

Biology of Yucatán Box Turtles (*Terrapene yucatana*) in Northern Yucatán

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ABSTRACT.—Yucatán Box Turtles (*Terrapene yucatana*) are the only fully tropical lineage of box turtles (*Terrapene* spp.). We studied the ecology, movements, behavior, and habitat associations of *T. yucatana* in northern Yucatán, México, over 218 field days from 2014–2019. We estimated the size of two subpopulations to comprise 36.6 and 3.0 turtles, with corresponding densities of 2.29 and 0.39 turtles/ha, respectively. We obtained 2,808 radio locations from radiotelemetry of 20 adults. We estimated an annual survivorship rate over a 5-yr period exceeding 0.989. For both sexes combined, the average annual 95% minimum convex polygon (MCP) home range size was 0.684 ha, and the average distance between consecutive annual home range centroids was 22.5 m. In 2 of 5 yr, males exhibited significantly larger 95% MCP home ranges than females. We observed feeding, courtship, and fighting in the wild between June and December. Females moved more than males in July, when gravid turtles were also observed. We found that *T. yucatana* was positively associated with *Mimosa* sp. and *Bromelia* spp. The use of aquatic habitats was infrequent (0.17%). Our findings support the conclusion that *T. yucatana*, an allopatric and fully tropical lineage, is an interior forest and thornscrub species that occurs at low densities. In such undisturbed contexts, *T. yucatana* may exhibit high survivorship rates, small home range size, and home range fidelity that underscore the importance of large-scale forest conservation efforts in concert with the targeted protection of documented Yucatán Box Turtle populations.

RESUMEN.—La tortuga de caja de Yucatán (*Terrapene yucatana*) es el único linaje completamente tropical de tortugas de caja (*Terrapene* spp.). Realizamos un estudio de la ecología, movimientos, comportamiento y asociaciones de hábitat de *T. yucatana* en el norte de Yucatán, México, durante 218 días de campo entre 2014 y 2019. Estimamos el tamaño de dos poblaciones comprendidas en 36,6 y 3,0 tortugas, respectivamente, con densidades correspondientes a 2,29 y 0,39 tortugas / ha. Obtuvimos 2,808 radiolocalizaciones de 20 tortugas adultas. Estimamos una tasa de supervivencia anual superior a 0,989 basado en el marcado y recaptura de 37 individuos. Para ambos sexos, el tamaño medio anual del área de distribución (95% del MCP) fue de 0,684 ha, y la distancia entre los centroides del área de distribución anual consecutivos fue de 22,5 m. Los machos exhibieron rangos de distribución significativamente mayores que las hembras en 2 de los 5 años. Observamos alimentación, cortejo y peleas en su estado natural entre junio y diciembre. Las hembras se movieron más que los machos en julio, cuando también se observaron tortugas grávidas. Encontramos que *T. yucatana* se asoció positivamente con *Mimosa* sp. y *Bromelia* spp. El uso de hábitats acuáticos fue infrecuente (0,17%). *Terrapene yucatana*, un linaje alopátrico y completamente tropical de las tortugas de caja de América del Norte, es una especie de bosque interior y matorrales espinosos que ocurre en densidades bajas. En ambientes no perturbados, *T. yucatana* puede exhibir altas tasas de supervivencia, un ámbito hogareño pequeño y una notable fidelidad a su ámbito doméstico, lo que acentúa la importancia de los esfuerzos de conservación de bosques a gran escala junto con la protección específica de poblaciones documentadas de tortugas de caja.

Yucatán Box Turtles (*Terrapene yucatana* Boulenger) are known from the interior and northern coastal regions of the Yucatán Peninsula in Yucatán, Campeche, and extreme western Quintana Roo (Buskirk, 1993; Dodd, 2001; Legler and Vogt, 2013; Kiester and Willey, 2015). The species-level taxonomic divisions within the wide-ranging, continental *Terrapene carolina* clade are complex, unresolved, and disputed (Minx, 1996; Fritz and Havaš, 2013; Martin et al., 2013; Fritz and Havaš, 2014) because of disagreement between the molecular phylogenies of Butler et al. (2011), Martin et al. (2013), and Spinks et al. (2009) (Fritz and Havaš, 2014). As a result, the Yucatán lineage is variously referred to as a subspecies of *T. carolina* (Lee, 1996; Kiester and Willey, 2015; Rhodin et al., 2021) or as the full species *T. yucatana* (Legler and Vogt, 2013; Rhodin et al., 2021). Pending a

comprehensive taxonomic revision based upon a synthesized analysis of mitochondrial DNA, nuclear genes, and morphology, the taxonomic classification of *T. yucatana* remains unresolved. *Terrapene yucatana* has been only peripherally treated in recent molecular analyses because of small sample sizes. The Yucatán lineage is related to *Terrapene mexicana* of Tamaulipas and adjoining states and *Terrapene triunguis* of the midwestern United States, together with which it may form a monophyletic clade (*Terrapene mexicana* sensu Martin et al., 2013). Despite the lack of clarity concerning the phylogenetic relationships within *T. carolina* sensu lato, the allopatry and relative isolation of *T. yucatana* are noteworthy; within the putative *T. mexicana* group, *T. yucatana* was estimated to have diverged from *T. c. triunguis* + *T. c. mexicana* ~9.2 million years ago (Martin et al., 2013). Populations of *T. yucatana* are isolated approximately 1,000 km (by land) from the nearest *Terrapene* populations in southern Tamaulipas (Pfau and Buskirk, 2006; Rhodin et al., 2021). Correspondingly, *T. yucatana* represents the only fully tropical lineage within the primarily temperate complex (Kiester and

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Wiley, 2015). The species is generally reported to be rare and seems to be in decline (Buskirk, 1993; Legler and Vogt, 2013).

