

ARE FEMALES MATERNAL MANIPULATORS, SELFISH MOTHERS, OR BOTH? INSIGHT FROM PYTHONS

DALE F. DENARDO^{1,4}, OLIVIER LOURDAIS^{1,2}, AND ZACHARY R. STAHLSCHMIDT^{1,3}

¹*School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA*

²*Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934, 79360 Villiers en Bois, France*

³*Department of Psychology and Neuroscience, Dalhousie University, Halifax, NS B3H 3Z1, Canada*

ABSTRACT: During reproduction, females often modify their behavior relative to the nonreproductive condition. These changes are frequently attributed to maternal efforts to optimize offspring development and survival (i.e., the maternal manipulation hypothesis). However, Schwarzkopf and Andrews (2012) recently challenged this concept as oversimplified, emphasizing that females should optimize their own lifetime fitness, and therefore maternal efforts may be directed at the female's future reproductive effort in addition, or even in contrast, to current reproductive effort. To provide insight into the relative importance of current versus future reproductive effort in shaping maternal behavior, we systematically explore a single study system—pythons. Pythons show distinct maternal behaviors during gravidity (modified basking effort), perioviposition (nest site selection), and postoviposition (egg brooding). By examining each component, we reveal that python maternal effort is predominantly aimed at current offspring. Yet, at times, females will make decisions that benefit their future reproductive potential at a cost to their current effort. Therefore, maternal behavior likely reflects a focused effort to maximize fitness through optimizing current reproductive investment, but such effort is not without consideration of future reproductive potential.

Key words: Brooding; Maternal Manipulation Hypothesis; Parental care; Snakes; Thermoregulation

INDIVIDUAL fitness is derived from fecundity as well as offspring quality because quality highly influences survival and fitness of the offspring (Fox, 1975; Sinervo and Doughty, 1996; Madsen and Shine, 1998). Therefore, maternal physiology and behavior during reproduction have received considerable attention. Females often modify their behavior and physiology when they are reproductive. The most commonly examined adjustment, at least among ectothermic vertebrates, is altered thermoregulatory behavior when females are gravid or pregnant compared to when they are nonreproductive. This change in maternal behavior is the basis of the "maternal manipulation hypothesis" (MMH; Shine, 1995), which posits that females actively regulate developmental conditions in order to optimize offspring quality. Indeed, embryonic thermal sensitivity is a universal feature of vertebrates (Farmer, 2000), and it has been widely demonstrated that maternal thermoregulation associated with reproduction accelerates development and enhances offspring quality in support of the MMH (for review, see Shine 2006).

Recently, Schwarzkopf and Andrews (2012) provided an alternate explanation for reproduction-associated changes in behavior and physiology. They "propose, more generally than the MMH and consistent with life-history theory in general, that females should behave in ways that maximize their own lifetime reproductive success (Wilson et al., 2005; Marshall and Uller, 2007)." They went on to state that "although maximizing lifetime reproductive output does not preclude providing benefits to offspring, it may also mean that females sometimes alter their behavior in ways that are neutral, or even detrimental, to offspring fitness . . ." For consistency with Shine (2012, in this issue), we will refer to Schwarzkopf and Andrews' (2012) alternate approach as the "selfish mother hypothesis" (SMH).

Although there is limited supportive empirical data, Schwarzkopf and Andrews provided a conceptual rationale for the SMH. First, females exposed to inadequate thermal conditions in the laboratory may abort and sometimes consume their offspring (Shine and Downes, 1999; Rock and Cree, 2003), thus maximizing future reproduction over the fitness of their current offspring. In both of the referenced papers, however, the condition

⁴ CORRESPONDENCE: e-mail, denardo@asu.edu

of the offspring at the time of abortion was unknown. If the offspring were already dead at the time that the female made the decision to abort, then the action occurred after failure of the current reproductive effort. Adaptive maternal cannibalism has been demonstrated in several taxa, with females selectively consuming stillborn offspring and undeveloped ova (reviewed in Stahlschmidt and DeNardo, 2010a). Additionally, less in support of the SMH but more to deemphasize current support of the MMH, Schwarzkopf and Andrews proposed that altered thermal profiles of females during pregnancy or gravidity may simply be the result of the physical burden imposed on the female by the mass and volume of the developing offspring rather than an active thermoregulatory shift.

