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Sexual size dimorphism and allometric growth of the smallest turtle in the world (Testudines: Kinosternidae)

Nadin E. López-González[1,2], Marco A. López-Luna[3] & Armando H. Escobedo-Galván[1]

[1] Centro Universitario de la Costa, Universidad de Guadalajara, Av. Universidad 203, 48280 Puerto Vallarta, Jalisco, México
[2] Turtle Island, Am Katzelbach 98, 8054 Graz, Austria
[3] División Académica de Ciencias Biológicas, Universidad Juárez Autónoma de Tabasco, Carr. Villahermosa-Cárdenas km 0.5, Villahermosa, Tabasco 86039, México

Corresponding author: Armando H. Escobedo-Galván, e-mail: elchorvis@gmail.com

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Variation in sexual size dimorphism (SSD) has been measured and compared within and among many species for decades. Some studies across invertebrates, fish, amphibians, and snakes have shown that females often show larger body sizes than males (Cox et al. 2007, Fairbairn et al. 2007), suggesting that a larger female confers advantages through enhanced fecundity selection, i.e., increased offspring production (Cox et al. 2003). In other groups such as birds, mammals, and lizards, males typically exhibit larger bodies than females, which may promote success in male–male competition for mates and territory (reviewed by Cox et al. 2007, Szekely et al. 2007). However, some exceptions related to habitat specialization, body traits, climate variability, and latitude have been observed within some groups (e.g., Stephens & Wiens 2009, Regis & Meik 2017). For instance, some studies have shown that semiaquatic and terrestrial chelonians species tend to exhibit male-biased SSD, while aquatic species tend to show female-biased SSD (Berry & Shine 1980, Agha et al. 2018). In a phylogenetic analysis encompassing data from 135 chelonians, Agha et al. (2018) observed that arid climates are associated with females being larger than males, whereas in wet climates males tend to be larger.

Ceballos & Iverson (2014) and Regis & Meik (2017) independently reviewed the available literature on kinosternid species (genera *Kinosternon* and *Sternotherus*). In the first study, Ceballos & Iverson (2014) showed that these species follow a pattern consistent with Rensch's rule, which proposes a positive association between SSD and body size in taxa where males are the larger sex (hyperallometry) and a negative relationship in groups where females are larger (hypoallometry; Abouheif & Fairbairn 1997, Fairbairn 1997). In the other study, Regis & Meik (2017) observed differing patterns depending on the body traits analyzed, showing female-biased SSD based on body mass, while linear measures of body size exhibited male-biased SSD.

Recent studies on the genus *Kinosternon* incorporating morphological and molecular data have supported the existence of previously undetected or weakly differentiated taxonomic diversity, although some of this diversity still needs formal description (e.g., Loc-Barragán et al. 2020, Caballero et al. 2022, Weaver et al. 2022, Hurtado-Gómez et al. 2024, Iverson & Berry 2024). Based on these publications, *Kinosternon* is the most species-rich genus of turtles in the world (Hurtado-Gómez et al. 2024). However, whether the newly identified evolutionary lineages exhibit similar SSD patterns to those previously identified remains unknown.

The Vallarta Mud Turtle, *Kinosternon vogti*, was described based on morphological characteristics (López-Luna et al. 2018). This species differs from its congeners in the proportions of its plastron and carapace scutes, body size, and the noticeable presence of a large yellow rostral shield in males (López-Luna et al. 2018, 2021). These morphological traits clearly differentiate *K. vogti* from all other species of the genus *Kinosternon*. At present it is considered the smallest turtle in the world (TTWG 2021) based on a maximum reported straight carapace length (SCL) of 10.2 cm only (Cupul-Magaña et al. 2022).

