf litter, around the bases of trees, in clumps of agave and cacti, in shallow depressions, and in woody debris as well as looking for evidence of "forms" (Stickel, 1950) and "bulldozing" (Dodd, 2001) in deciduous leaf litter, which often indicated the presence of one or more turtles in the immediate vicinity.

Upon capture, the location of each turtle was recorded using handheld GPS (Etrex; Garmin International Inc., Olathe, Kansas). We recorded body size (straight carapace length [SCL$_{\text{min}}$], straight plastron length [SPL$_{\text{min}}$], plastron width at the hinge, carapace width at the 8th marginal scute, and carapace height at the highest point; Ernst and Lovich, 2009) using dial calipers and body mass using a spring-loaded scale (2500 g Medio Line scale; Pesola, Baar, Switzerland). Turtles were marked individually by filing the marginal scutes with a triangular file (Cagle, 1939) and following the numbering scheme provided by Ernst et al. (1974). A unique bloc of numbers (e.g., 1 to 99, 100 to 199, etc.) was assigned to each island where turtles were observed. Turtles were released at the capture location after <15 min of restraint.

Data Analysis.—To estimate the effort needed to detect Box Turtles on an island where they occur, we analyzed the intervals between turtle detections on islands with documented populations in a survival-analysis framework. Each interval was treated as a separate survey sample that terminated when the next turtle was found. We used the cumulative distribution of interval lengths to approximate the search effort required to detect turtles. Although these intervals are not strictly independent, this method gave us more insight into our surveys than simply calculating the mean search effort per Box Turtle. We would be unable to perform statistical tests on the single value produced by calculating the overall mean effort per turtle because statistical tests, by definition, require multiple values. Instead, our method generated a distribution of interval lengths which allowed us to conduct seasonal analyses of detection rates and quantify our confidence in survey results on islands where we detected no turtles. To examine the effect of season on our ability to detect turtles, we conducted an analysis of variance (ANOVA) using month and site as predictor variables and search interval as the response.

To estimate the probability of finding Box Turtles on each island, given our total search effort there, we matched the sum of search effort on an island to the appropriate percentile in our search interval distribution. We then used these probabilities in a simulation under a likelihood statistical framework. In R, we considered alternate possible realities in which turtles were actually present on a varying number of islands. For each number of total islands potentially containing turtle populations (0–18), we randomly assigned these populations to islands 10,000 times. For each such scenario, we then simulated surveys that lasted the same length as the sum of our actual survey effort on each island. For islands where turtles were detected, we truncated the survey lengths at the time when we first observed a turtle. We included observations of both live and dead turtles in parameterizing this analysis. We simulated surveys by sampling from binomial distributions with probabilities corresponding to the 18 estimated detection probabilities. We then calculated the frequency with which the number of islands where turtles were detected in simulations matched the number of islands where we detected turtles in our actual data, allowing us to estimate the number of additional islands within our sample that are likely to hold undetected turtle populations.

We compared body sizes of males and females, as well as live and dead turtles at Site B, using Student's *t*-tests, evaluated differences in body size on different islands using ANOVA, and calculated the sexual size dimorphism index (SDI) for adult turtles (Lovich and Gibbons, 1992) in R (R Development Core Team, 2012).

To estimate population size at our reference islands (i.e., those with more-intensive survey effort), we used the results of our repeated surveys to fit Jolly-Seber open population models (Cormack 1985, 1989) using the package Rcapture (Baillargeon and Rivest, 2007, 2009) and the statistical software R (R Development Core Team, 2010). We used open population models rather than closed population models because the surveys took place over multiple years, and some marked turtles were known to have died during or between survey events (as evidenced by the observation of the remains of turtles marked previously on three of the islands). We used models to estimate both overall population size as well as survival rates between sampling events and capture probabilities. Pearson residuals and a chi-square goodness of fit test (Baillargeon and Rivest, 2007) were evaluated for each site's open population model to assess lack of fit. Population estimates were converted to density estimates by dividing by the total upland habitat area of the island. Habitat area was calculated for each island by digitizing each island's upland boundary (including insolated mangrove areas but excluding peripheral mangrove areas) from 2011 aerial imagery in GoogleEarth (Google, Inc., Mountain View, CA) and then using the University of New Hampshire Cooperative Extension kml tools (http://extension.unh.edu/kmlTools/index.cfm) to calculate area.

