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Source: Journal of Herpetology, 44(2) : 320-326

Published By: Society for the Study of Amphibians and Reptiles

URL: <https://doi.org/10.1670/08-333.1>

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Geographic Variation in Sexual Size Dimorphism in Painted Turtles (*Chrysemys picta*)

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ABSTRACT.—Geographic variation in body size may reflect adaptations to local environments, and sexual size dimorphism (SSD) arises from ultimate and proximate factors acting differently on males and females in those environments. The Painted Turtle (*Chrysemys picta*) is a wide-ranging North American freshwater turtle species with known female-biased SSD. We hypothesized that, in more seasonal environments, the disparity between adult female and male body size would be more pronounced (i.e., the sexual dimorphism index [SDI, female body size/male body size] would be higher) than in more moderate environments because selective pressures on females to maximize reproductive output would result in relatively larger body sizes (fecundity advantage hypothesis) in extreme environments. We predicted that the SDI would be higher in populations at northern latitudes and middle longitudes than in southern and coastal populations. We conducted linear and nonlinear regression analyses using data from the literature and museum records, extrapolated data, and unpublished data on adult male and female carapace and plastron lengths from 65 locations. In contrast to our prediction, SDI decreased with increasing latitude. With respect to longitude, the trend supported our prediction in that the SDI was slightly higher for interior populations and lower for coastal populations; however, the relationship was not significant. Future research should examine sex differences in carapace height and body volume which may more directly reflect selective pressures on female fecundity than straight-line shell lengths.

Geographic variation in body size may reflect adaptations to local environments, and sexual size dimorphism (SSD) arises from ultimate and proximate factors acting differently on males and females in those environments. Sexual size dimorphism can result from sexual selection, selection for increased female fecundity, and ecological niche divergence (Hendrick and Temeles, 1989; Shine, 1989; Andersson, 1994). Sexual selection occurs through male-male competition or through female mate choice, both potentially resulting in large male body size relative to females (Weckerly, 1998; Cox et al., 2003). Relatively large female body size may evolve if maximization of body cavity volume maximizes the capacity for ovarian development (Darwin, 1871; Fairbairn and Shine, 1993; Honek, 1993). Ecological niche divergence refers to environmental pressures such as sex-specific food requirements and differences in trophic structures that result in body size differences (Selander, 1966; Nudds and Kaminski, 1984; Shine, 1989; Temeles et al., 2000). In addition, proximate factors such as conspecific variation in growth rates (Shine, 1990; Rutherford, 2004), age and size at maturity (Gibbons and Lovich, 1990; Shine, 1990; Lovich et al., 1998; Zuffi et al., 2006), and sex-specific patterns of mortality (Stewart, 1985; Shine, 1990; Haenel and John-Alder, 2002) have been shown to affect SSD in reptile populations.

Among freshwater turtle species, conspecific patterns of SSD have been attributed to habitat type combined with male mating strategy (Berry and Shine, 1980), sex-specific mobility (Bonnet et al., 2001; Kaddour et al., 2008), sex-specific feeding ecology (Tucker et al., 1995; Lindeman and Sharkey, 2001; Lindeman, 2006), and female-biased SSD has been linked to fecundity advantage (Berry and Shine, 1980; Gibbons and Lovich, 1990; Brophy, 2006; Munoz

and Nicolau, 2006). Because a turtle's shell cannot expand to accommodate growing ovaries and embryos, larger female body size should be favored by selection as a means of maximizing clutch size, egg size, or both (Gibbons et al., 1982), which in turn could result in higher fitness. Female-biased SSD should be pronounced in turtle species with no male-male competition or forcible insemination and, thus, no directional selection on males for larger size (Berry and Shine, 1980; Gibbons and Lovich, 1990). Furthermore, in seasonal (i.e., extreme) environments with short growing seasons, clutch frequency is lower than in more moderate (i.e., mild) environments (Iverson and Smith, 1993; Litzgus and Mousseau, 2003, 2006). Increased clutch size will offset this low clutch frequency, and to increase clutch size, female body size must increase because of the immobility of the shell. For example, Spotted Turtle (*Clemmys guttata*) females in a northern population (i.e., extreme environment) had larger clutch sizes and lower clutch frequencies than conspecifics in the south; however, the reproductive output per female per year was the same in both populations as a result of population-specific variation in clutch size and clutch frequency (Litzgus and Mousseau, 2006). Selective pressures on females to maximize reproductive output through increases in clutch size in seasonal environments may result in more extreme female-biased SSD in northern and interior populations relative to southern and coastal conspecific populations (Cox et al., 2003).