Based on Rensch's rule, we initially hypothesized that *K. vogti* would not exhibit significant sexual dimorphism in body size (SCL: maximum carapace length). Ceballos & Iverson (2014), however, observed that for small kinosternid turtles (SCL ~110 mm) females exhibited larger body sizes than males, whereas Regis & Meik (2017) suggested a female bias in body mass. To settle this controversy, we compared nine morphological traits between the sexes of *K. vogti*, expecting that females would present larger features than males.

From 2019 to 2024, we collected 175 individuals of *K. vogti* within its distribution in the Bahía de Banderas Valley, México (Cupul-Magaña et al. 2022). We transported each turtle individually in a plastic box to the Laboratory of Biodiversity and Ecosystem Services at the Centro Universitario de la Costa of Universidad de Guadalajara, Mexico. In the laboratory, we recorded nine standard morphometric characters (Legler & Vogt 2013). Examined characters were: maximum straight-line carapace length (SCL), maximum length of the plastron (PL), bridge length (BR), maximum carapace height (CH), plastral width at the humeropectoral suture (PWHP), midline abdominal scute length (AB), maximum plastral hindlobe width at the midfemoral area (PWMF), length of the third central scute (LC3), and width of the fourth central scute (WC4). We also measured body mass (BM) with an analytical balance (± 0.01 g). The measurements were taken within 24 hours after the turtles had been captured. The sex of individuals was determined using the criteria of Berry & Shine (1980), where the males exhibited a long, prehensile, spine-tipped tail and clasping organs on the rear legs.

In addition, adult males are easily recognizable by the presence of a large yellow rostral shield in males (López-Luna et al. 2018).

All measurements were $\log_{10}$ transformed before data analysis. We first examined the allometric relations between SCL and morphological traits (PL, BR, CH, PWHP, AB, PWMF, LC3, WC4, and BM) for each sex. To test the isometric relation (null hypothesis, Charnov 1993), we considered a slope with a 95% confidence interval (CI) including the expected value of 1.0 to show isometry, while slopes with a 95% CI below or above 1.0 were interpreted as hypoallometric or hyperallometric, respectively (Fairbairn 1997). For the determination of SSD only adult turtles were included in the analyses. Females were considered adults if their SCL exceeded the previously reported reproductive SCL of 88.4 mm, while males were classified as adults if their SCL was greater than 78.7 mm as reported by Rosales-Martínez et al. (2022). We initially conducted a Mann-Whitney U-test to compare SCL between sexes. Subsequently, an analysis of covariance (ANCOVA) was used to assess sexual dimorphism adjusted to body size using SCL as the covariate. Finally, we also ran a derived discriminant function analysis wherein residuals were used to assess the percentage of sex assignment.

Of 175 captured individuals of *K. vogti*, 46 were classified as adult females and 34 were identified as adult males. Females exhibited a hypoallometric relationship for CH (slope < 1). PL, PWHP, AB, PWMP LC3, and WC4 were consistent with the null hypothesis (slope = 1). BR and BM showed a hyperallometric relationship (slope > 1; Table 1). For males, PL, BR, AB, PWMF, LC3, WC4, and BM were isoallometric, while CH and PWHP exhibited hypoallometry (Table 1).

The SCL of adult females ranged from 88.5 to 101.6 mm with a mean of 93.7 ± 3.6 mm SD, while adult males exhibited a SCL ranging from 78.8 to 95.3 mm with a mean of 83.3 ± 4.0 mm SD. A comparison of mean SCLs between sexes suggests that females were on average 8.8% larger than males, which was significantly different based on the Mann-Whitney U-test ($U_{46,34} = 71.0$, $p < 0.01$; Fig. 1A). Based on analysis of covariance adjusted to body size us-

