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POPULATION STRUCTURE AND NATURAL HISTORY OF CREASER'S MUD TURTLE (*KINOSTERNON CREASERI*) IN CENTRAL YUCATÁN

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***Abstract*.—Creaser's Mud Turtle (*Kinosternon creaseri* Hartweg, 1934) is a kinosternid turtle that is widely distributed across the three states of the Yucatán Peninsula in southeastern México. Although its distribution and habitat associations have been established for nearly three decades (Iverson 1988), primarily anecdotal data are available on local population structure and natural history. We conducted a capture-recapture study of *K. creaseri* in small, limestone depressions (*haltunes*) distributed over about 650 ha of forested hills in the Puuc Hills Region of south-central Yucatán. We used baited funnel traps in seven *haltunes* with surface areas ranging from 2.3 to 54.9 m^2 for a combined total of 445 trap hours, and manually searched 20 additional small *haltunes* (≤ 1.5 m semi-major axis). We captured, marked, and released 174 individual turtles. Our sample included 21 adults (12 males and nine females) and 139 juveniles or hatchlings with carapace lengths < 90 mm. Turtle densities ranged from 1.55–5.11 turtles/m^2 of surface water. Preliminary results from our two-year sampling period provide no evidence of individual turtle movement between ponds. Further, we report on novel ecological interactions of *K. creaseri*, such as attempted depredation of hatchlings by giant water bugs (*Lethocerus* sp.), feeding behavior of trapped turtles on adult Rio Grande Leopard Frogs (*Lithobates berlandieri*), and shared rock-crevice aestivation with the Furrowed Wood Turtle, *Rhinoclemmys areolata*. We also compiled new occurrence data for the species and report an expanded known distribution of this poorly known species.**

Key Words.—capture-mark-recapture; demography; density; sex ratio

INTRODUCTION

Creaser's or Yucatán Mud Turtle (*Kinosternon creaseri* Hartweg 1934, syn: *Cryptochelys creaseri*) is an endemic species known primarily from shallow rainwater pools, roadside ditches, limestone ponds, and adjacent uplands in the Mexican states of Yucatán, Campeche, and Quintana Roo in the Yucatán Peninsula (Iverson 1988; Iverson 1992; Hernández-Gallegos et al. 2003), where it is apparently allopatric from its sister taxon, the Tabasco Mud Turtle (*Kinosternon acutum*; Iverson 1980, 1983; Lee 1996). *Kinosternon creaseri* is believed to exhibit terrestrial dormancy during the Yucatán winter-spring dry season (Iverson 1988; Buskirk 1993; Legler and Vogt 2013). Though considered a species of Least Concern by the International Union for Conservation of Nature (IUCN; van Dijk et al. 2007) because of its apparent local abundance (Iverson 1988), several authors have urged direct attention toward range-wide population status and local population trends (e.g., van Dijk et al. 2007; Legler and Vogt 2013).

Kinosternon creaseri was found to be locally abundant along the perimeter of the Sian Ka'an Biosphere Reserve, north of Felipe Carrillo Puerto in central Quintana Roo (Cálderon-Mandujano et al. 2005). Iverson (1988) reported that *K. creaseri* primarily inhabits the wet region of the northeastern Yucatán Peninsula; however, more recently, isolated observations in the drier areas of northwestern Yucatán have provided evidence of a broader range (Buskirk 1997; Hernández-Gallegos et al. 2003). It is now evident that the species is widely distributed in the northern part of Yucatán Peninsula, but its entire distribution and range margins are poorly understood, as are many aspects of its ecology. We investigated the population ecology of *K. creaseri* in the central Puuc Hills region of southern Yucatán as a first step in understanding the distribution and abundance of this poorly known species. Our primary objective