RESULTS

We conducted 576.4 person-hours of surveys during 10 separate sampling bouts between March 2006 and March 2014, including 154.15 h of exploratory surveys at Site K from 2006–2009. Our initial exploratory surveys were excluded from the survey effort analyses, leaving a standardized survey dataset of 422.2 survey hours from 2010–2014. We observed Box Turtles on seven islands distributed throughout the study area (Table 1). From 2006–2014, we observed 250 live Box Turtles 346 times and 96 dead Box Turtles. The vast majority of live (314) and dead (95) turtle detections occurred during the 2010–2014 standardized surveys, yielding an average catch per unit effort of 0.74 live and 0.23 dead turtle captures/person-hour across all 18 islands.

Of the 341 live turtle observations for which turtle activity was recorded, 142 (41.6%) were in a leaf litter or organic substrate "form" (Stickel, 1950), five (1.5%) were entering forms, and nine (2.6%) were emerging. An additional 134 (39%) were quiescent but visible on the ground surface when detected. We found others walking ($n = 33$, 9.7%), "bulldozing" in leaf litter ($n = 13$, 3.8%), paired in apparent courtship ($n = 4$, 1.1%), or actively feeding ($n = 1$, 0.3%). The majority ($n = 220$, 65%) of live turtle observations were in hardwood hammock while fewer observations occurred in red mangrove ($n = 32$, 9.3%), scrub ($n = 22$, 6.5%), and cactus ($n = 14$, 4.1%), and an additional 50 observations (14.6%) occurred in ecotones between these cover classes. Live turtles were not observed in completely exposed shell barrens or under thick Brazilian pepper canopy, though deceased remains of Box Turtles were observed in these habitat types. The percentages of turtles observed in each habitat type is likely not representative of actual habitat use because availability of each of these habitat types was variable across islands, and detection rates likely varied between habitat types.

The sex ratio of males to females among live adult turtles was 0.85 : 1.0 ($n = 248$) and the sex ratio among turtles found dead that we were able to sex ($n = 84$) was 0.38 : 1.0. However, many shells were lacking plastra so our identification of sex is tentative, and we could not confidently identify the sex of 11 sets of remains. Three juveniles were found (two live and one dead), all at Site C. Sixty of the dead turtles (63%) were found at a single island (Site B). None of the turtles initially found dead appeared to have died recently, as none had remains of soft tissue present and many were disarticulating. Two turtles marked while alive at Site K and one at Site B were found dead in subsequent surveys. Ten shells found in various stages of deterioration were monitored from 2010 to 2014 to observe the rate of continued deterioration, and although most that retained keratinous scutes when found lost them during this period, they otherwise remained little changed. Of the turtles found dead, it was possible to infer the cause of mortality in only two instances: an adult male was found dead in a dry cement foundation on Site J and an adult female was found dead in a cement cistern on Site C.

Among living turtles, male SCL_{min} averaged 141.4 mm (SD = 9.7) and female SCL_{min} averaged 125.3 mm (SD = 7.6). The smallest living adult turtle observed was a female (SCL_{min} 107.2) and the largest living adult turtle was a male ($SCL_{min} = 165.0$). Pooled across sites, the SSDI equaled -1.13. Body size varied significantly across islands for both males ($F_{3,109} = 15.37$, $P < 0.001$) and females ($F_{3,122} = 5.63$, $P = 0.001$). We considered it noteworthy that the largest turtles detected during the surveys were three dead males found on three different islands (Sites P, K, and N; SCL_{min} 166.9, 172.2, and 175.5, respectively), and the four smallest, apparently adult, turtles were dead females at a single site (Site B; SCL_{min} 103.6, 104.9, 105.0, and 106.0).

At one site with sufficient samples of both living and dead turtles (Site B), there is a significant difference in body size between dead ($SCL_{max} = 130.6$ mm, $n = 7$) and living ($SCL_{max} = 139.0$ mm, $n = 41$) males ($t = 2.66$, df = 8.8, $P = 0.03$). However, the sample of dead male turtles is small and the sample sizes of live and dead animals are very different. Pooled across sites, the difference between dead ($SCL_{max} = 119.5$ mm, $n = 58$) and living ($SCL_{max} = 125.1$ mm, $n = 129$) female Box Turtles is also significant ($t = 4.41$, df = 100.9, $P < 0.001$).