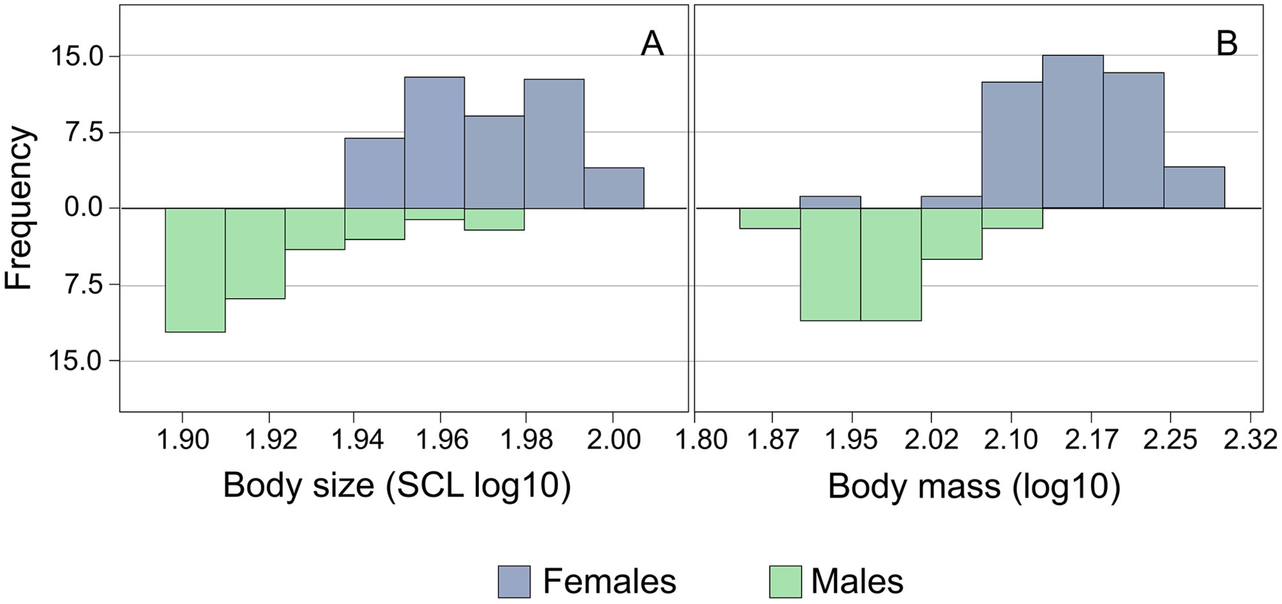

Figure 1. Comparison of body size (A) and body mass (B) between adult females and adult males of *Kinosternon vogti*.

Table 1. Allometric relations between body size and morphological traits of *Kinosternon vogti*.

Independent variable	Dependent variable	n	r^2	p	Slope (a)	95% CL	Result	Y intercept
Females								
SCL	PL	46	0.60	<0.001	0.86	0.65–1.03	Isometry	0.17
	BR	46	0.43	<0.001	1.59	1.11–2.01	Hyperallometry	-1.90
	CH	46	0.18	0.002	0.62	0.24–0.94	Hypoallometry	0.34
	PWHP	46	0.09	0.038	0.91	0.21–1.53	Isometry	-0.3
	AB	46	0.35	<0.001	1.11	0.64–1.55	Isometry	-0.87
	PWMF	46	0.31	<0.001	0.88	0.49–1.26	Isometry	-0.27
	LC3	46	0.15	0.006	0.61	0.25–1.00	Isometry	0.10
	WC4	46	0.14	0.010	0.82	0.19–1.50	Isometry	-0.27
	BM	46	0.40	<0.001	2.43	1.46–3.22	Hyperallometry	-2.63
Males								
SCL	PL	34	0.63	<0.001	0.85	0.30–1.12	Isometry	0.16
	BR	34	0.20	0.006	0.91	-0.03–1.49	Isometry	-0.67
	CH	34	0.03	0.294	0.23	-0.26–0.57	Hypoallometry	1.03
	PWHP	34	0.05	0.169	0.35	-0.13–0.83	Hypoallometry	0.75
	AB	34	0.21	0.005	0.69	0.21–1.12	Isometry	-0.10
	PWMF	34	0.10	0.055	0.55	0.04–1.14	Isometry	0.32
	LC3	34	0.15	0.019	0.67	0.28–1.54	Isometry	-0.07
	WC4	34	0.06	0.144	0.4	-0.11–1.21	Isometry	0.52
	BM	31	0.36	<0.001	1.84	0.50–2.50	Isometry	-1.56