The Painted Turtle (*Chrysemys picta*) is an excellent model organism for examining conspecific patterns in SSD because it is relatively common, well studied, widely distributed throughout southern Canada and most of the United States, and is known to have female-biased SSD (Fitch, 1981; Rowe, 1997; Ernst and Lovich, 2009). Four subspecies have been described (Ernst and Lovich, 2009): the Western Painted Turtle (*Chrysemys picta bellii*) occurs in western Canada and

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TABLE 1. Data sources and locality information used in the meta-analysis of geographic variation in sexual size dimorphism in Painted Turtles (*Chrysemys picta*). The data are presented roughly from western to eastern North America. When not given in the original publication, subspecies were inferred from range maps. Locations are given by province (Canada) or state (United States).

Subspecies	Location	Sources
<i>C. p. bellii</i>	British Columbia	St. Clair and Gregory, 1990; St. Clair et al., 1994
<i>C. p. bellii</i>	Colorado	Cooley et al., 2003
<i>C. p. bellii</i>	Nebraska	Rowe, 1997; J. B. Iverson, pers. comm., 2006
<i>C. p. bellii</i>	New Mexico	Christiansen and Moll, 1973
<i>C. p. bellii</i>	Wisconsin	Moll, 1973; Christiansen and Moll, 1973
<i>C. p. bellii</i>	Minnesota	Gamble and Simmons, 2004
<i>C. p. bellii</i>	Saskatchewan	MacCulloch and Secoy, 1983
<i>C. p. bellii</i>	Manitoba	Hart, 1982; W. Weller, pers. comm., 2006
<i>C. p. bellii</i> or <i>dorsalis</i>	Louisiana	Hart, 1982
<i>C. p. bellii</i> or <i>marginata</i>	Wisconsin	Ream and Ream, 1966
<i>C. p. bellii</i> or <i>marginata</i>	Illinois	Cagle, 1954; Moll, 1973; W. Weller, pers. comm., 2006
<i>C. p. bellii</i> or <i>marginata</i>	Michigan	Cagle, 1954; Gibbons 1968a,b; Frazer et al., 1991; Congdon et al., 1986, 1992
<i>C. p. marginata</i>	Indiana	J. B. Iverson, pers. comm., 2006
<i>C. p. marginata</i>	Michigan	Rowe and Parsons, 2000; Rowe, 2003
<i>C. p. marginata</i>	Ontario	Williams and Crossman, 1977; Balcombe and Licht, 1987; F. Cook, pers. comm., 2006; N. Rollinson, pers. comm., 2006; W. Weller, pers. comm., 2006
<i>C. p. marginata</i>	Quebec	F. Cook, pers. comm., 2006; W. Weller, pers. comm., 2006
<i>C. p. marginata</i> or <i>picta</i>	New York	Pough and Pough, 1968
<i>C. p. marginata</i> or <i>picta</i>	Pennsylvania	Ernst, 1971a,b
<i>C. p. picta</i>	Virginia	Mitchell, 1994 cited in Bowne and White, 2004
<i>C. p. picta</i>	North Carolina	Grayson and Dorcas, 2004
<i>C. p. dorsalis</i> or <i>marginata</i>	Tennessee	Moll, 1973

the United States; the Southern Painted Turtle (*Chrysemys picta dorsalis*) is found in the south-central United States; the Midland Painted Turtle (*Chrysemys picta marginata*) is found in central United States and south-central Canada; and the Eastern Painted Turtle (*Chrysemys picta picta*) occurs along the Atlantic coast. Each subspecies differs mainly in appearance of plastral pigmentation and scute alignment, and the subspecies are often found as intergrades between their respective ranges (Wright and Andrews, 2002).