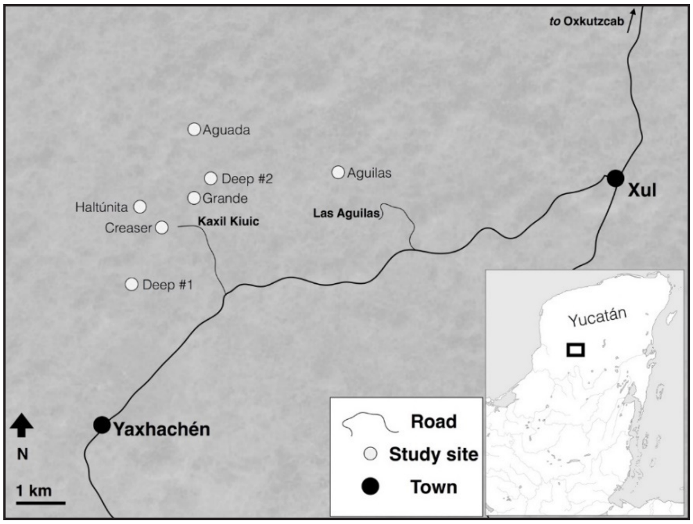

Figure 1. Map of the study area of the Creaser's Mud Turtle (*Kinosternon creaseri*) in the Puuc Hills Region of southwestern Yucatán, México, showing the *haltunes* locations.

was to establish a baseline measurement of abundance, population structure, and individual-based occurrences to allow future investigations of metapopulation dynamics in a landscape with limited, sporadically distributed, and often seasonal aquatic habitats.

Materials and Methods

Study site.—Our study ponds are distributed across approximately 650 ha of mature tropical forest within the Kaxil Kiuic Reserve (Helen Moyers Biocultural Reserve), in the Puuc Hills Region 27 km southwest of Oxkutzcab, Oxkutzcab Municipality, Yucatán, México (Fig. 1). The Puuc Hills belong to the Sierra de Ticul, a topographic system that extends from western Yucatán to northern Campeche, reaching a maximum elevation of 270 m (Lee 2000). As an area of high topographic relief, the Puuc Region is distinct from the generally flat areas farther north in the Yucatán Peninsula, and our study sites ranged in elevation from 95 m to 130 m. The dominant vegetation association of the region is Tropical Deciduous Forest (Challenger 1998), and our study sites were situated in a complex aggregation of primarily forested, low hills juxtaposed with small archeological clearings and surrounded by low-intensity agriculture. The climate in central Yucatán is warm, with a pronounced rainy season from July through October (García 2004).

Most of our study sites are karst-derived limestone solution ponds locally referred to as *haltunes* or sartenejas. These ponds vary in size and depth, but most have a benthic substrate of organic material and leaf litter, though some have been sealed or lined with plastic by reserve staff to retain water for longer periods. Compared with other pond types in this region such *bajos* (seasonal ponds in the forest floor) and *aguadas* (large and permanent bodies of water in the forested), *haltunes* are smaller, do not have a connection with groundwater, and are well defined. Lee (1996, 2000) provides a complete description of Yucatán Peninsula wetlands.

We established two primary study ponds: *Haltun Grande* (HG; 20.0965°N, 89.5476°W) and Creaser's *Haltun* (CrH; 20.0910°N, 89.5542°W; separated by 920 m), where we trapped at repeated intervals over multiple nights in July 2014, October 2014, January 2015, and November 2016. In addition, we conducted overnight trap assessments of four additional *haltunes* and an *aguada* under management (a plastic liner) to hold more water (Fig. 1). We also manually sampled (by inspecting the organic substrate) approximately 20 additional small *bajos* with minimal standing water (< 0.5 m^2) or only saturated organic substrate consisted of organic muck, leaf litter, and woody debris (Table 1).

Trapping protocol.—We trapped seven individual waterbodies for periods of time ranging from 4–48 h during four separate periods from July 2014 to November 2016 for a combined total of 445 trap hours. We completed eight distinct sampling events during the two years of field work. We used collapsible funnel traps that expanded to 91.4 × 30.48 cm with 0.63 cm polyethylene netting baited with sardines in soy oil. We secured traps to surrounding woody vegetation using a 2 m piece of twine. We further assured the buoyancy of the trap by inserting at least one empty, 2 L soda bottle. Traps were GPS-referenced in the field and checked daily. Additionally, we searched rock piles and Mayan ruins near *haltunes* to detect dormant turtles on land.

