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## Biphasic Geographic Variation in Sexual Size Dimorphism of Turtle (*Mauremys leprosa*) Populations Along an Environmental Gradient in Morocco

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**ABSTRACT.** – The varying influences of selective forces throughout a species’ range can result in geographic variation in sexual size dimorphism (SSD). The Moroccan turtle, *Mauremys leprosa*, occupies an extremely wide variety of ecoregions and habitats, including coastal rivers, mountain streams, oases, and intermittent rivers in the northern fringe of the Sahara Desert. To assess geographic variation in SSD, we collected specimens along an environmental gradient in central Morocco, including Oued (River) Ksob on the Atlantic coast, Oued Zat in the High Atlas Mountain foothills, and Oued Drâa in the Sahara Desert. Only turtles with conspicuous secondary sexual characteristics were included in our analysis. We calculated a sexual dimorphism index (SDI) using the mean size of the larger sex divided by the mean size of the smaller sex and subtracted one from that ratio. The direction of SSD was biphasic: in one population males and females exhibited the same body size, whereas, in two other populations, females were larger than males. Mean straight-line carapace lengths of males and females were not statistically different at Oued Ksob (SDI = 0.08), and females were relatively small. In contrast, females from Oued Zat were significantly larger than males (SDI = 0.56) and females were larger than those from Oued Ksob. SSD was most dramatic at Oued Drâa (SDI = 0.92) and much greater than any value previously reported for the species, with females exhibiting a mean carapace length greater than those in the other 2 rivers. A 2 × 3 factorial analysis of variance that compared the mean size of the sexes among the 3 sites yielded a significant SEX × LOCALITY interaction ( $p < 0.001$ ), which demonstrated geographic variation in SSD. Geographic variation in SSD appears to represent the interaction of natural and sexual selection on growth rates and maturity schedules of males and females in different environments.

**KEY WORDS.** – Reptilia; Testudines; Geoemydidae; *Mauremys leprosa*; turtle; sexual size dimorphism; natural selection; sexual selection; maturity; Morocco

Sexual size dimorphism (SSD) is a common feature of many species of turtles, with one sex achieving a consistently larger mean adult body size relative to the opposite sex. In many turtle species, females are larger than males, although there are other species in which the reverse situation is observed, or males and females have similar sizes (Berry and Shine 1980; Gibbons and Lovich 1990). Thus, there are 3 potential phases of SSD in turtles. It is unusual, but not unknown, for one turtle species to exhibit more than one phase of SSD among populations or subspecies (Iverson 1985; Lovich and Lamb 1995; Yasukawa et al. 1996).

The causes of SSD have been debated in the literature, and there are 2 fundamental adaptive explanations for its evolution: those based on natural selection and those based on sexual selection (see reviews in Gibbons and Lovich 1990; Fairbairn et al. 2007). Natural selection proponents maintain that differential interactions between the sexes and their environment lead to SSD, sometimes through competition for food. The evolution of different body sizes

may allow the sexes to occupy different niches and eat prey of different sizes, conceivably reducing resource competition. In contrast, sexual selection, not environmental factors, can result in SSD if one sex competes for access to the other sex. If large body size confers an advantage in intrasexual competition for mates or if larger mates are preferable (e.g., because of increased fecundity), then SSD may evolve because of sexual selection. Comparative phylogenetic analyses provide support for alternative nonadaptive explanations for the evolution of SSD (Cox et al. 2003), including phylogenetic inertia in turtles (Gosnell et al. 2009).

Although there are about 319 species of turtles (Turtle Taxonomy Working Group 2007), geographic variation in SSD has been quantified in only a few species (Iverson 1985; Gibbons and Lovich 1990; Lovich and Lamb 1995; Yasukawa et al. 1996; Lovich et al. 1998; Zuffi et al. 2006), which represent but 3 of the 14 families recognized by Fritz and Havaš (2007), despite the common occurrence of this phenomenon in polytypic

reptile species (Fitch 1981). In this article, we demonstrate the incidence of extreme geographic variation in SSD among 3 very different populations of the turtle *Mauremys leprosa* along an environmental gradient in central Morocco. In addition, we discuss environmental factors and selective forces, past and present, that appear to have contributed to the variation observed.