Painted Turtles display geographic variation in life-history traits. In northern populations, body size and clutch size are larger, whereas annual clutch frequency is lower compared to more southern populations (Ernst, 1971a; Moll, 1973; Iverson and Smith, 1993; Cooley et al., 2003), and individuals in northern populations mature later and at larger body sizes than conspecifics in southern populations (Moll, 1973; St. Clair et al., 1994). Geographic patterns of life-history trait variation suggest that female turtles in cool seasonal climates are under selective pressure to increase body size as a means to increase fecundity compared to those in warmer predictable climates. We tested hypotheses about the evolution of SSD in Painted Turtles using published and unpublished body size data from populations located throughout the species' distribution. We hypothesized that in more seasonal environments, the disparity between adult female and male body size, as measured by the sexual dimorphism index (SDI = female body size/male body size; Lovich and Gibbons, 1992) would be

greater than in more moderate environments. Selective pressures on females to maximize reproductive output would result in relatively larger body sizes (fecundity advantage hypothesis) in extreme environments, whereas males would not be under the same pressure to be large. We predicted that the SDI would be higher in populations at northern latitudes and interior longitudes than in southern populations where the growing season is longer and climate more predictable and than in coastal populations where oceans moderate climate. Specifically, we predicted a positive linear relationship between SDI and latitude and a nonlinear parabolic relationship (inverted U) between SDI and longitude.

MATERIALS AND METHODS

We surveyed the literature for papers containing data on the ecology of Painted Turtles, including all four subspecies. Data were included in the meta-analysis if they included information on either mean carapace length (CL) or mean plastron length (PL) of both males and females separately for a given location or population. Additional data were gathered from unpublished sources (J. B. Iverson, pers. comm., 2006; W. Weller, pers. comm., 2006) and museum records (Canadian Museum of Nature, F. Cook, pers. comm., 2006). In total, body size data from 65 locations across the North American distribution of *C. picta* were obtained (Table 1). Sample sizes ranged between two and 990 turtles per population (mean \pm SE and median sample sizes for females were 59 ± 10

individuals and 30, respectively, and for males were 83 ± 22 and 26, respectively). The data spanned 17.87° of latitude ($32.51\text{--}50.38^\circ\text{N}$) and 43.06° of longitude ($72.09\text{--}115.15^\circ\text{W}$). Latitude and longitude values were obtained from the publications or museum records or by locating study sites reported in the literature on maps of Canada and United States.

To maximize the representation of populations across the range of latitudes and longitudes, we used regressions to predict CL and PL values for populations in which one or the other variable were not reported in the literature. The equations were derived from populations for which we had CL and PL measurements for the same individuals. We conducted regression analyses between CL and PL separately for both males and females, creating equations that enabled calculation of an unknown CL or PL from a known PL or CL, respectively. The regression between PL and CL for females was represented by the equation $\text{CL} = 0.94 (\text{PL}) + 18.58$ ($R^2 = 0.73$; $P < 0.0001$) and for males was $\text{CL} = 1.08 (\text{PL}) + 3.90$ ($R^2 = 0.87$; $P < 0.0001$). Using the equations increased the sample size for population CL SDI from $N = 46$ to $N = 65$ populations. The regression between CL and PL for females was represented by the equation $\text{PL} = 0.78 (\text{CL}) + 25.90$ ($R^2 = 0.73$; $P < 0.0001$) and for males was $\text{PL} = 0.81 (\text{CL}) + 12.39$ ($R^2 = 0.87$; $P < 0.0001$), increasing the sample size for population PL SDI from $N = 27$ to $N = 65$ populations.

