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C. L. Morjan; N. Valenzuela

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Is Ground-Nuzzling by Female Turtles Associated with Soil Surface Temperatures?

C. L. MORJAN¹ AND N. VALENZUELA

Department of Zoology and Genetics, Iowa State University, 339 Science II, Ames, Iowa 50011, USA

Nest-site choice in reptiles has elicited considerable interest because of its implications for offspring fitness. Nest location may directly affect offspring survivorship, in terms of predation risk, hatching success, and emergence success (Whitmore and Dutton, 1985; Temple, 1987; Horrocks and Scott, 1991; Wilson, 1998). Environmental variation among oviposition sites, such as temperature and hydric conditions, influences survivorship and various offspring traits including sex, growth, and behavior (Bull 1980; Gutzke and Crews, 1988; Packard et al., 1993; Shine and Harlow, 1996; for a review, see Deeming and Ferguson, 1991). Given these consequences of incubation conditions on offspring survivorship and phenotype, selection may exist for females to detect environmental cues correlated with offspring fitness and to oviposit at sites exhibiting these cues (see Resetarits, 1996).

This study assesses the role of ground temperature as a cue for nest-site choice in painted turtles (*Chrysemys picta*). In painted turtles, temperatures in natural nests affect offspring sex (Schwarzkopf and Brooks, 1987) and survivorship (Packard et al., 1997; Weisrock and Janzen, 1999). In some evolutionary models, the ability of females to discriminate among nesting environments with different thermal characteristics is a critical assumption for the maintenance of temperature-dependent sex determination (Roosenburg, 1996). We specifically focused on a behavior present in many turtles that is thought to aid in nest-site choice through the detection of environmental

cues. Female turtles frequently exhibit a stereotypical behavior during nesting forays, in which the head and ventral side of the neck are pressed on the ground surface before choosing a nest site. This so-called ground-nuzzling or sand-smelling is particularly interesting because of its presence across a wide array of chelonian taxa (Table 1) and may be a conserved mechanism for detecting temperature, olfactory, or other cues during nest-site selection (Carr et al., 1966; Ehrenfeld, 1979; Stoneburner and Richardson, 1981). No study has investigated the correlation between this behavior and any potential environmental cue. Because it is uncertain whether this behavior is in fact an olfactory sensory mechanism, and because it occurs not only in sand, we will refer to it as ground-nuzzling rather than sand-smelling.

We observed natural nesting events of painted turtles to examine whether surface temperatures experienced by females while ground-nuzzling differed from surface temperatures at nesting or while walking. We further evaluated the potential utility of surface temperature as a cue to nesting females by investigating whether surface temperatures at the time of nesting were correlated with vegetation cover over nests (a known thermal indicator at this site), sex ratios, predation rates, and hatching success of nests.

We observed nesting painted turtles (*C. picta bellii*) on the south nesting beach at the Thomson Causeway Recreation Area in Thomson, Illinois (41°57'N, 90°07'W). The nesting beach is level and fairly uniform in soil moisture levels, and trees are dispersed across the site, providing a wide range of thermal environments for nest placement (Janzen, 1994). This site is a public recreation area, and nesting turtles consequently have become fairly tolerant to human observation. Forty-seven turtles were observed following their emergence onto the nesting beach between 28 May and 30 June 1998. During this time, we searched the nesting beach for females at least once hourly from sunrise until sunset. Each turtle was observed from the time she was first discovered (usually shortly after emergence from the water) until she either commenced nesting or left the nesting beach and returned to the water. Most turtles emerged during the afternoon (1400–2000 h), although some emerged in the morning (0700–1000 h).