ing SCL, females were also larger than males in PL ($F_{1,77} = 82.07$, $P < 0.01$), BR ($F_{1,77} = 49.08$, $p < 0.01$), CH ($F_{1,77} = 67.23$, $p < 0.01$), AB ($F_{1,77} = 41.00$, $P < 0.01$), PWMF ($F_{1,77} = 16.27$, $p < 0.01$) and length of the C3 ($F_{1,77} = 41.54$, $p < 0.01$), while PWHP ($F_{1,77} = 1.73$, $p = 0.19$), and WC4 was similar between sexes ($F_{1,77} = 1.45$, $p = 0.23$). The BM of adult females ranged from 90 to 198 g with a mean of 145.5 ± 21.3 g SD. The adult males exhibited a BM ranging from 70 to 130 mm with a mean of 95.2 ± 14.3 g SD. The body mass was statistically different between females and males ($F_{1,74} = 14.01$, $p < 0.01$; Fig. 1B). Our derived discriminant functional analysis showed that between 100% and 96.7% (log-transformed data) were correctly attributed to adult females and adult males, respectively.

Our results showed significant sexual dimorphism in body size and mass, with female bias in six of ten morphological traits. Most of them were related to PL, BR, CH, AB, and PWMF, which was expected since male kinosternids typically exhibit reduced plastral size (Legler & Vogt 2013, among others). The female bias in the traits mentioned above may relate to allometric relationships. While males showed mainly isometric and few negative relationships, females showed positive and isometric relationships. In other words, females exhibited proportionally larger features (e.g., bridge length and body mass), while males exhibit shorter maximum carapace height and plastral width at the humeropectoral suture. The use of different morphological characteristics can provide a more comprehensive understanding of sexual dimorphism (e.g., Scharf & Meiri 2013, Goldberg et al. 2024); whereas using a single measurement, such as SCL, for the comparison of body sizes might overlook trait differences in the smaller sex, as each of them could experience different selective pressures. For example, a small plastron (midline abdominal scute length + maximum plastral hindlobe width at the midfemoral area + maximum length of the plastron) allows males to have long, prehensile tails, while a large plastron in females could provide more protection from predators during nesting forays. A large plastron in females also could help reduce forcible inseminations by small males; however, this idea is untested.

Brejcha & Kleisner (2016) examined whether head colouration is associated with sexual size dimorphism and sexual behaviour in 35 turtle species from six families. The authors showed that for species where females are larger than males, the males often exhibit conspicuously coloured head ornamentation, whereas in species where males exceed female sizes, males lack the conspicuous colouring. In *K. vogti*, adult males exhibit a large yellow rostral shield (unique among all kinosternids; López-Luna et al. 2018), which would be in line with this hypothesis. However, *Kinosternon cora*, the sister species of *K. vogti*, is of similar size, but males do not present any conspicuous colouration despite being smaller than females (Loc-Barragán et al. 2020, Loc-Barragán et al. in press). This suggests that the interaction of head colouration and SSD in turtles may be more complicated than has been previously envisioned.

In a recent molecular analysis encompassing data from 25 *Kinosternon* species, Hurtado-Gómez et al. (2024) showed that Nearctic *Kinosternon* species possess clasping organs (organs on the hind legs used during copulation), whereas Neotropical species exhibited at least four independent transitions from absence to presence of clasping organs. Although *K. vogti* was not included in the analysis, the sister species *K. cora* was analysed, and both exhibit clasping organs and SSD favouring females. Surprisingly, their sister group (*K. oaxacae* and *K. integrum*) lacks the clasping organs, shows a male-biased SSD with males lacking conspicuous colour (Macip-Ríos et al. 2009, Vázquez-Gómez et al. 2016, Aparicio et al. 2018). However, *K. oaxacae* and *K. integrum* are much larger, and follow Rensch's rule.

