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## Spatial dynamics of nesting behavior: Lizards shift microhabitats to construct nests with beneficial thermal properties

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**Abstract.** Because temperature affects the growth, development, and survival of embryos, oviparous mothers should discriminate carefully among available nesting sites. We combined a radiotelemetric study of animal movements with a spatial mapping of environmental temperatures to test predictions about the nesting behavior of the eastern fence lizard (*Sceloporus undulatus*). Females made large excursions from their typical home ranges to construct nests in exposed substrates. These excursions appeared to be related solely to nesting because all females returned to forested habitat immediately afterward. On average, <1% (range = 0–8%,  $n = 19$ ) of the area used by a female during nesting was contained within the area used before and after nesting. The selection of nesting sites matched predictions based on laboratory studies of embryonic performance; specifically, females nested in extremely open habitat at a mean of 6 cm depth. Spatial mapping of soil temperatures revealed that temperatures of nesting areas exceeded those of areas typically used by females, indicating that females preferred to construct warm nests that speed embryonic growth and development. However, this behavior could reduce the survivorship of females because of the need to rapidly navigate unfamiliar and exposed terrain.

**Key words:** artificial neural network; eastern fence lizard; microhabitat; nesting; reptiles; *Sceloporus undulatus*; temperature; thermoregulation.

When a mother lays her eggs, she possibly initiates her single greatest influence on the success of her offspring (Bernardo 1996). The choice of a nesting site determines the abiotic and biotic conditions experienced by developing embryos. These early environmental conditions affect virtually all aspects of the phenotype, including behavior, physiology, morphology, survivorship, and reproduction (see reviews by Deeming and Ferguson 1991, Packard 1991, Cagle et al. 1993, Kam et al. 1996, Shine and Harlow 1996). Therefore, natural selection should favor genotypes that discriminate carefully among potential nesting sites. Yet, such discrimination requires mothers to assess environmental heterogeneity on several scales. Given the environmental effects on embryonic development, we should wonder whether mothers successfully analyze the spatial com-

plexity of their environment and identify microhabitats that maximize the performance of offspring.

Spatially implicit studies of nesting behavior indicate that mothers can direct offspring toward desirable microhabitats. For instance, insects tend to lay eggs on plants that offer better nutrition or fewer competitors (Thompson 1988; but see Nylin et al. 1996, Messina 1998, Pappers et al. 2002). Similarly, both insects and amphibians avoid laying eggs in ponds that contain predators (Resetarits 1996, 2001). Abiotic factors, such as temperature and water, also influence the sites of oviposition (Roosenburg 1996, Ward et al. 1999). Although these examples suggest that females can oviposit adaptively on a fine spatial scale, several aspects of previous research limit the strength of this inference. First, most researchers have underestimated the spatial complexity of the environment by converting continuous variables (e.g., temperature) into discrete variables (e.g., warm vs. cool patches). Second, few researchers have analyzed the selection of nesting sites in the context of the relative availability of different microhabitats. Finally, researchers who have analyzed both selected and available microhabitats have not done so in a

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spatially explicit framework. This last point seems most critical because the costs of nesting depend on the spatial distribution of preferred sites relative to the spatial distributions of other resources (e.g., food, refuge). The ability to test quantitative predictions about nesting in a spatially explicit framework should improve our understanding of the benefits, costs, and constraints that shape the evolution of this behavior.

We combined a radiotelemetric study of animal movements with a spatial mapping of environmental temperatures to test an a priori hypothesis about the nesting behavior of the eastern fence lizard (*Sceloporus undulatus*). As with any organism, the phenotype of *S. undulatus* depends strongly on the temperatures experienced during embryonic development. Relatively high temperatures speed development without affecting the size of offspring at hatching (Andrews et al. 2000, Angilletta et al. 2000, Oufiero and Angilletta 2006), yet excessive heat leads to poor survival (Sexton and Marion 1974, Angilletta et al. 2000). In contrast, hydric conditions of the nest have a much smaller effect on the phenotype; at a constant temperature of 28°C, water potentials ranging from -530 to -150 kPa did not affect the development, thermoregulation, locomotion, growth, or survival of offspring (Warner and Andrews 2002a). Based on laboratory experiments, Angilletta and colleagues (2000) concluded that lizards in New Jersey (USA) should nest in unshaded microhabitats at least 4 cm in depth. Their reasoning was simple. The high temperatures of unshaded patches would enable rapid development, while  $\geq 4$  cm depth would prevent embryos from reaching lethally high temperatures. This prediction has important implications for the spatial distribution of lizards, because unshaded patches occur rarely in forested habitats and their surfaces reach lethal temperatures for nesting females. We show that females shift microhabitats abruptly during nesting, which maximizes the probability of choosing an optimal site while minimizing the probability of experiencing a lethal temperature.