We tested for relationships between the population SDI and latitude using linear regression analyses. We tested for a nonlinear, parabolic relationship between population SDI and longitude using second order polynomial regression analyses (Statistica 6.1; Statsoft, Tulsa, OK). We analyzed the data in two ways: by using only the values directly measured in each population, and by using the measured data plus the estimated data created from the body size regressions. We evaluated whether results obtained using direct and estimated shell length measurements were consistent by conducting analyses of the two datasets separately.

RESULTS

SSD Variation with Latitude.—We found a significant negative relationship between PL SDI (female body size/male body size) and latitude (Fig. 1A) when the analysis was conducted using the measured data only ($N = 27$, $R^2 = 0.20$, $P < 0.05$) and when the estimated data were combined with the measured data ($N = 65$, $R^2 = 0.091$, $P < 0.05$); however, in both cases, little of the variation in PL SDI was explained by latitude (as indicated by the low R^2 -values). Similarly, we found a significant negative relationship between CL SDI and latitude (Fig. 1B) when the analysis was conducted using the measured data combined with the estimated data ($N = 65$, $R^2 = 0.11$, $P < 0.01$); the relationship was not significant when the analysis was conducted using the measured data only ($N = 46$, $R^2 = 0.014$, $P = 0.43$); and again, little of the variation in CL SDI was explained by latitude.

SSD Variation with Longitude.—We detected no significant relationships between PL SDI and longitude or between CL SDI and longitude when conducting the analyses with the measured data only (PL: $N = 27$, $R^2 = 0.13$, $P = 0.20$; CL: $N = 46$, $R^2 =$

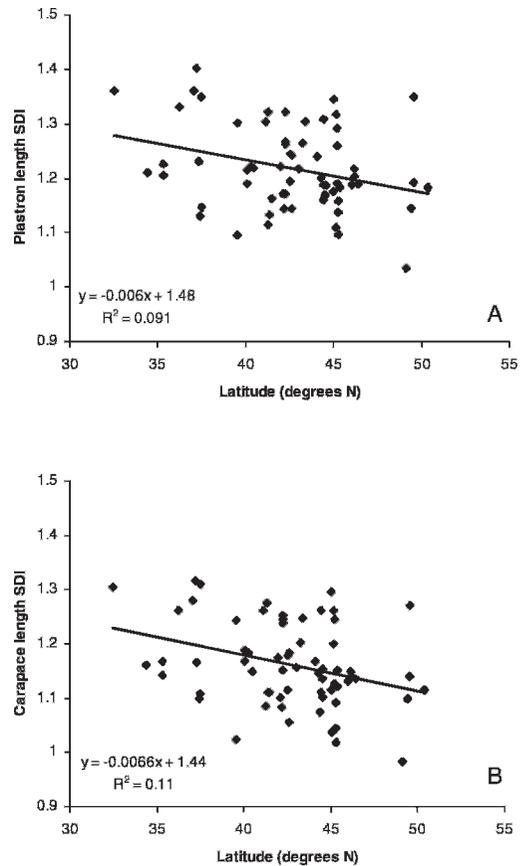


FIG. 1. Geographic variation in sexual size dimorphism (SDI, female body size/male body size; Lovich and Gibbons, 1992) with latitude for 65 populations of Painted Turtles (*Chrysemys picta*) in North America. Sample sizes ranged between two and 990 turtles per population. The negative linear relationship between plastron length SDI (A) and latitude was significant ($P < 0.05$). Similarly, the relationship between carapace length SDI (B) and latitude was significant ($P < 0.01$).

0.015 , $P = 0.73$) or when combining the measured and estimated data (PL: $N = 65$, $R^2 = 0.035$, $P = 0.33$; CL: $N = 65$, $R^2 = 0.043$, $P = 0.26$; Fig. 2). However, the data followed a nonlinear trend; the SDI for both size measures was highest at midlongitudes, peaking at approximately 95°W , and lower at the extreme west and east coastal longitudes (Fig. 2).

