

Nest Temperature Is Not Related to Egg Size in a Turtle with Temperature-Dependent Sex Determination

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A recent hypothesis posits that temperature-dependent sex determination (TSD) in reptiles may be maintained if females can assess thermal conditions and lay eggs accordingly to produce the sex benefiting most from maternal investment. Specifically, females should lay large eggs in environments likely to produce the sex benefiting most from larger egg size. This relationship has been demonstrated in diamondback terrapins. To evaluate the generality of this hypothesis, we examined two components of this hypothesis using painted turtles (*Chrysemys picta*), a reptile with TSD. Vegetation cover around nests at oviposition significantly and negatively influenced nest temperatures during embryonic development, particularly during the period of sexual differentiation. However, no relationship existed between egg mass and either nest temperatures or vegetation cover around nests at oviposition. Therefore, large eggs were not laid in specific thermal microenvironments as a mechanism to match egg size with offspring sex ratio. These results do not support a general relationship between thermally based nest-site choice and maternal investment (egg mass) in reptiles with TSD.

THE adaptive significance, if any, of temperature-dependent sex determination (TSD) in reptiles remains unclear. The variation in patterns of TSD and its widespread occurrence across many reptilian taxa have elicited several competing hypotheses for why this enigmatic sex-determining system exists. One of the most promising hypotheses, developed by Charnov and Bull (1977), proposed that environmental sex determination (of which TSD is a form) would be adaptive primarily when particular environmental conditions benefit one sex more than the other. Offspring would then benefit most if their sex remained undetermined until they encountered environmental conditions that favor a particular sex. This assumption regarding differential fitness of the sexes has received some support for several reptiles (e.g., Joanen et al., 1987; Bobyn and Brooks, 1994; for a review, see Shine, 1999), but no general mechanistic explanation has yet emerged.

A recent adaptation of the Charnov-Bull model includes the ability for parents to influence offspring sex ratios and provides insight into how this condition may be beneficial for organisms with environmental sex determination (Roosenburg, 1996; Roosenburg and Niewiarowski, 1998). If fitness of male and female offspring varies according to maternal investment (e.g., egg size or some other maternal quality), females that can adjust sex ratios toward the sex that benefits most from maternal investment should have a selective advantage (in accordance with Trivers and Willard, 1973). There-

fore, TSD would be maintained as a mechanism for a female to manipulate sex ratios according to her investment (Roosenburg, 1996; Roosenburg and Niewiarowski, 1998).

Roosenburg (1996) empirically assessed three important conditions of this new hypothesis in the diamondback terrapin (*Malaclemys terrapin*), a turtle with TSD. First, some quality or condition that varies among females should differentially benefit offspring of one sex over those of the other. Specifically, egg size was identified as an important influence on offspring size, growth rates, and ages of maturity for female *M. terrapin* but not necessarily for males (Roosenburg and Kelley, 1996). Second, nesting females should discriminate among environmental cues likely to produce a particular sex, and third, they should manipulate offspring sex ratios based on maternal investment. Indeed, *M. terrapin* tended to lay small eggs in cooler, male-producing areas with greater vegetation cover and large eggs in warm, female-producing microenvironments with less vegetation cover (Roosenburg, 1996). This maternal condition-dependent choice hypothesis (MCDC) remains an exciting avenue for linking a definite mechanism of sex ratio manipulation with maternal investment and may provide general insight into how TSD may be maintained in reptiles (Roosenburg, 1996).

To test the generality of the MCDC hypothesis (Roosenburg, 1996), we evaluated the three necessary conditions using painted turtles (*Chrysemys picta*), a widespread North American

species with TSD. In a previous study, we examined the first condition by evaluating effects of egg size and incubation temperatures on growth rates and juvenile size in painted turtles (Janzen and Morjan, 2002). We found that larger eggs were associated with faster hatchling growth rates and larger juvenile sizes for at least one year posthatching for both sexes but that females grew faster than did males prior to maturity (Janzen and Morjan, 2002).

Although further study is required to confirm relationships between fecundity and body size in females versus males, evaluating patterns of nest-site choice is also critical for assessing whether females use the effects of egg size on growth to benefit the sexes differentially. In the following study, we thus evaluated the two remaining conditions: (1) a realistic environmental cue for nest-site choice exists that predicts nest temperature during embryonic sex determination; and (2) a relationship exists between egg size and thermal characteristics of the nests, as in *M. terrapin* (Roosenburg, 1996).