Despite their great isolation from other North American *Terrapene* species and likely ecological distinctiveness, empirical studies of *T. yucatana* in the wild are lacking. Since Buskirk's (1993) thorough review of the species' natural history, based largely on his own interviews and field trips to Yucatán, mostly brief or anecdotal notes have been published on the species' distribution (Lee, 1996; Smith et al., 1996; Buskirk, 1997; Ázquez et al., 2000; Ochoa-Ochoa et al., 2006; Pfau and Buskirk, 2006; Legler and Vogt, 2013), behavior and performance (Pfau and Buskirk, 2006; Butterfield and Macip-Rios, 2019; Butterfield et al., 2021), trophic position (Butterfield et al., 2021), parasitology (Rodríguez-Vivas, et al. 2016), and paleodistribution (Gotz and Sosa, 2011).

Relatively little is known about the detailed habitat associations and requirements of *T. yucatana*. For example, Lee (1996) reported that the species was primarily associated with open habitats, whereas Legler and Vogt (2013) indicated that the species was primarily found in forested habitats. Legler and Vogt (2013) also noted that the species is found primarily in tropical deciduous scrub forest, whereas Lee (1996) reported their occurrence in "marshy areas, pastures, thorn forests, and tropical evergreen forest." Several authors have noted the probable tendency of the species to use aquatic habitats (Lee, 1996; Legler and Vogt, 2013), as *Terrapene carolina major* does frequently (Meck et al., 2020). Throughout the Yucatán Peninsula, this species is referred to as *coc ac*, *kokak*, or *xkokak* and is locally considered a medicinal treatment for various respiratory ailments (Carr, 1991; Buskirk, 1993). Because, to our knowledge, there have been no previous detailed or long-term studies of their spatial ecology, population biology, or seasonal activity, we undertook a targeted study of the ecology, movements, behavior, and preliminary floristic associations of a population of *T. yucatana* in northern Yucatán from 2014–2019.

MATERIALS AND METHODS

Study Area.—We established two distinct study areas in the northern part of Yucatán State, hereafter referred to as Site A and Site B. We have chosen to withhold further site locality data because of the risk of illegal collection. Both sites are within the "Yucatán Dry Forests" ecoregion (Bezaury Creel et al., 2000) and the "Plain with Low and Medium Deciduous Tropical Forest" ecoregion (i.e., the EPA Level III designation described by Wiken, 2011). Site A is a 16.0-ha forested parcel bounded on three sides by unpaved farm roads, set within a primarily forested matrix approximately 950 ha in size. Site B is located 4.3 km west of Site A and comprises a 17.0-ha forest fragment surrounded by fenced pasture, exposed rocky barrens, isolated areas of scrub, and limestone sinkholes associated with the margin of the Chicxulub impact feature (Pope et al., 1996). Although their surrounding context is different, the forested sites are superficially similar floristically and are dominated by low, deciduous, sclerophyllous, tropical thornscrub forest with interspersed clearings dominated by columnar and epiphytic cacti, *Bromelia* spp., vines, graminoids, and herbaceous species (Fig. 1). Both sites are actively grazed by cattle in low-intensity rotation.

Field Surveys.—In January 2013, July 2013, and January 2014, we conducted de novo visual encounter surveys in forested habitats within areas where Yucatán Box Turtles had been previously reported. During these surveys, one to five observers searched for Box Turtles in leaf litter, woody debris, rock walls,



FIG. 1. Thornscrub habitat of *T. yucatana* in northern Yucatán. Photo: M. T. Jones.

roots, and tree tip-ups. Our initial surveys were not standardized. In addition, in January 2014, we affixed radios to two female *T. yucatana* that had been incidentally collected by local resident people along the farm road that traversed from Site A to Site B, forming the southern margin of Site A. From our discussions with the people who discovered the turtles, we determined there was a reasonable probability of releasing the turtles within a kilometer of their capture location. The radio-tagged turtles were located by telemetry in July 2014 and served as "Judas" turtles, or a form of "snowball" sampling, that facilitated the detection of the first five naive study animals (Keegan et al., 1994; Campbell and Donlan, 2005). Upon locating the "Judas" turtles with radios by radiotelemetry at 5 mo after their release, we located a core group of five wild *T. yucatana*, which formed the initial basis of this study. Following the deployment of radios on naive, wild turtles, we discontinued tracking the "Judas" turtles, and their movements are not described here. Opportunistic visual encounter surveys continued throughout the duration of the radiotelemetry study until December 2019.

Processing Turtles Upon Initial Capture.—Box Turtles detected in the wild were measured (straight carapace length, straight plastron length, length of anterior plastron lobe, length of posterior plastron lobe, plastron width at the hinge and at the humeral-pectoral seam, carapace width, and shell depth), weighed using a digital pharmaceutical scale, and uniquely marked by filing the marginal carapace scutes (Ernst et al., 1974). We took high-resolution carapace and plastron photographs of every turtle in shade for future reference and noted the extent of injuries, keratin loss, fusion of the seams between the plastral scutes, and *Amblyomma* sp. tick infestation. We compared morphometric measurements between males and females by using Welch's two-sample *t*-test in R. Box Turtles found in situ in the wild were radio equipped with very-high-frequency transmitters (R-1860; Advanced Telemetry Systems). Radio transmitters had a 12-h on/off duty cycle and were generally programmed to operate from 0800 h to 2000 h. We secured the radios with a fast-curing epoxy to the posterior carapace near the seam between the fourth costal scute and the marginal scutes. The radio weight was 17 g, and the total weight with epoxy and an added iButton thermochron (usually model DS1921G-F5, which logged ambient temperature for another study), was generally less than 30 g, or less than 5% of total Box Turtle body mass.