#### METHODS

During 2001 and 2002, we used radiotelemetry to monitor the movements of nesting females on a 4-ha plot in Wharton State Forest (Burlington County, New Jersey, USA). The site was marked with grid stakes every 10 m, enabling us to estimate the position of an animal to the nearest meter. The forest consisted of pitch pine (*Pinus rigida*) with an understory of scrub oak (*Quercus ilicifolia*), huckleberry (*Gaylussacia baccata*), and blueberry (*Vaccinium corymbosum*). Sandy roads and an abandoned railway transected the plot along its east-west axis, providing exposed substrates. Gravid females were captured in late May, and transmitters were glued to their dorsal surfaces. These transmitters weighed <5% of a lizard's body mass and possessed a battery life of 3-4 weeks (Model BD-2; Holohil Systems,

Ontario, Canada). Females were released at their site of capture within one hour. We used a handheld receiver to locate each female every two to three hours. Females were captured once per day between 06:00 and 09:00 to verify reproductive status by palpation. Thus, we were able to specify a narrow window of time during which nesting had occurred, even if we did not observe a female during nesting. Twenty-one females were monitored for a mean of 20 d (range = 4-31 d); nineteen of these females were monitored for at least one week before and after nesting.

Nesting sites were determined by a combination of direct and indirect observations. Because we located females at regular intervals, we observed 15 of the 21 individuals in the act of either digging a nest or laying eggs. Ovipositing females ( $n = 10$ ) did not respond to our presence; therefore, we approached these individuals slowly and placed a marker next to the nesting cavity. We excavated marked nests and measured the depth at which the eggs were deposited. For females that were not observed during oviposition ( $n = 11$ ), we estimated the location of each nest from the position of the female just after oviposition. Because distances between the locations of females before and after oviposition were very small (range = 0-3 m), estimated sites were likely to have environmental characteristics similar to those of actual sites.

During the incubation period, we measured the shading, temperature, and moisture of each nest. Canopy cover was estimated using a spherical densiometer (Model A; Forest Densimeters, Bartlesville, Oklahoma, USA). Temperature was recorded hourly by a miniature data logger (Thermochron iButton; Dallas Semiconductors, Dallas, Texas, USA); data loggers were placed in nests within two weeks of oviposition and were retrieved in the middle of August, after hatchlings had emerged. Because the data loggers were approximately the size of a lizard egg (Angilletta 1999, Angilletta and Krochmal 2003), they did not disrupt the transfer of heat between eggs and the surrounding soil. When nesting sites were estimated, data loggers were placed at the mean depth of eggs in actual nests ( $\approx 6$  cm). Soil moisture, estimated as the percentage of water, was determined from soil cores taken in late June and early August, which correspond to the beginning and end of the incubation period, respectively. We also measured the operative temperatures of nesting females using hollow copper electroforms (Bakken and Gates 1975). These physical models accurately reflect the steady-state temperatures of *S. undulatus* (Niewiarowski 2001). Pairs of models were placed within a meter of actual nests ( $n = 10$ ); one model was positioned as if it were digging a nest, and the other was positioned as if it were laying eggs (see Fig. 1A).

We compared the characteristics of nesting sites with those of 100 randomly selected locations on our study plot. At each location, we measured canopy cover, soil

temperatures, and soil moisture as we did at nesting sites. Randomization tests were performed to compare environmental conditions at nesting sites to those at random sites. These tests make no assumptions about the distributional properties of data (Manly 1997, Good 1999). First, we calculated the observed mean difference between nests and random locations. Next, values for all locations were combined and redistributed randomly as “nesting sites” and “random sites,” and a mean difference was recalculated. This procedure was performed 10 000 times. The significance of the test was reported as the proportion of mean differences from the randomized data that were greater than or equal to the observed mean difference.