## METHODS

We collected *Mauremys leprosa* during a rapid assessment of populations along a coastal-to-inland transect in 3 drainage systems in central Morocco during May 2008 (Fig. 1). Most sampling was concentrated in less than 500 m of stream length at each site. Climatic data reported below are from Le Houerou (1989) unless indicated otherwise and are reported as mean minimum and mean maximum annual temperatures, and mean annual rainfall. Environmental temperatures affect turtle growth and maturity patterns directly through digestion efficiency and length of growing season and indirectly through effects on ecological productivity (Steyermark 2008).

The first population was Oued (River) Ksob, about 20 km south of Essaouira and about 25 m above sea level. The study site was less than 10 km from the river estuary on the Atlantic Ocean. The climate in this area is coastal Mediterranean, with mild to cool temperatures (9.6°C–22.2°C) because of the moderating influence of cold offshore ocean currents. The average annual rainfall is 295 mm. Oued Ksob is an intermittent rocky stream, and the pools we sampled were turbid because of suspended sediment and thus had relatively low primary productivity of filamentous algae or aquatic macrophytes.

The second study site was Oued Zat, a major tributary of Oued Tensift in the coastal foothills of the High Atlas Mountains, 40 km east of Marrakech, Morocco, at 760 m above sea level. Oued Zat is a perennial mountain stream, fed largely by snowmelt, with a substrate of cobble. The clear water supports dense accumulations of filamentous algae on the rocky substrate (Gasith and Resh 1999). The climate in this area is Mediterranean as well, with cool rainy winters and hot dry summers (5.2°C–37.1°C), with an average annual rainfall of 382 mm (Saïdi et al. 2006).

The third study site was Oued Drâa, a major snowmelt river that arises on the Sahara Desert side of the High Atlas Mountains, located about 90 km southeast of Ouarzazate at 880 m above sea level. Although the mouth of the river enters the Atlantic Ocean, annual flows are rarely adequate to carry water that far through the desert. A major dam (Al Mansour) near Ouarzazate provides additional regulation of flows on the river. During our study, the river was intermittent, with large pools separated by dry reaches. The climate in this area is Saharan with cool continental winters, extremely high summer temperatures (2.2°C–41.5°C), and limited rainfall

(108 mm per year). The hot sunny conditions create a eutrophic system, with high primary production of aquatic macrophytes and filamentous algae.

The straight-line distance between our Oued Ksob and Oued Drâa study sites is about 350 km. The observed differences in climate and productivity among the 3 study sites provide an environmental gradient from maritime to increasingly continental climates and oligotrophic to eutrophic productivity for assessing geographic variation in body size for this species.

Turtles were captured by hand or in hoop traps baited with canned sardines and released after data acquisition. Specimens were sexed by using secondary sexual characteristics (primarily precloacal tail length; Muñoz and Nicolau 2006). Straight-line mid-carapace length (CL) was measured with calipers accurate to the nearest 0.1 mm or 1 mm, depending on the caliper size used. Estimates of sexual maturity are best when based on primary sexual characteristics (e.g., the ability of females to produce eggs or males to produce viable sperm). By basing our criteria for sexual maturity on secondary sexual characteristics, our samples may have included individuals that were immature, but this would be consistent across study sites. Males as small as 64.2 mm CL fully everted their penises when handled at both Oued Ksob and Oued Zat, a criterion for confirming sex that has previously been used for this species (Keller 1997a). In addition, Naimi (unpubl. data) confirmed that females in central Morocco mature at small body sizes. The CL of the smallest female observed with shelled eggs in Morocco's Oued Tensift, not far from its confluence with the Oued Zat was only 124.0 mm. We recognize that, when including smaller, possibly immature, individuals in a sample tends to inflate estimates of a sexual dimorphism index (SDI) as shown for the turtle *Trachemys scripta* (Gibbons and Lovich 1990). However, the information above and a review of the literature (see Discussion) supports the assumption that the body sizes we included are reasonable for specimens that are mature or nearly so.

