Population Characteristics of the Mexican Spotted Wood Turtle (*Rhinoclemmys rubida perixantha*) Along the Pacific Coast of Mexico

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Abstract.—The natural history and population ecology of the Mexican Spotted Wood Turtle (*Rhinoclemmys rubida perixantha*) is poorly known. The Mexican Spotted Wood Turtle inhabits the tropical deciduous forest along the western coast of Central Mexico. From 2012 to 2017, we conducted a capture-mark-recapture study on the coast of Jalisco, Mexico to estimate basic population characteristics of the Mexican Spotted Wood Turtle such as abundance, density, size structure, and sex ratio. We captured 234 turtles during seven sampling events. Estimated population size was 1,051 turtles and estimated density was 43 individuals/ha within the 24.6 ha surveyed. Sex ratio was slightly skewed toward males (1.2:1) but not significantly, and the population was structured, comprised mostly of adults. Females were significantly larger in carapace length, plastron length, carapace width, and heavier than the males. The population seems healthy, and because we captured some hatchlings during the study, we think the population has recruitment. Even with several years of sampling, the recapture rate was low, which means more fieldwork is needed to better understand the population dynamics of the Mexican Spotted Wood Turtle.

Key Words.-abundance; density; population structure; sex ratio; sexual size dimorphism

INTRODUCTION

About half of all turtle species are considered threatened or endangered by the International Union for Conservation of Nature (IUCN; 2018), making them the most threatened group of reptiles in the world (Böhm et al. 2013; Rhodin et al. 2018). The family Geoemydidae is the most diverse turtle family and contains about onequarter of all turtle species (Spinks et al. 2004). Despite this diversity, Geoemydidae has a disproportionate number of species considered threatened or endangered. For example, Geoemydidae dominates the list of the most endangered turtle species of the world, representing 48% of the top 25 and 40% of the top 50 endangered species (Stanford et al. 2018; Turtle Conservation Coalition 2018). This is extremely high compared to the second most diverse turtle family, Emydidae, which only has two species on the list of the top 50 most endangered turtles (Stanford et al. 2018; Turtle Conservation Coalition 2018). The main reason why many geoemydids are endangered is because the majority occur in southeast Asia where for decades they have been highly sought after for traditional medicine, food, or the illegal pet trade (Cheung and Dudgeon 2006; Gibbons and Lovich 2019). In the New World, Geoemydidae is represented only by the genus *Rhinoclemmys*, which is composed of nine species that range from northern Mexico to South America (Turtle Taxonomy Working Group 2017). Unlike many geoemydids in southeast Asia, populations of *Rhinoclemmys* in the New World appear to be more stable, providing researchers with the opportunity to study these species in the wild.

Because so many turtles are imperiled, basic research on understudied, rare, or endangered species has become a necessity. Basic information on a population such as abundance, sex ratio, population structure, and density are required to make any sort of effective conservation decision (Gibbs and Amato 2000). The majority of information that is available on population ecology in geoemydids is mainly on Old World representatives (Muñoz and Nicolau 2006; Ernst et al. 2008; Chen and Lue 2010; Lin et al. 2010; Baruah et al. 2016). In the New World, the only information that exists on the nine species of Rhinoclemmys belongs to those of the Spotted-legged Turtle, R. punctularia (Wariss et al. 2012), Large-nosed Wood Turtle, R. nasuta (Garcés-Restrepo et al. 2013, 2014, 2019), and Mexican Spotted Wood Turtle, R. rubida (see below). The information that exists on the population ecology of other Rhinoclemmys is anecdotal (Alvarado-Díaz et al. 2003; Vogt et al. 2009; Legler and Vogt 2013).