To enable a spatially explicit analysis of nesting behavior, we modeled the soil temperatures of patches within the entire study plot. We used a feed-forward artificial neural network (Rumelhart et al. 1986, Lek and Guégan 1999, Basheer and Hajmeer 2000) to predict the spatial distribution of maximal soil temperatures at the mean nest depth. Other researchers have used neural networks to estimate environmental temperature because of its strong, but nonlinear, relationship with other physical characteristics of the habitat (Bryant and Shreeve 2002). Input data for the neural network consisted of red–green–blue values extracted from a digital orthophoto quadrat (Chatsworth, New Jersey, USA; 1-m resolution); the source of this image was an aerial photograph recorded on 16 April 1995, about one month before the typical onset of the nesting season. Rather than use the raw pixel values, we used ratios of each color band to all color bands to account for differences in pixel illumination that might have resulted from solar angles, cloud cover, or other factors. As training targets for the neural network, we used the soil temperatures recorded at randomly selected sites (as previously described). These data were partitioned into two sets: 80% were randomly allocated for training the model, and the remaining 20% were used as testing data to prevent overfitting of the model. Because neural networks can learn to perfectly predict data in the training set, we stopped training when the sum of squares error was minimized in the testing set. After training the neural network, we projected the spatial distribution of daily maximal temperatures by iterating the model over all pixels of the digital orthophoto quadrat. The model provided reasonably accurate estimates of soil temperature; observed temperatures of the testing sites were highly correlated with predicted temperatures ( $r = 0.82$ ; absolute deviation =  $2.6^\circ \pm 2.4^\circ\text{C}$  [mean  $\pm$  SD]). We used the resulting map to characterize the thermal quality of home ranges. To compare the use of habitat during nesting with that during other periods, we estimated two home ranges for each female. The nesting home range was defined as the minimum convex polygon of observed positions during the period of nest-site selection. The

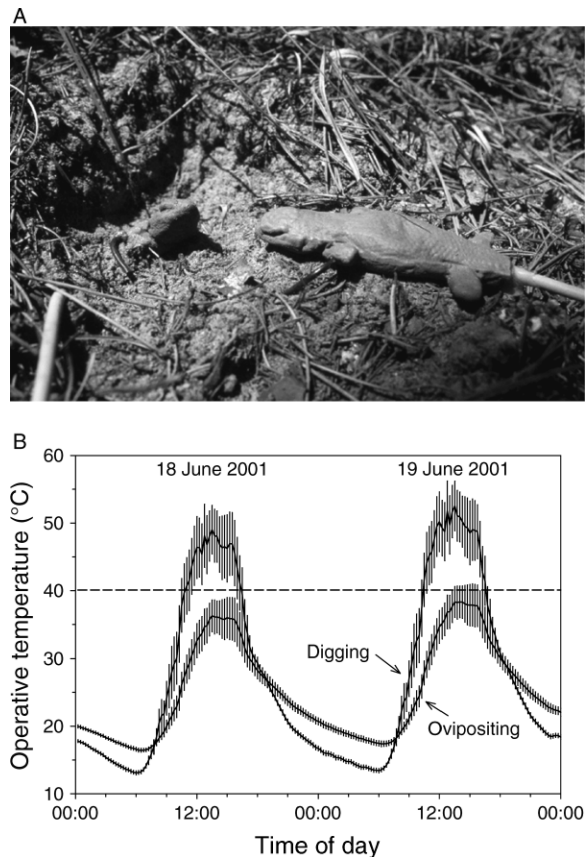


FIG. 1. (A) Operative environmental temperatures near nesting sites were recorded with physical models of lizards. At each site, one model was positioned as if it were digging a nest, and another was positioned as if it were laying eggs. (B) Operative environmental temperatures at unshaded sites prohibited nesting during most of the day. The data shown here were recorded for two clear days during the nesting period of 2001. Error bars represent 95% confidence intervals. The dashed line marks the critical thermal maximum for *Sceloporus undulatus* (Angilletta et al. 2002). Thus, lizards nesting between 10:00 and 17:00 would have reached lethal body temperatures. Operative temperatures estimated for digging females exceeded those estimated for ovipositing females because digging exposes a female's entire body to solar radiation while ovipositing exposes only the female's head to solar radiation.

non-nesting home range was defined as the minimum convex polygon of observed positions before and after this period. The nesting period was defined by a stereotypical pattern of movement, beginning 2–4 days prior to nesting and ending on the day after nesting (see *Results and discussion*). A randomization test was used to compare the daily maximal soil temperatures of nesting and non-nesting home ranges. Any spatial or environmental distinction between these home ranges would indicate that lizards nest in habitats that lie outside those habitats used for other activities.