Statistical analyses, including Student *t* tests, analysis of variance (ANOVA) and post hoc comparisons were conducted with SYSTAT software. Following Lovich et al. (1998) and King (2000), all data were natural log-transformed before statistical analysis to improve linearity and reduce or remove heteroscedasticity of variances. Visual analysis of a normal probability plot of log-transformed CL confirmed the effectiveness of that transformation. A 2 × 3 factorial ANOVA with CL as the dependent variable was used to test for effects due to sex and locality. A significant SEX × LOCALITY interaction would demonstrate geographic variation in SSD (Lovich et al. 1998). The SDI was calculated by using the method of Lovich and Gibbons (1992) where:

$$SDI = \left( \frac{A}{B} \right) - 1$$

*A* is the mean size of females, and *B* is the mean size of



**Figure 1.** Map of Morocco, showing the locations of our 3 study sites. From west to east, they are Oued Ksob, Oued Zat, and Oued Drâa.

males, when females are larger than males. The utility of this metric in analyses of SSD was validated by Smith (1999), and straight-line CL has been demonstrated to be a good measure of body size and SSD in turtles (Gibbons and Lovich 1990; Lovich et al. 1990).

## RESULTS

The mean CL of turtles captured in traps ( $n = 42$ ) was not significantly different from turtles captured by hand ( $n = 12$ ), so the data were combined (ANOVA;  $F = 0.007$ ;  $df = 1, 52$ ;  $p = 0.93$ ), including measurements for one dead female from Oued Drâa. Males exhibited secondary sexual characters at CL that ranged from 61.1 to 129 mm (Table 1). Females with secondary sexual characters ranged from 80 to 216 mm CL, depending on locality. Mean female CL was significantly greater than that of males in samples from Oued Zat ( $t = 5.21$ ;  $df = 23$ ;  $p < 0.001$ ) and Oued Drâa ( $t = 7.36$ ;  $df = 7$ ;  $p < 0.001$ ) but not Oued Ksob ( $t = 0.76$ ;  $df = 19$ ;  $p = 0.46$ ) (Fig. 2). Mean male CL was not significantly different among locations (ANOVA,  $F = 1.20$ ,  $df = 2, 31$ ;  $p = 0.32$ ). Post hoc tests of males by using Tukey's honestly significant difference test showed that none of the pairwise comparisons of mean CL were different: Oued Drâa vs. Oued Ksob,  $p = 0.93$ ; Oued Drâa vs. Oued, Zat  $p = 0.51$ ; and Oued Ksob vs. Oued Zat,  $p = 0.39$ . In contrast, mean female CL was significantly different among sites (ANOVA;  $F = 21.80$ ;  $df = 2, 18$ ;  $p < 0.001$ ), including post hoc tests of all pairwise comparisons: Oued Drâa vs. Oued Ksob,  $p < 0.001$ ; Oued Drâa vs. Oued Zat,  $p = 0.002$ ; and

**Table 1.** Comparison of straight-line mid-carapace length statistics for the turtle *Mauremys leprosa* from 3 rivers (Oueds) in Morocco. All measurements are in millimeters.<sup>a</sup>

	Oued Ksob		Oued Zat		Oued Drâa	
	♂	♀	♂	♀	♂	♀
N	15	6	16	9	3	6
Minimum	64.7	80.0	61.1	105.3	84.5	159.0
Maximum	129.0	151.0	122.0	166.0	115.2	216.0
Mean	98.3	106.5	89.1	138.8	102.2	196.0
Standard deviation	19.8	25.2	21.7	20.3	15.9	19.9

