

Temporal and Spatial Complexity of Maternal Thermoregulation in Tropical Pythons

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ABSTRACT

Parental care is a widespread adaptation that evolved independently in a broad range of taxa. Although the dynamics by which two parents meet the developmental needs of offspring are well studied in birds, we lack understanding about the temporal and spatial complexity of parental care in taxa exhibiting female-only care, the predominant mode of parental care. Thus, we examined the behavioral and physiological mechanisms by which female water pythons *Liasis fuscus* meet a widespread developmental need (thermoregulation) in a natural setting. Although female *L. fuscus* were not facultatively thermogenic, they did use behaviors on multiple spatial scales (e.g., shifts in egg-brooding postures and surface activity patterns) to balance the thermal needs of their offspring throughout reproduction (gravidity and egg brooding). Maternal behaviors in *L. fuscus* varied by stage within reproduction and were mediated by interindividual variation in body size and fecundity. Female pythons with relatively larger clutch sizes were cooler during egg brooding, suggesting a trade-off between reproductive quantity (size of clutch) and quality (developmental temperature). In nature, caregiving parents of all taxa must navigate both extrinsic factors (temporal and spatial complexity) and intrinsic factors (body size and fecundity) to meet the needs of their offspring. Our study used a comprehensive approach that can be used as a general template for future research examining the dynamics by which parents meet other developmental needs (e.g., predation risk or energy balance).

Introduction

Parental care (any nongenetic contribution of an adult that increases the fitness of its offspring) represents an adaptation of broad importance because it has evolved independently in a broad range of taxa—from insects to mammals (Clutton-Brock 1991). Parental care often represents a parent-offspring trade-off wherein costs to parents (e.g., reduced survival or future fecundity) are offset by benefits to offspring (e.g., increased survival or growth rate). In addition to influencing the fitness of parents and offspring, parental care may be inextricably involved in other evolutionary processes, such as sexual selection (Trivers 1972) and the evolution of endothermy (Farmer 2000) and viviparity (Webb et al. 2006).

Parental care typically benefits offspring by enhancing one or several aspects of development, including offspring thermoregulation, energy balance, and predation avoidance. Parental care has been well studied in birds, where multiple parental behaviors are essential to offspring survival. Researchers have elegantly demonstrated that avian parental behavior exhibits temporal and spatial complexity (e.g., egg incubation, nest defense, and nestling provisioning) and that behavior is influenced by a number of variables, including fecundity (e.g., clutch size; Wright et al. 1998), parent-offspring communication (e.g., begging behavior in chicks; Godfray 1991), environmental factors (e.g., food availability; Chalfoun and Martin 2007), and mating system (e.g., polygamy vs. monogamy; Olson et al. 2008). Birds generally mitigate parent-offspring trade-offs by sharing parental obligations between both parents (Clutton-Brock 1991). In contrast, most caregiving taxa exhibit female-only care (reviewed in Clutton-Brock 1991; Stahlschmidt 2011). Thus, in a majority of parental care systems, maternal care alone must meet the needs of offspring despite constraints due to time (e.g., prolonged duration of care) and space (e.g., moving appreciable distances to acquire resources for offspring). Understanding the mechanisms by which females alone meet offspring needs in a natural setting may provide considerable insight into the evolution of parental care across taxa (e.g., the roles of adaptation and physical constraint).

Pythons have recently emerged as a useful model to address questions related to the mediation of parental care trade-offs. Pythonidae is an oviparous family of snakes that exhibits female-only care. Pythons display striking behavioral and physiological traits of maternal care that differentially enhance several developmental variables (e.g., embryonic thermoregulation, water balance, and predation avoidance), and these traits exhibit temporal and spatial complexity (reviewed in Stahlschmidt and DeNardo 2011). The dynamics of thermoregulatory tactics in pythons are of particular interest because py-

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thon embryos are extremely temperature sensitive (Shine et al. 1997), which is a trait shared by most other taxa (e.g., invertebrates: Moran and Woods 2007; Parker et al. 2009; other oviparous vertebrates: Deeming and Ferguson 1991; Watkins and Vraspir 2006; viviparous vertebrates: Edwards et al. 2003; Webb et al. 2006). Importantly, it is now quite feasible to quantify the thermoregulatory tactics of free-ranging animals in real time because of recent technological advances in miniature temperature data loggers (e.g., Davis et al. 2008).

As with most other squamates (lizards and snakes) that have been examined, female pythons choose nests that are thermally favorable (water python *Liasis fuscus* Peters 1873: Madsen and Shine 1999; Z. R. Stahlschmidt, R. Shine, and D. F. DeNardo, unpublished manuscript; Children's python *Antaresia childreni* Gray 1842: Stahlschmidt et al. 2011a). Regardless, female pythons also brood their eggs (fig. 1a), and this behavior can vary in intensity (e.g., duration) within and among species (e.g., Madsen and Shine 1999; reviewed in Stahlschmidt and DeNardo 2011). During egg brooding, pythons employ several physiological and behavioral thermoregulatory tactics. Some species of pythons are facultatively thermogenic and can produce heat when the nest temperature (T_{nest}) is low (Burmese python *Python molurus* Linnaeus 1758: Vinegar et al. 1970; diamond python *Morelia spilota spilota* Lacépède 1804: Harlow and Grigg 1984; Slip and Shine 1988b). In turn, this heat can raise clutch temperature (T_{clutch}) up to 7°C higher than T_{nest} (*P. molurus*; Vinegar et al. 1970). However, increasing evidence demonstrates that facultative thermogenesis is relatively rare among the Pythonidae (reviewed in Stahlschmidt and DeNardo 2011). Although most species lack significant thermogenic capability, brooding pythons can behaviorally thermoregulate their eggs in two ways. First, a brooding female can use subtle shifts in her body posture to alter thermal resistance between

the nest and clutch environments (e.g., females increase tight coiling when the nest is cooling; *A. childreni*: Stahlschmidt and DeNardo 2009a). Second, a brooding female may temporarily leave her clutch to gather heat radiated from the sun or conducted from the substrate and then return to her nest to transfer heat to her clutch (black-headed python *Aspidites melanocephalus* Krefft 1864: Johnson et al. 1975; southern African rock python *Python natalensis* Gmelin 1788: Alexander 2007).

Studies of captive pythons continue to elucidate the effects of thermoregulatory tactics on offspring at specific stages within reproduction, including during gravidity (egg bearing; Lourdaïs et al. 2008), at oviposition (Stahlschmidt et al. 2011a), and during egg brooding (Stahlschmidt and DeNardo 2009a). However, the tactics by which wild female pythons meet the thermal needs of offspring are still unclear because researchers have yet to comprehensively examine the physiological and behavioral aspects of maternal thermoregulation in a natural population of pythons. For example, wild pythons may adjust brooding posture, surface activity patterns, thermogenesis, or some combination thereof to meet the thermal needs of their embryos. Further, adjustments in maternal thermoregulatory tactics may be influenced by temporal factors (e.g., specific stages within reproduction) or fecundity-related factors (e.g., clutch size).