Rather than survey the considerable literature on ectotherm maternal efforts, we examined the merits of the MMH and SMH by limiting our assessment to a single study system—pythons. By reviewing the literature on python maternal efforts, we revealed that the regulation of maternal effort is best understood when the MMH and SMH are considered collectively. That is, the MMH correctly emphasizes the importance of current offspring fitness, but fails to recognize the importance of future reproduction in influencing maternal decisions. Contrarily, the SMH gainfully introduces the role of future reproductive success, but undervalues the predominant importance of the current reproductive effort.

INSIGHT FROM PYTHONS

Recent work on pythons has proven valuable in expanding our understanding of parental efforts (reviewed by Stahlschmidt and DeNardo, 2010a). Not surprisingly, Schwarzkopf and Andrews (2012) specifically discussed pythons. They acknowledged that “egg attendance in free-ranging water pythons creates a warmer, more stable environment for developing embryos, and includes a reproduction-related shift in behavioral thermoregulation, which improves offspring phenotype . . .” They went on to state “at the same time, prolonged egg attendance and, thus, prolonged periods of elevated T_b [body temperature], reduces females’ rates of sur-

vival and reproduction (Madsen and Shine, 1999).” They therefore concluded that “observations of brooding pythons thus support the MMH . . .”

Although nest attendance by female pythons clearly supports the MMH, python maternal care has several additional components that can also be evaluated in terms of the MMH and SMH. Egg brooding by female pythons lacks the complexity that is seen in parental care provided by birds and mammals. Brooding female pythons provide no energy resources to their offspring during brooding, as energy investment into the offspring is made during follicular development (i.e., lecithotrophy, Speake et al., 2003). Furthermore, neonatal pythons are independent, with no maternal support after hatching. Regardless of the lack of these classic facets of endotherm parental care, python maternal care has a considerable degree of complexity in its own right. Pythons use a suite of maternal behaviors that exhibit appreciable temporal and spatial complexity (e.g., Stahlschmidt et al., 2012), and influence several developmental variables (reviewed in Stahlschmidt and DeNardo, 2010a). Examining each of these maternal behaviors provides insight into further understanding the MMH and the SMH, and, in the end, suggests that these two hypotheses likely reflect coexisting rather exclusive driving forces that influence maternal effort.

Complex Egg-brooding Behavior

In the broadest sense, as pointed out by Schwarzkopf and Andrews, egg attendance in itself imposes female costs when measured either in the short term (e.g., reduced body condition, muscle mass, and performance measures; Madsen and Shine, 1999; O. Lourdais et al., 2012, personal observation) or long term (reduced survival and reduced future reproduction; Madsen and Shine, 1998). These costs to the female are countered by benefits to offspring morphology and behavior (Shine et al., 1997). Offspring benefits from maternal attendance, however, are not derived from a single behavior (i.e., “coiling” around the eggs); rather, a female uses a suite of behaviors while brooding her eggs. Most simply, coiling behavior can be

divided into two types (Stahlschmidt and DeNardo, 2008; Stahlschmidt et al., 2008; Stahlschmidt et al., in press). First, tight coiling occurs when the female's coils completely encompass the eggs, even to the point of limiting gas exchange between the eggs and the environment. Tight coiling promotes maintenance of developmental temperature (e.g., Stahlschmidt and DeNardo, 2009a; Stahlschmidt et al., in press). However, more dramatically, tight coiling limits egg desiccation (Aubret et al., 2003; Lourdaïs et al., 2007; Stahlschmidt et al., 2008). In contrast, loose coiling consists of a set of behaviors in which the female repositions her head or coils to expose varying amounts of the clutch to the nest environment. Brooding female pythons spend the majority of their time tightly coiled around their eggs, but periodically and temporarily assume a loose coiling posture (Stahlschmidt and DeNardo, 2008; Stahlschmidt et al., 2008). Such switching between tight and loose coiling most certainly would have little effect on future reproduction of the female, but this relatively minor positional shift greatly alters the developmental environment—loose coiling events elevate clutch oxygen availability, but increase water loss and heat conductance from the clutch (Stahlschmidt and DeNardo, 2008, 2009a), all parameters known to influence hatching success, morphology, and performance of neonatal pythons (Vinegar, 1973; Shine et al., 1997; Aubret et al., 2005a; Stahlschmidt and DeNardo, 2009b). Additionally, the rate of loose coiling is dynamic in that the female alters the frequency and duration of loose coiling behavior depending on nest conditions (Stahlschmidt and DeNardo, 2009a, 2010b). Therefore, this behavior manages a complex trade-off that occurs between embryonic oxygen provisioning, thermoregulation, and egg water balance. Egg brooding provides strong support for the MMH, because it clearly enhances offspring fitness, but can reduce both short-term and long-term fitness-related measures in the female (Madsen and Shine, 1998, 1999; O. Lourdaïs et al., personal observation).