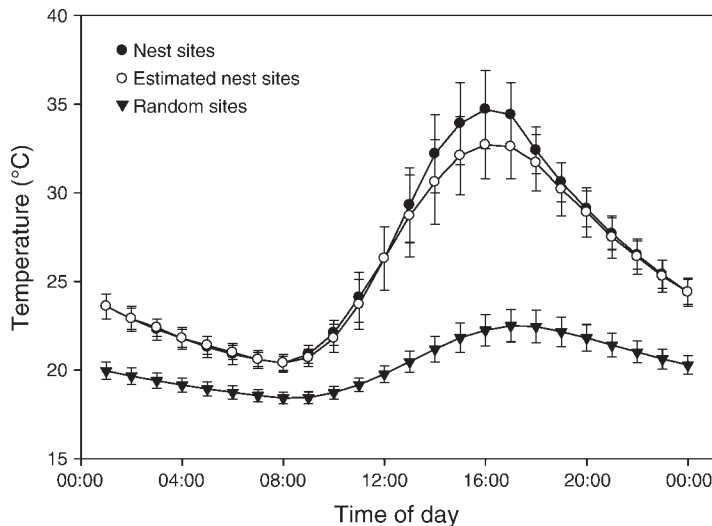


FIG. 2. Nesting sites ( $n = 10$ ) and estimated nesting sites ( $n = 11$ ) were considerably warmer than randomly selected sites ( $n = 100$ ), particularly during daylight hours. Data are mean hourly temperatures for the period between the middle of June and the middle of August. Error bars represent 95% confidence intervals.

#### RESULTS AND DISCUSSION

Observed nesting behaviors corresponded strongly with the prediction based on the thermal sensitivity of embryonic performance. First, females nested at sites with a relatively sparse canopy compared to random sites. The mean densities of canopy cover were 50% and 80% at nesting sites and random sites, respectively ( $P < 0.0001$ ). In fact, the two distributions of canopy cover overlapped very little; the upper quartile of canopy cover at nesting sites was only 56%, whereas the lower quartile of canopy cover at random sites was 75%. Second, females placed eggs at mean minimal and maximal depths of 4.7 and 6.4 cm, respectively. This correspondence between predicted and observed behaviors seems extraordinary, given that the prediction stemmed from experiments using constant temperatures instead of realistic cycles of temperature (e.g., see Oufiero and Angilletta 2006). All nesting activities that we observed occurred during the night; indeed, a lizard nesting during the day would have reached a lethal body temperature while digging its nest (Fig. 1B).

Nesting behavior provided a distinct thermal environment for embryos. At all times of the day, nesting sites were significantly warmer than random sites ( $P < 0.0001$  for each of 24 hourly periods). An average nest reached temperatures  $>28^{\circ}\text{C}$  for approximately 8 hours per day, but an average random site never exceeded  $23^{\circ}\text{C}$  (Fig. 2). Although embryos of *Sceloporus undulatus* can develop at  $23^{\circ}\text{C}$  (Andrews et al. 2000), the incubation period would be greatly extended, possibly having deleterious consequences for the fitness of offspring (Qualls and Shine 2000). Other data corroborate the significance of temperature during nest-site selection. When placed in an artificial thermal gradient, fence lizards from Virginia, USA, constructed nests that provided mean temperatures between  $23.8^{\circ}$  and  $28.2^{\circ}\text{C}$

(Warner and Andrews 2002b); these data corresponded remarkably well with the mean temperatures of nests in our study, which ranged from  $23.4^{\circ}$  to  $27.9^{\circ}\text{C}$ . Furthermore, hydric requirements were unlikely to have driven nesting behavior because the water content of soil surrounding nests ( $1.3\% \pm 0.5\%$  and  $0.4\% \pm 0.2\%$  in June and August, respectively) did not differ significantly from the water content of soil at random sites ( $5.0\% \pm 3.0\%$  and  $1.0\% \pm 0.8\%$  in June and August, respectively; both  $P \geq 0.20$ ). More likely, nesting behavior enhanced offspring success by providing embryos with temperatures that accelerate growth and development.