Thus, we use concepts and hypotheses borne out of controlled laboratory experiments as a framework to examine the behavioral and physiological mechanisms by which parents meet a widespread developmental need (thermoregulation) in a natural setting. Our approach explores the complexity (temporal and spatial) and fecundity dependence of maternal thermoregulation using real-time assessments of multiple temperature variables (surface, nest, and maternal body temperatures). Specifically, we used miniature data loggers and video methods to test four hypotheses related to how wild female *L. fuscus*

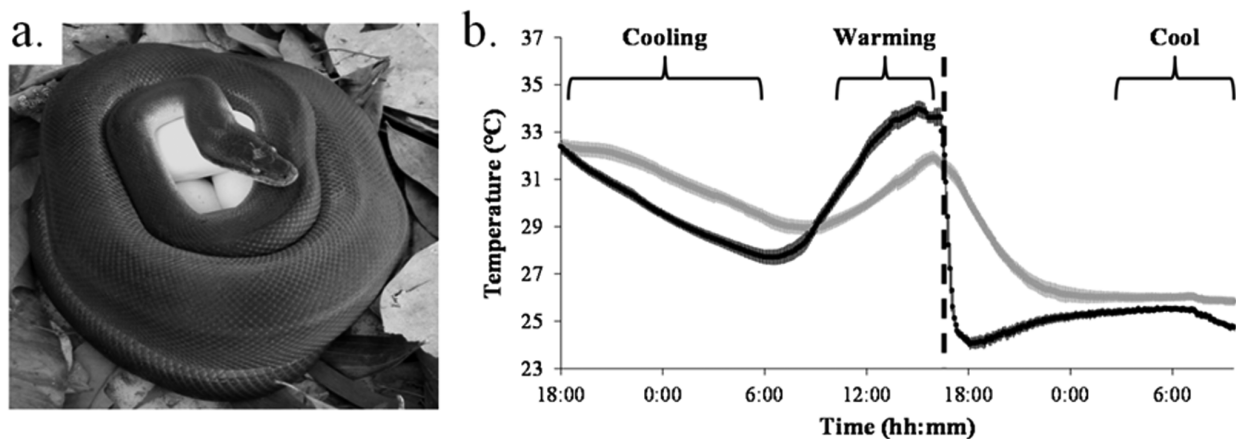


Figure 1. Egg-brooding behavior and temperature relations in the water python *Liasis fuscus*. Egg-brooding female *L. fuscus* (a) and the temperature of *L. fuscus* egg clutches (b; gray line) and nest boxes (black line) during three temperature treatments: cooling (clutch temperature > nest temperature), warming (clutch temperature < nest temperature), and constantly cool (nest at $25 \pm 1.5^\circ\text{C}$). Values are from data collected from each of nine females every 5 min and displayed as group mean \pm SEM. The dashed vertical line indicates the point at which each nest box was moved to a temperature-stable room (see text for details). Photograph by Z. R. Stahlschmidt. A color version of this figure is available in the online edition of *Physiological and Biochemical Zoology*.

adjust their body temperature (T_{body}) and what factors influence thermoregulatory shifts.

1. Egg-brooding females are not facultatively thermogenic (capable of intrinsically increasing T_{body} during egg brooding) based on available information in other pythons (reviewed in Stahlschmidt and DeNardo 2011). Thus, we predict T_{clutch} will gradually conform to T_{nest} when T_{nest} is cooling (dropping below preferred developmental temperature of 32°C; Shine et al. 1997; Lourdaïs et al. 2008).

2. During egg brooding, females assess the differential between T_{nest} and T_{clutch} and make behavioral adjustments to enhance the thermal microenvironment of their developing offspring. Nonthermogenic female *A. childreni* coil tightly around their eggs less often when the nest is warming compared with when it is cooling, which increases beneficial heat transfer into eggs during nest warming and reduces detrimental heat loss by eggs during nest cooling (Stahlschmidt and DeNardo 2009a, 2010). Thus, we predict egg-brooding *L. fuscus* females will similarly respond to shifts in T_{nest} and use fine-scale behavioral decisions to enhance the thermal environment of their developing offspring.

3. The surface activity patterns of females will vary according to reproductive state. Relative to when they are nonreproductive, reproductive female *L. fuscus* and *A. childreni* adopt warmer, more stable T_{body} (Madsen and Shine 1999; Lourdaïs et al. 2008). Additionally, reproductive females typically do not forage (Madsen and Shine 1999). Because reproductive females prioritize thermoregulation over food intake, we predict that surface activity by reproductive females will occur during the warmer parts of the day, when thermal benefits can be obtained. Contrarily, nonreproductive female activity will entail longer foraging periods at night, when their primary prey (dusky rat *Rattus colletti* Thomas 1904; Shine and Madsen 1997) is active.

4. Because females are likely under selection to maintain embryos at the optimal temperature for development, the stage within reproduction and reproductive output will influence patterns of thermoregulatory behavior. We predict that to keep embryos at or near 32°C, females will exhibit more midday surface activity during brooding than during gravidity because of stage-specific differences in the efficiency by which heat is transferred to embryos; that is, radiated or conducted heat is rapidly transferred to embryos in a gravid female during basking, whereas it is less efficiently transferred in a brooding female because a brooding female loses heat as she shuttles between basking on the surface to brooding in the nest. We also predict females with larger reproductive outputs will be larger in body size and thus will require more time on the surface to sufficiently raise T_{body} during reproduction because of thermal inertia (e.g., Shine and Madsen 1996).

Material and Methods

Study Species and Area

Liasis fuscus are large (≥ 2 m total length), semiaquatic, non-venomous snakes found throughout northern Australia (Wilson and Swan 2008). Their ecology has been intensively studied

for the past 3 decades at Fogg Dam (60 km southeast of the city of Darwin) on the Adelaide River floodplain in the wet-dry tropics (12°34'S, 131°18'E). This area is characterized by high temperatures year-round (monthly mean maximum: 31°–34°C) and highly seasonal rainfall (>75% of annual rain fall [1,300 mm] occurs during the wet season from December to March; Madsen and Shine 1996; Shine and Brown 2008). Our study area was approximately 10 km south-southeast of Fogg Dam on Beatrice Hill Farm, a government-operated cattle farm situated on the Adelaide River floodplain. Some of the snakes we caught at Beatrice Farm were animals that had been marked at Fogg Dam, suggesting some degree of interchange of individuals between the two areas. However, such interchange likely involves only a small proportion of the population (Ujvari et al. 2011). Mating in this population occurs in the dry season (July and August), with oviposition occurring 1–2 mo later (Madsen and Shine 1996).

