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Egg Size, Incubation Temperature, and Posthatching Growth in Painted Turtles (*Chrysemys picta*)

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Incubation temperature has profound and pervasive effects on phenotypes of developing embryos and offspring of oviparous reptiles (reviewed in Deeming and Ferguson, 1991). Perhaps the most compelling impact involves sex determination in many of these species. Indeed, this temperature-dependent sex determination (TSD) in reptiles has received considerable attention (reviewed in Bull, 1983; Ewert and Nelson, 1991; Janzen and Paukstis, 1991; Shine, 1999).

Most adaptive explanations for the existence and persistence of TSD hypothesize that incubation temperatures benefit the sexes differentially (sensu Charnov and Bull, 1977). Incubation temperature does, in fact, influence many traits that may affect fitness and examining such traits may disclose sex-specific effects in accord with the Charnov-Bull model. A number of studies have adopted this exploratory approach, yet no general explanation for the adaptive significance of TSD in reptiles has been validated empirically (reviewed by Shine, 1999).

One promising hypothesis suggests that the evolutionary persistence of TSD in reptiles could be explained by a covariance between egg size, nest thermal environment, and sexual size dimorphism (Roosenburg, 1996; Roosenburg and Niewiarowski, 1998). That is, a key trait (i.e., egg size) might have sex-specific (i.e., incubation temperature-specific) effects on fitness by influencing posthatching growth rates and ages of maturity. Specifically, (1) egg size must be correlated with eventual size of an individual; (2) incubation temperature must influence posthatching growth rates; (3) any covariance between egg size and temperature affecting growth must be sex-specific; (4) nesting females should be able to discriminate among environmental cues related to nest temperature; and (5) these females should use such environmental cues to manipulate offspring sex ratio according to their egg sizes.

The only attempt to evaluate this hypothesis produced considerable support. In diamondback terrapins (*Malaclemys terrapin*), a turtle with TSD and large-female sexual size dimorphism in adulthood, egg size influenced posthatching growth rates and ages of maturity for females but not for males (Roosenburg and Kelley, 1996). Fieldwork showed subsequently that nesting terrapins generally laid larger eggs in warmer, female-producing microhabitats and smaller eggs in cooler, male-producing microhabitats (Roosenburg, 1996).

Our study is a first attempt at testing the generality

of Roosenburg's hypothesis. We evaluated the first three key conditions of the hypothesis (see above) using painted turtles (*Chrysemys picta*), an emydid turtle with TSD and large-female sexual size dimorphism [the remaining two conditions involving nesting biology are evaluated elsewhere (unpubl. data)]. Specifically, we explored the effects of egg size and incubation temperature on posthatching body size and growth. We expected to obtain results concordant with those of Roosenburg and Kelley (1996) given the similarity of painted turtles to terrapins phylogenetically and in patterns of TSD (Paukstis and Janzen, 1990) and sexual size dimorphism (Ernst et al., 1994).

Eggs from 13 fresh nests were collected during June 1989 near the Thomson Causeway, an island in the Mississippi River near Thomson, Carroll County, Illinois (41°57'N, 90°07'W; Janzen, 1994). These eggs were weighed to the nearest 0.01 g with an Ohaus portable electronic balance and then transported immediately to the University of Chicago. In the laboratory, a subset of these eggs was chosen for this experiment. Eggs were assigned randomly to a position in a 3 × 8 matrix in 4 shoeboxes containing moist vermiculite (−150 kPa = 300 g dry vermiculite : 337 g deionized water). Two shoeboxes each were then placed in incubators set at either 26 (male-producing) or 30°C (female-producing) (Schwarzkopf and Brooks, 1985; Paukstis and Janzen, 1990). These temperatures are well within the range experienced by natural nests in this population during embryonic sexual differentiation (Weisrock and Janzen, 1999:fig. 1; for a detailed explanation on comparing constant and fluctuating incubation temperatures, see Georges, 1989). Containers were rehydrated weekly to replace any lost water and were rotated daily within incubators to minimize the effects of thermal gradients. Dissections of carcasses of turtles that died during the study confirmed that 26 of 27 individuals incubated at 26°C were male (the single female suffered severe deformities) and 17 of 17 individuals incubated at 30°C were female.