Rhinoclemmys rubida is fully terrestrial and endemic to the Tropical Dry Forests (TDF) along the western coast of Mexico from the states of Jalisco to Chiapas and within the Balsas River basin up into Michoacán, Guerrero, and the state of Mexico (Lagler and Vogt 2013; Rhodin et al. 2017). There are two recognized subspecies: R. r. perixantha (Colima Wood Turtle), which occurs in Jalisco, Colima, Michoacán, and parts of Guerrero; and R. r. rubida (Oaxaca Wood Turtle), which is only known to occur in Oaxaca and Chiapas (Rhodin et al. 2017). Recent work by Butterfield (2015) and Butterfield et al. (2014; 2018) has contributed to the knowledge of how terrestrial Rhinoclemmys interact with their environment. Yet there are no population or demographic data published on either subspecies of R. rubida.

Given the paucity of information on population parameters of *R. rubida* and other *Rhinoclemmys* species, the aim of this paper was to provide a baseline understanding on the population ecology of the subspecies *R. r. perixantha*. To do this, we present results of a capture-mark-recapture study on a population of *R. r. perixantha* that began in 2014. With these data, we were able to estimate abundance, density, population structure, and sex ratio. We also summarize patterns of sexual dimorphism. Altogether, this information, along with previously published data on this species (Butterfield et al. 2018), can be used to address the basic conservation needs and inform future conservation decisions for this species.

MATERIALS AND METHODS

Study site.---We conducted this study on the Pacific coast of Mexico at the Estación de Biología Chamela (EBCh), located near Chamela, Jalisco, México. Vegetation at the EBCh is characterized as Lowland Tropical Deciduous (dry) Forest with marked seasonality in precipitation, where 80% (average = 748 mm) falls during the four-month wet season (June-September). Mean annual temperature is 24.9° C with a range from 14.8–32° C (Bullock 1986). The landscape throughout the EBCh is characterized by small undulating hills with elevations ranging from 30 to 140 m. Two main habitat types have been described in this landscape, deciduous and semi-deciduous forest (Lott et al. 1987). Deciduous forest is the most abundant habitat type throughout the EBCh and semi-deciduous forest is restricted to larger drainages (Lott et al. 1987). Thirteen kilometers of walking-access trails are maintained throughout the EBCh and the majority of sampling occurred along these trails and in the adjacent forests. The total estimated sampling area where we regularly searched for turtles, including the trails and patches of forest off of the trails, was approximately 24.6 ha.

Sampling protocol.—We sampled for turtles between July 2012 and September 2017 in both dry and wet seasons. To calculate population size, our sampling effort was divided into seven sampling periods: July 2012, August 2014, October 2014 to May 2015, June to September 2015, July to September 2016, June to July 2017, and August to September 2017. Each sampling period ranged from 1-8 mo, depending on the length of the field season. During the sampling periods (or events), we conducted intensive searches for turtles in the study area from 6–7 d a week. We found turtles by walking on the trails and in potential turtle habitat off the trails. Upon locating a turtle, we captured individuals by hand and we recorded the geographic location using a GPS, at which time we marked and measured all individuals. We individually numbered turtles by filing notches in the marginal scutes with a triangular file using a numbering system similar to that developed by Cagle (1939). We measured straight line carapace length (SCL), plastron length (PL), and carapace width (CW) with an analog caliper to the nearest ± 0.05 mm (Spi Swiss Precision Instruments, Inc. Melville, New York, USA). We weighed turtles with a spring scale to the nearest \pm 1.0 g (Pesola ®, Schindellegi, Switzerland). We identified males by secondary sexual characteristics such as concave plastron and a longer tail with the cloacal orifice located posterior to the carapace. We identified females by their flatter plastrons and shorter tails (Ernst and Barbour 1989). To examine the size structure of this population, we used 11 body size (SCL) categories starting at 40 mm, which represent hatchlings/yearlings, and increasing by 10 mm increments up to 140 mm, which represent old/asymptotic females (Stamps and Andrews 1992). We used nine categories to assess the size structure of body mass that were divided into 50 g increments ranging from 50-450 g.