In August 2010, we captured adult water pythons and gently manipulated each snake to ascertain its sex and reproductive status. We transported 22 gravid (egg-bearing) snakes to the laboratory at the University of Sydney's Tropical Ecology Research Facility (TERF; <10 km from the study area). We randomly assigned nine snakes to participate in the egg-brooding behavior study at TERF and assigned the remaining snakes to participate in the surface activity study at our study area. All procedures were approved by the Arizona State University Institutional Animal Care and Use Committee (protocol 08-968R) and the Northern Territory (Australia) Parks and Wildlife Commission (permit 37045).

Egg-Brooding Behavior

After capture, we housed each of the nine females in this component of the study in a 58 × 39 × 35-cm translucent container (nest box) in a building at TERF that maintained a diel cycle of approximately 27°–34°C. We kept nest boxes under dimly lit to dark conditions throughout the study to mimic the subterranean nests chosen by free-ranging females. At oviposition, a female python brings her moist eggs together. As the parchmentlike eggshells dry, the eggs adhere to one another and form a clutch conglomerate around which the female can coil and uncoil without altering the positioning of the eggs within the clutch. Within 12 h of oviposition for each female, we gently inserted a miniature temperature data logger (Thermochron iButton, model DS1921G, Maxim Integrated Products, Sunnyvale, CA) within the clutch conglomerate to record T_{clutch} every 5 min. Also at this time, we attached a temperature-humidity data logger (DS1923, Maxim Integrated Products) to the inside wall of each nest box to record the temperature and humidity of the nest environment every 5 min. We used dew point (the temperature to which air must be cooled for water condensation to occur) as our humidity metric because unlike relative humidity, dew point is directly proportional to vapor pressure independent of temperature.

We conducted all trials less than 1 wk postoviposition. To measure the effects of shifts in T_{nest} on thermal and behavioral

dynamics, we examined T_{clutch} , T_{nest} , and egg-brooding behavior in the building at TERF described above. To avoid disturbance, we monitored trials in darkness with an infrared camera and recorded real-time video for later analysis of brooding behavior.

From 1800 hours on day 1 to 0600 hours on day 2, the nest boxes were cooling, and $T_{\text{clutch}} > T_{\text{nest}}$ (fig. 1b). From 1000 to 1600 hours on day 2, the nest boxes were warming, and $T_{\text{clutch}} < T_{\text{nest}}$ (fig. 1b). After the warming treatment, we moved each nest box into a room in TERF maintained at $25^{\circ} \pm 1.5^{\circ}\text{C}$ to measure the effect of a constant cool nest on T_{clutch} and brooding behavior from 0300 to 0900 hours on day 3 (fig. 1b). After the cool treatment, we removed each female from her clutch to measure the mass of the female and clutch (± 0.1 g) and counted the number of viable shelled eggs (clutch size). We conducted each female's trial in this same order (cooling followed by warming followed by constantly cool) to (1) create a more natural dial cycle (i.e., cooling period and warming period adjacent to each other) and (2) impose a distinct change in temperature when the females were shifted to the constant cool temperature, which enabled us to assess insulatory effects of brooding.

As described previously, we categorized egg brooding into two behavior types that are strongly associated with nest-clutch thermal, hydric, and respiratory dynamics (Stahlschmidt and DeNardo 2008, 2009a, 2010; Stahlschmidt et al. 2008). We defined tight coiling to be when a female was motionless and tightly coiled around her clutch. We considered postural adjustments as individual behavioral events only if they were >30 s removed from another postural adjustment.

Surface Activity

We intracoelomically implanted each of 13 gravid snakes with a radio transmitter (13 g model SI-2, Holohil Systems, Carp, Ontario) and a miniature temperature data logger (Thermochron iButton, model DS1921G, Maxim Integrated Products) using methods similar to those described previously for rattlesnakes (Taylor et al. 2004). The temperature data loggers were programmed to collect hourly measurements of T_{body} for the duration of the study. Before each snake's recovery from anesthesia, we measured each snake's mass and snout-vent length (SVL), and we measured its clutch size using ultrasonography (Stahlschmidt et al. 2011b). We returned snakes to their location of capture within 24 h of surgery. From the snakes' release through reproduction (gravidity and egg brooding), we ascertained the location of each snake using radiotelemetry every morning (0700–1000 hours) and zero to two times per evening (1800–2100 hours). After a snake ceased brooding, we captured it and surgically removed the radio transmitter and temperature data logger. As before, we returned snakes to their location of capture within 24 h of surgery.

The interval between initial release and oviposition was the gravid period (mean \pm SEM = 32 ± 1 d). Because snakes at our area nested in inaccessible areas (typically in abandoned burrows excavated by varanid lizards), we estimated oviposition date indirectly. The captive snakes from the egg-brooding be-

havior study oviposited fairly synchronously (SEM < 2 d), so we used the mean date of oviposition by captive snakes as a proxy for the oviposition date of free-ranging snakes. The interval between oviposition and nest abandonment was the brooding period (mean \pm SEM = 37 ± 7 d). We assumed that a snake had abandoned its nest when it was away from its nest for 24 h. The interval between abandonment and final capture was the postreproductive period (mean \pm SEM = 9 ± 3 d).

Throughout the study, we measured the temperature and dew point of the surface environment (T_{surface} and $\text{DP}_{\text{surface}}$, respectively) at a single central point within the study area using another DS1923 temperature-humidity data logger. We positioned the surface environment logger 1 m above the ground and suspended it in a polyvinyl chloride pipe (12-cm diameter, 30-cm length) to reduce the effects of solar radiation. We set the logger to record hourly and uploaded the data monthly. To estimate each snake's surface activity, we used temperature-based activity estimation (TBAE; Davis et al. 2008). Briefly, we compared the profile of T_{surface} with each snake's T_{body} and considered a snake to be underground when T_{body} was relatively constant, with little to no response to changes in T_{surface} (fig. 2). Additionally, we considered the snake to have initiated surface activity when there was a sudden shift in T_{body} toward surface temperature, and we surmised the snake ended surface activity when T_{body} began to shift away from surface temperature and again became relatively constant (fig. 2). Using TBAE, we were able to estimate the frequency and duration of surface activity as well as the thermal conditions (warming or cooling) of the surface during bouts of activity. Activity bouts during warming occurred when T_{body} increased with the initiation of surface activity, while bouts during cooling occurred when T_{body} decreased with the initiation of surface activity (e.g., activity bouts in fig. 2 were during warming periods).