Radiotelemetry.—We recorded weekly to monthly radio locations from July 2014 to December 2019 by using a handheld receiver (R-1000; Communications Specialists) and “rubber ducky” antenna (Telonics, Inc.). Turtles were located precisely, usually within 1 m, and were generally confirmed visually. We did not use triangulation to estimate the turtles’ locations. Incidental Box Turtle detections without the assistance of radiotelemetry were noted. In each case, we continued to search for new and marked turtles while conducting radiotelemetry. When a turtle was located by radiotelemetry, we categorically recorded the turtle’s behavior (hidden, alert, walking, feeding, fighting, courting/copulating, and aquatic). We recorded their global positioning system location and associated habitat data, including dominant plant species within a 5-m-radius circle. Incidental detections of all other turtle species were noted. Radiotelemetry generally occurred in the morning. While conducting radiotelemetry, we searched opportunistically for turtles.

Population Estimation.—We used live survey returns from all three survey bouts in conjunction with log-linear models and the package Rcapture (Rivest and Baillargeon, 2014) in R (R Core Team, 2019) to estimate the total number of live turtles at Site A between 2014–2019 and Site B between 2017–2019. Following Rivest and Baillargeon (2014), we selected the closed population model that accounted for sources of variation resulting in the best fit (using Akaike information criterion) and applied a bias correction for small sample size as suggested in Rivest and Lévesque (2001) and Rivest and Baillargeon (2014). Following Rivest and Baillargeon (2014), we also estimated the total population size with a log-linear open population model by using the function openp.

Movement Analysis.—To facilitate comparison with previous *Terrapene* sp. studies, home range sizes were calculated as 95% minimum convex polygon (MCP) on an annual basis for all turtles with more than 23 locations in a given year, using the R package adehabitatHR (Calenge, 2006) in R (R Core Team, 2019). We also calculated 95% MCP for each turtle by using all locations from 2015–2019. Differences in movement patterns between the sexes were evaluated for each year using Welch’s two-sample *t*-test, using only individuals with more than 23 locations in that year. To calculate home range fidelity, we calculated the interannual distance between home range centroids for each consecutive year that a turtle was tracked. As an additional measure of fidelity, we also calculated the interannual distance between consecutive dry-season dormancy locations. Measures of fidelity were also compared between the sexes using Welch’s *t*-test.

We evaluated seasonal movement patterns by calculating distance (m) moved per day since the last location for each consecutive location and visually assessed seasonal movement patterns graphically. We evaluated the difference in daily movement rates between males and females by using the mixed effects models fit with the lme4 package (Bates et al., 2015) in R (R Core Team, 2019) with individual as a random effect. We summarized turtle activity by sex and season and assessed correlations between the frequency of courtship, home range size, and body size by using the Pearson’s correlation coefficient.

Vegetation Analysis.—Following the first 2 yr of radiotelemetry study at Site A, we established a network of 42 5-m-radius circular plots at fixed intervals across the 16-ha study area. At each location, we measured the same habitat variables collected at each turtle location. In addition, we visually estimated the total

percent canopy cover, shrub cover, and *Bromelia* cover within 5 m, as well as categorical information (high/medium/low/none) regarding cactus (all species), leaf litter, exposed rock, soil, and herbaceous cover. Measurements for the standardized plot network were made in December 2015 and December 2016.

To evaluate the importance of specific plant species, we recorded the dominant plant species within 5 m of every turtle location. To compare associated plants with those generally available in the study site, we calculated the frequency of turtle locations sites in 2016 that were dominated by each of the 14 most frequently occurring plant species and compared them with the frequency of dominance of those plants in the 42 vegetation plots by using Fisher’s exact test in R (R Core Team, 2019).

To further evaluate habitat characteristics associated with turtle locations, we calculated the number of radiotelemetry points within calendar year 2016 (to correspond most closely with the time frame of vegetation plot data) that occurred within 10 m of each of the 42 vegetative plots. We used these counts as the response variable in generalized linear models. Because the counts were overdispersed (i.e., residual deviance values were much larger than degrees of freedom for Poisson regression, and formal evaluation of goodness of fit using residual deviance suggested a lack of fit of Poisson regression models), we used a negative binomial error structure. We fit univariate negative binomial regression models in R with percent canopy, shrub cover, and *Bromelia* cover as well as the categorical information collected at each of the fixed vegetative plots as predictors. Model residuals were evaluated using the DHARMA package (Hartig, 2019) in R (R Core Team, 2019).

RESULTS

Capture Statistics.—We captured and recorded 36 wild, in situ *T. yucatana* between July 2014 and December 2019 at Sites A and B. At Site A, we captured 33 turtles a total of 103 times, including 21 females captured 65 times, and 11 males captured 37 times. At Site B, we captured three female *T. yucatana* a total of seven times. We captured one subadult female one time at Site A (F37). We attached radios to 17 *T. yucatana* at Site A (8 males, 9 females) and 3 *T. yucatana* at Site B (3 females). We also found six dead *T. yucatana* within Site A, including one turtle that was initially marked in 2014 (F22). We found a single dead male *T. yucatana* at Site B. We also found two long-dead adult *T. yucatana* in the area between Site A and B during our initial de novo surveys, providing evidence of recent occupancy and possible connectivity within the area between our two study sites.