Statistical analysis.—Because of the low recapture rate, we estimated population size with a jackknife estimate of heterogeneity model (Mh; Chao 1989). This model assumes that each member of the population has its own probability of capture, in contrast with most capture-mark-recapture models, when equal catchability is assumed between sampling events. The Mh models underestimate population size, which works with low recapture rates and their high standard error estimates (Chao 1989). This analysis was done with the CARE1 (Charo et al. 2001) package in R (R Core Team 2018). We calculated capture probabilities using a log-linear model in Rcapture (Baillargeon and Rivest 2007) within R (R Core Team 2018). We used a Chisquared test (with Yates Correction) to determine if the sex ratio differed significantly from 1:1 (Zar 1999). We calculated density by dividing the number of turtles calculated for abundance by the available forest area



FIGURE 1. Structure based on straight-line carapace length (mm) of a population of a subspecies of the Mexican Spotted Wood Turtle (*Rhinoclemmys rubida perixantha*) located near Chamela, Jalisco, México.

in the study. To determine if there were differences in body size and other morphological measurements between males and females, we used a Student's *t*-test. We tested if parametric assumptions for normality and homogeneity were meet for tests using Shapiro-Wilks and Bartlett tests (Zar 1999) and we used JMP v5.0.1 (SAS Institute 2002) for all statistical analyses with α = 0.05.

RESULTS

We marked 234 *R. r. perixantha* during our study period and only recaptured 29 individuals (11.46%). We captured 205 individuals only once, 20 twice, seven turtles three times, and we captured two turtles four times. Recaptured individuals were distributed among almost all of the size classes: one in 40 mm size class (SC), two (60 mm SC), one (80 mm SC), four (90 mm SC), eight (100 mm SC), four (120 mm SC), eight (130 mm SC), and only one in the 140 mm SC. We recaptured 12 males, 14 females, and three immature turtles.

Estimated abundance using the Mh Chao model was 1,050.6 (standard deviation = 217.4) individuals (lower confidence interval = 721.8, upper confidence interval = 1,627) occupying 24.6 ha. Capture probabilities (P) during sampling events ranged from 0.17 to 0.41, with an average $P = 0.31 (\pm 0.10)$. Using the estimated abundance and total area sampled, the estimated density of *R. r. perixantha* in Chamela is about 43 individuals/ ha. Of the 234 marked turtles, we could identify 120 as males and 80 as females. The sex ratio was significantly biased in favor of males (1.5:1; $\chi^2 = 7.605$, P = 0.006).

The population structure was composed mainly of adults, but we also captured juveniles, including subadults and at least four hatchlings (Fig. 1). Weights ranged from 40 to 450 g (Fig. 2). Secondary sexual characters were evident at > 80 mm SCL for both sexes. Using the 200 adult individuals for which we could determine sex, we tested for sexual dimorphism in body size (SCL, PL, and PW) and body mass (weight).



FIGURE 2. Distribution of body mass (g) among males, females, and juveniles of a population of a subspecies of the Mexican Spotted Wood Turtle (*Rhinoclemmys rubida perixantha*) located near Chamela, Jalisco, México.

Females were significantly larger than males in SCL (females: 128.0 ± 16.7 , males: 103.6 ± 8.4 mm; t = 12.07, df = 106, P < 0.001), in PL (females 114.9 ± 15.6 , males 88.3 ± 6.5 mm; t = 14.34, df = 97, P < 0.001), and CW (females 79.0 ± 12.7 , males 65.9 ± 5.8 mm; t = 8.63, df = 101, P < 0.001). Females (280.3 ± 92.1 g) were also significantly heavier (t = 13.18, df = 91, P < 0.001) than males (139 ± 31.05 g).

DISCUSSION

Rhinoclemmys rubida perixantha is a small terrestrial turtle that is endemic to the tropical dry forests of western Mexico. Previous work has shown that this subspecies occupies small home ranges along hilltops in the dry forest and that individuals are active mainly during the wet season (Butterfield et al. 2018). Our population size estimate suggests that this species is abundant and found in relatively high densities (43 individuals/ha) in the Chamela forest. The population was primarily composed of adults with a sex ratio skewed towards males, which are significantly smaller than females.