We also used principal components analysis to generate principal components (PC) scores for each individual's surface activity patterns at each reproductive stage based on the percentage of time each female was on the surface each hour of the day. Hourly surface activity patterns exhibited high multicollinearity (e.g., the percentage of time a female was on the surface at 0900 hours was strongly correlated with the percentage of time she was on the surface at 1000 hours). Thus, we omitted odd-numbered hours (e.g., 0100 and 0300 hours) from subsequent PC analyses. Because our data were likely not independent, we used an oblique rotation (Promax; $K = 4$) rather than an orthogonal rotation (Field 2005). The resultant eigenvalues were 10.3 for PC1 and 1.9 for PC2, and these PCs explained 79% and 14% of the variation, respectively. We elected to use only these two PCs because all subsequent PCs had eigenvalues less than 1 and explained less than 7% of the variation in the data. Generally, PC1 loaded with the overall percentage of surface activity; that is, females had higher PC1 scores if they spent more time on the surface regardless of the time of day (fig. 3). On the other hand, PC2 generally reflected diurnal basking because it loaded positively on diurnal surface activity and negatively on nocturnal surface activity (fig. 3).

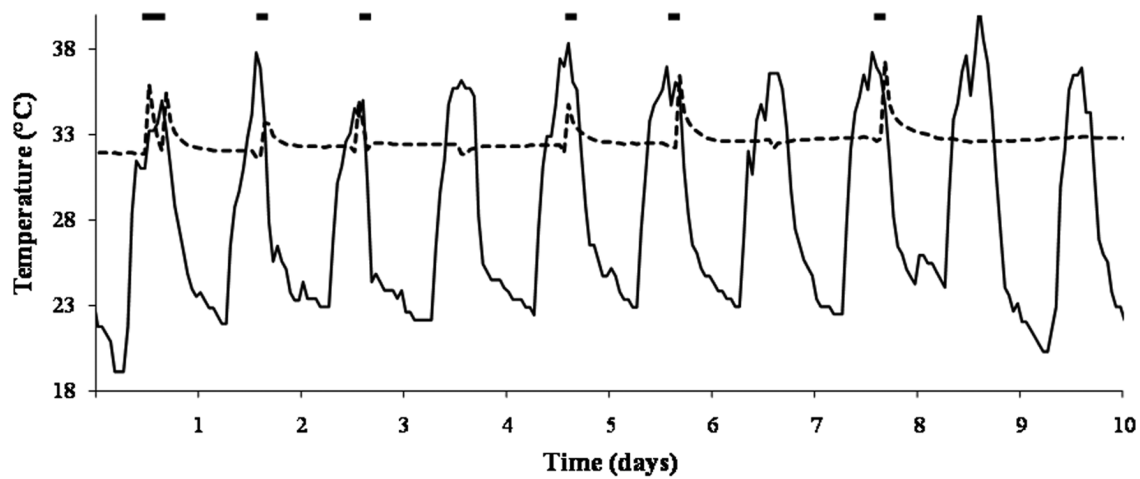


Figure 2. Hourly body temperature of one free-ranging *Liasis fuscus* female during egg brooding (dashed line) as well as the corresponding surface temperature (solid line). Most of the time, the female maintained a relatively constant body temperature and was presumed to be underground. However, initiation of surface activity can be identified by sudden shifts in body temperature toward surface temperature, and cessation of activity can be identified when body temperature shifts away from surface temperature and becomes relatively constant. Periods of surface activity are depicted by the bold horizontal lines at the top of the graph.

Nest Characteristics

To verify the ecological relevance of the conditions in our lab-based egg-brooding behavior study, we compared data from the DS1923 loggers used in the brooding behavior study with data from actual nest conditions. Using DS1923 temperature-humidity data loggers, we measured the hourly temperature and dew point of each free-ranging female's nest environment (T_{nest} and DP_{nest} , respectively) for 48-h periods beginning at three time points: 0–10 d (early incubation; mean \pm SEM = 6 ± 1 d), 26 d (middle incubation; 26 ± 0 d), and 52 d (late incubation; 52 ± 0 d) postoviposition. We housed the nest loggers in nonrigid wire mesh spheres (3–4-cm diameter) tethered to wire and inserted into the nest openings (mean \pm SEM = 49 ± 4 -cm depth). We compared the temperature and dew point of these nests during early incubation with the temperature and dew point of nest boxes during the egg-brooding behavior study that occurred over a similar period of time (<7 d postoviposition).

Statistical Analyses

Data met the appropriate assumptions of parametric statistics or were transformed as necessary and were analyzed using SPSS, version 19. We used repeated-measures ANOVA (rmANOVA) to examine differences in tight coiling due to temperature treatment (cooling, warming, and cool; within-subjects effects). We also used rmANOVA to test for differences in the percentage of time females were on the surface because of reproductive stage (gravid, egg brooding, and postbrooding; within-subjects effect), time of day (warming or cooling; within-subjects effect), and a stage \times time interaction. We also used rmANOVA to examine differences in PC1, PC2, and average values of specific

metrics of surface activity for each female (e.g., frequency of activity bouts) due to reproductive stage (within-subjects effect). In rmANOVA analyses with significant sphericity, we used χ^2 -tests with ϵ -adjusted Greenhouse-Geisser tests. For post hoc analyses, we used Bonferroni-corrected paired t -tests to correct for experiment-wise Type I error rate. To specifically test for differences in midday surface activity between gravidity and brooding for hypothesis 4, we used a paired t -test on scores

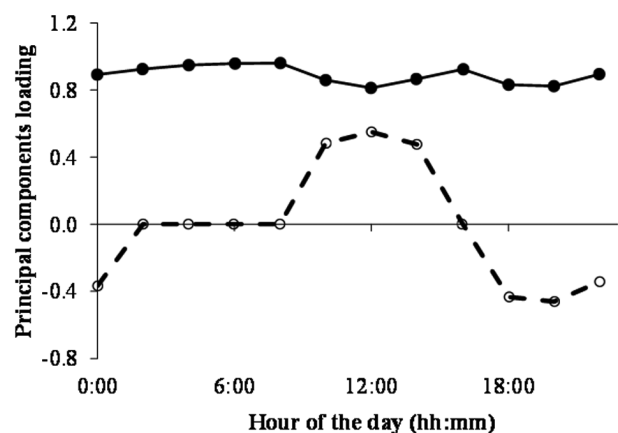


Figure 3. Principal components (PC) loadings for female *Liasis fuscus* surface activity patterns at each reproductive stage based on the percentage of time each *L. fuscus* female was on the surface each hour of the day. Greater PC1 (solid line) values correspond to greater overall percentage of surface activity regardless of the time of day. PC2 (dashed line) values generally reflected diurnal basking because PC2 loaded positively on diurnal surface activity and negatively on nocturnal surface activity.

for PC2, which is a proxy for diurnal basking (fig. 3). To test for differences between nest boxes and actual nests, we used two-sample *t*-tests. To test relationships among individuals, we used simple linear regression analysis. All values are displayed as mean \pm SEM, and two-tailed significance was determined at $\alpha < 0.05$ for all tests.