Terrapene yucatana was part of a four-species chelonian community at our study sites. During the study period, we incidentally observed, captured, and marked two juvenile Furrowed Wood Turtles (*Rhinoclemmys areolata*) a total of three times at Site A. We captured two juvenile Mesoamerican Sliders (*Trachemys venusta*) in limestone rainwater pools at Site A and found the remains of one dead adult. We observed three juvenile and two male Scorpion Mud Turtles (*Kinosternon scorpioides*) in rainwater pools in Site A and found one dead adult *K. scorpioides*. Although present in the vicinity, no Creaser’s Mud Turtles (*Kinosternon creaseri*) were observed within the two study sites.

Morphology.—Male *T. yucatana* averaged 147.7 mm minimum straight carapace length (SCLmin) (range = 134–159 mm; SD = 7.1 mm; *n* = 11) and females averaged 146.8 mm SCL (range = 135–155 mm; SD = 5.6 mm; *n* = 23). The difference was not



FIG. 2. Male *Terrapene yucatana* from Site A in northern Yucatán, Mexico, illustrating partial to complete fusion of the plastral scutes. Photos: M. T. Jones.

significant ($t_{16.26} = -0.402$; $P = 0.69$). Males and females were also not significantly different in carapace width ($t_{24.88} = 1.60$; $P = 0.12$). Male *T. yucatana* averaged 108.8 mm in carapace width (range = 104–116 mm; SD = 3.5 mm; $n = 11$) and females averaged 111.1 mm SCL (range = 102–120 mm; SD = 4.4 mm; $n = 23$). Wild-caught male *T. yucatana* averaged a mass of 607.4 g (range = 502.0–705.8 g; SD = 56.7 g; $n = 11$) and females averaged 663.7 g (range = 493.4–769.0 g; SD = 73.0 g; $n = 23$), which demonstrated a significant difference ($t_{25.5} = 2.43$, $P = 0.022$). The single subadult animal found at either study site (F37) had an SCLmin of 106 mm and a mass of 238.8 g. Two of 11 males at Site A exhibited pronounced fusion of the plastral scutes, as did the single dead male from Site B (Fig. 2).

Population Size and Density.—We estimated the total population size of Site A across all years to be 37.1 (SE = 2.6) using the closedp.bc function in Rcapture. The openp function provided a similar estimate of 36.6 (95% confidence interval = 33.0–43.4) across all sampling periods, an equivalent to roughly 2.29 adult *T. yucatana* per ha on the 16-ha Site A. We captured no juveniles and only one subadult turtle (F37). Using the openp function of Rcapture, we estimated a total of 3.0 turtles within Site B, indicating that we captured all of the living *T. yucatana* within that area. The density of turtles at Site B was 0.39 *T. yucatana* per ha on the 7.6-ha site, which was approximately one-sixth the density of turtles at Site A.

Radiotelemetry Statistics.—In total, we conducted 193 visits to Site A and 22 visits to Site B. We obtained 2,808 radio locations of 20 adult *T. yucatana* between 2014–2019. We set a cut-off of 23 radiotelemetry locations within a year to be included in subsequent analyses. We obtained sufficient radiotelemetry location data to estimate annual home range parameters for 17 adult turtles (8 males, 9 females) at Site A. We obtained a total of 88 annual cycles of turtle movement data at Site A, and numbers of turtles tracked steadily increased with each new year of effort, as follows: 2014 ($n = 5$ turtle-years); 2015 ($n = 16$ turtle-years), 2016 ($n = 16$ turtle-years), 2017 ($n = 17$ turtle-years), 2018 ($n = 17$

turtle-years), and 2019 ($n = 17$ turtle-years). The average number of radio locations per turtle at Site A varied by year, as follows: 2014 ($n = 25.0$); 2015 ($n = 37.9$), 2016 ($n = 38.2$), 2017 ($n = 34.5$), 2018 ($n = 25.5$), and 2019 ($n = 23.1$). Although we radio tracked three females at Site B during 2017–2019, we did not obtain sufficient radio locations to confidently estimate movement parameters, and they are excluded from home range size calculations.

Survivorship.—Based on continuous monitoring and confirmation that all 20 turtles from Site A and Site B were still alive on 31 December 2019, we obtained 34,173 days of turtle survivorship information between July 2014 and December 2019. None of the 20 radio-tagged turtles originally found in the wild died during the study, and because all observations were right censored, we could not use standard survivorship methods (e.g., Kaplan-Meier estimator). We, therefore, estimated a minimum annual survival rate by calculating the rate had there been a single death during the study. By this method, we estimated an annual survivorship rate, during our study, of greater than 0.989. During the year following the study reported here, 1 of the 20 radio-tagged study animals was, in fact, found dead from unknown causes (possibly mammalian depredation), suggesting that adding one single death is a reasonable approximation for the mortality rate in this population.

Detection.—Using the total number of visual, nontelemetry captures at each site and the total number of visits to conduct radiotelemetry to each site, we estimated that we incidentally located 0.53 turtles per visit (i.e., without the direct assistance of radiotelemetry) at Site A and 0.31 turtles per visit at Site B. Our visits generally averaged a minimum of 2.5–3.0 h, depending on the exact method of estimation, although effort typically varied across visits from 1–7 h. The turtles per visit figures are equivalent to an average individual-based detection rate per survey, based on the modeled number of turtles of each site, of 1.4% and 10.6% of the populations, respectively, in the context of an ongoing radiotelemetry study.