Our population estimate of 1,050 individuals in the 24.6 ha sampled is similar only in gross numbers to those observed in other species such as R. nasuta in Colombia (990 individuals in 0.4 ha; Giraldo et al. 2012); however, due to the different sampling areas, habits (R. r. perixantha is mainly terrestrial, and R. *nausta* is mainly aquatic), and type of habitat (Tropical Dry Forest versus Tropical Rainforest), both populations are quite different in their densities, even given the variation in our estimate (standard deviation = 217.4). It is likely that these estimates are study specific. For example, in our study the Chamela population likely exceeds 1,050 individuals. The area that we surveyed comprised only about 24.6 ha of a 3,319-ha reserve with similar habitats that likely also harbor R. r. perixantha. If it were possible to survey the entire reserve, it is likely that the population would exceed 1,050 individuals. Therefore, because population estimates vary depending

on sampling methods, population density seems a more appropriate parameter for comparing turtle populations.

Estimating population density allows an estimate of turtle biomass, which can be used to understand the relative contribution that turtle populations make to ecosystem processes (Iverson 1982; Lovich et al. 2018). Our density estimate (43 individuals/ha) aligns with our personal observations that turtles seem to be common at Chamela, and exceeds the density observed in other small terrestrial turtles. For example, most information on population density in small terrestrial turtles has been derived from studies of box turtles (Terrapene spp.), in which estimates range from 2.9-5.0 individuals/ha (T. ornata; Doroff and Keith 1990) to 17.3-34.6 individuals/ ha (T. carolina; Schwartz and Schwartz 1974). Our population estimate of 43 individuals/ha suggests that the standing crop biomass of R. r. perixantha is very high. This result underscores the capability of small terrestrial turtles to reach high densities, and their importance in the dry forest ecosystem (Iverson 1982). For instance, the high density of turtles, coupled with their potential to be important seed dispersers for Blollies (Guapira macrocarpa), figs (Ficus sp.), and cacti (Opuntia spp; Butterfield and Rivera-Hernandez 2014; pers. obs.), means that these turtles could make an important contribution to maintaining the composition of forest structure. Future work should look deeper into the potential impact that R. r. perixantha has on ecological processes, such as determining the composition and structure of plant communities.

In Chamela, the population of R. r. perixantha is primarily composed of adult turtles. According to Crouse et al. (1987) and Congdon et al. (1994), stable turtle populations tend to be composed of more juvenile than adult turtles due to the delayed maturity in turtles. If so, our results suggest that the R. r. perixantha population is not stable. Nevertheless, the fact that we did observe hatchlings and juveniles suggests that this population is recruiting new individuals and there could be other explanations for fewer juveniles, such as high rates of mortality in smaller turtles (Gibbons and Semlitsch 1982; Iverson 1991; Congdon et al. 1994). Another possible explanation is low detectability of young individuals; it could be more difficult to observe these turtles in the dense vegetation of Tropical Dry Forest. Similar population structures have been observed in other species of Rhinoclemmys (Giraldo et al. 2012; Wariss et al. 2012; Garcés-Restrepo et al. 2014), and even though these populations are dominated by adults it does not necessarily mean that they are not stable or growing (Seburn 2003; Bowne et al. 2018). Investigation of reproductive success and juvenile survivorship in R. r. perixantha is needed to understand the stability of this population and its future viability.

This population of R. r. perixantha was composed of more males that were significantly smaller than females. This finding coincides with a general pattern observed across turtle populations in which males outnumber females when they are the smaller sex (Lovich et al. 2014). The proximate cause of sexual size dimorphism is the timing at which individuals attain maturity, with the smaller sex maturing faster (Seger and Stubblefield 2002). Also, female sexual size dimorphism was suggested as an ancestral character state (Ceballos et al. 2013). Courtship patterns have been used to explain the ultimate cause of sexual size dimorphism. For example, male-male combat and forced insemination are common courtship behaviors in populations of turtles in which males are larger than females (Berry and Shine 1980). Female choice seems to be more common in populations of turtles in which males tend to be smaller than females (Berry and Shine 1980). If R. r. perixantha conforms to these patterns, we would expect that female choice is an important aspect in their courtship and reproduction. The observation that males are larger than females in the southern subspecies, R. r. rubida (Legler and Vogt 2013), suggests that comparisons of R. r. perixantha and R. r. rubida could lead to more detailed insights on what evolutionary processes drive differences in sexual size dimorphism.