During 2010–2014 surveys, our overall encounter rate on the seven islands where Box Turtles were detected was 1.24 person-hours per live Box Turtle. The month in which surveys were conducted had a significant effect on the interval between turtle encounters ($P \ll 0.001$) while the effect of site was not statistically significant in our analysis ($P = 0.6$). February had the longest intervals between encounters (mean = 3.1 h, SD = 3.4) and August had the shortest intervals between encounters (mean = 0.6 h, SD = 0.9; Fig. 2). However, these two months received only one survey bout each and so intervals are confounded with weather and observer.

Using the intervals between turtle encounters as observations in a survival-analysis framework, we were able to estimate the amount of effort needed to find a turtle (Fig. 3). On islands with documented turtle populations, 95% of search intervals lasted less than 4.5 person-hours before encountering a turtle, 85% of

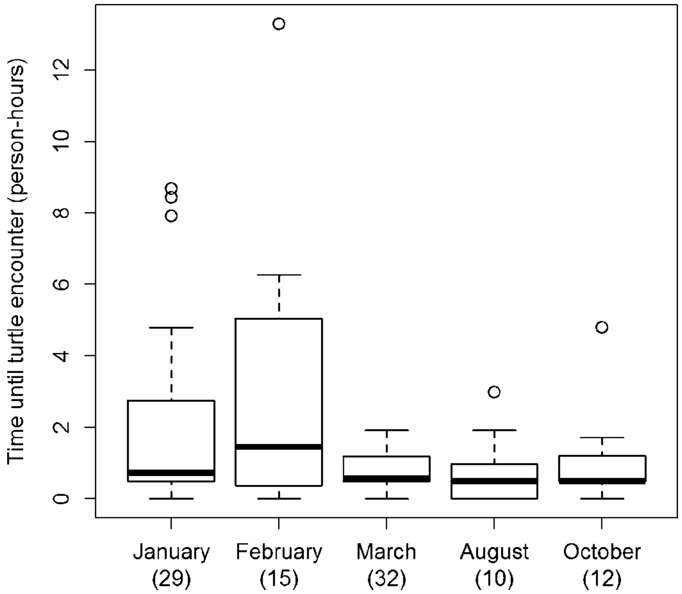

FIG. 2. Time between *Terrapene carolina bauri* encounters vs. month of survey at Site K in the Ten Thousand Islands region, Collier County, Florida, United States. We only plotted data from Site K because survey effort was not distributed evenly among islands and seasons, and our largest survey effort was focused on Site K. Sample sizes are reported in parentheses below each month.

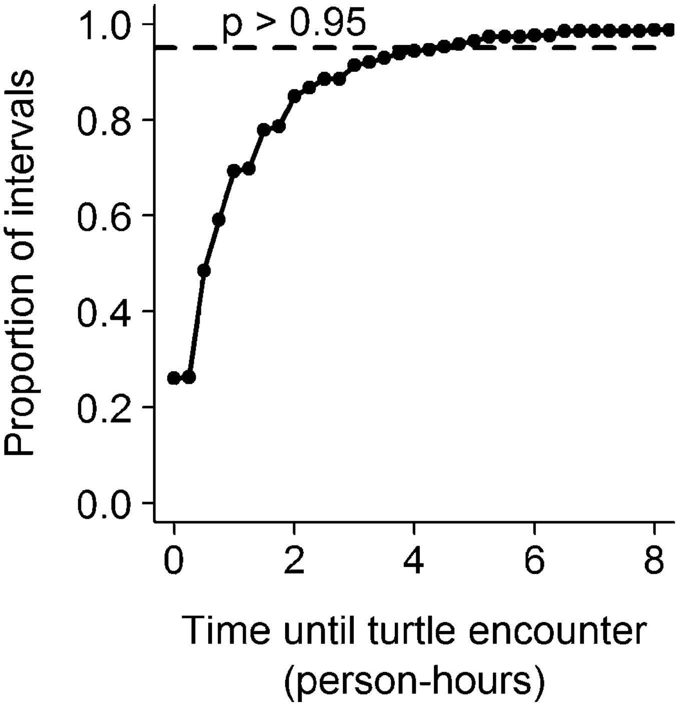

FIG. 3. Cumulative distribution of search intervals between *Terrapene carolina bauri* encounters on islands with documented turtle populations in the Ten Thousand Islands region, Collier County, Florida, United States. Ninety-five percent of the search intervals ended with a Box Turtle encounter in less than 4.5 person-hours.

search intervals lasted less than 2 person-hours, and 69% of search intervals lasted less than 1 person-hour. In our simulations, we found that the scenarios in which 7 to 9 of the 18 islands actually held turtle populations were the most likely to produce results matching our observed data (Fig. 4), with eight occupied islands being most likely, suggesting we likely missed turtles on at least one island. None of the 10,000 iterations with turtles occupying all 18 islands reproduced our data, and only one simulation with turtles occupying more than 15 islands reproduced our data, suggesting that it is highly unlikely that turtles occur on all of the natural islands.