Turtle processing protocol.—We measured, weighed, uniquely marked, and photographed all turtles

Table 1. Morphometry of water bodies in the study area of the Creaser's Mud Turtle (*Kinosternon creaseri*), Puuc Hill Region, southwestern Yucatán State, México.

Body of water (acronym)	Surface Area (m^2)	Shape	Seasonality	Depth (m)	Origin
Haltun Grande (HG)	54.9	Elliptical	Permanent	1	Natural
Creaser's *Haltun* (CrH)	25.1	Elliptical	Semi-permanent	2	Natural
Deep *Haltun* #1 (DH1)	< 2.0	Circular	Permanent	3–4	Natural
Deep *Haltun* #2 (DH2)	< 2.0	Circular	Permanent	2–3	Natural
Small *Haltun* (SH)	< 2.0	Circular	Seasonal	0.5	Natural
Eagles *Haltun* (EH)	6.3	Elliptical	Permanent	—	Natural
Aguada (A)	149.2	Elliptical	Permanent*	—	Anthropogenic

at the point of capture. We immediately released all turtles at the capture site following processing. For turtles > 50 mm, we uniquely notched individuals with a triangular file (Ernst et al. 1974) using a modification of the Cagle notching code (Cagle 1939), and we gave turtles < 50 mm a single mark to denote the *haltun* of their first capture. We measured carapace length (CL), plastron length (PL), carapace height (CH), and carapace width (CW) on each turtle with digital calipers (Mitutoyo America Corporation, Aurora, Illinois, USA) and weighed body mass (BM) with an electronic portable scale (0.1 g; American Weigh Scale, Norcross, Georgia, USA). Where visible, we recorded lines of arrested growth on the abdominal scute as an estimate of growing periods (Germano and Bury 1998; Wilson et al. 2006). We defined adult turtles by the presence of secondary sexual characters in males: a long and bulky tail, a well-developed spine at the end of the tail, a prominent notch in the hind lobe of the plastron, and a concave plastron. We defined adult females by size; any turtle that was at least the minimum size of a mature male (90 mm CL) but with a flat plastron, lacking the prominent notch in the hind lobe of the plastron, and with a spine-tipped tail (Macip-Ríos et al., 2011).

Population analysis.—We assessed population structure by classifying turtles by body size: we considered turtles with a CL < 40 mm hatchlings or that was hatched in the year of sampling. These individuals also lacked growth rings in their plastral scutes. We considered turtles 40–80 mm CL juveniles (secondary sexual characters absent or barely visible); turtles 80–90 mm CL sub-adults (secondary sexual characters were partly visible: tails were not fully differentiated, but notch in hind lobe and concave plastron possibly present); turtles 90–100 mm CL small adults (minimum size reported with enlarged follicles in females [Iverson, 1988] and full secondary sexual characters visible in males); and turtles > 100 mm CL large (± old) adults (Iverson 1988; Macip-Ríos et al. 2011).

We evaluated the sex ratio of small and large adults by *haltun* and across all bodies of water using a chi-square test (Gibbons 1990; Seger and Stubblefield 2002). We compared body sizes between *Haltun Grande* (HG) and Creaser's *Haltun* (CrT) using a Student's *t*-test. We tested data for normality using a Shapiro-Wilk test and variance homoscedasticity was tested with a Bartlett's test. We compared age class proportions between HG and CrH using contingency table. We estimated capture probabilities (*P*) per period or event by a log-linear model (Baillargeon and Rivest, 2012). We used a Wilcoxon test to compare capture probabilities between *haltunes*. We estimated the population size for CrH and HG using the log-linear Jolly-Seber model for open populations in the Rcapture package (Baillargeon and Rivest 2012) in R (R Core Team 2015). We were unable to estimate population size from the other *haltunes* and *aguada* sampled (DH1, DH2, SH, EH, and A) due to limited capture rates. For all statistical analyses, $\alpha = 0.05$.