After hatching in August 1989, 77 turtles were weighed to the nearest 0.01 g and then placed in an enclosed 3 × 3 m outdoor concrete pond with a sloping bottom ranging from 0.3 m to >1 m. This pond, which received partial sun during the day, was used to rear turtles from April to November. Turtles were hibernated indoors at 5 C from December through March. Juveniles were fed waxworms, trout feed, and Reptomin ad libitum three times per week during the growing period. In addition, insect larvae and algae were naturally abundant in the pond for feeding. Individual mass was measured in late summer for each subsequent year of survival through 1992. However, we only report data for the first year of growth because many turtles were stolen in 1991, which greatly reduced sample sizes.

Growth for hatchlings for the first year was calculated as the mass gained by an individual from hatching to one year of age, and differences between males (26°C) and females (30°C) were compared using a *t*-test. We then evaluated the relative effects of egg mass and incubation temperature on hatchling and juvenile masses by performing two analyses of covariance. With incubation temperature, egg mass, and their interaction as effects, we used hatchling mass as a response in the first analysis and mass at one year

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TABLE 1. Mass ($\bar{x} \pm$ SD) of female and male painted turtles (*Chrysemys picta*) at hatching and at one year of age.

Year	Sex	Mass (g)	N	t	P
1989 (hatchling)	female	4.47 \pm 0.13	37	0.016	0.87
	male	4.45 \pm 0.13	40		
1990	female	14.73 \pm 0.62	13	4.61	0.0001
	male	11.07 \pm 0.50	20		

in the second. Because females hatched on average two weeks earlier than males, we also used analysis of covariance to evaluate the relative effects of age (in days), hatchling mass, and incubation temperature on juvenile mass at approximately one year of age. We could not include clutch as a factor in our analyses because of the small sample sizes caused by low hatching success and low first-year survival. We also could not statistically separate the effects of incubation temperature and sex on growth in this study because these factors were confounded. Consequently, we use the terms "incubation temperature" and "sex" interchangeably throughout the manuscript. All statistical analyses were performed using JMP version 3.2.1 (SAS Institute, Inc., Cary, NC, 1997).

Of the 96 eggs incubated for this experiment, 40 (83%) hatched at 26°C and 37 (77%) hatched at 30°C. Of these 77 hatchlings, only 20 (50%) from 26°C and 13 (35%) from 30°C survived to the end of the following summer (i.e., August 1990). Most of this mortality, which had no obvious causes, occurred in November 1989 just before hibernation and in spring 1990 shortly after removal from hibernation. The 33 turtles that survived to at least one year posthatching form the basis of our growth analyses.

Although no differences existed in mass at hatching between males (eggs incubated at 26°C) and females (eggs incubated at 30°C), females were significantly heavier than males after the first year of growth (Table 1). When considering strictly the subset of individuals that survived to their first year, no significant differences in hatchling mass existed between males and females ($N = 33$, $t = 1.12$, $P = 0.27$). During the first year, however, these females grew significantly more than males ($\bar{x}_{\text{females}} = 10.20$ g \pm 0.53, $\bar{x}_{\text{males}} = 6.27$ g \pm 0.43, $t = 5.76$, $P < 0.0001$, $df = 31$).

No egg mass by incubation temperature interaction was present among the analyses (hatchling mass: $F_{1,73} = 0.39$, $P = 0.54$; mass at one year: $F_{1,29} = 0.030$, $P = 0.86$; Table 2); therefore egg mass affected hatchling and juvenile size similarly between the sexes (Fig. 1), and this interaction effect was excluded from further analyses. Egg mass significantly and positively affected hatchling mass, whereas incubation temperature

marginally affected hatchling mass in a negative direction. At one year of age, both incubation temperature and egg mass significantly and positively affected juvenile mass. Even accounting for the fact that females (eggs incubated at 30°C) hatched 14 days earlier than males on average (eggs incubated at 26°C), age (in days) did not significantly affect juvenile mass at one year after accounting for the effects of incubation temperature and hatchling mass (age: $F_{1,29} = 0.52$, $P = 0.47$; incubation temperature: $F_{1,30} = 38.14$, $P < 0.0001$; hatchling mass: $F_{1,30} = 14.63$, $P < 0.001$). In summary, although female painted turtles grew faster than males during their first year, larger eggs produced larger hatchlings for both sexes (Fig. 1).