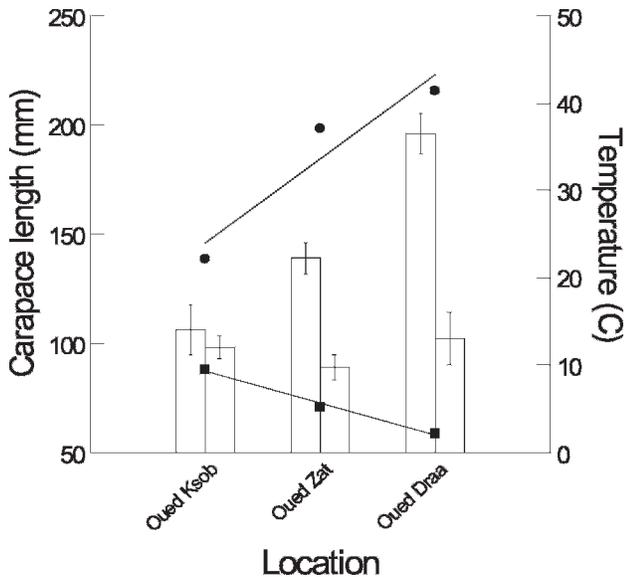
<sup>a</sup> ♂ = male; ♀ = female.

Oued Ksob vs. Oued Zat,  $p = 0.013$ . SDIs for the populations were as follows: Oued Ksob = 0.08, Oued Zat = 0.56, and Oued Drâa = 0.92 (Fig. 2). Previously reported SDIs for this species range from only 0.10 to 0.32 (Table 2). A  $2 \times 3$  factorial ANOVA that compared mean CL between sexes and among our 3 localities demonstrated that mean size differed significantly among localities, as did the degree of SSD, the latter was indicated by a significant interaction between sex and locality (Table 3).

## DISCUSSION

Although sexual dimorphism is well known in *M. leprosa*, as documented most recently by Muñoz and Nicolau (2006) for a population in Spain, our study is the first to demonstrate geographic variation in the degree of sexual dimorphism exhibited by this species. Surprisingly, we also noted that SSD was biphasic, a very unusual phenomenon in turtles, with males and females in one population exhibiting similar body sizes, whereas females were much larger than males in the other populations. Various intraspecific phase shifts in SSD were reported for other turtle species by Lovich and Lamb (1995), Iverson (1985), and Yasukawa et al. (1996), the latter for the congener *Mauremys mutica*. In all cases, the direction of size superiority (or equality) varied according to the population or subspecies sampled.

The greatest degree of SSD previously reported shows the mean size of *M. leprosa* females to be up to 32% larger than that of males (Table 2). Our sample from Oued Drâa in Morocco indicates that adult females were, on average, almost 92% larger than males, the most extreme value ever reported for *M. leprosa* and one of the largest female-biased values ever reported for turtles (Gibbons and Lovich 1990; after adjusting the values reported per our Methods). Again, we recognize that the possible inclusion of immature specimens tends to inflate estimates of SDI (Gibbons and Lovich 1990). Most of the variation in SSD we observed was because of size differences of females among populations, because mean male size was essentially invariant (Table 3).



**Figure 2.** Mean and standard error bars for midline straight carapace length of *Mauremys leprosa* from 3 localities in Morocco. Female data are shown with open bars, whereas males are crosshatched. Mean minimum (squares) and mean maximum (circles) temperature data for recording stations nearest to the respective study sites are plotted and fitted with linear smoothers. Refer to Methods for details. Locations are arranged from west (left) to east (right) along an increasingly arid and continental climate continuum.