Using Jolly-Seber open population models, we estimated population size on the four reference islands to range from approximately 43.5 (95% CI = 36–50) turtles to 270 (95% CI = 207–748) turtles; equivalent to densities of 2.7 turtles/ha and 12.3 turtles/ha (Table 1). Estimates of survival rates between sampling events ranged from 0.35 (SE = 1.6) and 1.0, and capture probabilities ranged from 0.0096 to 0.4. Pearson residuals were low for all models, and goodness of fit tests showed no evidence for lack of fit ($P > 0.05$) for any of the four models.

DISCUSSION

Box Turtles were detected only on anthropogenic, prehistoric shell work islands. The islands where we detected turtles were generally larger and closer to the mainland (Fig. 5), as would be expected from island biogeography theory (MacArthur and Wilson, 1967). While we detected no turtles on natural islands, this could be because of insufficient search time per island area, the fact that natural islands tended to be farther from the mainland, turtle behavioral differences, habitat differences, historic differences, or other factors. Our analysis of between-turtle search intervals suggests that approximately 2–5 h should be sufficient to detect Box Turtles if they are present at densities similar to those of the documented populations. We searched all islands for at least 1.1 person-hours and all but two for at least 2 person-hours. It is likely that we failed to detect turtles on some individual islands where turtles are actually present. However, our search effort analysis suggests that it is extremely unlikely that all 18 islands support Box Turtle populations. It is most likely that between 7 and 9 of the 18 islands support turtles, and we only failed to detect turtles that were present on two or fewer additional islands.

The male-biased sexual size dimorphism is consistent with reports from other portions of this species range (Ernst et al., 1998; Dodd, 2001; Verdon and Donnelly, 2005). The largest turtle, a dead male found at Site P (SCL_{min} 175.5), is near the upper end reported for this species (Dodd, 2001) but substantially smaller than several very large, captive *T. c. bauri* of uncertain origin described by Jackson and Brechtel (2006).

The estimated density of Box Turtles at Sites B and C (9.3 and 8.7 turtles/ha) is similar to that observed by Verdon and Donnelly (2005) in a pine rockland habitat on Big Pine Key, Monroe County (4.8–10.2 turtles/ha) and lower than the densities observed by Langtimm et al. (1996) for Egmont Key (11.4–18.5 turtles/ha). The estimated density of Box Turtles at Site K (2.7 turtles/ha) is lower than most reported estimates from Florida (Ernst and Lovich, 2009). We conducted most surveys during the winter, or dry season, when turtles may be more difficult to detect (Fig. 2). While the timing of our surveys may have reduced our detection rates and thus our total sample sizes, this should not have biased the mark–recapture population estimates. Continued sampling in multiple seasons should confirm or contradict this assumption. Although the Jolly-Seber models suggested relatively low capture probabilities (0.01–0.40) during survey events, these were three to ten times higher than that observed for the Ornate Box Turtle, *Terrapene ornata* (0.003), by Refsnider et al. (2011), and our catch per unit effort