We chose to measure ground temperatures at fixed time intervals rather than at fixed distances during the turtles' nesting forays, because females rarely walked a straight path during their nesting forays while covering a long distance from the water to the nest. Furthermore, no tracks were left by the turtles as they traveled over the short grass of the nesting beach, and marking the turtle's path would likely interfere with normal nesting behavior. We observed turtles by standing motionless at a vantage point 5–10 m away from the turtle during her nesting foray. Surface temperatures were measured with a factory-calibrated Raytek® Raynger ST8 noncontact, infrared thermometer (accuracy $\pm 1^\circ\text{C}$). This thermometer functions by pointing a sighting laser directly at a surface and measuring the temperature of the surface remotely from the point of the laser. This instrument has a 30:1 distance-to-spot ratio, meaning that, at a 10-m distance, the instrument records surface temperatures from a circle with a 33-cm diameter, centered on the laser

¹ Corresponding Author. E-mail: milne@iastate.edu

TABLE 1. Turtles reported to exhibit the "ground-nuzzling" behavior.

<i>Cryptodira</i>	
Cheloniidae	
<i>Caretta caretta</i>	(Stoneburner and Richardson, 1981)
<i>Chelonia mydas</i>	(Carr and Hirth, 1962)
<i>Eretmochelys imbricata</i>	(Carr et al., 1966)
<i>Lepidochelys</i>	(Hirth and Carr, 1970)
Emydidae	
<i>Chrysemys picta</i>	this study
<i>Clemmys guttata</i>	(Ernst et al., 1994)
<i>Clemmys insculpta</i>	(Harding and Bloomer, 1979)
<i>Clemmys muhlenbergii</i>	(Holub and Bloomer, 1977)
<i>Emydoidea blandingi</i>	(Linck et al., 1989)
<i>Graptemys ernsti</i>	(Ernst et al., 1994)
<i>Graptemys nigrinoda</i>	(Ernst et al., 1994)
<i>Malaclemys terrapin</i>	(Lazell and Auger, 1981)
<i>Pseudemys concinna</i>	(Jackson and Walker, 1997)
<i>Terrapene carolina</i>	(Messinger and Patton, 1995)
<i>Trachemys gaigeae</i>	(Morjan and Stuart, 2001)
<i>Trachemys scripta</i>	(Moll and Legler, 1971)
Testudinidae	
<i>Testudo hermanni</i>	(Swingland and Stubbs, 1985)
<i>Pleurodira</i>	
Pelomedusidae	
<i>Podocnemis expansa</i>	N. Valenzuela, pers. obs.

point visible on the ground's surface. Temperatures were measured every 30 sec during the turtle's nesting foray by pointing the infrared thermometer directly at the ground surface in front of the turtle's nose. We aimed the sighting laser at a short distance in front of the turtle (10–20 cm) in an effort to measure the ground's surface temperature while excluding the turtle's temperature from the measurements as much as possible. If the turtle stopped moving for > 1 min, recording was stopped until she resumed movement.

Temperature and the behavior of the turtle were registered into a tape recorder. Four behaviors were identified: walking, standing, ground-nuzzling, and nest digging. We recorded every time the female performed the ground-nuzzling or nest digging behavior, such that the remaining time corresponded to walking or standing, which were thus combined into a third behavioral category (walking/standing). These three behavioral categories were considered for statistical analysis. When a female commenced nest digging, she usually initiated this behavior by turning 180° immediately after a ground-nuzzling episode and digging at this site with her hind legs. However, females frequently exhibited the ground-nuzzling behavior at several sites during their nest-site selection process before nesting at the final site.

To exclude repeat nesters (maximizing the independence of the data), turtles were identified on completion of nesting by examining unique patterns of notches on the marginal scutes, made during previous studies at the site. If no marks were present, she was given a new marking pattern. Eggs from nests were excavated, counted, and reburied in their original orientations. Vegetation cover, the amount of canopy veg-

etation over the nest, was recorded over each nest while facing each of the four cardinal directions with a Model-A spherical densiometer as in Janzen (1994). This variable was considered important to measure because, within each nesting season, nest temperatures and offspring sex ratios are correlated with vegetation cover from the south and west directions over nests (Janzen, 1994; Weisrock and Janzen, 1999; C. L. Morjan and F. J. Janzen, unpubl. data). Air temperatures were recorded at the field site every 40 min from 30 May until the end of the study using a HOBO TEMP® datalogger placed out of direct sunlight at 0.3 m above the ground (Weisrock and Janzen, 1999).