Why does SSD vary geographically in *M. leprosa* populations in Morocco? It has been suggested that the populations we sampled represent distinct taxa, with the blue-eyed population at Oued Drâa described as *Mauremys leprosa vanmeerhaeghei* (Bour and Maran 1998). If multiple subspecific taxa are involved, then perhaps they have different expressions of traits such as SSD, as previously reported for a small number of other turtle species (see above). Eight subspecies of *M. leprosa* were recognized in the past (Schleich 1996; Bonin et al. 2006), including 7 in Morocco, but recent research does not support this high degree of diversity. Sequence data from the mitochondrial cytochrome *b* gene supports recognition of only 2 clades: one north and one south of the High Atlas Mountains (Fritz et al. 2005). As a result of their analysis, Fritz et al. (2005) synonymized 7 of the previously recognized subspecies (including *M. l. vanmeerhaeghei*) as *Mauremys leprosa leprosa* and recognized a second blue-eyed subspecies as *Mauremys leprosa saharica*. Thus, all 3 of our sampled populations are recognized as the same taxon, *M. l. leprosa* (Turtle Taxonomy Working Group 2007). Even if the population at Oued Drâa is excluded from our analysis as a separate subspecies, populations at Oued Ksob and Oued Zat still show geographic variation in SSD.

Estimates of SSD can vary because of the influence of several factors, including 1) sampling bias, 2) inappropriate measures of dimorphism, 3) incorrectly estimating the size of maturity, 4) geographic variation in

growth or body size, and 5) geographically variable selective pressures (Gibbons and Lovich 1990; Lovich et al. 1990; Lovich and Gibbons 1992). Sampling bias must be considered in any demographic analysis. Although our sample size is small, especially for Oued Drâa where turtles were more difficult to capture, we found no statistically significant difference in log-transformed CL between hand captures and traps, which suggests that sampling bias because of the method of capture was not a problem in our analyses. In addition, the fact that no pairwise comparisons of male CL were significantly different suggests that our results were robust, despite sample size limitations. However, if our samples were biased toward one sex or size group of turtles, then our estimates of SSD might be likewise skewed. Given that we were able to sample turtles of almost every stage, including recently emerged hatchlings, juveniles, and adults, we believe our estimates of SSD are representative of the populations sampled.

Another potential source of sampling bias could be attributed to local or commercial harvesting of turtles for food or traditional uses. For example, if larger specimens were preferred for food or other purposes, then populations might exhibit size class distributions that are biased toward smaller individuals, as observed in populations of *Testudo graeca* in west-central Morocco (Znari et al. 2005). However, we did not see live *M. leprosa* or their body parts for sale in the souks (bazaars) we visited in Marrakech, Essaouira, or Zagora (despite an abundance of other animals for sale, including large numbers of *T. graeca*), which suggests that local or regional exploitation of *M. leprosa* was not a significant problem for the populations we sampled.

The size and age of maturity for *M. leprosa* varies according to sex and location, with males maturing at a smaller size (and presumably younger age) than females. Data from Algeria suggest that males mature at about 90 mm CL, whereas females mature at 130 mm (Combescot 1954). Ernst and Barbour (1989) reported a 110-mm male courting and copulating with a female of unreported size. In a population from southern Morocco, females appeared to grow faster than males, especially after an estimated age of 5–7 years, which corresponded with a CL of about 80–90 mm (Meek 1987). Because growth in turtles slows dramatically with the onset of sexual maturity (Gibbons and Lovich 1990), those figures likely represent the age and size range of maturity for males in that population.

The smallest reproductive female collected by da Silva (1995) in southwestern Spain had a CL of 153 mm, although smaller sizes of 140–150 mm and 130 mm have been reported elsewhere in Spain (Pérez et al. 1979) and Algeria (Combescot 1954), respectively. These small sizes of maturity are supported by Keller (1998), who found that the smallest female from southwestern Spain with eggs, as shown by radiography, was 137.3 mm. This is larger than the CL of the smallest female (124.0 mm)

**Table 2.** Measures of adult body size in male and female *Mauremys leprosa*. See text for details on calculation of the sexual dimorphism index (SDI). All measurements are in millimeters.<sup>a</sup>