The beneficial temperatures of nests resulted from a marked shift in microhabitat during nesting. Just a few days before oviposition, each female moved rapidly from the interior of the forest to an area of exposure (Fig. 3). These excursions appeared to be related solely to nesting because females returned to the forest on the day after oviposition. On average, only 1% of the area used by a female during nesting overlapped with the area used before and after nesting (range = 0–8%,  $n = 19$  lizards). Researchers have documented similar shifts in microhabitat by other reptiles (Cree and Daugherty 1990, Rovero and Chelazzi 1996, Randriamahazo and Mori 2001, Shine et al. 2002). For example, many turtles favor open areas (e.g., Kolbe and Janzen 2002), which could confer greater survivorship to their offspring (Weisrock and Janzen 1999). Our spatial analysis revealed a far greater aggregation of home ranges during nesting than existed before and after nesting (Fig. 3). Females nested in a linear tract that was consistently exposed to solar radiation, thus creating a more thermally homogeneous habitat (Table 1). Although small patches within their usual home ranges could have provided similar temperatures (Fig. 3, Table 1), these ephemeral patches probably shrank as surrounding vegetation grew throughout the summer. We could test this hypothesis

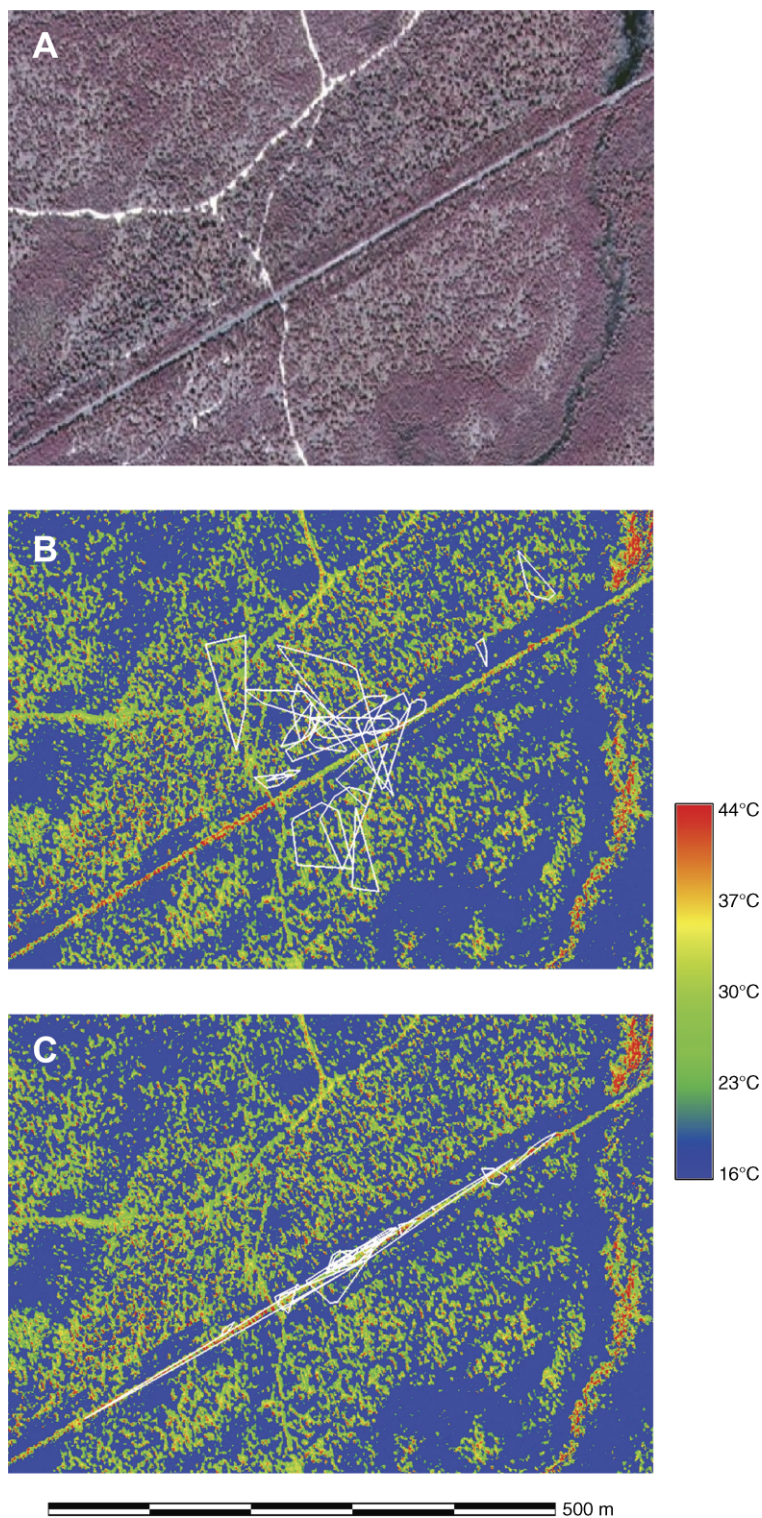


FIG. 3. An artificial neural network was used to convert (A) an aerial photograph of the study area into (B and C) a thermal map. The map shows tremendous spatial variation in the predicted daily maximum of soil temperature at a depth of 6 cm (pixel size = 1 m<sup>2</sup>). Home ranges of females ( $n = 19$ ), estimated as minimum convex polygons, were more dispersed (B) before and after nesting than they were (C) during nesting. Thermal characteristics of these home ranges are described statistically in Table 1. Females converged on an abandoned railway, which offered relatively unshaded and hot soils.

TABLE 1. Predicted thermal characteristics of the nesting and non-nesting home ranges shown in Fig. 3.

Temperature	Nesting range (°C)	Non-nesting range (°C)	P
Mean daily maximum	26.8 ± 1.0	23.6 ± 0.3	<0.0001
Minimal daily maximum	18.7 ± 1.3	17.2 ± 0.2	0.0003
Maximal daily maximum	36.2 ± 1.1	37.5 ± 0.7	0.9703

Notes: Descriptive statistics are means (and 95% confidence intervals) of the mean, minimum, and maximum of daily maximal temperature within each home range. Randomized paired *t* tests were used to compare descriptive statistics between nesting and non-nesting home ranges.

by constructing a temporal series of thermal maps from spring to fall, assuming we could obtain aerial photographs over this period.