In early September 1998, hatchlings were removed from 14 of the 15 nests that survived predation. The remaining nest was part of an ongoing study concerning overwinter survivorship, and these hatchlings were removed in March 1999. Hatching success was defined as the number of hatchlings divided by the number of eggs in an intact nest. Up to six hatchlings per nest were euthanized by injection of a 1:1 solution of sodium-pentobarbital ("Sleepaway") and deionized water into the cardiac cavity. Hatchlings were sexed by macroscopic examination of the gonads and preserved in ethanol in the laboratory at Iowa State University.

We first determined whether the relationship between air temperature (taken within 20 min of surface temperature measurements) and surface temperature was homogeneous for all nesting forays. ANCOVA using female identity as an effect, air temperature as the covariate, and surface temperature as the response variable showed significant differences among females (equal slopes but different intercepts). Therefore, all

the analyses that follow were conducted taking into account female identity. Residuals of the regression of surface temperature on air temperature used in the previous analyses were tested for the presence of serial autocorrelation using the Durbin-Watson test (Neter et al., 1996). We corrected for this serial autocorrelation by performing a three-way Mantel test (Smouse et al., 1986) of residual temperature by behavioral category (walking/standing, ground-nuzzling, or nesting), holding time and female constant. We generated four distance matrices corresponding to the time, behavioral category, turtle ID and residual temperature variables. We then combined the time and turtle ID matrices into a new design matrix where time values were kept only in those cells corresponding to same-female comparisons and all other cells corresponding to comparisons across females were given a value of zero. By performing the three-way Mantel test of residual temperature by behavioral category holding this new design matrix constant, we tested for differences in temperatures among behavioral categories while simultaneously holding the effects of time and female constant.

Finally, we tested whether surface temperature at nesting was correlated with vegetation cover over the nest, nest predation, hatching success, and hatchling sex ratios. Residuals were taken from the regression of air temperatures on surface temperatures at time of nesting. Percent vegetation cover was calculated by converting the values taken from the south and west densiometer readings into percentages and calculating their average. We performed a linear regression of residual temperature of the surface over the nest site at time of nesting on percent vegetation cover over the nest. Then we performed a series of logistic regression analyses to investigate the effect of residual temperature on nest predation ($N = 17$ nests), hatching success ($N = 12$ nests), and sex ratios (percent females) for nests producing hatchlings ($N = 12$ nests).

Of the 49 turtles observed during the study, 26 successfully constructed nests. The ground-nuzzling behavior was significantly associated with nesting (Fisher's Exact test; $P = 0.0002$). Only one of the turtles that nested was not observed to exhibit ground-nuzzling. Of the 23 turtles that did not nest, 12 were never observed to exhibit the ground-nuzzling behavior, four were frightened from nesting because of known disturbances unrelated to the study, and three abandoned nest cavities for unknown reasons. Based on these observations, and given an incidence of false crawls (emergence without nesting) up to 71% in some nesting turtle populations (Andre and West, 1981), we are confident that observing the females in this population did not cause disturbance to their normal nesting behavior.

Using ANCOVA, we found a significant relationship between air temperature and surface temperature, which was homogeneous among females (parallel slopes, $F = 0.960$, $df = 39$, $P = 0.5423$). Residual ground temperatures were serially autocorrelated (Durbin-Watson index = 0.58, $P < 0.001$). No significant differences among behavioral categories in residual ground temperatures were evident, even while accounting for female effects and serial autocorrelation ($P = 0.66$).