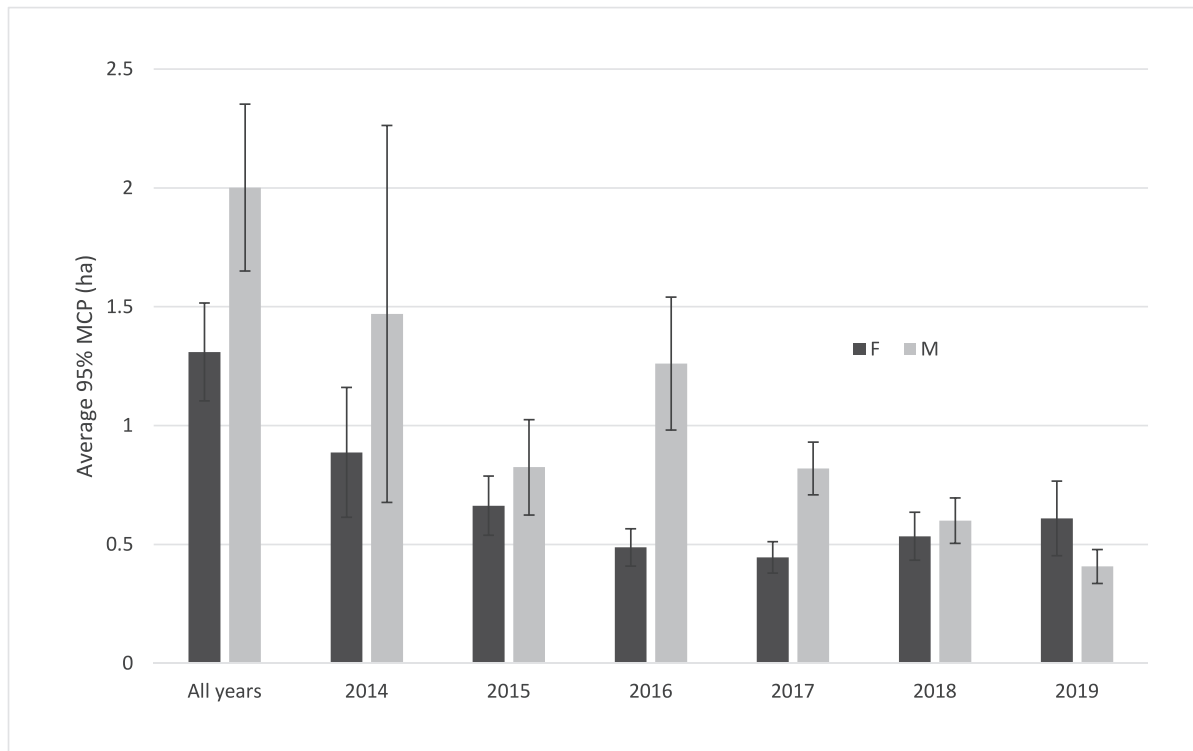


FIG. 3. Home range size (MCP) in hectares (ha) of *T. yucatana* in northern Yucatán, Mexico, illustrating the size of 5-yr pooled home ranges and average home range size by year (includes only turtles with greater than 23 locations).

Home Range.—Across all turtles of both sexes from 2014–2019 at Site A, average annual 95% MCP home range size was 0.684 ha (0.604 ha, SD = 0.159 for females and 0.915 ha, SD = 0.398 for males) (Fig. 3). Across all turtles of both sexes at Site A, the average individual home range encompassing all locations from all years (2014–2019) combined was 1.635 ha (SD = 0.93) (Table 1). Although males tended to have larger home ranges than females, this difference was only significant in 2 of 5 yr at Site A (2016: $t_{6,94} = -2.66$, $P = 0.03$; 2017: $t_{11,58} = -2.89$, $P = 0.01$; all other years: $P > 0.05$).

Home Range Fidelity.—Across all turtles of both sexes that we observed between 2014–2019, the average distance between consecutive annual home range centroids comprising all radio-telemetry locations was 22.5 m, with the average ranging

annually from 17.2–29.3 m. The smallest interannual centroid drift was 1.5 m (F6, 2017 to 2018), and the largest interannual home range centroid drift was 77.3 m (F7, 2018 to 2019). There was no significant difference in home range fidelity between the sexes ($P > 0.05$ in all cases). The distance between consecutive year dry-season dormancy locations ranged 1.5 m–251 m and averaged 50.5 m ($n = 86$) across all turtles in all years (Table 2).

Seasonal Movements.—Turtles moved less than 2 m per day on average from January through May (corresponding roughly to the dry season) and moved greater distances during other months with a peak between July and October (Fig. 4), varying by year (Fig. 5). Throughout the year, males showed significantly greater daily movements than females ($t_{3,12} = 15.66$, $P = 0.007$, using a mixed effects model with individual turtle as a random effect).

Feeding.—We observed instances of feeding on five occasions in June, July, and October. Food items included an unidentified species of snail, the fruit of an unidentified climbing vine, ripe fruit of the Pitahaya (*Hylocereus* sp.), ripe fruit of the cactus

TABLE 1. Home range size (ha) of *Terrapene yucatana* in northern Yucatán across study years (includes individuals with >23 locations in a given year).

Year	Movement metric (% MCP)	Females (ha)	Males (ha)	Overall average (ha)
2014	95	0.89	1.47	1.12
2014	100	0.84	2.41	1.36
2015	95	0.66	0.82	0.73
2015	100	1.05	1.17	1.10
2016	95	0.49	1.26	0.83
2016	100	0.66	1.42	0.99
2017	95	0.44	0.82	0.62
2017	100	0.60	1.11	0.84
2018	95	0.53	0.60	0.57
2018	100	1.00	1.05	1.02
2019	95	0.61	0.41	0.51
2019	100	0.89	0.82	0.86
All years	95	1.31	2.00	1.64
All years	100	2.39	2.80	2.58

TABLE 2. Distances between dry-season dormancy locations of *Terrapene yucatana* in northern Yucatán in each year of study, averaged across all years.