DISCUSSION

Our findings did not support the hypothesis that the degree of female-biased SSD would be more pronounced in northern populations caused by strong selective pressure on females to increase fecundity in seasonal environments. In contrast to our prediction, the SDI decreased with increasing latitude (Fig. 1); however, the relationship is likely not very biologically meaningful because little of the variation in SDI (i.e., the relationship had a low R^2 -value) was explained by latitude per se. It appears that both

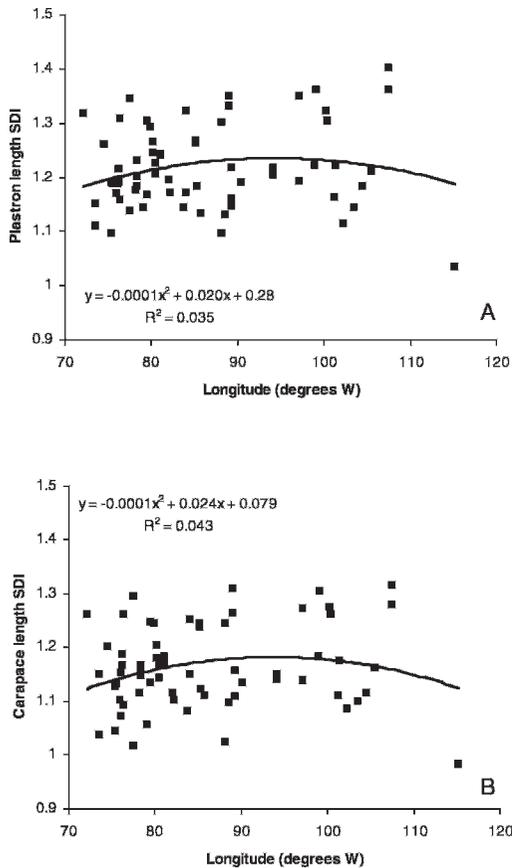


FIG. 2. Geographic variation in sexual size dimorphism (SDI, female body size/male body size; Lovich and Gibbons, 1992) with longitude for 65 populations of Painted Turtles (*Chrysemys picta*) in North America. Sample sizes ranged between two and 990 turtles per population. The second order polynomial relationship between plastron length SDI (A) and longitude was not significant ($P = 0.33$). Likewise, the relationship between carapace length SDI (B) and longitude was not significant ($P = 0.26$).

females and males have larger body sizes in northern compared to southern populations. Similarly, in a study examining geographic variation in SSD in Stinkpot Turtles (*Sternotherus odoratus*), Tinkle (1961) found that, in northern populations, males were larger than females, and, in southern populations, females were larger than males. In Fitch's (1981) preliminary study of geographic variation in SSD in Painted Turtles, no significant pattern of variation was detected, and Iverson (1985) found no relationship between SSD and latitude or altitude in Rough-Footed Mud Turtles (*Kinosternon hirtipes*). These results point to some other ecological, rather than purely reproductive, causes for the variation in the SDI, even though northern females are larger and have larger clutch sizes than their southern counterparts (Christiansen and Moll, 1973; Moll, 1973; Iverson and Smith, 1993; Rowe, 1994). Perhaps larger clutch sizes in