Facultative Thermogenesis

Another well-documented feature of python maternal care is facultative thermogenesis, in

which an increase in brooding female metabolic rate results in increased body and clutch temperatures (Hutchison et al., 1966; Vinegar et al., 1970). Facultative thermogenesis is often referred to as shivering thermogenesis because of the conspicuous muscular twitching that occurs. However, because it is unclear whether additional mechanisms of heat production may be involved (Van Mierop and Barnard, 1976, 1978), we use the broader term facultative thermogenesis, which includes both shivering and nonshivering mechanisms of intermittent heat production (Argyropoulos and Harper, 2002). At no time other than brooding do females use facultative thermogenesis, suggesting that this physiological response is aimed at enhancing the developmental thermal environment to optimize offspring phenotype at the expense of the female's energy balance (i.e., support for the MMH).

Schwarzkopf and Andrews (2012) argued that enhanced thermoregulation (e.g., increased preferred temperature or increased thermoregulatory precision) during reproduction, as provided by facultative thermogenesis, might be for the benefit of the female more than for the benefit of the offspring, and as such may provide support for the SMH rather than the MMH. However, although there is considerable evidence for offspring benefits from tight control of the egg's thermal environment, there is no support for any such benefit to the mother. Suggesting that altered thermoregulatory effort during reproduction supports a female benefit over an offspring benefit is akin to suggesting that altered thermoregulation associated with meal consumption (e.g., Lysenko and Gillis, 1980; Touzeau and Sievert, 1993) or infection (i.e., behavioral fever, Burns et al., 1996) are not for digestion and disease resistance, respectively, but more for a female performance trait unrelated to digestion or immunity. Although both scenarios are possible, they are much less likely than the thermoregulatory changes being associated with the predominant activity at that time. Using this logic, facultative thermogenesis (and modified maternal thermal behavior in general) in pythons likely serves to buffer embryonic developmental

conditions and improve offspring quality in support of the MMH.

Facultative thermogenesis in pythons has only been documented in two species, *Python molurus* (Hutchison et al., 1966; Vinegar et al., 1970) and *Morelia spilota* (Harlow and Grigg, 1984; Slip and Shine, 1988). These species represent the two major python clades (*P. molurus* represents the Afro-Asian clade and *M. spilota* represents the Indo-Australian clade; Rawlings et al., 2008). Although most species remain to be examined, the lack of facultative thermogenesis has been documented in 11 species of pythons (Stahlschmidt and DeNardo, 2010a; Stahlschmidt et al., 2012), covering eight of the nine secondary clades of python. Interestingly, the two species known to be facultatively thermogenic represent the southernmost and northernmost species of pythons. In fact, *M. s. imbricata* and *M. s. spilota* represent the two highest-latitude subspecies of *M. spilota* (*M. s. imbricata* in southwestern Australia and *M. s. spilota* in southeastern Australia), and both of these subspecies are facultatively thermogenic (*M. s. spilota*: Slip and Shine, 1988; *M. s. imbricata*: Pearson et al., 2003). However, the conspecific *M. s. cheynei*, which is more tropical in distribution, is not facultatively thermogenic (Stahlschmidt and DeNardo, 2010a). Because facultative thermogenesis in pythons is limited to higher latitudes despite close phylogenetic relationships across latitudes, there are likely considerable metabolic costs that must be balanced with significant gain in a thermally constraining (cold) environment. In fact, the metabolic rates of *P. molurus* and *M. spilota* are 12 and 16 times greater, respectively, during brooding than during resting (*P. molurus*, Van Mierop and Barnard, 1978; *M. spilota*, Harlow and Grigg, 1984). Because nonreproductive females at the same time of year, or males, never use facultative thermogenesis, the benefit most likely is being realized by the developing embryos.

Preoviposition Maternal Efforts

Although python maternal tactics are predominantly considered postoviposition, preoviposition (i.e., gravid) behaviors also warrant attention when considering the MMH and SMH. As with many viviparous reptiles, gravid

female pythons maintain higher and more precise preferred temperatures than do nonreproductive females (Lourdais et al., 2008). Although pythons are oviparous, temperature during early development within the female substantially influences offspring phenotype. Maintaining gravid females at a thermal cycle typical of nonreproductive females detrimentally alters hatchling morphology, antipredator behavior, strength, and metabolism, even when all eggs are incubated under identical conditions (Lorion et al., 2012). Additionally, access to preferred temperature is more relevant to offspring quality than is mean temperature during development (Lorion et al., 2012). These data suggest that the maternal thermal shift during gravidity is "driven" by specific embryonic requirements. Importantly, thermally driven maternal care is nondepreciable, because offspring share the same optimum (Ladyman et al., 2003), and the gravid female has virtually no option to adjust her thermal environment without compromising her entire current reproductive effort.