Year	No. of locations available to compare with previous year	Avg. distance from the previous year (m)	Minimum distance from last year's location (m)	Maximum distance from last year's location (m)
2016	16	46.3	2.3	197.9
2017	17	65.2	7.8	251.0
2018	19	38.0	4.4	125.6
2019	19	52.8	1.5	136.2
All years	86	50.5	1.5	251.0

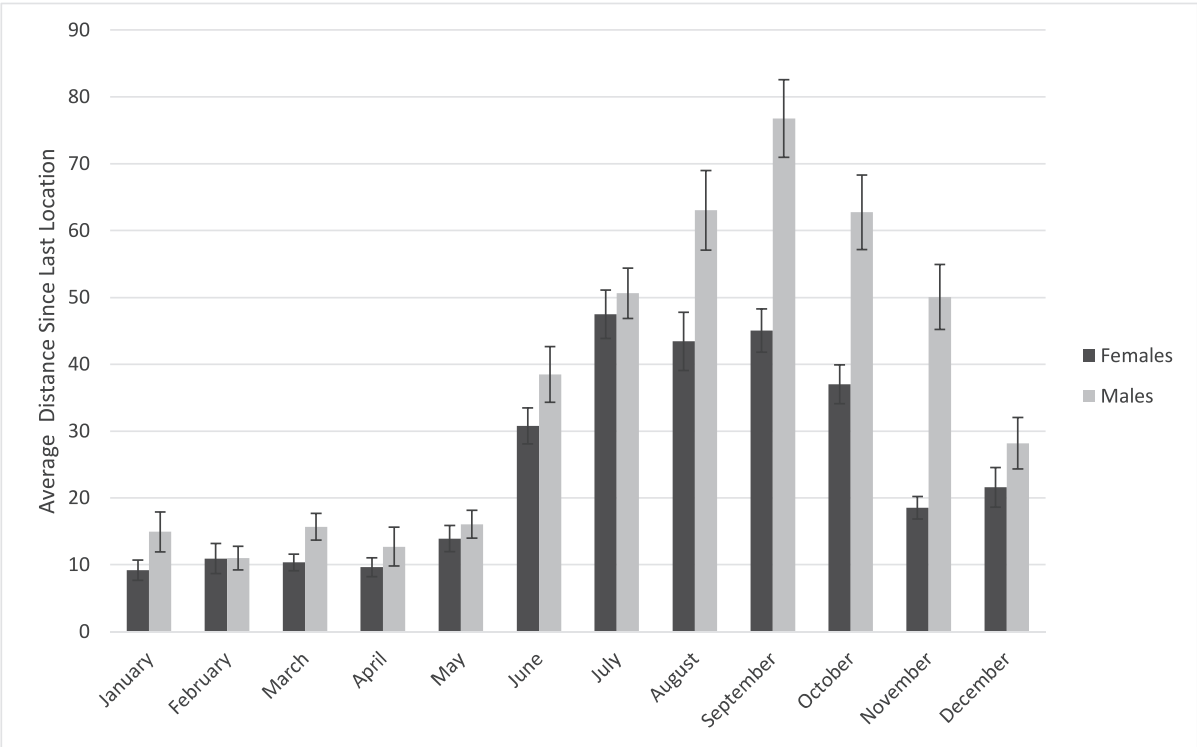


FIG. 4. Seasonal movements in meters (m) of *T. yucatana* in northern Yucatán, Mexico, illustrating generally larger average daily movements by males in all months except July and a typical activity peak between June and December.