northern populations are a beneficial byproduct of selection for larger body sizes for reasons independent of fecundity, such as decreased surface area : volume ratios for heat retention in seasonal environments (i.e., Bergmann's Rule; Lindsey, 1966; Atkinson and Sibly, 1997; Ashton and Feldman, 2003; Litzgus et al., 2003) or increased capacity for energy stores to support metabolism during aphagia in the long northern winters (Galbraith et al., 1989; Brooks et al., 1992). Differences in body size among geographically disjunct Painted Turtles may be linked to diet, particularly to the degree of carnivory; more northern populations tend to be more carnivorous (Cooley et al., 2003). These explanations would also explain why male body size increases with latitude and, thus, why the SDI does not favor females to the degree we predicted for northern populations. Alternatively, variation in SSD may be attributable to environmental factors that elicit phenotypically plastic responses under different habitat, thermal, and seasonal conditions (Tucker et al., 1998; Bonnet et al., 2001; Daza and Paez, 2007; Lubcke and Wilson, 2007) that affect the sexes differently. It has been proposed that the sex-specific growth rates and the resulting size at which each sex reaches maturity may be the underlying cause of SSD in turtles (Lagarde et al., 2001), with the smaller sex maturing at a smaller size and younger age than the larger sex (Gibbons and Lovich, 1990; Lovich et al., 1998; Zuffi et al., 2006). Attainment of sexual maturity may be a plastic trait, and at northern latitudes, male Painted Turtles may benefit from delaying maturity to a larger size relative to southern conspecifics (for the reasons cited above); this could be another explanation for why the SDI does not favor females to the degree we predicted. Finally, even if fecundity advantage drives the evolution of larger body size in female turtles in extreme environments, males may also increase in size to facilitate successful mating with large females. That is, selection for rapid growth of both sexes in extreme environments may be occurring.

With respect to longitude, we did not detect a significant relationship with SDI; however, visual inspection of the data (Fig. 2) indicates that SDI was slightly higher for interior populations and lower for coastal populations. It is possible that, as hypothesized, the pattern in SDI we found reflects fecundity pressures on females to maximize body size and, thus, reproductive output (Ernst et al., 1998; Zuffi et al., 1999; Bonnet et al., 2001; Munoz and Nicolau, 2006) in more seasonal interior locales. It is interesting that the SDI pattern mirrors the distribution of the subspecies; for example, *C. p. bellii*, *C. p. picta*, and *C. p. marginata* have similar latitudinal distributions but differ in their east-west distributions (Ernst et al., 1994), and Moll (1973) found that body size and clutch size in Painted Turtles were more strongly correlated with subspecies distribution than latitude. We were unable to test relationships pertaining directly to each subspecies because no data were available for *C. p. dorsalis*, the smallest subspecies; the majority of the data we used were from *C. p. marginata*, the most well-studied subspecies. Although several studies on turtles have examined variation in SSD with latitude, to our knowledge, ours is the first study to examine variation in SSD with longitude. Although the Painted Turtle is

widely distributed in North America, little body size data are available in the literature on western populations (see Table 1), likely because populations in the extreme west are endangered (COSEWIC, 2006) and so few individuals are available to be measured. Any conclusions regarding longitudinal patterns in SSD await data from western populations.

The lack of statistical support for our predictions may have arisen from sampling biases, different measurement protocols, and inconsistencies in sampling methods among studies. However, the effects of any such biases should have been minimized because of our relatively large sample sizes. Turtles have a convex carapace but are typically measured using calipers to obtain straight-line measurements, which do not incorporate the height of the shell. In addition, even if they are measured, shell height data are rarely reported. Females have broader and deeper shells than males (Mosimann, 1958; Jolicoeur and Mosimann, 1960; Munoz and Nicolau, 2006), features that would not be detectable from straight-line CL measurements. The more domed carapace of females would encase a larger total body volume and, thus, increase the capacity for larger clutch sizes (Rowe, 1997; Ernst et al., 1998; Zuffi et al., 1999; Kaddour et al., 2008). Future work should examine SDI with respect to carapace height because it may more directly reflect selective pressure on females for increased fecundity. In addition, body size data for Painted Turtles from the western and southern range extremes are needed (see Table 1) and their inclusion in analyses such as ours may elucidate significant geographic patterns in SSD.

Acknowledgments.—We thank J. B. Iverson and W. Weller for providing unpublished data and for correspondence during the data collection part of the project. M. Steigerwald, the late R. M. Rankin, and F. Cook of the Herpetology Collection at the Canadian Museum of Nature, Ottawa, Ontario, provided access to the collection and unpublished data. A. Dunnett helped with data input. A. I. Schulte-Hostedde helped with the nonlinear statistical analyses and provided feedback on an earlier draft of the manuscript.

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Accepted: 11 September 2009.