Geoemydids from the Old World such as the Yellow Pond Turtle (Mauremys mutica; Yasukawa et al. 1996), Amboina Box Turtle (Cuora amboinensis) in southeast Asia (Ernst et al. 2016), and Mediterranean Turtle (M. leporsa; Lovich et al. 2010) did not show differences between males and females in body size. Emydids of about the same body size, such as the European Pond Turtle (Emys orbicularis) also did not show differences in sexual size dimorphism (Zulfi et al. 2006). Other geoemydids such the Western Caspian Turtle, Mauremys rivulata (Ayaz and Budak 2008), did show evidence of sexual size dimorphism. The sexual size dimorphism hypothesis based on habitat type (Berry and Shine 1980) still has support from large data sets and comparative phylogenetic analyses (Ceballos et al. 2013; Agha et al. 2017), with a basic trend of sexual size dimorphism biased toward males in terrestrial and semi-aquatic habitats, and sexual size dimorphism biased to females in aquatic habitats: however, other factors such variation in temperature, precipitation, and aridity seems to affecting sexual size dimorphism in local populations (Agha et al. 2017). This evidence also gave support to the suggestion that male body size could be driven by ecological selection instead of fecundity selection for female body size.

This is the first report of the basic population ecology for a subspecies of the Mexican Spotted Wood Turtle, an understudied species. We found this subspecies to be abundant in the Chamela forest; however, this species has high value in the illegal pet trade (Legler and Vogt 2013). Therefore, protecting populations like those found in Chamela is necessary for the future conservation of this species. Future research should focus on assessing the abundance of this species in other parts of its geographic distribution to better assess the conservation of this species.

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LITERATURE CITED

- Agha, M., J.R. Ennen, A.J. Nowakowski, J.E. Lovich, S.C. Swat, and B.D. Todd. 2017. Macroecological patterns of sexual size dimorphism in turtles of the world. Journal of Evolutionary Biology 31:336–345.
- Alvarado-Díaz, J., A. Estrada-Virgen, D. García-Parra, and I. Suazo-Ortuño. 2003. *Rhinoclemmys rubida* (Mexican Spotted Wood Turtle). Diet. Herpetological Review 34:363.
- Ayaz, D., and A. Budak. 2008. Distribution and morphology of *Mauremys rivulata* (Valenciennes, 1833) (Reptilia: Testudines: Geoemydidae) in the lake district and Mediterreanean region of Turkey. Turkish Journal of Zoology 32:137–145.
- Baillargeon, S., and L.P. Rivest. 2007. Rcapture: Loglinear models for capture-recapture in R. Journal of Statistical Software 19:1–31.
- Baruah, C., P. Devi, and D.K. Sharma. 2016. Comparative morphometry and biogeography of the freshwater turtles of genus *Pangshura* (Testudines: Geoemydidae: *Pangshura*). International Journal of Pure and Applied Zoology 4:107–123.
- Berry, J.F., and R. Shine. 1980. Sexual size dimorphism and sexual selection in turtles (Order Testudines). Oecologia 44:185–191.
- Böhm, M., B. Collen, J.E.M. Baillie, P. Bowles, J. Chanson, N. Cox, G. Hammerson, M. Hoffmann, S.R. Livingstone, M. Ram, et al. 2013. The conservation status of the world's reptiles. Biological Conservation 157:372–385.
- Bowne, D.R., B.J. Cosentino, L.J. Anderson, C.P. Bloch, S. Cooke, P.W. Crumrine, J. Dallas, A. Doran, J.J. Dosch, D.L. Druckenbrod, et al. 2018.

Effects of urbanization on the population structure of freshwater turtles across the United States. Conservation Biology 32: 1150–1161.