In addition, the Neartic species *K. baurii* and *K. subrubrum hippocrepis* possess both conspicuous head colours and clasping organs (though *K. subrubrum subrubrum* lacks head stripes, as does *K. steindachneri*) (Lovich & Lamb 1995), their body sizes slightly exceed that of *K. vogti* and *K. cora*, but these taxa are paraphyletic (Hurtado-Gómez et al. 2024). On the other hand, *K. s. subrubrum* did not show sexual size dimorphism in South Carolina (Gibbons & Lovich 1990), whereas *K. baurii* in Florida showed body size and body mass skewed toward females in at least some populations (Johnston et al. 2021). These data suggest that sexual dimorphism in kinosternids emerges from a complex interplay of evolutionary history, sexual behaviour, and environmental pressures. Future research should focus on comparing species with similar ecological niches while accounting for specific landscape features and climatic conditions to better understand these adaptive patterns. This targeted approach may help unravel how these various factors collectively shape sexual dimorphism across different kinosternid species.

Finally, the smaller size in male *K. vogti* may be associated with the interplay among growth, male dispersal, trophic niche partitioning, and the importance of adequate female fecundity in such a small turtle. Some authors have observed that species with sexual size dimorphism are skewed in favour of smaller size for the sex that matures earlier (Lovich & Gibbons 1990). For the Vallarta Mud Turtle, Cupul-Magaña et al. (2022) suggested that females reach a body size (straight carapace length) of 82.2 mm around the age of five years in wild conditions. The earliest courtship behaviour in females was reported from captive conditions, at an SCL of 88.4 mm, while the smallest female observed laying eggs measured 90.7 mm. The size at sexual maturity of males was estimated to be smaller, at around 78 mm (Rosales-Martínez et al. 2022). Although investigating the sex ratio of *K. vogti* was not the main objective here, we captured more adult females than adult males (1.35♀:1.0♂). We assumed that our sampling method was not biased towards capturing one sex more frequently than the other, so we expected to capture a greater number of males than females (Lovich et al. 2014). The female-biased sex ratio in our captured individuals could be related to dispersal behaviour of males. For example, males may be more susceptible to predation or vehicle strikes. Berry & Shine (1980) discussed the benefits of small body size for aquatic bottom-walking turtles such as kinosternids, focusing on how small body size could maximize energy investment in movements to find females. Nevertheless, the differential mortality between males and females has been suggested as a bias in turtle sex ratio (e.g. Steen et al. 2006), which must be evaluated in greater detail in future studies.

Regarding diet observations, studies of sympatric species like *K. integrum* and *K. hirtipes*, which have similar body sizes, have shown that males and females consume similar foods (Macip-Ríos et al. 2010, Platt et al. 2016). However, it has been suggested that food availability influences the sexual size dimorphism of *K. hirtipes* (Iverson 1985). For our study species, Ramírez-Ramírez et al. (2019) classified *K. vogti* as omnivorous, based on the presence of plants, seeds and insects in the diet. Recently, 24 individuals were captured (17 females, 7 males), and stomach flushing yielded 13 different prey items, including seeds, freshwater shrimps, and snails as the most common items, indicating a dietary overlap between the sexes (N. E. López-González unpubl. data). Therefore, interspecific competition and food availability may be working to promote a similar body size of females and males of *K. vogti*, but this possibility should be explored in further studies. In addition, further research is needed to elucidate the adaptive significance of the morphological traits and to investigate the potential role of environmental factors and phylogenetic relationships in shaping sexual size dimorphism patterns within the genus *Kinosternon*.

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