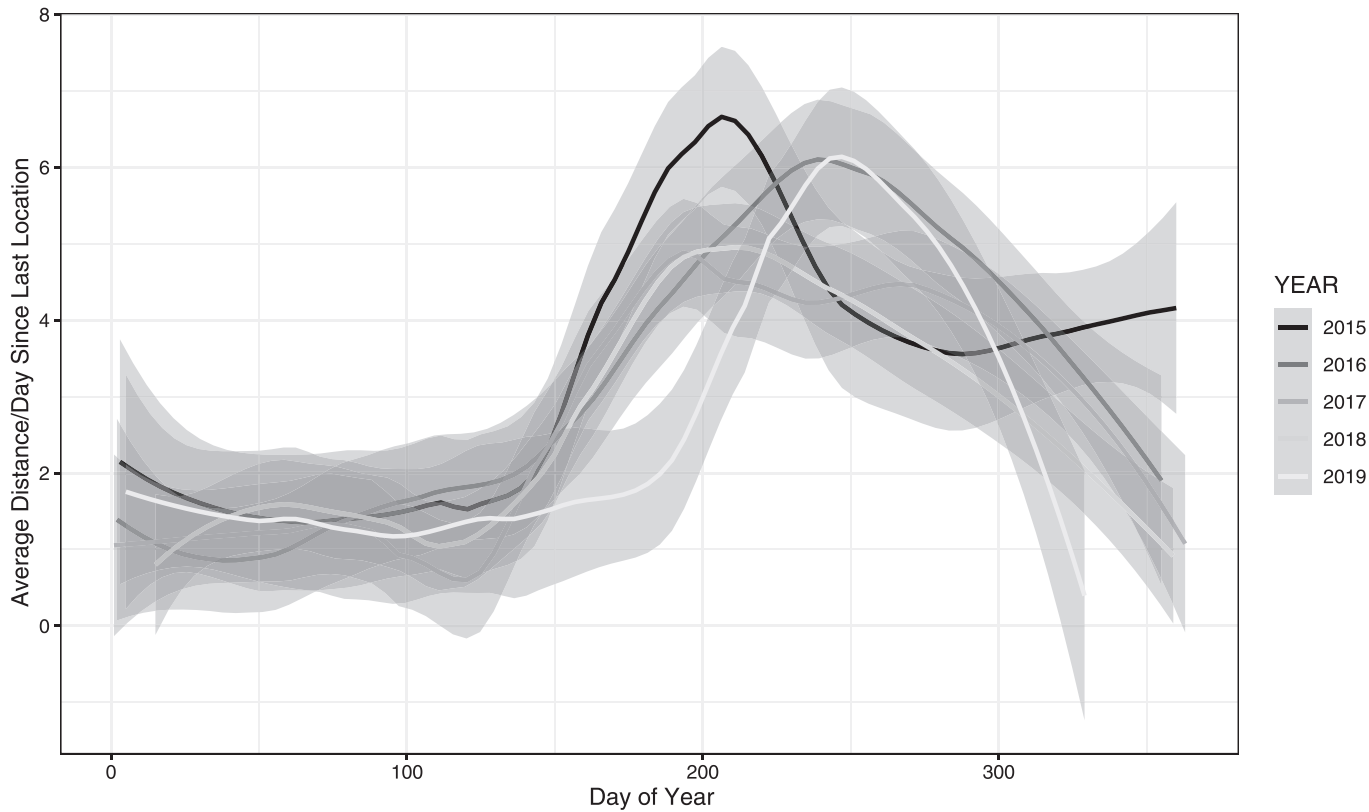


FIG. 5. Seasonal variation in average daily movement in meters (m) of *T. yucatana* in northern Yucatán from 2015–2019, illustrating activity peaks from June to December in most years, with substantial interannual variability.

Acanthocereus tetragonus, and ripe fruit of the usté (*Malpighia souzai*).

Reproduction.—We observed and recorded 25 instances of courtship. Courtship occurred in the summer and fall, with 23 instances (92%) occurring between July and October. The earliest observed date was 24 June and the latest was 22 November, with a median day of year, across all years, of 3 September. We observed only a single instance of courtship in June and November (4% each), with most observations in July ($n = 4$, 16%), August ($n = 5$, 20%), September ($n = 7$, 28%), and October ($n = 7$, 28%). Courtship was observed throughout the day and associated with air temperatures ranging 24.0–32.9°C (median = 30.9°C) and relative humidity of 85.5%–100% (median = 100%). Only two instances occurred during cloudy weather (8%); the remainder of instances occurred during clear or sunny weather conditions. We observed only diurnal courtship, but we did not track turtles at night. The 8 males in our radiotelemetry sample were observed courting on 22 occasions with an average of 2.25 females per male and an average of 1.22 bouts per mate. The number of observed courtship attempts and the number of mates per male were not significantly correlated with total home range size (Pearson's $r_7 = 0.19$, $P = 0.63$) or average distance between centroids (Pearson's $r_7 = 0.28$, $P = 0.47$), although the smallest males appeared to exhibit courtship behavior on more occasions per year (Pearson's $r_7 = 0.51$, $P = 0.16$). The 9 females in our radiotelemetry sample were observed courting 19 times with an average of 1.78 males and average of 1.19 courtship bouts per mate. We observed no instances of nesting or oviposition. At least two turtles were determined by palpation to be gravid in July 2017.

Antagonistic Encounters.—We observed a total of five putative, antagonistic encounters between males, including one observed event in each month from August to November. In four instances, two males were observed immediately adjacent to each other, with one enclosed in its shell and the other alert. On one occasion, a lone male was observed on its back and we inferred that it had been flipped by another male, although it could have been a predator. Based on our limited observations, it appears that male–male antagonistic encounters begin and end later in the season than courtship.

Habitat Characterization.—Our network of 42 fixed, 5-m plots revealed the forest structure and available ecological contexts and associations. Canopy closure within 5 m averaged 34.2%. Shrub cover averaged 42.7%. Large, nonepiphytic *Bromelia* spp. (*Bromelia karatas* L. and *Bromelia pinguin* L.) were present in 29 of 42 plots (69.1%) and averaged 12.2% cover within plots. The most frequent tree species (>3-m canopy height), including all species detected more than twice, were identified as *Acacia* cf. *pennatula* (Schltdl. and Cham.) Benth. (19.1% of plots), *Guaiacum sanctum* L. (9.5%), *Bursera simaruba* (L.) Sarg. (9.5%), *Guazuma ulmifolia* Lam. (7.1%), *Apoplanesia paniculata* C. Presl. (7.1%), *Mimosa* sp. (7.1%), *Caesalpinia yucatanensis* Greenm. (4.8%), *Gymnopodium floribundum* Rolfe in. Hook. (4.8%), *Piscidia piscipula* (L.) Sarg. (4.8%), *Esenbeckia pentaphylla* Griseb. (4.8%), and *Ceiba* cf. *pentandra* (L.) Gaertn. (4.8%).

When comparing the presence of dominant plants at turtle location sites with those in the 42 vegetative plots by using Fisher's exact tests, we found that turtles selected sites that were dominated by *Mimosa* sp. disproportionately to its availability in vegetative plots ($P = 0.025$). Turtles appeared to use sites with *G. sanctum* more frequently than the plant occurred in vegetative plots, but not significantly so ($P = 0.42$). Negative binomial regression models suggested that turtles' use of



FIG. 6. Head coloration of a male *T. yucatanana* in northern Yucatán, Mexico. Photo: M. T. Jones.

vegetation plots was positively associated with *Bromelia* spp., cactus, soil, rock, canopy, and shrub cover and negatively associated with leaf litter and herbaceous cover. However, the only significant association was the amount of *Bromelia* cover ($z = 2.02$, $P = 0.043$). Models met assumptions using diagnostics in the package DHARMA (Hartig, 2019).