RESULTS

Trapping results.—We captured, marked, and released 174 *K. creaseri*, including 170 turtles detected in seven *haltunes* during 445 h of trapping, and four adults detected in terrestrial habitats. Among the marked individuals, we recaptured 34 (19.76%), but we recaptured only seven (4.12%) during different sampling events. In the entire sample, we captured 21 adults (12.20%; 12 males, and nine females) and 139 immature individuals with carapace length < 90 mm. Some of the immature turtles exhibited partial secondary sexual characters, but we did not consider them as adults because they fell below the lower size limit in our study. We captured and marked, but did not measure, 12 individuals. These 12 were not included in the population structure analysis but were included in the capture-recapture analysis. Additionally, we observed but were unable to capture an additional 33 individuals while setting or checking traps. A single adult male *K. creaseri* was found dead from unknown causes, immediately adjacent to a *haltun.*

Morphology.—Overall, adult males had a mean CL of 109.21 ± 8.86 mm (range, 91.0–120.0 mm) and

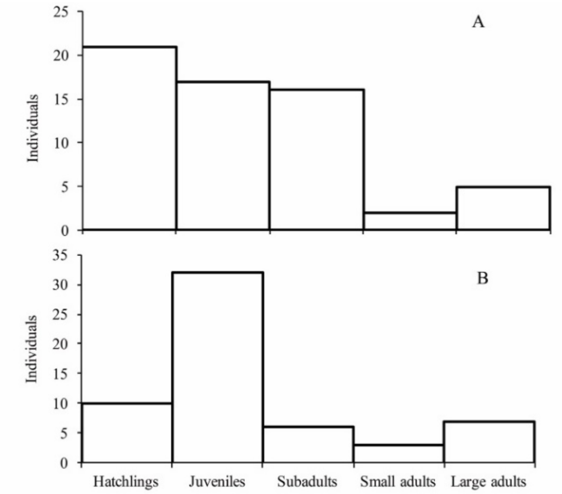

Figure 2. Population structure of the Creaser's Mud Turtle (*Kinosternon creaseri*) from (A) Creaser's *Haltun* and (B) *Haltun* Grande, in the Puuc Hills Region of southwestern Yucatán, México.

averaged 158.54 ± 38.54 g (range, 89.0–210.3 g) BM. Females had a mean CL of 102.87 ± 4.85 mm (range, 94.0–108.0 mm) and 144.88 ± 19.55 g (range, 114.0–166.5 g) M. Hatchlings had a mean CL of 36.18 ± 2.72 mm (range, 29.0–39.5 mm) and 6.95 ± 1.83 g (range, 2.6–10.0 g) BM. Individuals recognized as juveniles or immatures ranged from 40.0–78.5 ± 12.10 mm CL, and 9 to 66.4 g ± 15.10 g BM.

The CL of hatchlings in HG (37.8 ± 2.00 mm) were significantly larger than those in CrH (35.57 ± 3.07 mm; $t = 2.10$, df = 20, $P = 0.047$); however, we found no differences in BM between sites ($t = 2.36$, df = 6, $P = 0.510$). Juvenile CL (mean ± SD) in CrH (71.33 ± 5.44 mm) were significantly larger than those in HG (55.90 ± 11.36 mm; $t = 6.41$, df = 46, $P < 0.001$), as was BM (CrH = 46.11 ± 8.58 gr, HG = 25.69 ± 13.46; $t = 5.69$, df = 35, $P < 0.001$). We did not find any difference in sub-adult CL ($t = 0.902$, df = 8, $P = 0.360$) or BM (not enough data for statistical analysis). It was not possible to evaluate the difference in body sizes between adult males and females by *haltun* due to low sample size; however, when we combined *haltun* samples and compared adult males with adult females, we did not find a significant difference in CL ($t = 2.05$, df = 17, $P = 0.054$) or BM ($t = 0.936$, df = 13, $P = 0.361$).