Source	Measure	Males	Females	SDI	Location	Comments
Busack and Ernst 1980	Mean greatest CL	105.1	139.1	0.32	Algeria, Dahomey (Benin), Libya, Morocco, Spain, Tunisia	
MEEK 1987	Mean CL	82.06	97.1	0.18	Southern Morocco	
da Silva 1995	Mean CL	–	180.9	–	Spain	Reproductive females only
Keller 1998	Mean CL	–	178.4	–	Spain	Reproductive females with eggs detected by inguinal palpation
	Mean CL	–	179.7	–	Spain	Reproductive females without eggs detected by inguinal palpation
Muñoz 2004	Mean CL	150.4	180.9	0.20	Central Spain	
Bonin et al. 2006	Maximum CL	–	250.0	–	Range-wide	
Muñoz and Nicolau 2006	Maximum CL	144.0	165.0	0.15	Central Spain	
Tarize 2007	Mean CL	134.9	148.4	0.10	Morocco (Oued Zat and Oued Tensift combined)	

<sup>a</sup> CL = carapace length.

observed with shelled eggs in Morocco's Oued Tensift, not far from its confluence with the Oued Zat (Naimi, unpubl. data). Yet another study in Spain found that males matured at 135–140 mm, whereas females matured at 138–150 mm (Pérez et al. 1979). Keller (1997a) concluded that males in southwestern Spain matured at around 85 mm CL during their second year of life, and Pérez et al. (1979) suggested that maturity is correlated with size rather than age. Collectively, these data support the claim of Keller (1997b, cited by Muñoz and Nicolau 2006) that males mature at smaller sizes than females.

It is interesting to note that the mean male body sizes reported in Table 2 are often larger than those we observed, particularly for turtles in Spain. Like mammals and birds, most turtles appear to follow Bergmann's rule, increasing in body size with increasing latitude (Ashton and Feldman 2003). As such, *M. leprosa* at higher latitudes in Spain might be expected to be larger than those at lower latitudes in Morocco. Also, the sizes reported by Tarize (2007) from Oued Tensift, Morocco, were larger than ours. Portions of Oued Tensift are badly polluted with sewage, a condition known to promote faster growth, larger body sizes, and earlier maturity in turtle populations (Ernst and McDonald 1989; Lindeman 1996).

**Table 3.** Factorial analysis of variance comparing mean  $\log_e$  transformed carapace length between sexually mature male and female *Mauremys leprosa* from samples in Morocco (N = 56).<sup>a</sup>

Source	SS	DF	MS	F	p
Sex	0.105	1	0.105	2.526	0.118
Locality	0.520	1	0.520	12.503	0.001
Locality × sex	0.751	1	0.751	18.040	< 0.001
Error	2.122	51	0.042		

<sup>a</sup> SS = sum of squares; DF = degrees of freedom; MS = mean squares; F = F distributional critical value.

We concluded that the variation we observed in SSD was a result of differences in growth or body size because of both geographically variable selective pressures and environmental conditions (Iverson 1985; Stillwell and Fox 2007). Size at maturity in turtles is influenced by the sometimes opposing forces of natural and sexual selection, and these ultimately interact to produce SSD as an outcome of male and female maturity patterns (Gibbons and Lovich 1990). Selection to attain a mean CL of about 90–100 mm must be very strong in males, because there is no significant difference in mean male CL among locations, despite the differences in primary productivity among sites. This same scenario has been documented for male slider turtles (*Trachemys scripta*) in similar comparisons (Gibbons et al. 1979, 1981).

Ultimately, organisms must apportion finite resources among the competing compartments of maintenance, growth, storage, and reproduction (Congdon 1989). Early maturity at a small body size conceivably allows males to begin breeding earlier by investing energy into locating females and mating instead of growth (Gibbons and Lovich 1990). Also, maturing at an early age and small size suggests that larger size does not confer an advantage in male–male competition for mates, as has been suggested for some turtles (Lovich et al. 1990, 1998), or via intersexual selection by females for larger males (Trivers 1972). Maturing at a small body size must be balanced by minimization of vulnerability to predation. Juvenile turtles are subject to predation by a host of predators (Ernst and Lovich 2009), so attaining a body size where vulnerability is minimized is critical. Chief predators of *M. leprosa* in Africa include herons and humans (Loveridge and Williams 1957), although doubtless there are others, including feral dogs, jackals, and various other predatory mammals and birds (Polo-Cavia et al. 2008). Maturing at a CL of about 90–100 mm would

certainly limit predation on male *M. leprosa* by species like herons but not larger predators, especially humans.