MATERIALS AND METHODS

Field methods.—Field research was conducted on a nesting population of painted turtles on the Thomson Causeway, an island in the Mississippi River near Thomson, Carroll County, Illinois (41°57'N, 90°07'W). The south beach of the Thomson Causeway has a large grassy area ($\approx 250 \times 75$ m), where more than 100 painted turtle nests were laid each year. This area consists of moist loamy soil, is almost uniformly level, and exhibits a complete range of light intensity accessible to the nesting turtles caused by varying densities of trees (Janzen, 1994a).

The study site was monitored for nesting activity from 26 May to 3 July from 1995 through 1998. Nesting activity during the 1995 through 1997 field seasons lasted approximately three weeks, peaking in mid-June. In 1998, nesting activity lasted for five weeks (26 May through 1 July), but nesting ceased for one week in June during rainy weather. Females were captured upon completing their nests, and their plastron lengths were measured with dial calipers. Some females had been marked prior to our study, but most females in this study were uniquely marked at capture by notching the marginal scutes with a file (Gibbons, 1968).

Eggs were weighed (± 0.01 g) immediately after nesting with an Ohaus portable electronic balance and were reburied in their original orientation in the nest cavity. Vegetation cover over each nest was measured shortly after nest construction using a Model-A spherical densiome-

ter, as described in Janzen (1994a). Vegetation cover, a measure of the amount of canopy vegetation directly above the nest, is correlated with offspring sex ratio in this population (i.e., nests under high vegetation cover tend to produce males) during years experiencing typical climatic conditions (Janzen, 1994a). This measurement does not change over a site throughout the nesting and incubation seasons (Janzen, 1994a), so it may act as a potential thermal cue for nesting females.

Nests that were selected for temperature monitoring met the following criteria: they survived until the end of June, came from identified females, and were representative of the entire range of south and west vegetation cover over nests at the field site. Temperatures were recorded approximately hourly from 11 nests in 1995, from 30 nests each in 1996 and 1997, and from 14 nests in 1998. HOBO[®] XT temperature loggers were enclosed in waterproof plastic containers and buried 1 m away from each monitored nest, with a probe extending underground from the temperature logger into the side of the middle of the nest (Weisrock and Janzen, 1999). During the 1995 through 1997 field seasons, two additional HOBO[®] loggers with internal probes recorded ambient temperatures at the field site. One logger was attached to the underside of a bench (~ 0.5 m above ground) to record air temperatures, whereas the other was placed < 2 m away inside the base of a hollow tree trunk to record surface temperatures. Neither logger received direct sunlight. Only ambient temperature was recorded in 1998. We focus on July temperatures in this study because they are most related to offspring sex ratio in painted turtles (Schwarzkopf and Brooks, 1985; Janzen, 1994b).

Statistical procedures.—Preliminary results suggested that densiometer measurements facing both south and west are most influential on temperatures experienced in the nests (Weisrock and Janzen, 1999) and on sex ratios of the hatchling turtles in this population (Janzen, 1994a); thus, only these two measures were used in subsequent analyses. All statistical analyses were performed using JMP version 3.2.1 (SAS Institute, Inc., Cary, NC), unless specified otherwise. Average vegetation cover was computed by converting the densiometer readings from the south and west into percentages of cover, and taking their average (Weisrock and Janzen, 1999).

To examine the effect of vegetation cover on nest temperature during the period of sex determination in this population, mean July nest

TABLE 1. SUMMARY STATISTICS FOR VEGETATION COVER (%) OVER NESTS AND EGG MASS (G) PER CLUTCH OF PAINTED TURTLES (*C. picta*).

Year	n	Vegetation cover			Egg mass		
		Mean	SE	Range	Mean	SE	Range
1995	83	45.6	20.5	4.2–92.7	6.14	0.91	4.22–8.16
1996	79	46.4	21.8	0.5–90.6	6.16	0.82	4.17–7.67
1997	112	41.5	22.1	0.5–87.5	6.45	0.71	4.53–8.07
1998	102	41.5	20.3	2.1–84.9	6.52	0.76	4.22–8.10

temperatures were regressed on average vegetation cover for each of the four field seasons. We also generated an analysis of covariance using year, vegetation cover (as the covariate) and their interaction as effects on mean July nest temperatures, to evaluate the similarity of slopes across the four field seasons. These analyses evaluated the utility of vegetation cover as a realistic thermal cue for nest-site choice.