Despite the positive correlation between enhanced thermoregulation and offspring phenotype, Schwarzkopf and Andrews (2012) pointed out that, while this higher preferred temperature during gravidity is often used to support the MMH, it might actually support the SMH. Higher temperatures typically lead to shorter gestation periods and reduce the duration of the physical burden of carrying the offspring. Indeed, gravid pythons maintained at the preferred temperature of reproductive females have a shorter duration of gravidity than do females maintained at a thermal cycle typical of nonreproductive females (Lorion et al., 2012). However, pythons offer additional insight into these disparate explanations. Oviposition in squamates tends to be at embryonic stages 28–30 and rarely beyond stages 32–33. However, python embryos are approximately at stage 35 at the time of oviposition (Shine, 1983; Harlow and Grigg, 1984). Based on Schwarzkopf and Andrews' (2012) rationale that females reduce the burden of reproduction by elevating body temperature to shorten gestation duration, the prolonged embryonic retention in pythons provides support for the MMH in that it imposes an extended burden

on the female. Finally, hastened embryogenesis may strongly benefit the offspring through maternal phenological effects (Wapstra et al., 2010), notably under constraining climatic conditions. In pythons, increased maternal temperature during gravidity hastens gestation and leads to an earlier hatching date (Lorion et al., 2012), which is known to increase neonate python survival (Madsen and Shine, 1998). Therefore, it is likely that modified maternal thermoregulation during gravidity simultaneously enhances offspring traits (support for the MMH) as well as shortens developmental duration (support for both the MMH and the SMH).

In addition to higher preferred body temperatures during reproduction, reproductive pythons use a specialized basking behavior. Gravid pythons will often position themselves so that the caudal half of the body is lying on a heat source in a supine position (Ross and Marzec, 1990; Lourdais et al., 2008). Thus, the heating effort is focused on the body region in which the embryos reside, which provides thermal benefits to offspring while limiting elevation in female whole-body temperature. Therefore, this behavior suggests benefits in line with the MMH rather than the SMH. However, further studies evaluating regional body temperatures are needed to evaluate the thermal implications of this behavior as well as its influence on offspring phenotype.

Nest Site Selection

The various maternal tactics used by female pythons discussed thus far are best explained by the MMH, with limited support for the SMH. However, some aspects of python reproduction clearly support the SMH. As with most oviparous reptiles, nest site selection in pythons is nonrandom, with females preferentially selecting nests based on temperature and humidity (Stahlschmidt et al., 2011). Madsen and Shine (1999) revealed that Water Pythons (*Liasis fuscus*) within a single population nest in two distinct microhabitats, root boles of paperbark trees and varanid burrow systems. The latter nest sites provide a superior thermal environment, but also pose a greater risk of egg predation and desiccation. The thermal limitations of the root boles can

be mitigated by egg brooding, yet some females lay their eggs in the warmer, higher-risk varanid burrows. These latter females typically abandon their clutches during the first week of incubation, whereas the females nesting in root boles tend to brood their eggs for the entire duration of incubation (mean = 58 d; Madsen and Shine, 1999). Furthermore, female pythons nesting in root boles tend to have reduced survivorship and future reproduction, likely as a result of the extended duration of brooding (Madsen and Shine, 1999). Therefore, selection of varanid burrows and early clutch abandonment can be better explained by the SMH than the MMH. That is, although both nest types can lead to similar offspring developmental temperatures, nest attendance would be required if the female selects root-bole nests. By selecting a varanid burrow, a female improves her chances of survival and her reproductive frequency, but increases offspring predation risk.

In a more recent study of an adjacent *L. fuscus* population where paperbark tree root boles are not present, Stahlschmidt et al. (2012b) demonstrated that females that nest in cooler retreats abandon their clutches during the first week of incubation whereas females nesting in warmer locations stay with their clutches throughout incubation. Although egg brooding would provide greater benefit to the offspring developing in cool nests, females who chose cool nests opted to abandon such nests and expose their eggs to cooler thermal regimes and increased predation risks. Furthermore, although brooding entails a small percentage of the total energy expenditure of females during reproduction (Aubret et al., 2005b; Stahlschmidt et al., 2012b), clutch abandonment benefits the female by avoiding metabolic and structural costs of brooding and increasing foraging opportunities (Madsen and Shine, 1999; Stahlschmidt et al., 2012b; O. Lourdais et al., 2012). Thus, the choice by the female to abandon her clutch promotes future reproductive effort over current effort and is better explained by the SMH than the MMH.