Results

Egg-Brooding Behavior

Female *Liasis fuscus* are not thermogenic during egg brooding because females could not keep T_{clutch} at or near preferred incubation temperature during the cooling and cool treatments (fig. 1b). We also did not detect any muscle contractions associated with shivering thermogenesis in facultatively thermogenic species (e.g., Vinegar et al. 1970). However, brooding females insulated their clutches sufficiently to provide some thermal buffering to their clutches during nest cooling even after 12 h of the cool treatment (fig. 1b). Tight coiling particularly provided a significant buffer to heat flux between the clutch and nest environments because the percentage of time spent tightly coiled was positively correlated with the gradient between T_{clutch} and T_{nest} during the warming treatment ($F_{1,7} = 6.8$, $P = 0.035$, $R^2 = 0.49$). The percentage of time spent tightly coiled was significantly affected by temperature treatment ($F_{2,16} = 11$, $P = 0.001$; fig. 4), and it was positively correlated with relative clutch mass (clutch mass divided by maternal mass) during the warming treatment ($F_{1,7} = 5.7$, $P = 0.049$, $R^2 = 0.45$) and overall (mean of all three temperature treatments: $F_{1,7} = 11$, $P = 0.014$, $R^2 = 0.60$). Female body size (SVL) was positively correlated with clutch size ($F_{1,7} = 18$, $P = 0.004$, $R^2 = 0.72$), clutch mass ($F_{1,7} = 40$, $P < 0.001$, $R^2 = 0.85$), relative clutch mass ($F_{1,7} = 7.2$, $P = 0.031$, $R^2 = 0.51$), and mean egg mass ($F_{1,7} = 9.7$, $P = 0.017$, $R^2 = 0.58$) but was not related to tight coiling during any temperature treatment.

Surface Activity

Females were warmer during reproduction than after reproduction ($F_{1,12} = 12$, $P = 0.004$). Post hoc analyses demonstrate that females were warmest during brooding (mean of all three incubation stages for each snake: $31.5^\circ \pm 0.2^\circ\text{C}$) followed by during gravidity ($30.3^\circ \pm 0.2^\circ\text{C}$), which was significantly higher than after reproduction ($28.9^\circ \pm 0.7^\circ\text{C}$). Reproduction also affected the standard deviation in T_{body} ($F_{1,15} = 7.8$, $P = 0.004$) whereby standard deviation during brooding ($0.9^\circ \pm 0.2^\circ\text{C}$) was lower than during gravidity ($1.5^\circ \pm 0.2^\circ\text{C}$) and after reproduction ($2.1^\circ \pm 0.3^\circ\text{C}$), and standard deviation during gravidity was similar to that during postreproduction.

Surface activity patterns were different among reproductive stages (gravidity, brooding, and postbrooding). The percentage of time females spent on the surface was affected by reproductive stage ($F_{1,13} = 8.8$, $P = 0.001$; post hoc: gravidity and brooding were lower than postbrooding), time of day ($F_{2,20} = 4.2$, $P = 0.038$), and a stage \times time interaction

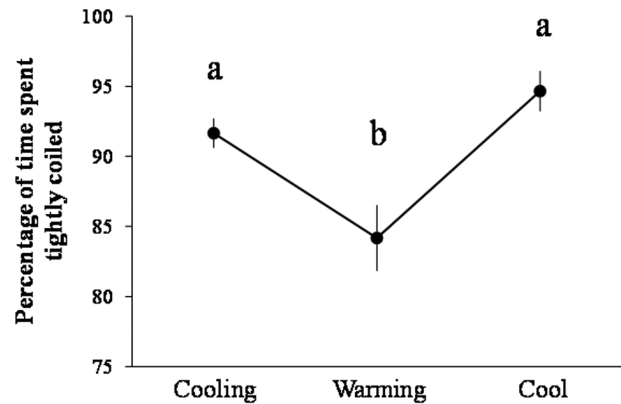


Figure 4. Temperature and egg-brooding behavior in female *Liasis fuscus*. Effect of temperature treatment on the amount of time female *L. fuscus* spent tightly coiled around their respective clutches ($n = 9$). Values are displayed as mean \pm SEM, and significant differences are denoted by lowercase letters ($a \neq b$).

($F_{4,42} = 4.0$, $P = 0.011$; fig. 5). The mean duration of surface activity was also significantly different among reproductive stages (h d^{-1} ; $F_{1,13} = 7.2$, $P = 0.018$; post hoc: gravidity and brooding were lower than postbrooding). Further, the percentage of surface activity that occurred during cooling was also significantly affected by reproductive stage ($F_{1,16} = 4.2$, $P = 0.048$; post hoc: only brooding was significantly lower than postbrooding). The frequency of all surface activity and of surface activity during cooling (bouts d^{-1}) was significantly different among reproductive stages (all: $F_{1,16} = 3.8$, $P = 0.037$; cooling: $F_{1,14} = 16$, $P = 0.001$; fig. 6a). The duration of all surface activity bouts (h bout^{-1}) was also significantly different among reproductive stages ($F_{1,13} = 7.2$, $P = 0.018$), but the duration of bouts during cooling was not significantly different among reproductive stages ($F_{1,5} = 5.2$, $P = 0.069$; fig. 6b). Thus, the total amount of time spent on the surface and the amount of time spent on the surface during cooling (h d^{-1}) were significantly affected by reproductive stage (total: $F_{1,13} = 7.5$, $P = 0.016$; cooling: $F_{1,12} = 14$, $P = 0.003$; fig. 6c).

PC analyses also revealed significant differences in surface activity due to reproductive stage. PC1, which reflected the overall percentage of time spent on the surface regardless of the time of day, was significantly affected by reproductive stage ($F_{1,15} = 4.2$, $P = 0.002$; post hoc: gravidity and brooding were lower than postbrooding). PC2, which reflected midday surface activity (diurnal basking), did not significantly vary among reproductive stages using rmANOVA ($F_{1,14} = 4.2$, $P = 0.11$). However, a pairwise comparison demonstrated that females exhibited more diurnal basking during brooding than during gravidity (PC2: $t_{12} = 2.3$, $P = 0.040$; fig. 5).