Populations.—Most of the captures were made in the two *haltunes* with the greatest water volume: CrH (n = 60; 17 recaptures) and HG (n = 58; 16 recaptures). Adult sex ratio for the overall sample was not different from 1:1 (12 males and nine females; $\chi^2 = 0.430$, $P = 0.511$). In individual *haltunes*, the sex ratio was male skewed 2:1 (four males and two females) for CrH, but approximately even (1.14:1; four males and three females) for HG; small sample sizes precluded statistical analyses.

Based on the number of unique individuals captured in each *haltun*, minimum turtle densities ranged from 0.8 to 3.6 turtles/m^2 of surface water available in the study site. Estimated population size of turtles in CrH was 104.8 turtles ± 22.5 SE (95% CL = 60.7–148.9), suggesting a density of 5.11 turtles/m^2 of surface water available in the study site. Estimated population size of turtles within HG was 85.4 ± 26.4 SE (95% CL = 33.63–137.24), suggesting a density of 1.55 turtles/m^2 of surface water.

Capture probabilities were low at both *haltunes*. For CrH, capture probabilities (P) during each sampling period were: 0.28 ± 0.10 SE (July 2014); 0.20 ± 0.07 (October 2014); 0.37 ± 0.22; 0.08 ± 0.05 (January 2015); and 0.20 ± 0.20 (November 2016). For HG, capture probabilities were: 0.11 ± 0.06, 0.08 ± 0.05, and 0.35 ± 0.18. No significant differences in capture probabilities were detected between *haltunes* ($S = 0.451$, $P = 0.790$). Nevertheless, cumulative capture probabilities (P_c) were high for CrH ($P_c = 0.84$) and moderate for HG ($\mathrm{P}_c = 0.62$).

The population structure for CrH and HG shared similar characteristics, including a small number of large adults (Fig. 2). The distributions of body size between populations were significantly different ($\chi^2 = 15.40$, df = 2, $P = 0.009$). We also captured individuals in other *haltunes*, *aguadas*, and in the forest (n = 20). Those turtles included 10 hatchlings, two sub-adult males, one adult male, one large adult female, and three large adult males.

Occurrence data and observations.—We updated the occurrence map of Iverson (1992) by adding new records from the field, from publications such as Buskirk (1993) and Hernández-Gallegos et al. (2003), and for CONABIO-SNIB (National System of Biodiversity Information) from the Mexican Federal Government. We built an updated database of 67 localities for the Yucatán Peninsula. Those records extend the distribution of *K. creaseri* by 152 km to the southwest at Campeche, 138 km northwest to Celestun on the border of Yucatán and Campeche, and 91 km the southwest to the known record of Quintana Roo, which locates *K. creaseri* a few kilometers from the Belize border (Fig. 3). It is noteworthy that many of the records occur along two major highways, Route 180D Mérida-Cancún highway and Route 307 Tulum-Felipe Carrillo Puerto highway, suggesting that areas away from highways may be under sampled.

We observed a hatchling that was attacked by a giant water bug (*Lethocerus* sp.), and after a 10-min struggle, successfully escaped the predator. We also observed *K. creaseri* feeding on a Rio Grande