The following statistical analyses concern the effects of egg mass on nest-site choice. Egg masses among clutches exhibited much greater variation than egg masses within clutches (ANOVA: 1995, $F_{82,805} = 67.39$, $P < 0.0001$; 1996, $F_{78,780} = 36.52$, $P < 0.0001$; 1997, $F_{111,1090} = 28.95$, $P < 0.0001$; 1998, $F_{101,1120} = 29.74$, $P < 0.0001$). Consequently, we considered mean egg mass a representative measure of egg mass within clutches. We compared the average percentage of vegetation cover from the south and west to mean egg mass in a clutch using linear regression for each year. We also conducted a power analysis to compare our combined data (since no significant differences in the relationship between mean egg mass and vegetation cover occurred across years) with the results found by Roosenburg (1996). The statistical power for our regression analysis and Roosenburg's (1996) could not be compared directly, since he used an ANOVA to compare mean egg mass of clutches across categories of vegetation cover. Instead, we converted both analyses to a common effect size (r) and tested the power of our analysis, given our sample size, and using the calculated r from Roosenburg (1996) as the alternative hypothesis. Conversion of F to r when F is from an ANOVA with more than two groups follows Rosenthal (1994). Power was calculated following Zar (1999).

To directly test potential associations between mean egg mass and mean July nest temperatures for the subset of nests where nest temperatures were taken, we conducted a regression using mean egg mass as an effect on mean July nest temperatures. Females sometimes nest more than once per season in this population;

when this occurred, only the first clutch was included in statistical analyses. However, to address possible patterns of behavioral adaptation in nest-site choice within a nesting season, changes in mean egg mass between nesting events for individual females were regressed on changes in average percentage of south and west vegetation cover in the corresponding nest sites.

RESULTS

Vegetation cover as a predictor of nest temperature.—Summary statistics for average vegetation cover are presented in Table 1. Vegetation cover over the nests was negatively correlated with mean July nest temperature, such that nests with more vegetation cover experienced cooler temperatures than more exposed nests (Fig. 1). Both year ($F_{3,75} = 9.66$, $P < 0.0001$) and vegetation cover ($F_{1,75} = 49.29$, $P < 0.0001$) significantly affected mean July nest temperatures, but no interaction of vegetation cover by year was present ($F_{3,75} = 0.0055$, $P = 0.43$). The intercept shifted according to yearly climate: the warmest summer occurred in 1995 and the coolest in 1996 (Table 2).

Egg mass and nest-site choice.—Summary statistics for mean egg mass are presented in Table 1. Mean egg size of clutches varied greatly among females (Table 1), which provided substantive opportunity for placement of different egg sizes among different thermal environments (Fig. 1). However, regression of average amount of vegetation cover on egg size of nests of *C. picta* showed no significant relationship between these attributes in any of the four field seasons (Fig. 2). We conducted a power test on the combined data ($r = 0.0512$) and found that the power for detecting an effect size as large as that found by Roosenburg (1996; $n = 344$, $r = 0.185$) was 0.943 with our sample size ($n = 376$). Because females may assess egg size relative to their own body size (e.g., relative investment) rather than to the distribution of egg sizes in

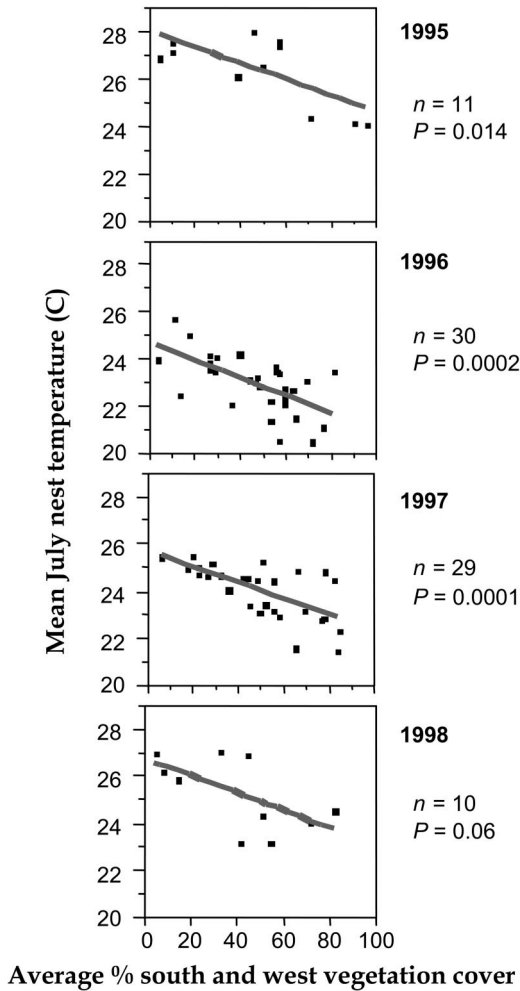


Fig. 1. Linear regressions of mean July nest temperatures on average percentage of south and west vegetation cover over natural nests of painted turtles (*Chrysemys picta*). The top panel is equivalent to figure 2 of Weisrock and Janzen (1999). Data for one nest in 1997 and four nests in 1998 were excluded because the temperature loggers malfunctioned.