Variation in absolute clutch size was positively related to body size (SVL: $F_{1,11} = 13$, $P = 0.004$, $R^2 = 0.54$), and the variation in both of these variables was positively correlated with several metrics of surface activity during reproduction (table 2). Relative clutch size (clutch size residuals from an SVL vs. clutch

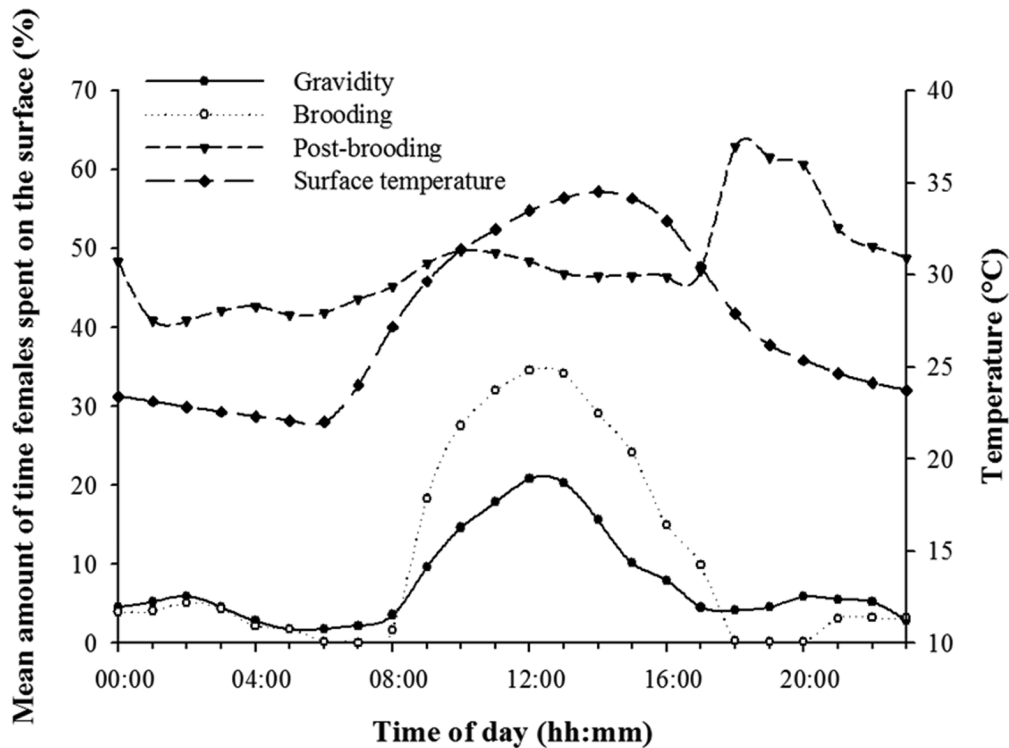


Figure 5. Surface activity patterns in female *Liasis fuscus* and corresponding surface temperature. Mean percentage of time female *L. fuscus* ($n = 13$) were on the surface each hour of the day during gravidity, egg brooding, and after egg brooding as well as the mean hourly temperature at the surface throughout the study.

size regression) was negatively correlated with mean T_{body} during brooding (table 2). However, absolute clutch size and SVL were not correlated with T_{body} (mean or variance) at any stage (table 2). After brooding, larger females tended to exhibit more surface activity during warming and less surface activity during cooling relative to their smaller counterparts (table 2).

Nest Characteristics

The nest boxes of captive females during the egg-brooding study exhibited similar daily thermal properties as actual nests during the same time period (table 1). However, nest boxes were significantly less humid than actual nests (table 1). Actual nests' maximum temperature ($F_{2,16} = 6.8$, $P = 0.007$; post hoc: early > middle) and mean temperature ($F_{2,20} = 14$, $P < 0.001$; post hoc: early > middle) varied by the stage of incubation, but dew-point variables were similar throughout incubation (table 1).

Discussion

In support of our first hypothesis, female *Liasis fuscus* were not thermogenic during egg brooding (fig. 1b). This result corroborates a growing body of literature that demonstrates facultative thermogenesis in pythons is the exception to the rule (reviewed in Stahlschmidt and DeNardo 2011). The potential rationale

for the occurrence of facultative thermogenesis in *Python molurus* and *Morelia spilota spilota* has been discussed in detail previously (Stahlschmidt and DeNardo 2011). To summarize, thermogenesis may occur in these pythons only because they live in more thermally challenging environments (e.g., higher latitude) and can minimize the appreciable costs of endogenous heat production (e.g., large body size in *P. molurus* and nest construction in *M. spilota spilota*; Stahlschmidt and DeNardo 2011). On the other hand, *L. fuscus* may not be under enough selective pressure for thermogenesis to offset the appreciable costs of endogenous heat production. For example, thermogenesis during egg brooding increases energetic expenditure by greater than 10-fold in pythons (Vinegar et al. 1970; Harlow and Grigg 1984). Alternatively or additionally, the benefits of facultative thermogenesis can be met through maternal behavior in *L. fuscus* (e.g., adaptive nest site selection: table 1; postural shifts: fig. 2; midday basking: fig. 5) and potentially in other pythons endemic to the tropics. Because *P. molurus* and *M. spilota spilota* are distantly related within Pythonidae (Rawlings et al. 2008), thermogenesis likely evolved independently in these two pythons and is a derived trait in pythons. If this is true, and behavioral thermoregulation is instead ancestral in pythons, the Pythonidae first established a close maternal-offspring relationship (prolonged embryo retention) involving shifts in maternal T_{body} to improve embryo development fol-

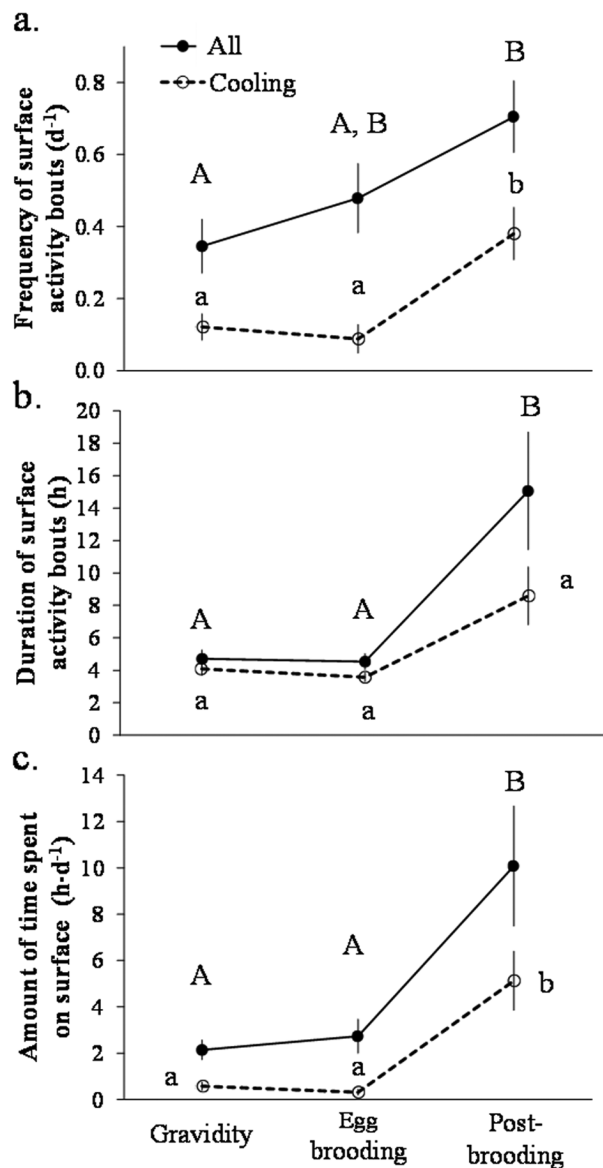


Figure 6. Surface activity metrics of *Liasis fuscus* females during and after reproduction. Frequency of surface activity bouts (a), duration of surface activity bouts (b), and amount of time spent on the surface during gravidity, egg brooding, and after egg brooding (c) in female *L. fuscus* ($n = 13$). Filled symbols represent all surface activity; open symbols represent activity bouts occurring only during cooling periods (those that resulted in decreased body temperature). Values are displayed as mean \pm SEM, and significant differences are denoted by letters ($a \neq b$, $A \neq B$).

lowed by facultative thermogenesis in support of the parental care model of the evolution of endothermy proposed by Farmer (2000).