Summary for Python Maternal Effort

By evaluating the myriad of maternal efforts of pythons, we conclude that the behaviors of

female pythons predominantly support the MMH, but that some actions of female pythons may also be explained by the SMH. Maternal behavior is best described as a balance between benefits to reproduction (improved offspring quality) and benefits to the female's future reproductive success. This presumption that maternal behaviors result from a trade-off between current and future reproductive effort is similar to the balance seen in energy investment. It has long been accepted that optimal energy allocation by females into reproduction (e.g., clutch mass) balances current and future reproductive performance. Individuals that make a larger investment into a current reproductive effort tend to have lower survivorship and future reproduction than those that make a more limited current investment (Madsen and Shine, 2000). In fact, extremely high costs of current reproduction in snakes can lead to semelparity (Bonnet et al., 2002). Because maternal behavior, like maternal energy investment, can be detrimental to future reproductive success, it is logical to expect that maternal behaviors similarly represent a trade-off between current and future reproductive success.

Although pythons are atypical among ectotherms in the complexity of maternal effort provided, it is unlikely that they are unique among reptiles in having the majority of their maternal effort being best explained by the MMH. Instead, the complexity of maternal effort in pythons provides a rare opportunity to examine the MMH and SMH at multiple levels in a single study system. Postoviposition egg brooding by pythons is among the most convincing evidence for the MMH. Attributing python preoviposition maternal effort to the MMH is less absolute, but the driving force for maternal effort is similar before and after oviposition. That is, regardless of developmental stage, offspring phenotype is enhanced when developmental temperature is above that preferred by a nonreproductive female. As result, gravid and brooding females selectively provide the offspring with a warmer, more stable developmental environment. To our knowledge, however, there is no evidence that maintaining warmer, more

stable body temperatures during gravidity or brooding benefits female pythons.

RECOMMENDATIONS FOR FUTURE RESEARCH

Future research should embrace the conceptual value of both the MMH and SMH, and not become consumed by either hypothesis to the point at which the other is ignored. Optimally, studies examining the motivation and implications associated with parental strategies should attempt to evaluate offspring fitness as well as female benefits, particularly as they pertain to future reproductive effort. However, offspring fitness and female lifetime reproductive fitness are difficult to evaluate singly, let alone together. Therefore, although Schwarzkopf and Andrews (2012) argued that fully testing the MMH requires knowing "the preferred temperature and thermoregulatory precision of females when gravid, the preferred temperature and precision when not gravid, and the effects of variation in these parameters on both females and offspring," it is sensible for logistical reasons for studies to focus on one aspect of reproductive effort and to use short-term assessments as predictive metrics of true offspring and female fitness.

Schwarzkopf and Andrews proposed that one revealing test would be to apply physical burdens (e.g., implanting weights) on nonreproductive females to determine whether the burden itself is responsible for the observed changes in female thermal profiles and behavior during reproduction. While we see value in examining the potential for thermal changes associated with reproduction being simply attributable to the physical burden, we also see problems with such a test. First, the "burden" of reproduction goes beyond that of mass and volume, as there are critical energetic and vascular demands that burden the female during reproduction. Second, many reptiles are capital breeders in that the energy to support reproductive effort comes from current energy stores. Thus, the mass of pregnant or gravid females often approximates their mass prior to the onset of the reproductive bout. Therefore, adding to a nonreproductive female weights equivalent in mass to the clutch would not accurately mirror the mass burden experienced by a reproductive female.

Despite the lack of substantial mass gain, reproductive females often show reduced locomotor performance, which is likely due to the redistribution of mass as well as the reallocation of energy from tissue vital to locomotion (e.g., muscle) to the offspring (Lourdais et al., 2004). Schwarzkopf and Andrews suggested that the response to an experimentally applied physical burden should be graded (heavier burdens having greater effects on performance and thermal profiles), and that such a result would challenge the MMH. We suggest that a simpler and more direct approach to evaluating the role of the "physical burden" of reproduction in influencing behavior and thermal profiles would be to determine whether reproduction-associated changes in behavior and thermoregulation are correlated with clutch mass. That is, are the responses graded to the mass of the clutch as Schwarzkopf and Andrews (2012) predicted they would be for the masses of the implanted loads? Lack of such a correlation would challenge the simplistic physical-burden hypothesis.