- Bullock, S.H. 1986. Climate of Chamela, Jalisco, and trends in the south coastal region of Mexico. Archives for Meteorology, Geophysics, and Bioclimatology, Series B 36:297–316.
- Butterfield, T.G. 2015. *Rhinoclemmys rubida perixantha* (Colima Wood Turtle) courtship and mating behavior. Herpetological Review 46:620.
- Butterfield, T.G., and O.F. Rivera-Hernandez. 2014. *Rhinoclemmys rubida perixantha* (Colima Wood Turtle) diet. Herpetological Review 45: 320–321
- Butterfield, T.G., A. Scoville, A. García, and D.D. Beck. 2018. Habitat use and activity patterns of a terrestrial turtle (*Rhinoclemmys rubida perixantha*) in a seasonally dry tropical forest. Herpetologica 74:226–235.
- Cagle, F.R. 1939. A system of marking turtles for future identification. Copeia 1939:170–173.
- Ceballos, C.P., D.C. Adams, J.B. Iverson, and N. Valenzuela. 2013. Phylogenetic patterns of sexual size dimorphism in turtles and their implications for Rensch's rule. Evolutionary Biology 40:194–208.
- Chao, A. 1989. Estimating population size for sparse data in capture-recapture experiments. Biometrics 45:427–438.
- Chao, A., P.K. Tsay, S.H. Lin, W.Y. Shau, and D.Y. Chao. 2001. The applications of capture-recapture models to epidemiological data. Statistics in Medicine 20:3123-3157.
- Chen, T.H., and K.Y. Lue. 2010. Population status and distribution of freshwater turtles in Taiwan. Oryx 44:261–266.
- Cheung, S.M., and D. Dudgeon. 2006. Quantifying the Asian turtle crisis: market surveys in southern China, 2000–2003. Aquatic Conservation: Marine and Freshwater Ecosystems 16:751–770.
- Congdon, J.D., A.E. Dunham, and R.C. van Loben Sels. 1994. Demographics of Common Snapping Turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. American Zoologist 34:397–408.
- Congdon, J.D., J.L. Greene, and J.W. Gibbons. 1986. Biomass of freshwater turtles: a geographic comparison. American Midland Naturalist 115:165– 173.
- Crouse, D.T., L.B. Crowder, and H. Caswell. 1987. A stage-based population model for Loggerhead Sea Turtles and implications for conservation. Ecology 68:1412–1423.
- Doroff, A.M., and L.B. Keith. 1990. Demography and ecology of an Ornate Box Turtle (*Terrapene ornata*) population in south-central Wisconsin. Copeia 1990:387–399.

- Enneson, J.J., and J.D. Litzgus. 2008. Using longterm data and a stage-classified matrix to assess conservation strategies for an endangered turtle (*Clemmys guttata*). Biological Conservation 141:1560–1568.
- Ernst, C.H., and R.W. Barbour. 1989. Turtles of the World. Smithsonian Institution Press, Washington, D.C., USA.
- Ernst, C.H., A.F. Laemmerzahl, and J.E. Lovich. 2008. A morphological review of the *Cuora flavomarginata* complex (Testudines: Geoemydidae). Proceedings of the Biological Society of Washington 12:391–397.
- Ernst, C.H., A.F. Laemmerzahl, and J.E. Lovich. 2016. A morphological review of subspecies of the Asian Box Turtle, *Cuora amboinensis* (Testudines, Geomydidae). Proceedings of the Biological Society of Washington 129:144–156.
- Eskew, E.A., S.J. Price, and M.E. Dorcas. 2010. Survivorship and population densities of Painted Turtles (*Chrysemys picta*) in recently modified suburban landscapes. Chelonian Conservation and Biology 9:244–249.
- Garcés-Restrepo, M.F., J.L. Carr, and A. Giraldo. 2019. Long-term variation in survival of a neotropical freshwater turtle: habitat and climatic influences. Diversity *11*(6), 97; https://doi.org/10.3390/ d11060097.
- Garcés-Restrepo, M.F., A. Giraldo, and J.L. Carr. 2013. Population ecology and morphometric variation of the Chocoan River Turtle (*Rhinoclemmys nasuta*) from two localities on the Colombian Pacific coast. Boletín Científico Museo de Historia Natural 17:160–171.
- Garces-Restrepo, M.F., A. Giraldo, and J.L. Carr. 2014. Variación demográfica temporal de la Tortuga de Río Chocoana, *Rhinoclemmys nasuta* (Geoemydidade), en Isla Palma, Bahía Málaga, Pacífico del Valle del Cauca. Acta Biológica Colombiana 19:489–497.
- Gibbons, J.W., and J.E. Lovich. 2019. Where has turtle ecology been, and where is it going? Herpetologica 75:4–20.
- Gibbons, J.W., and R.D. Semlitsch. 1982. Survivorship and longevity of a long-lived vertebrate species: how long do turtles live? Journal of Animal Ecology 51:523–527.
- Gibbs, J.P., and G.D. Amato. 2000. Genetics and demography in turtle conservation. Pp. 207–217 *In* Turtle Conservation. Klemens, M.W. (Ed.). Smithsonian Institution Press, Washington, D.C., USA.
- Gibbs, J.P., and D.A. Steen. 2005. Trends in sex ratios of turtles in the United States: implications of road mortality. Conservation Biology 19:552–556.
- Giraldo, A., M.F. Garcés-Restrepo, J.L. Carr, and J.