Our intent was to investigate three key conditions of a recent hypothesis to explain the adaptive maintenance of temperature-dependent sex determination (TSD) in reptiles (Roosenburg, 1996). Specifically, we evaluated the effects of (1) initial egg mass and (2) incubation temperature (sex) on juvenile growth for one year posthatching in painted turtles and (3) whether any egg and temperature effects on growth were sex-specific. We detected persistent effects of egg mass on juvenile mass through one year of age, as well as differential growth rates between males (eggs incubated at 26°C) and females (eggs incubated at 30°C). We did not observe a sex-specific covariance between effects of egg mass and temperature on juvenile mass.

Our results for these three conditions of Roosenburg's hypothesis are largely consistent with those of Roosenburg and Kelley (1996) for diamondback terrapins. However, we detected a positive relationship between egg mass and juvenile mass at one year of age for both sexes (incubation temperatures) in painted turtles (Fig. 1), whereas egg size significantly affected juvenile size for only females in diamondback terrapins (Roosenburg and Kelley, 1996). Furthermore, although egg mass was an important factor for juvenile body size for both sexes throughout early growth in painted turtles, the persistence of such effects until age of maturity is currently unknown. Preliminary information from mark-recapture work in our study population indicates rapid maturation (~3 years in males and ~5 years in females; FJJ, unpubl.), so rapid

TABLE 2. Results from two analyses of covariance evaluating the effects of egg mass and incubation temperature on mass of painted turtles (*Chrysemys picta*) at hatching and at one year of age.

Age (N)	Effect	Estimate \pm SE	F (df = 1)	P
Hatchling (77)	Egg Mass	0.72 \pm 0.039	331.57	< 0.0001
	Incubation Temperature	-0.040 \pm 0.020	3.97	0.050
One year (33)	Egg Mass	1.27 \pm 0.37	11.49	0.002
	Incubation Temperature	0.98 \pm 0.17	32.01	< 0.0001

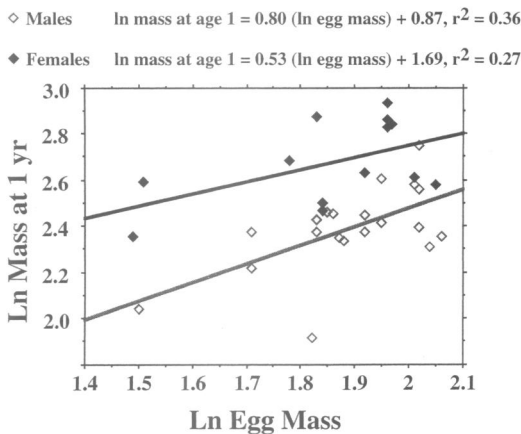


FIG. 1. Mass at 1 yr for male (open diamonds) and female (filled diamonds) painted turtles as a function of initial egg mass. The regression lines for sexes (= incubation temperatures) were significantly different from 0 but not from each other.

growth even to one year of age is likely to be important ecologically in this case.

The sex-specific benefits of larger body size and faster growth in painted turtles have yet to be documented definitively. Mature females are certainly larger (reviewed by Ernst et al., 1994) and typically grow faster as juveniles (reviewed by Ernst et al., 1994; St. Clair et al., 1994; but see Wilbur, 1975) than males under natural and seminatural conditions (Table 1). Most crucially, fecundity scales positively with body size in females (reviewed in Iverson and Smith, 1993), but apparently scales negatively with body size in males (S. McTaggart, unpubl.). In other words, larger females produce more eggs and smaller males sire more offspring. More information on mating patterns would be helpful to confirm the body size/fitness results for males, but the current implications are that females are likely to benefit more than males from larger body size in painted turtles.

If indeed larger body size benefits females more than males, then our results support several key conditions of Roosenburg's hypothesis for the adaptive maintenance of TSD in reptiles (Roosenburg, 1996). Larger painted turtle eggs lead to larger juveniles of both sexes (incubation temperatures), but this effect of accelerating growth may only (or primarily) be beneficial for females. The stage is thus set for further empirical evaluation of Roosenburg's hypothesis by examining the mating system, nesting biology, and general evolutionary ecology of painted turtles in the field.