Air temperatures and surface temperatures at nesting were highly correlated ($N = 17$, $R^2 = 0.53$, $P = 0.001$), so residual ground temperatures were used to assess the association between surface temperatures at nesting and nest characteristics. Residual ground temperatures at nesting were uncorrelated with the percentage of vegetation cover over the nest ($N = 17$, $R^2 = 0.06$, $P = 0.35$). Although vegetation cover over nests was not correlated with hatchling sex ratio ($N = 14$, $\chi^2_{(1)} = 2.37$, $P = 0.12$), there was a significant relationship between residual ground temperatures at nesting and sex ratio such that relatively warmer sites tended to produce more females ($N = 12$, $\chi^2_{(1)} = 7.65$; $P < 0.006$; $R^2 = 0.09$). Residual ground temperatures had no significant effect on whether a nest was depredated ($N = 17$, $\chi^2_{(1)} = 0.16$, $P = 0.69$) or on the hatching success of a nest ($N = 12$, $\chi^2_{(1)} = 0.72$, $P = 0.40$). All analyses using unstandardized ground temperatures in the place of residual ground temperatures were not significant.

In conclusion, we found that ground-nuzzling in *C. picta* was significantly associated with nesting, but no differences in ground temperature existed among the three behavioral categories (walking/standing, ground-nuzzling, and nesting). If females select nest sites based on thermal cues, it might be expected that temperatures at the nest site should differ from those encountered prior to nesting during the search for a nest site. Stoneburner and Richardson (1981) reported that female loggerhead turtles (*Caretta caretta*) nested when they encountered an abrupt increase in temperature ($> 2.0^\circ\text{C}$) on the nesting beach. They speculated that the ground-nuzzling behavior exhibited in this species may act as a possible mechanism to detect such thermal cues. However, Wood and Bjorndal (2000) noted the observed thermal differences may have been artifactual (overturned sand during the nest digging process may have influenced the results) and that other characteristics such as slope may instead influence nest-site choice. Our results showed no consistent significant thermal differences among the behavioral categories studied among females; thus, females are unlikely to be choosing warmer sites for oviposition based on surface temperatures, as found by Stoneburner and Richardson (1981).

Ground temperatures at nesting for *C. picta* did not differ overall from temperatures encountered during the nesting foray in this study. These results suggest that females either do not use surface temperatures as a cue for nesting or that females may in fact choose to nest at sites exhibiting a broad range of intermediate temperatures and simply avoid areas exhibiting extreme temperatures. Nests of *C. picta* in Ontario experience significantly warmer temperatures than random sites, and females probably use slope and absence of vegetation as cues to select their nesting site (Schwarzkopf and Brooks, 1987). With this possibility in mind, we investigated potential relationships between vegetation cover, surface temperatures, survivorship, and hatchling sex ratios. We did not consider slope in these analyses because the nesting beach was uniformly level. We found a negative, but not significant relationship, between vegetation cover and proportion of female hatchlings for the focal females in this study. Although the trend was in the expected direction, our small sample size for this analysis ($N =$

14 nests) is likely responsible for the weak association between these two variables. Indeed, vegetation cover significantly affected hatchling sex ratios for the entire study site in 1998 (F. J. Janzen, pers. comm.). However, we did find a positive and significant relationship between the residual ground temperatures at nesting and sex ratio, but this correlation had a very low predictive power ($R^2 = 0.09$). Despite the fact that vegetation cover negatively affects offspring sex ratios in this population and that relatively warmer sites at nesting also positively affected sex ratios, we found no significant relationship between the surface temperatures at nesting and vegetation cover over the nest with our sample size.