In contrast, females benefit from continued growth beyond the size that males mature because of the advantage that body size confers on clutch and egg size in many turtle species (Gibbons and Lovich 1990; Ryan and Lindeman 2007), including *M. leprosa* (Muñoz and Nicolau 2006). A key question is why females from the various localities sampled do not all achieve the same mean body size if there is such strong selection for large body size because of a fecundity advantage. Although quantitative measures of productivity were not collected in the 3 rivers sampled, qualitative assessment suggested that the order of productivity from lowest to highest was Oued Ksob, Oued Zat, and Oued Drâa. This proposed productivity continuum was characterized by a change from more-maritime to more-continental climates, with lower high-average annual air temperatures and higher low-average annual air temperatures in the west relative to the east (Fig. 2). Because it is a desert stream exposed to high ambient temperatures and more days of sunshine, Oued Drâa supported the greatest visible abundance of submerged macrophytes and appeared to be highly eutrophic. Oued Ksob is close to cold ocean currents that moderate regional temperatures and produce a greater number of cloudy days (oligotrophic to mesotrophic), whereas Oued Zat was intermediate, with filamentous algae production dominating the system (mesotrophic). Concomitantly, female body size tracked our qualitative assessment of productivity, with the smallest females in the coolest, least-productive river and the largest females in the warmest most-productive river (Fig. 2), which suggests that resource availability can limit female *M. leprosa* growth to the point that they mature at a smaller size and begin allocating resources to egg production earlier in less-productive environments. Iverson (1985) also suggested that food limitation was responsible for geographic variation in SSD of the turtle *Kinosternon hirtipes*.

Environmental conditions play an important role in affecting SSD (Stillwell and Fox 2007), as documented in other species. Primary productivity has been suggested as a cause of ecogeographic variation in SSD of marsupial mammals in the genus *Petaurus* (Quin et al. 1996). However, small body size caused by low feeding rates of male carpet pythons (*Morelia spilota*) relative to females may reflect genetic control more than local prey availability, as shown in another study of geographic variation in SSD of reptiles (Pearson et al. 2002). In another study of geographic variation, in SSD of snakes (*Natrix natrix*), in which males are smaller than females, the investigators suggested that marked differences in body size and SSD reflected the influence of prey availability but not genetic factors (Madsen and Shine 1993). They further concluded that, because males are smaller, tend to eat less, and grow more slowly than females, food scarcity is less likely to impact males than

females. Such a scenario is a plausible explanation for the variation we observed in *M. leprosa*. The factors that determine male and female body size in adult turtles may ultimately be determined by the pattern of temperature-dependent sex determination. Ewert and Nelson (1991) demonstrated that species with pattern Ia (males produced by cool incubation temperatures; females produced by warm incubation temperatures) often exhibit female-biased size dimorphism. Data for *Mauremys reevesii* confirmed this relationship (Du et al. 2007), but in *M. mutica*, there is pattern Ia sex determination (Zhu et al. 2006) without female-biased SSD (Yasukawa et al. 1996). However, the model presented by Ewert and Nelson (1991) does not explain geographic variation in SSD.