Aquatic Habitat Use.—We did not observe the frequent use of aquatic habitats by *T. yucatanana*, although there are seasonal ponds in the immediate vicinity of both sites. We observed only 5 instances out of 2,808 radio locations (0.17%) in which the turtle was submerged in rainwater pools. In one case, it appeared that an adult male had been apparently displaced from his shelter site under a tree trunk by rainwater flooding. In another instance, a pair was observed courting in a rainwater pool.

DISCUSSION

Our findings represent the first quantitative estimates of population density, home range size, and habitat associations for *T. yucatanana*. Here, we have reported basic ecological data from two distinct subpopulations within an agriculture–forested landscape, and the degree of connectivity between them (or relative isolation) is unknown. Contrary to earlier accounts (Legler and Vogt, 2013), we did not observe pronounced sexual size dimorphism, although females were significantly heavier. We did, however, observe striking chromatic dimorphism between the sexes consistent with that reported by Legler and Vogt (2013) (Fig. 6). The largest turtle in our study, a male with SCL = 159 mm, was larger than the maximum reported by Legler and Vogt (2013).

The estimated population density of the two populations was strongly different and was the only measure by which the two sites could be quantitatively compared. The estimated density at Site A, which is set within a large contiguous block of forested habitat, was six times higher than that at Site B, which is similarly sized but surrounded by nonforested habitats. The estimated density of Site A, 2.29 turtles/ha, was lower than most reported estimates for subspecies of *T. carolina* (Kiester and Willey, 2015) but comparable to reported densities of *T. carolina* in Delaware (Nazdrowicz et al., 2008), Massachusetts (Willey, 2010), and North Carolina (Kapfer et al., 2013). The estimated density of Site B, namely, 0.39 turtles/ha, was generally lower than other reported density estimates but must be interpreted with caution because not all assumptions of the models were

met. Regrettably, the two sites could not be furthered compared in regard to movements and home range, site fidelity, behavior, or habitat associations because the logistical difficulties of regular access precluded the same frequency of radiotelemetry at Site B as that at Site A.

The apparent survivorship within our network of study locations was higher than that generally reported for northern subspecies of *T. carolina*, which were summarized by Kiester and Willey (2015) to generally range below 96% annually. It is possible that this species is notably long-lived under stable landscape conditions, although this 5-yr study would not have adequately characterized the mortality rates and population dynamism associated with stochastic or catastrophic events such as fire and forest clearing (both of which are frequent throughout northern Yucatán). In addition, we found only one juvenile at either study site, indicating that there may be low rates of recruitment. Alternatively, it is likely that juveniles are more difficult to find than adults or they may use different habitats than adults.

Comparisons of annual home ranges of Yucatán Box Turtles in this study to more northerly subspecies of *Terrapene* are made difficult because of methodological and analytical differences. However, it seems clear that individual *T. yucatana* in our study area moved less on an annual basis than individual Box Turtles in most published studies in the United States. The average annual home range observed in our study (0.68 ha) was exceeded by that in most published studies (Kiester and Willey, 2015). Even the average total 5-yr MCP home range (1.64 ha) observed in Yucatán is lower than the annual estimates of other subspecies, which generally exceed 2 ha on average (Kiester and Willey, 2015). However, this population of *T. yucatana* was consistent with other studies of *Terrapene* in not exhibiting strong differences in generalized space use between the sexes (Cook, 2004; Kapfer et al., 2013; Kiester and Willey, 2015). We noted that the absolute values for movement and home range should be interpreted with some caution because we set an arbitrary cut-off of 23 radio locations for inclusion in our analyses, and it is likely that the actual values are higher.

The observed rates of interannual home range centroid drift in our study were exceptionally low and include some of the smallest values reported (Cook, 2004; Kiester and Willey, 2015). It appeared that, in this area, individual *T. yucatana* can occupy relatively small areas less than 1 ha with notably high interannual home range fidelity. The continued use of the same small areas of interior forest by individuals over the course of several years underscores the importance of forest conservation for this rare and declining species.

As reported by Legler and Vogt (2013) and Buskirk (1993), Yucatán Box Turtles exhibit a strong seasonal activity pattern positively associated with summer and fall rains. From our own observations, it is not clear whether increased surface activity results in increased rates of collection but probably does result in increased rates of roadway mortality. Although permanent freshwater ponds and seasonally flooded pools were available at both sites, *Terrapene yucatana* did not actively use them. In contrast, *T. carolina* has been reported to regularly use aquatic habitats when available (Latham, 1916; Nichols, 1917; Allard, 1948; Dickson, 1953; Madden, 1975; Rossell et al., 2006; Jones et al., 2015; see review in Donaldson and Echternacht, 2005, and Kiester and Willey, 2015).

Our preliminary floristics and habitat studies indicated that in this part of Yucatán, *T. yucatana* is primarily a species of tropical deciduous forests. The northern subspecies of *T. carolina*, in

contrast, is most frequently associated with edge habitats, ecotones, and early-successional habitats (Madden, 1975; Kiester and Willey, 2015). Yucatán Box Turtles are an interior forest species that occurs at variable, but very low, densities in the northern Yucatán landscape. In undisturbed contexts, Yucatán Box Turtles may exhibit high survival rates and possibly extreme longevity, small home range size, and fidelity for home range areas. As an allopatric and fully tropical lineage of North American Box Turtles, *T. yucatana* warrants dedicated conservation efforts based on large-scale forest conservation programs.

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