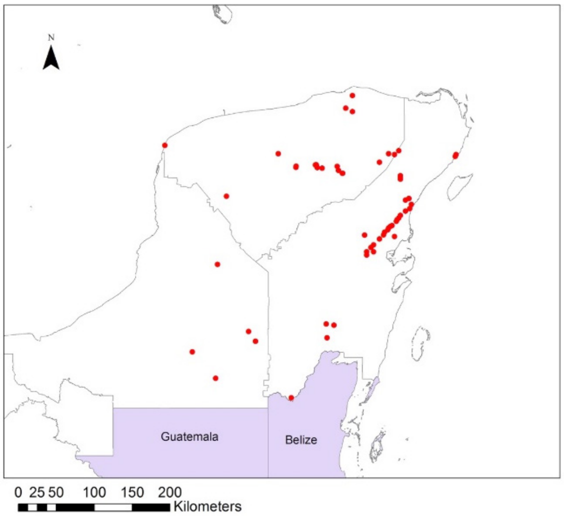

Figure 3. Known records of the Creaser's Mud Turtle (*Kinosternon creaseri*) in the Yucatán Peninsula.

Leopard Frog (*Lithobates berlandieri*) while caught in a trap. This species of frog is abundant in the water bodies where turtles were trapped. Additionally, during upland surveys, we observed one *K. creaseri* sharing an aestivation site under rocks on the forest floor with a *Rhinoclemmys areolata*. Though we witnessed this event only once, additional *K. creaseri* and *R. areolata* were individually found in similar habitat suggesting that this could happen on a regular basis.

Discussion

Previous knowledge of *K. creaseri* is based on an intensive natural history paper (Iverson 1988), notes on its geographic distribution throughout the Yucatán Peninsula (Buskirk 1997; Hernández-Gallegos et al. 2003), and anecdotal observations in herpetological inventories of the Yucatán Peninsula and México (Lee 1996; Calderon-Mandujano et al. 2008; Legler and Vogt 2013), with no previous quantitative estimates of population structure. Contrary to the conclusion by Iverson (1988) that *K. creaseri* exclusively inhabits *bajos* (temporary forest pools), we observed it in permanent and semi-permanent limestone pools (*haltunes* and an *aguada*).

We recorded population structure as remarkably different from other kinosternid species, in which adults and sub-adults are usually the most common individuals (Iverson 1991a; Frazer et al. 1991; Stone 2001; Macip-Ríos et al. 2009; Vázquez-Gómez et al. 2016) due to low survivorship of hatchlings and immatures (Iverson 1991b). The abundance of hatchling and juvenile *K. creaseri* that we observed has been previously reported by Iverson (1988) and could be related to an explosive hatching process during the rainy season. Other species, such as the Mexican Mud Turtle (*K. integrum*), have been observed to exhibit similar hatchling and juvenile densities (Rodrigo Macip-Ríos, per. obs.). At our study site, *haltunes* are the only aquatic habitat that remains in the dry season, and when water is low, the limestone walls could trap turtles for several days or even months, until they are replenished by rainfall. *Haltun* trapping might also play a role in the structuring a population dominated by hatchling and young individuals observed in the study site. Another possibility is that adults are highly terrestrial, only using water to forage during the night, as observed in the Tabasco Mud Turtle (*K. acutum*; Richard C. Vogt, pers. comm.) and other kinosternids from seasonal environments, such as the Sonora Mud Turtle (*K. sonoriense*; Ligon and Stone 2003; Stone et al. 2015). Regardless, the *haltunes* appear to be an important habitat feature on the landscape where populations congregate for feeding, and potentially mating, and they may facilitate growth across size classes. Additional capture-recapture data in the Puuc Hills region are needed to determine hatchling survival and recruitment to the subadult and adult age classes, and to adequately describe population dynamics. Future work should also evaluate the importance of aquatic versus terrestrial habitats, whether the adults found in the *haltunes* are contributing to recruitment, and at what rate individual turtles move among *haltunes*.

Based upon our preliminary data, there was no difference in body size between adult males and females, which is different from other species of kinosternids (Iverson 1991; Iverson et al. 1991; Macip-Ríos et al. 2009, 2011). Whether this lack of sexual dimorphism is real or an artifact of our limited sampling remains to be tested. Due to the complex *haltun* system in the study site and the potential terrestrial moments of the species, long-term studies should be undertaken to reveal apparent adaptations and metapopulation dynamics associated with this highly seasonal environment.

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