Loaiza. 2012. Tamaño y estructura poblacional de la Tortuga Sabaletera (*Rhinoclemmys nasuta*, Testudines: Geoemyidade) en un ambiente insular del Pacífico Colombiano. Caldasia 34:109–125.

- Hellgren, E.C., R.T. Kazmaier, D.C. Ruthven, and D.R. Syntazske. 2000. Variation in tortoise life history: demography of *Gopherus berlandieri*. Ecology 81:1297–1310.
- International Union for Conservation of Nature (IUCN). 2018. The IUCN Red List of Threatened Species. Version 2018-2. http://www.iucnredlist.org.
- Iverson, J.B. 1982. Biomass in turtle populations: a neglected subject. Oecologia 55:69–76.
- Iverson, J.B. 1991. Patterns of survivorship in turtles (order Testudines). Canadian Journal of Zoology 69:385–391.
- Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Privately Printed, Richmond, Indiana, USA.
- Kabigumila, J. 2002. Size composition and sex ratio of the Leopard Tortoise (*Geochelone pardalis*) in northern Tanzania. African Journal of Ecology 39:393–395.
- Legler, J.M., and R.C. Vogt. 2013. The Turtles of Mexico: Land and Freshwater Forms. University of California Press, Berkeley, California, USA.
- Lin, Y.F., S.H. Wu, T.E. Lin, J.H. Mao, and T.H. Chen. 2010. Population status and distribution of the endangered Yellow-margined Box Turtles *Cuora flavomarginata* in Taiwan. Oryx 44:581–587.
- Lott, E.J., S.H. Bullock, and J.A. Solis-Magallanes. 1987. Floristic diversity and structure of upland and arroyo forests of coastal Jalisco. Biotropica 19:228– 235.
- Lovich, J.E., J.R. Ennen, M. Agha, and J.W. Gibbons. 2018. Where have all the turtles gone, and why does it matter? BioScience 68:771–781.
- Lovich, J.E., J.W. Gibbons, and M. Agha. 2014. Does the timing of attainment of maturity influence sexual size dimorphism and adult sex ratio in turtles? Biological Journal of the Linnean Society 112:142–149.
- Lovich, J.E., M. Znari, M.A.A. Bamrane, M. Naimi, and A. Mostalih. 2010. Biphasic geographic variation in sexual size dimorphism of turtle (*Mauremys leprosa*) populations along an environmental gradient in Morocco. Chelonian Conservation and Biology 91:45–53.
- Mitro, M.G. 2003. Demography and viability analyses of a Diamondback Terrapin population. Canadian Journal of Zoology 81:716–726.
- Moskovits, D.K. 1988. Sexual dimorphism and population estimate of the two Amazonian tortoises (*Geochelone carbonaria* and *G. denticulata*) in northwestern Brazil. Herpetologica 44:209–217.
- Muñoz, A., and B. Nicolau. 2006. Sexual dimorphism

and allometry in the Stripe-necked Terrapin, *Mauremys leprosa*, in Spain. Chelonian Conservation and Biology 5:87–92.