Several lines of reasoning lead us to hypothesize that the shift in microhabitat during nesting reflected philopatry. First, females from different areas of the forest converged rapidly on a relatively restricted nesting area. Second, several females passed through other exposed areas during their migration, even though these areas offered soil temperatures that were comparable to the nesting area. Finally, fence lizards and their congeners can home over distances of 50 m or more (Ellis-Quinn and Simon 1989, Hein and Whitaker 1997), which suggests these lizards possess the ability to return to a natal site. Evolutionary models predict that philopatry should occur only in extremely stable environments (Doligez et al. 2003, Schmidt 2004). Consistent with this view, the exposed area in which lizards nested has been maintained by human activity for decades. This temporal stability could have favored a philopatric strategy over strategies based on environmental cues. Still, some females moved for a few days within the exposed area before constructing a nest. These small-scale movements could reflect a search for specific microclimates even if large-scale movements involved homing (Warner and Shine 2008). Our hypothesis about philopatry could be evaluated by transplanting eggs among habitats and observing the nesting behavior of those hatchlings that survive to reproduce.

The nesting behavior of lizards could slow the evolution of thermal physiology in a heterogeneous environment (Huey et al. 2003). If nesting females provide warm environments for their offspring, embryos would not need to grow and develop rapidly at low temperatures. This phenomenon could have important consequences for geographic variation in thermal tolerance and evolutionary responses to global warming. On the other hand, natural selection might favor both embryonic and maternal strategies that promote growth and development. In common garden experiments, embryos from cold environments (including New Jersey) hatched earlier and grew more efficiently than embryos from warm environments (Oufiero and Angilletta 2006, Niewiarowski and Angilletta 2008). These patterns indicate that embryonic physiology has played some

role in adaptation to thermal heterogeneity. Thus, we should consider the coadaptation of maternal and embryonic strategies when developing a theoretical perspective on the evolution of nesting behavior (Angilletta et al. 2005). A spatially explicit perspective of thermal ecology will likely be necessary to understand these evolutionary dynamics.

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