In support of our second hypothesis and in agreement with results in *Antaresia childreni* (Stahlschmidt and DeNardo 2009a, 2010), *L. fuscus* females used subtle behavioral shifts (tight coiling and postural adjustments) to enhance T_{clutch} through alterations in thermal resistance (decreased tight coil-

ing during warming T_{nest}). Unlike *A. childreni*, *L. fuscus* females exhibited significantly greater tight coiling during constant cool T_{nest} relative to during nest warming (Stahlschmidt and DeNardo 2009a, 2010). Although the low humidity of nest boxes may have played a role in this result (see below), it may also be explained by the larger body mass and thus greater thermal inertia of *L. fuscus*. Specifically, tight coiling during prolonged periods of constant cool T_{nest} by *A. childreni* has little consequence on T_{clutch} because of the relatively low thermal buffering capacity of the relatively small *A. childreni*. Environmental temperature influences the proportion of time parents spend in their nests in other taxa, such as the duration of nest attendance bouts in birds (Conway and Martin 2000) and the rate of egg-tending bouts in fish (Green and McCormick 2005). However, the dynamics of within-nest parental behaviors (e.g., shifts in body posture in pythons) are less understood, particularly as they pertain to thermoregulation. Though not true parental care, honeybee (*Apis mellifera* Linnaeus 1758) workers are thermogenic during brood attendance and adjust their body postures to more efficiently transfer heat to pupae (Bujok et al. 2002). On the other hand, some offspring behaviorally thermoregulate within the nest (e.g., nestling birds seek shade to avoid heat-loading solar radiation; Glassey and Amos 2009). Similarly, some embryos can behaviorally thermoregulate; that is, embryos shift positions and orient toward higher temperatures within their respective eggs to increase their T_{body} (turtles; Du et al. 2011). Therefore, within-nest interactions among temperature, parental behavior, and offspring behavior may be widespread, and their investigation may be an important avenue for future research in parental care.

In support of our third hypothesis, free-ranging *L. fuscus* females adopted warmer, more stable T_{body} during reproduction (particularly egg brooding), although $T_{surface}$ during reproduction was cooler than after reproduction (Kruskal-Wallis test; mean daily $T_{surface}$: $K_2 = 28$, $P < 0.001$; minimum daily $T_{surface}$: $K_2 = 30$, $P < 0.001$; for mean and minimum: gravidity < brooding < postreproduction). Rather, reproduction-related shifts in T_{body} were due to largely limiting the time they were on the surface to midday (figs. 4, 5). Also, female surface activity after reproduction occurred more often during cooling periods (fig. 6), particularly at night (fig. 5). We attribute this shift to stage-specific motivations. During reproduction, females predominately basked during midday (fig. 5) to maintain a high T_{body} that enhances development (Shine et al. 1997; Lorigou et al. 2012). After reproduction, females were motivated to forage, which obligated surface activity during cooling periods and resulted in cooler, more variable T_{body} . Interestingly, nonreproductive females were also active during warming periods when prey were not active (fig. 5), which suggests that thermoregulation was still somewhat important after reproduction (possibly because of digestion needs). This trade-off between foraging and reproduction is common in snakes (oviparous and viviparous; reviewed in Brischoux et al. 2011) in contrast to endotherms, which typically increase foraging during reproduction to meet the increased energy demands of parental care (e.g., milk production in mammals). Anorexia during repro-

Table 1: Daily thermal and hydric characteristics of the nest boxes during the egg-brooding study on captive *Liasis fuscus* and of actual nests of free-ranging *L. fuscus* at three stages of incubation

Daily thermal and hydric characteristics (°C)	Nest boxes in captive egg-brooding study ($n = 9$)	Natural nests ($n = 13$)		
		Early	Middle	Late
Maximum temperature	34.1 \pm .3	34.4 \pm .7	30.9 \pm .5	31.8 \pm .9
Minimum temperature	27.0 \pm .8	27.2 \pm .4	26.7 \pm .4	27.6 \pm .5
Mean temperature	30.4 \pm .2	31.2 \pm .4	28.7 \pm .3	29.9 \pm .5
Maximum dew point	25.8 \pm .8 ^a	30.1 \pm .7	29.9 \pm .5	30.9 \pm .8
Minimum dew point	19.3 \pm 1.3 ^a	23.7 \pm 1.1	24.9 \pm .3	26.5 \pm .6
Mean dew point	22.8 \pm .5 ^a	27.8 \pm 1.0	27.9 \pm .3	28.8 \pm .5

Note. Early, middle, and late: mean 6, 26, and 52 d postoviposition, respectively. We statistically compared only between nest boxes and early nests because all captive measurements were taken within 1 wk of oviposition. Values are displayed as mean \pm SEM.

^aSignificantly lower than natural nests during early incubation.

duction in snakes has been attributed to adaptation (e.g., foraging during reproduction imposes increased risk of predators or detrimental shifts in the magnitude or variance of T_{body}) or physical constraint (e.g., retained or brooded eggs interfere with digestion or the efficient locomotion required for prey acquisition; reviewed in Brischoux et al. 2011). Pythons typically ingest large meals (5%–65% of body mass; Slip and Shine 1988a; Secor and Diamond 1997) of nocturnal prey (e.g., rodents), have large reproductive investments (relative clutch mass of 25%–50%; reviewed in Stahlschmidt and DeNardo 2011), and exhibit greater temperature sensitivity as embryos than as adults (e.g., Shine et al. 1997). Thus, a foraging-reproduction trade-off in pythons is likely due to thermoregulatory concerns and physical constraints.