the population, we also evaluated the effects of relative egg size on vegetation cover over nests using female plastron length as a covariate. However, results did not differ from those using absolute egg size (results not shown). Females apparently laid eggs randomly in terms of vegetation cover with respect to egg size.

We also directly evaluated potential relationships between mean egg mass and nest temperatures. No significant relationship between mean egg mass and nest temperatures was found ($n = 83$, $r = 0.078$, $P = 0.48$). Therefore, no relationship between egg mass and actual nest temperatures was present, regardless of

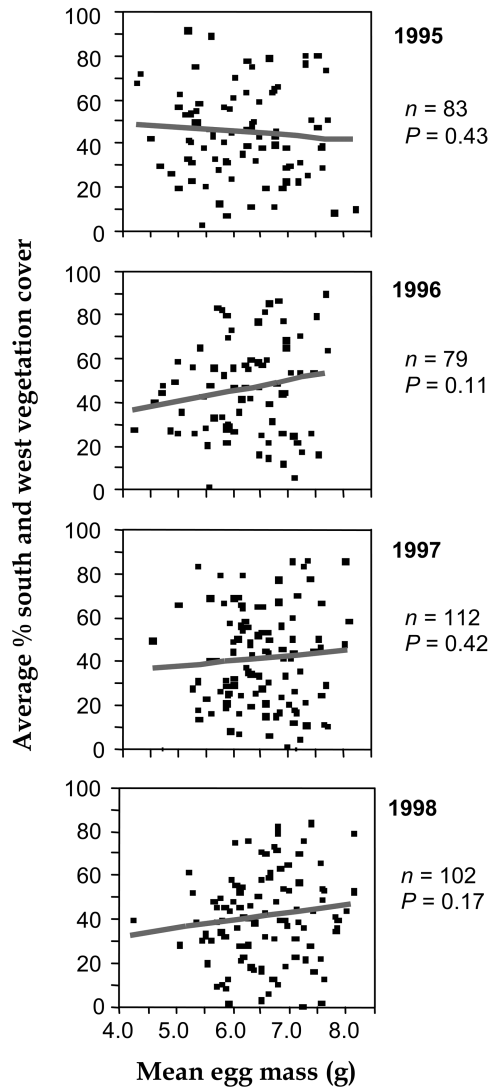


Fig. 2. Linear regressions of average percentage of south and west vegetation cover over natural nests of painted turtles (*Chrysemys picta*) on mean egg masses.

what criteria females may use for nest-site choice.

For females nesting twice in a season, based on Roosenburg's (1996) MCDC hypothesis, we would expect a significant relationship between the change in egg mass within a female between first and second clutches and the change in the amount of average vegetation cover over the corresponding nest sites. However, analysis of these attributes by linear regression revealed no pattern in choice of average vegetation cover in relation to a change in mean egg mass ($r = 0.028$, $n = 83$, $P = 0.80$). For example, females whose mean egg mass changed between the first

TABLE 2. JULY TEMPERATURES FOR THE THOMSON CAUSEWAY FIELD SITE.

Year	Temperature (C, $\bar{x} \pm SD$)	
	Ambient (bench)	Surface (tree)
1995	25.32 \pm 3.58	25.88 \pm 3.25
1996	22.14 \pm 3.47	20.77 \pm 2.08
1997	23.46 \pm 4.20	21.33 \pm 2.35
1998	24.01 \pm 3.25	NA

and second nesting events within a season did not correspondingly nest in more or less heavily vegetated sites the second time. These results demonstrate that, for painted turtles, females do not choose warmer or cooler nest sites in response to within-year changes in egg size.

DISCUSSION

Our objective was to evaluate two important conditions required to test the generality of a recent hypothesis to explain the maintenance of TSD in reptiles (Roosenburg, 1996). These conditions were that (1) an environmental cue exists at the time of oviposition, which indicates nest temperatures at the time of embryonic sex determination, and (2) females match egg size with this environmental cue. We found support for condition (1); however, we did not find support for condition (2), which brings into question the generality of egg size as a basis for nest-site choice concerning the maintenance of TSD in reptiles (Roosenburg, 1996).