An alternative adaptive explanation for the extremely large body size achieved by females at Oued Drâa relates to past natural selection to avoid predation by Nile crocodiles, *Crocodylus niloticus*. Although no longer present at Oued Drâa, Nile crocodiles persisted there until about 1950 (Bons and Geniez 1996; de Smet 1999) but were not found in other rivers in Morocco. Crocodylians are known to eat turtles (e.g., Delany and Abercrombie 1986), and some investigators (Gibbons and Lovich 1990; Pritchard 1979, p. 134) have suggested that the large body size and domed architecture of various turtle species within the range of the American alligator (*Alligator mississippiensis*) are a response to predation by the latter. Indeed, the largest female yellow-bellied slider turtles (*Trachemys scripta*) are known to occur in habitats with high densities of alligators (Gibbons et al. 1979; Gibbons and Harrison 1981). The body size–past predation hypothesis potentially explains why female *M. leprosa* still reach larger sizes at Oued Drâa, whereas selection among males may operate differently because the maximum body size attainable by males may not have been sufficient to avoid crocodile predation. Size selection would presumably be a slow process that could take many generations. Now that crocodiles are extirpated, perhaps there will be an opportunity to see if selection eventually favors smaller body sizes.

The phenomenon of male and female turtles exhibiting different sizes at maturity even over a small geographical area is well documented (Gibbons et al. 1979, 1981). In the slider turtle, *Trachemys scripta*, males in both natural and thermally enhanced environments (with higher-quality diets) attain maturity at about the same body size, but males in enhanced environments mature at an earlier age. In contrast, females in thermally enhanced and diet-enhanced environments delay maturity to a larger body size (but at about the same age) relative to females in natural environments (Gibbons and Lovich 1990), similar to what we observed for *M. leprosa*.

As stated by Gibbons and Greene (1990), “The complexity of the interaction between age, size, maturity, and other life history traits continues to be one of the most perplexing problems in the study of turtles”. Additional research on growth, diet, and environmental productivity

will be required to more clearly identify the determinants of maturity and ultimately sexual size dimorphism in *M. leprosa*. Nonetheless, the current study shows that SSD can vary dramatically, and biphasically, in this species along an environmental gradient.

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#### RÉSUMÉ

Les influences variables sur les forces sélectives à travers l'aire de répartition d'une espèce peuvent avoir comme conséquence la variation géographique du dimorphisme sexuel de taille (DST). L'émyde lépreuse du Maroc, *Mauremys leprosa*, occupe une gamme d'écotones et d'habitats extrêmement variés comprenant les rivières côtières, les cours d'eau de montagne, les oasis et les rivières intermittentes au niveau de la frange nord du désert du Sahara. Afin d'évaluer la variation géographique du DST, nous avons collecté des spécimens le long d'un gradient environnemental au Maroc central incluant Oued (Rivière) Ksob sur la côte atlantique, Oued Zat au niveau du piémont du Haut Atlas et Oued Draa au Sahara. Seules les tortues montrant des caractères sexuels secondaires remarquables ont été incluses dans notre analyse. Nous avons calculé un indice de dimorphisme sexuel (IDS) utilisant le rapport de la taille moyenne du sexe le plus grand à celle du plus petit sexe et diminué de un. Le sens du DST était diphasique: dans une population, les mâles et les femelles ont montré la même taille corporelle tandis que dans les deux autres, les femelles étaient plus grandes que les mâles. Les longueurs linéaires moyennes de la carapace des mâles et des femelles n'étaient pas statistiquement différentes à Oued Ksob (IDS = 0.08) et les femelles étaient relativement de petite taille. En revanche, les femelles de Oued Zat étaient sensiblement plus grandes que les mâles (IDS = 0.56) et les femelles étaient plus grandes que celles d'Oued Ksob. Le DST était impressionnant à Oued Draa (IDS = 0.92) et beaucoup plus important par rapport à toutes les valeurs rapportées auparavant chez cette espèce, avec les femelles présentant une taille moyenne de la carapace plus importante que celles des tortues dans les deux

autres rivières. Une ANOVA à deux critères de classification comparant la taille moyenne des deux sexes entre les trois sites d'étude, a révélé une interaction SEXE × LOCALITÉ significative ( $p < 0.001$ ) démontrant la variation géographique variation du DST. Cette variation géographique semble représenter l'interaction entre les sélections naturelle et sexuelle exercées sur les taux de croissance et les âges d'acquisition de la maturité sexuelle des mâles et des femelles dans différents environnements.

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