In support of our fourth hypothesis, we detected differences in diurnality of surface activity between gravidity and egg brooding. Brooding *L. fuscus* females may restrict their surface activity to the midday because (1) they can warm up quickly during this period, (2) they can be away from their clutch during the period of the day in which T_{nest} warms the clutch, and (3) staying on the surface for a longer duration may result in costly elevated T_{body} (fig. 5). Other taxa similarly adjust their egg-attending behaviors (e.g., duration of nest-attending bouts) in response to time of day, which strongly dictates ambient temperature and dissolved oxygen concentration (birds: Conway and Martin 2000; fish: Green and McCormick 2005). Birds also shift the rate or duration of parental care behaviors because of stage within reproduction (e.g., egg incubation vs. nestling attendance; reviewed in Clutton-Brock 1991). However, to our knowledge, we present the first evidence that both diel patterns and the specific stage within reproduction can influence parental care behaviors in a taxon demonstrating female-only care (fig. 5), the most prevalent mode of parental care in internally fertilizing animals.

Also in support of our fourth hypothesis, females with larger reproductive outputs were larger and spent more time on the surface relative to less fecund, smaller females. However,

fecundity-related variation in surface activity was solely due to size because relative clutch size was not significantly correlated with any variable of surface activity (table 2). Despite increased surface activity during warming periods, larger females were not warmer than smaller females. Additionally, surface activity during warming periods was favored by larger females after reproduction. Together, these results indicate that the fecundity dependence of surface activity patterns during reproduction is simply the by-product of size-dependent fecundity and thermal inertia. However, female body size was not related to egg-brooding behavior, which demonstrates that not all fecundity-related effects on maternal behavior could be attributed to body size. Female pythons with relatively larger clutch sizes were cooler while brooding (table 2), which suggests a trade-off between reproductive quantity (size of clutch) and quality (developmental temperature). Similarly, European starling (*Sturnus vulgaris* Linnaeus 1758) parents of experimentally enlarged broods exhibit higher provisioning rates to their offspring but deliver food of lower quality (lower fat and higher ash content), which results in reduced body mass of nestlings and reduced survival of fledglings (Wright et al. 1998). Thus, many parents may navigate a similar quantity-quality trade-off, although the currency of “quality” may differ. Our results demonstrate that quantity and quality may be maintained through maternal behavior alone at one stage of development (gravidity) but not at another stage (brooding) possibly due to physical constraint (e.g., stage-specific variation in the efficiency of embryo thermoregulation), adaptation (e.g., embryo sensitivity to temperature decreases over time), or both.

Biologists strive to understand how organisms function in and respond to their natural environment by examining organism processes in controlled laboratory settings that closely mimic natural environmental conditions. Therefore, acquiring in-depth measurements of natural conditions is quite important (Calisi and Bentley 2009) but often logistically difficult or not feasible. Because we measured actual nest and surface temperatures in real time throughout reproduction, we were able

Table 2: Summary of significant relationships between maternal morphological traits and maternal surface activity patterns and body temperature during gravidity, egg brooding, and after egg brooding

	SVL	Absolute clutch size	Relative clutch size
Gravidity:			
Frequency of all surface activity (bouts d ⁻¹)	+	+	NS
Frequency of surface activity during warming (bouts d ⁻¹)	+	+	NS
Time spent on the surface during warming (h d ⁻¹)	+	+	NS
PC2 (diurnality of surface activity)	+	+	NS
Egg brooding:			
Frequency of all surface activity (bouts d ⁻¹)	+	NS	NS
Frequency of surface activity during warming (bouts d ⁻¹)	+	NS	NS
Duration of surface activity (h bout ⁻¹)	+	NS	NS
Duration of surface activity during warming (h bout ⁻¹)	+	NS	NS
Time spent on the surface during warming (h d ⁻¹)	+	NS	NS
Diurnality of surface activity (PC2)	+	NS	NS
Mean maternal body temperature	NS	NS	—
Postbrooding:			
Proportion of all surface activity bouts occurring during warming (%)	+	NS	NS
Proportion of all surface activity bouts occurring during cooling (%)	—	NS	NS

Note. SVL = snout-vent length; PC = principal component. Plus signs (+) denote positive relationships, minus signs (—) denote negative relationships, and NS denotes nonsignificant relationships.

to assess the accuracy of previous conditions at which python egg-brooding trials were performed. Experimental T_{nest} treatments used in this and previous python egg-brooding behavior studies were similar to natural nests of *L. fuscus*, but humidity treatments were lower than natural nests (Stahlschmidt and DeNardo 2008, 2009a, 2010; table 1). Low nest dew-point treatment (16°C) reduced thermal responsiveness of egg-brooding behavior in *A. childreni* (females exhibited high rates of tight coiling regardless of temperature treatment; Stahlschmidt and DeNardo 2010). Thus, our significant results of T_{nest} treatment on brooding behavior are likely still reliable, but nonsignificant results (e.g., cooling vs. constant, cool T_{nest}) require cautious interpretation (fig. 4). Like *A. childreni*, *L. fuscus* females with relatively heavy clutches coiled tightly more often. This may be interpreted as a general tactic by pythons to promote egg water balance because python eggs rapidly lose water through their parchmentlike shells when they are not brooded, and egg water loss is dramatically reduced by tight coiling (Lourdais et al. 2007; Stahlschmidt et al. 2008). Pythons also promote egg water balance through nest site selection because in nature they choose nest sites that are more humid than surface conditions (*L. fuscus*; Z. R. Stahlschmidt, R. Shine, and D. F. DeNardo, unpublished manuscript) and, when given the choice under controlled conditions, they choose more humid nest sites (*A. childreni*; Stahlschmidt et al. 2011a). However, a parental behavior may benefit one developmental need at the expense of another need (intraoffspring trade-off), and these trade-offs are relatively understudied (but see Lissaker and Kvarnemo 2006 for fish and Stahlschmidt and DeNardo 2009b for reptiles) but may play an important role in the evolution of parental care across taxa.

Together with previous research, we demonstrate that wild female *L. fuscus* balance the thermal needs of their offspring

through a suite of parental behaviors that span time (monthly: before, at, and after oviposition; hourly: diel cycle of surface activity and body postures) and space (large scale: nest site selection; moderate scale: surface activity patterns; and fine scale: egg-brooding body posture). We also demonstrate that maternal behaviors in *L. fuscus* are mediated by interindividual variation in body size and fecundity. In nature, caregiving parents of all taxa must navigate both extrinsic factors (temporal and spatial complexity) and intrinsic factors (body size and fecundity) to balance the needs of their offspring with their own needs. We investigated maternal thermoregulation because temperature sensitivity of embryos is incredibly widespread, but our study provides a useful template for future research examining the dynamics by which parents meet other developmental needs (e.g., predation risk or energy balance). Notably, maternal behavior in pythons is capable of improving as many developmental variables as the behavior of two bird parents (e.g., embryonic water balance, temperature, and predation avoidance; Stahlschmidt and DeNardo 2011; this study). Thus, we encourage the future investigation of temporal and spatial complexity in other systems of female-only parental care to develop a broader synthesis of the costs, benefits, and behavioral mechanisms of parental care across taxa.

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