- Páez, V.P., M.A. Morales-Betancourt, C.A. Lasso, O.V. Castaño-Mora, and B.C. Bock (Eds.). 2012.
 V. Biología y Conservación de las Tortugas Continentales de Colombia. Serie Recursos Hidrobiológicos y Pesqueros Continentales de Colombia, Instituto Alexander von Humbolt. Bogotá, Colombia.
- R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project. org/.
- Rhodin, A.G.J., C.B. Stanford, P.P. van Dijk, C. Eisemberg, L. Luiselli, R.A. Mittermeier, R. Hudson, B.D. Horne, E.V. Goode, G. Kuchling, et al. 2018.
 Global conservation status of turtles and tortoises (Order Testudines). Chelonian Conservation and Biology 17:135–161.
- SAS Institute. 2002: JMP. Statistical Discovery Software. Version 5.0.1. SAS Institute, Cary, North Carolina, USA.
- Seburn, D.C. 2003. Population structure, growth, and age estimation of Spotted Turtles *Clemmys guttata*, near their northern limit: an 18-year follow-up. Canadian Field-Naturalist 117:436–439.
- Schwartz, C.W., and E.R. Schwartz. 1974. The Threetoed Box Turtle in central Missouri: its population, home range and movements. Missouri Department of Conservation Terrestrial Series 5:1–28.
- Seger, J., and W. Stubblefield. 2002. Models of sex ratio evolution. Pp. 2–25 *In* Sex Ratios. Concepts and Research Methods. Hardy, I. (Ed.). Cambridge University Press, Cambridge, UK.
- Spinks, P.Q., H.B. Shaffer, J.B. Iverson, and W.P. McCord. 2004. Phylogenetic hypotheses of the turtle family Geoemydidae. Molecular Phylogenetics and Evolution 32:164–182.

- Stamps J.A., and R.M. Andrews. 1992. Estimating asymptotic size using the largest individuals per sample. Oecologia 92:503–512.
- Turtle Conservation Coalition (Stanford, C.B., A.G.J. Rhodin, P.P. van Dijk, B.D. Horne, T. Blanck, E.V. Goode, R. Hudson, R.A. Mittermeier, A. Currylow, C. Eisemberg, et al. [Eds.]). 2018. Turtles in trouble: the world's 25+ most endangered tortoises and freshwater turtles - 2018. International Union for Conservation of Nature SSC Tortoise and Freshwater Turtle Specialist Group, Turtle Conservation Fund, Chelonian Research Foundation, Conservation International, Wildlife Conservation Society, and Global Wildlife Conservation, Ojai, California, USA.
- Turtle Taxonomy Working Group (Rhodin, A.G.J., J.B. Iverson, R. Bour, U. Fritz, A. Georges, H. B. Shaffer, and P.P. van Dijk). 2017. Turtles of the world: annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status (8th Edition). Chelonian Research Monographs 7:1–292.
- Yasukawa, Y., H. Ota, and J.B. Iverson. 1996. Geographic variation and sexual size dimorphism in *Mauremys mutica* (Cantor, 1842) (Reptilia: Bataguridae), with description of a new subspeces from the southern Ryukyus, Japan. Zoological Science 13:303–317.
- Wariss, M., V.J. Isaac, and J.C. Brito-Pezzuti. 2012. Habitat use, size structure and sex ratio of the Spotlegged Turtle, *Rhincolemmys punctularia punctularia* (Testudines: Geoemydidae), in Algodoal-Maiandeua Island, Pará, Brazil. Revista de Biología Tropical 60:413–424.
- Zar, J. 1999. Biostatistical Analysis. 4th Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Zuffi., M.A.L., F. Odetti, R. Batistoni, and G. Mancino. 2006. Geographic variation of sexual size dimorphism and genetics in the European Pond Turtle, *Emys orbicularis* and *Emys trinacris*, of Italy. Italian Journal of Zoology 73:363–372.



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