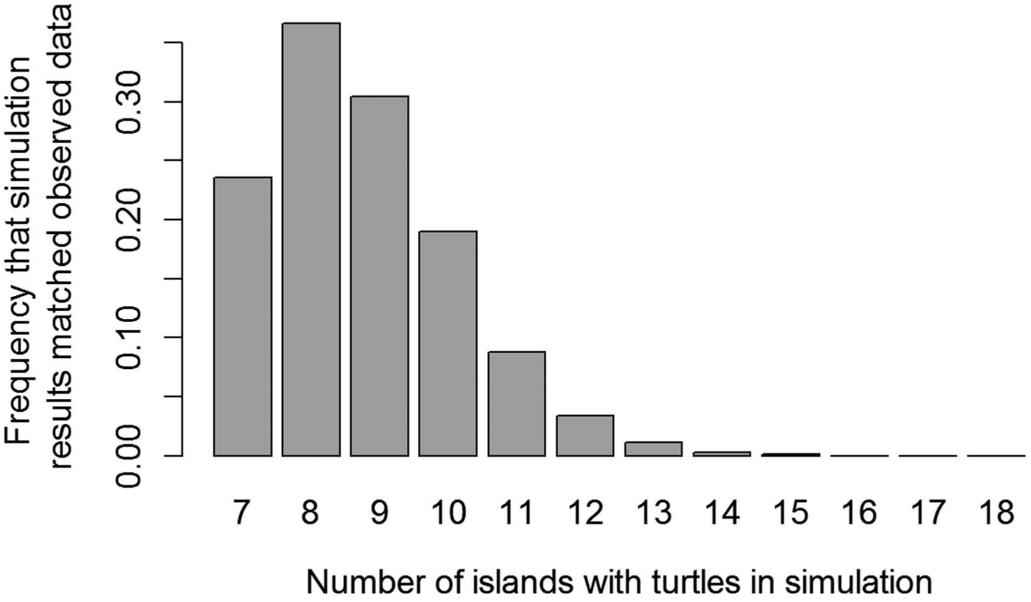

FIG. 4. The frequency with which simulations resulted in detecting *Terrapene carolina bauri* on the same number (7) of islands as in our surveys of 18 islands in the Ten Thousand Islands region, Collier County, Florida, United States. Each bar represents 10,000 simulations of the corresponding number of *T. c. bauri* populations distributed randomly amongst the 18 islands.

(0.74 live and 0.23 dead turtle captures/person-hour) was an order of magnitude higher (0.08 turtles/person-hour) than that observed by Refsnider et al. (2011), despite similar population density estimates (6.4 turtles/ha for *T. ornata*). These differences suggest that either: 1) visual encounter surveys may be more effective in this system than for *T. ornata*; 2) observer experience is extremely important, as all observers conducting standardized Florida box surveys from 2010–2014 had multiple years' experience surveying for Box Turtles while those surveying for *T. ornata* did not; or 3) surveys targeting the Box Turtle specifically are more effective than general herpetological surveys, which was the focus of the Refsnider et al. (2011) surveys.

The large number of dead turtles that we encountered suggests that: 1) the environment and associated species present on the islands allow Box Turtle shells to remain intact at the surface for long periods of time (supported by the shells we observed that remained structurally intact for more than 4 yr but contradicted by evidence provided by Dodd, 1995); 2) mortality may be unusually high in this system compared to those systems described above; or 3) a mass die-off caused by a stochastic disturbance, such as hurricane overwash or a pathogen such as ranavirus, occurred at some point in the past on Site B. Average survival estimates between (approximately annual) survey events were highly variable and ranged from 0.68–1.0, both lower and higher than those observed by Dodd et al. (2012) (0.911 and 0.923 for females and males, respectively). High mortality in the recent past, such that the population size dropped dramatically before stabilizing, could also explain the high density of dead turtles relative to live turtles.

High mortality rates or low recruitment might help explain the low densities we observed compared to other locations. Though we can only speculate as to the cause of mortality, turtles in this extreme environment may be subject to heat stress, overwash events, depredation events as predators move onto the islands, or canopy closure caused by natural succession or exotic Brazilian pepper (*S. terebinthifolius*), which forms dense mats on several of the islands. Low densities may also be the result of the recent (within 70 yr) agricultural land use on the larger islands.

Box Turtle populations may also be affected negatively by the TTI Common Raccoon, *Procyon lotor marinus* L., which are well-documented to be distributed throughout our study region (Garmestani and Percival, 2005) and which have been inferred to attack adult Box Turtles at Egmont Key (Dodd, 2001). We observed raccoon skulls and scat on each of the four reference islands. Further, it is noteworthy that the lowest population densities were also observed at the only island with a recreational trail. It is possible that increased recreational access could result in potentially elevated mortality because of collection.

It is noteworthy that living or dead Box Turtles were only detected on seven of the larger prehistoric shell work islands. No Box Turtles were observed on naturally formed barrier islands or on shell work islands smaller than 7.3 ha. To our knowledge, these island populations are unusual because in addition to being apparently isolated from one another and the mainland by several kilometers of seawater, they appear to exist entirely on nonnatural (manmade) islands. The shell work islands offer rare upland hardwood habitat in a system dominated by mangrove and seawater and provide some of the highest terrain in the region at over 6 meters above sea level (Wilder and Barry, 2012). This system of islands of suitable habitat in a matrix of inhospitable salt water may offer an opportunity to study population dynamics in isolation in a system of long-lived vertebrates, and the sustainability of these populations may have implications for mainland populations fragmented by anthropogenic means.