The ground-nuzzling behavior may be related to the detection of olfactory cues. Hatchling *Lepidochelys kempi* preferentially oriented to seawater that was in contact with substrate from where they were incubated and hatched (Grassman et al., 1984). If hatchlings imprint to chemical properties of the incubation and hatching substrate, and natal philopatry exists, ground-nuzzling behavior in nesting females could act as a mechanism to detect these chemical properties when returning to natal beaches. Carr and Hirth (1962) observed that female green turtles (*Chelonia mydas*) exhibited the ground-nuzzling behavior in shallow water even before emerging from the surf and that the tip of the snout, rather than the entire neck, was placed on the sand. The ground-nuzzling behavior was usually terminated long before the nest-site selection process was completed for females of this species (table 4 in Carr et al., 1966). At least for green turtles, it would be difficult to explain why this behavior might be used to detect temperature rather than olfactory cues for emerging at a particular nesting beach. *Chrysemys picta* females are philopatric to nesting areas (Schwarzkopf and Brooks, 1987; Scribner et al., 1993); thus it is possible that they employ ground-nuzzling to aid in philopatry.

One important result from our study is that our data allowed us to rule out temperature as a factor related to ground-nuzzling. It is quite surprising that this behavior has received so little attention despite being widespread among chelonian taxa (Table 1). Further studies should test whether this behavior is instead an olfactory sensing mechanism.

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Relationships of *Hemidactylus* (Reptilia: Gekkonidae) from the Cape Verde Islands: What Mitochondrial DNA Data Indicate

JOSÉ JESUS,¹ ANTÓNIO BREHM,¹ MARGARIDA PINHEIRO,² AND D. JAMES HARRIS^{3,4}

¹Centro de Ciências Biológicas e Geológicas, University of Madeira, Penteada, 9000 Funchal, Portugal

²Centro de Zoologia, Instituto de Investigação Científica Tropical, Ministério da Ciência e Tecnologia, Lisbon, Portugal

³Centro de Estudos de Ciência Animal (CECA), ICETA-U.P., Campus Agrário de Vairão, 4485-661 Vila do Conde, Portugal; E-mail: james@mail.icau.pt

Colonizers in archipelagos frequently invade nearby islands and often show high genetic diversity between islands (Castilla et al., 1998). Because island populations have a higher risk of extinction than mainland populations (Frankham, 1997), investigation and protection of intransient forms is particularly important. Because geckos are frequently introduced anthropogenically, we examined gekkonids of the genus *Hemidactylus* in the Cape Verde islands. The Cape Verde archipelago (Fig. 1) lies between 380 and 460 km from the coast of Africa and consists of volcanic islands, which have never been connected to the continent (Mitchell-Thome, 1983). Two species of *Hemidactylus* have been reported from the islands; *Hemidactylus bouvieri* is endemic to the islands, whereas *Hemidactylus brooki* is extremely widespread, found in sub-Saharan Africa, India, Indonesia, Mexico, and elsewhere (Mertens, 1955; Joger, 1993; Powell et al., 1998).

Six *H. brooki* (CV36, CV122, Hb37, Hb38, Hb42, Hb43) and four *H. bouvieri* (CV38, CV125, CV165 and HBV1) from the Cape Verde islands were taken from the collections of the University of Madeira and Centro de Zoologia, IICT, Lisbon. One juvenile specimen that could not be adequately identified using morphological characters was also included (BichoA), as was one sample of *H. brooki* from Guinea, Africa (HbG1). Total genomic DNA was extracted from tail pieces using standard methods. Polymerase Chain Reaction (PCR) primers used in amplification and sequencing were cytochrome b1 and b2, and 12Sa and 12Sb (Kocher et al., 1989). PCR conditions were as those used by Harris et al. (1998), and successful PCR products were sequenced from both strands on an Applied Biosystems DNA Sequencing System.

Sequences were aligned using Clustal W (Thompson et al., 1994). The cytochrome *b* sequences were 317 base pairs long, and contained no indels. The codon reading frame was inferred by comparison with published sequences of *Tarentola mauritanica* and *Tarentola delalandii* (Nogales et al., 1998), which were included as outgroups. Cytochrome *b* sequences from *Hemidactylus turcicus* (Nogales et al., 1998) and *Hemidactylus*

⁴Corresponding Author. E-mail: james@mail.icau.pt

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