Vegetation cover as a predictor of nest temperature.—Nests with more vegetation cover tended to be cooler than nests with less vegetation cover across all years of the study (see also Weisrock and Janzen, 1999). Nest temperatures, in turn, influence offspring sex ratios. Nests with mean July temperatures near 24 C at this field site tended to produce strongly male-biased sex ratios, whereas nests experiencing higher mean July temperatures ranged from producing mixed sex ratios to all females (Weisrock and Janzen, 1999).

Janzen (1994a) found that nests under higher vegetation cover tended to produce male-biased sex ratios in a three-year study on this population of *C. picta*. However, this relationship only existed for two of the years; the remaining year was unusually cool and produced highly male-biased sex ratios overall. Indeed, yearly climate strongly affects offspring sex ratios in this population (Janzen, 1994b), and during some years vegetation cover and offspring sex ratio are not

correlated (Janzen 1994a; Valenzuela and Janzen, 2001). The consistent relationship between vegetation cover and nest temperatures across all years in our study indicates a negative relationship between vegetation cover and nest temperatures regardless of climatic condition and provides a previously undocumented functional link between vegetation cover and offspring sex ratios. Because vegetation cover over nests also remains consistent throughout the nesting season and the period of embryonic development at this site (Janzen, 1994a), it provides a realistic environmental cue that females may use during oviposition to predict relative temperatures the nests will experience during the ensuing summer.

Nest-site choice and the maintenance of TSD.—Although female diamondback terrapins tend to lay larger eggs in areas with less vegetation cover (Roosenburg, 1996), we found no evidence for such a trend in *C. picta*. In fact, in painted turtles, larger eggs were not laid in areas likely to produce males either. Our results are inconsistent with the relationship found in diamondback terrapins. However, painted turtles possibly have less discernable advantages of larger egg size for one sex over the other. Egg size significantly affected size of three-year-old females in diamondback terrapins, but not for males (Roosenburg and Kelley, 1996). Although the persistence of such effects until age of maturity is unknown, Roosenburg and Kelley (1996) suggested females from larger eggs are likely to reach maturity at an earlier age than those hatched from smaller eggs. In painted turtles, females grow faster than males and egg mass exerted significant positive effects on juvenile mass during the first year of life; however, both sexes benefited by egg mass equally (Janzen and Morjan, 2002). Nevertheless, our study demonstrates that females still did not match egg size to expected nest temperatures regardless of which sex might be expected to benefit most from large egg size.

It could be argued that female painted turtles could still benefit from large egg size in the long term. Female painted turtles are larger than males (Gibbons, 1968; Mitchell, 1988; Zweifel, 1989) and are thought to grow faster than males (Ernst, 1971; Rickard et al., 1989; but see Wilbur, 1975). Fecundity is positively correlated with body size for females (Iverson and Smith, 1993), and some evidence suggests that fecundity is negatively correlated with male body size (S. McTaggart, unpubl. data). However, the relative value of any lasting benefits of large egg size and faster growth for females ver-

sus males remains unaddressed in painted turtles (and perhaps in all turtles). More information about mating patterns in turtles would contribute to such an understanding.

Our results may also demonstrate a key difficulty in falsifying hypotheses related to Trivers and Willard (1973) concerning maternal investment (Brown, 2001). Given the variety of ways that maternal investment can be measured (e.g., egg size, clutch size, yolk steroid hormones, etc.) it is almost impossible to reject a theory as long as alternative adaptive mechanisms can be conceived (Brown, 2001). Specifically, although no correlation was found between nest-site choice and egg mass, it could be argued that Roosenburg's (1996) hypothesis is not rejected because the proper variables had not been measured. For example, females may choose their nest sites as a consequence of factors other than egg mass (e.g., yolk steroid hormones), or nest placement may not be based only on the amount of south and west facing vegetation. Therefore, we focused only on direct comparisons to Roosenburg's (1996) data.

Painted turtles could instead choose a nest site primarily to ensure completion of egg development (Schwarzkopf and Brooks, 1987) or overwinter survival of hatchlings (Weisrock and Janzen, 1999), rather than to influence offspring sex ratio. Variation in hydric conditions (Cagle et al., 1993) and predation pressures among nests may also diminish the relevance of egg size to life-history parameters in painted turtles (Iverson and Smith, 1993). Considering the wide variety of environmental effects across clutches in the field (e.g., predation pressures, flooding, thermal and hydric conditions), egg size may not play an important role in nest-site choice for many oviparous reptiles.

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