Painted turtle nests with more overstory vegetation cover tend to be cooler than nests with less overstory vegetation cover at our study site (Weisrock and Janzen, 1999). Because overstory vegetation cover around a given nest is constant throughout embryonic development at this site (Janzen, 1994), this variable provides a realistic environmental cue that a turtle could use during oviposition to predict relative nest temperatures during subsequent sexual differentiation of embryos. Evaluating patterns of nest-site choice would

elucidate whether females take advantage of the documented effects of egg size on juvenile growth to benefit the sexes differentially. If Roosenburg's (1996) hypothesis holds, we predict for painted turtles that (1) body size will correlate positively with reproductive success for females but not for males and (2) individuals with relatively large eggs will oviposit in warmer, less vegetated, female-producing sites than painted turtles with relatively small eggs.

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Rain-Harvesting Behavior in Agamid Lizards (*Trapelus*)

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The ability of arid region reptiles to use the body surface as a collector of water has been known for many years, although it has been described only in a small number of species. Bentley and Blumer (1962) demonstrated that *Moloch horridus* (Agamidae) drink the water film passively transported by capillary action of the skin to the mouth, thus contradicting a theory that water is absorbed transcutaneously in this species (Buxton, 1923). Gans et al. (1982) reexamined *Moloch* skin with the aid of scanning electron microscope (SEM) photographs and attributed the water

flow to capillary forces generated by grooves between scales. Schwenk and Greene (1987) described a similar system in another agamid, *Phrynocephalus helioscopus*, and reported that capillary forces pull water through interscalar channels. In addition, they described a stereotyped posture that was exhibited when this species was sprayed with water. This posture involved lowering the head, raising the splayed hindquarters, and protruding the tongue. Comparable behavior has not been observed in *Moloch* (Sherbrooke, 1993). In the iguanid lizard *Phrynosoma cornutum* a similar behavior was described by Sherbrooke (1990). His term “rain-harvesting” is used for a complex of behavioral and morphological characters associated with this form of water collection (Sherbrooke, 1990, 1993; Withers, 1993). More recently, such behavior has been described in *Phrynosoma platyrhinos* (Peterson, 1998).

Herein, we report rain-harvesting in three agamids (*Trapelus pallidus*, *Trapelus flavimaculatus*, and *Trapelus mutabilis*). Examination of two additional species of the same genus (*Trapelus ruderatus* and *Trapelus sanguinolentus*) did not reveal the presence of this behavior. All the animals examined have relatively similar biology, inhabiting more or less open arid to semiarid areas of Northern Africa, the Near East, and the Middle East.

During 1998, 41 specimens of *Trapelus* were examined for the presence or absence of rain-harvesting behavior. Numbers of specimens and their origin are as follows: *T. pallidus* (Reuss, 1834), 16 specimens from the Eastern Desert, Jordan; *T. flavimaculatus* (Rüppell, 1835), three specimens obtained from a commercial dealer; *T. mutabilis* (Merrem, 1820), 10 specimens from northern Egypt; *Trapelus ruderatus ruderatus* (Olivier, 1804), nine specimens, from the Amman region, western Jordan; *T. sanguinolentus* (Pallas, 1827), three specimens obtained from a private reptile keeper. Lizards were housed in glass terraria with sand or gravel substrate. Terraria were heated by incandescent lamps and illuminated by fluorescent tubes. Lizards were fed crickets, wormsmealworms, and *Zophobas morio* larvae, with vitamin-mineral supplement every two to three days. Water dishes were placed in each terrarium, and the enclosures were sprayed twice per week.

The drinking behavior of each animal was observed and recorded. Water was not available for three days prior to each trial. During trial observations, the subject was sprayed with water using a hand pump sprayer. Spraying lasted 3 min, and time to the beginning of drinking (movement of the jaw and tongue) was recorded. Additionally, the type and duration of rain-harvesting posture, and the presence or absence of wet stone licking was recorded. Minimum and maximum duration of these behavioral characters were measured in seconds. Animals exhibiting typical rain-harvesting posture were photographed using Nikon F90 camera with Sigma 90 mm macro-lens and Nikon SB 27 speed light. Each subject was observed in three separate trials with an interval of two weeks between trials.

The ability of skin to carry water by capillary action in interscalar channels was tested in two individuals of each species. The experiments were similar to those of Schwenk and Greene (1987). The animals were wetted by light spraying, then blotted dry with a paper tissue and placed back into the enclosure. Next, water

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