The 18 to 59 cm sea level rise projected to occur over the coming century by the Intergovernmental Panel on Climate Change (IPCC, 2007) is expected to have major effects on the coastal habitats of Florida (Michener et al., 1997; Doyle, 1998), altering habitat availability, community structure, and species diversity. The average expected sea level rise could result in an 80% loss of dry land in the TTI region (Glick and Clough, 2006) and would inundate the lowest of the prehistoric shell work

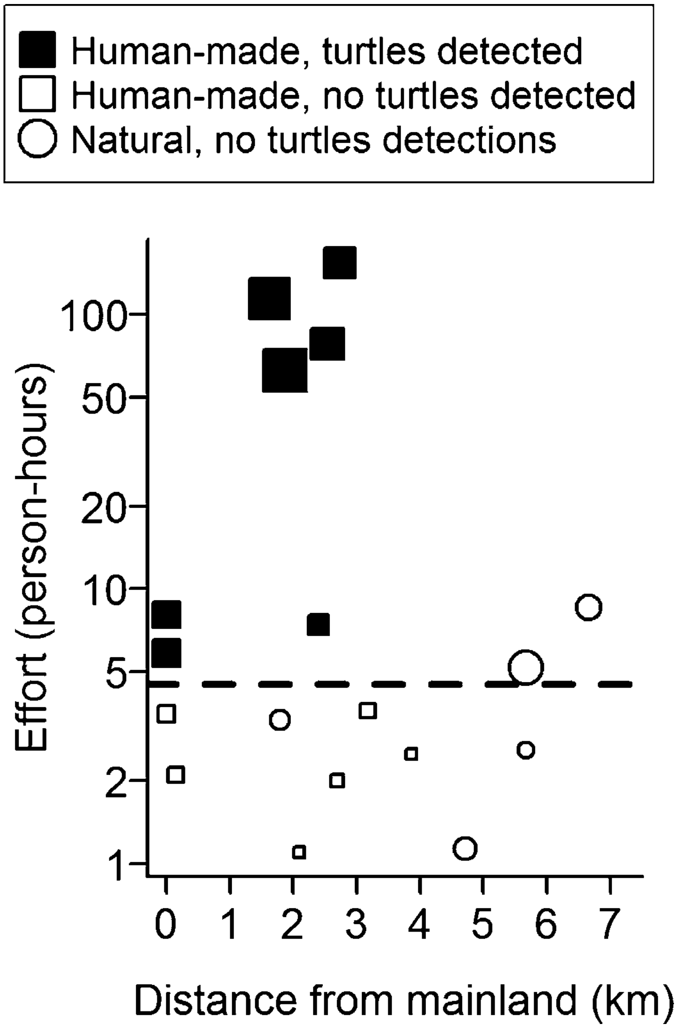

FIG. 5. *Terrapene carolina bauri* search effort at 18 natural and human-made islands in the Ten Thousand Islands region, Collier County, Florida, United States. Symbol size is proportionate to island size (contiguous area of upland habitat). Shaded points represent islands where turtles were found. Horizontal line represents approximate effort needed to demonstrate absence of turtle populations with densities similar to the documented populations, with 95% confidence.

islands and cause the higher islands to shrink in area. This would effectively make subpopulations fewer and farther apart, with the remaining subpopulations confined to smaller land areas. This increased isolation could affect demographics and genetic exchange of species and community structure. Future studies should explore the genetic relationships between island and mainland populations to illuminate the possible colonization sequence and whether metapopulation dynamics are possible, given the seawater isolation of each island.

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APPENDIX 1

Selected specimens of Florida Box Turtles from southwest Florida indicate widespread distribution in mainland and offshore areas. Lee County: Sanibel Island (UCM 56919); Collier County: Chokoloskee (CAS 172103 and 172104), Immokalee (CM 88330 and 21634; KU 141809), Naples (KU 211182), Ochopee (CM 116961; KU 319227; LACM 61073); Monroe County: Cape Sable (LACM 61072), Key West (LACM 23505). Museum abbreviations: CAS = California Academy of Sciences, CA; CM = Carnegie Museum of Natural History, PA; KU = University of Kansas Biodiversity Institute, KS; LACM = Natural History Museum of Los Angeles County, CA; UCM = University of Colorado Museum of Natural History, CO (HerpNet, 2012).