Along with Shine (2012), we also encourage work on thermal heterogeneity. Temperature should be measured at multiple internal locations of both reproductive and nonreproductive females with the locations coinciding with critical organ (e.g., brain, heart, liver, and oviduct). The elongate form of snakes makes them exceptional models for such a study. Although behavioral observations of regional basking by snakes suggest that reproductive females target their developing offspring, there would be stronger support for the MMH if temperature differences between nonreproductive and reproductive females were greatest at the oviduct.

No one study can fully test a hypothesis, but carefully designed yet reasonably feasible studies can provide considerable insight into the validity of a given hypothesis or idea. In accepting the need for experimental simplification for logistical reasons, one must also acknowledge the limitations that experimental constraints have on the results. Acknowledging and accommodating experimental logistics is especially important for testing hypotheses that address a topic as ubiquitous as lifetime fitness.

CONCLUSIONS

Animals are complex organisms, and, as such, few behavioral or physiological responses are isolated events. Instead, most responses, whether considered adaptive or not, provide some benefit but also have consequential impacts, if not detriments, on other aspects of an animal's biology. Schwarzkopf and Andrews (2012) stated that "some researchers separate 'adaptive maternal effects' (defined as those maternal effects that increase offspring fitness; Bernardo, 1996) from maternal effects that are neutral or have negative effects on offspring fitness, which are often interpreted as physiologically unavoidable (e.g., Fox and Czesak, 2000)." We propose that even individual maternal behaviors can be seen as adaptive, yet also entail negative effects to offspring. For example, tight coiling by female pythons benefits offspring thermoregulation and water balance, but it also creates a hypoxic environment that can alter offspring metabolism, morphology, and performance. Loose coiling, on the other hand, has the opposite effects. Therefore, effective brooding entails a combination of the two postures to solve complex developmental trade-offs (Stahlschmidt and DeNardo, 2008; Stahlschmidt et al., 2008). Yet even dynamic coiling behavior has inherent costs to the offspring. That is, while the thermal and hydric conditions provided by brooding enhance offspring phenotype, the processes involved in providing these benefits have unavoidable costs due to hypoxia (Stahlschmidt and DeNardo, 2008, 2009a).

As brooding pythons use a suite of behavioral and physiological responses to address trade-offs between critical developmental conditions, it is reasonable to suspect that female maternal behavior also entails trade-offs to optimize both current and future reproductive output. Because the impact on maternal behaviors is more likely to be realized by current rather than future offspring, it can be expected that maternal behaviors would emphasize current offspring. Yet, as demonstrated by nest site selection in pythons, current maternal decisions are associated with long-term reproductive fitness. Therefore, while experimental designs might focus on either the MMH or the SMH, it is

imperative to keep both hypotheses in mind in order for our understanding of maternal decisions to progress.

Acknowledgments.—First and foremost we thank L. Schwarzkopf and R.M. Andrews for their insightful contribution that promotes an open-minded approach to scientific inquiry. We also thank the editors of *Herpetologica* for inviting this response as well as the National Science Foundation, the Arizona State University School of Life Sciences, and the Fyssen Foundation for supporting our scientific efforts. Additionally, we wish to thank the many colleagues who have contributed to the broadening of our understanding of python maternal care.

LITERATURE CITED

- Argyropoulos, G., and M. Harper. 2002. Invited review: Uncoupling proteins and thermoregulation. *Journal of Applied Physiology* 92:2187–2198.
- Aubret, F., X. Bonnet, R. Shine, and S. Maumelat. 2003. Clutch size manipulation, hatching success and offspring phenotype in the Ball Python (*Python regius*). *Biological Journal of the Linnean Society* 78:263–272.
- Aubret, F., X. Bonnet, R. Shine, and S. Maumelat. 2005a. Why do female Ball Pythons (*Python regius*) coil so tightly around their eggs? *Evolutionary Ecology Research* 7:743–758.
- Aubret, F., X. Bonnet, R. Shine, and S. Maumelat. 2005b. Energy expenditure for parental care may be trivial for brooding pythons, *Python regius*. *Animal Behaviour* 69:1043–1053.
- Bernardo, J. 1996. Maternal effects in ecology. *American Zoologist* 36:83–105.
- Bonnet, X., O. Lourdais, R. Shine, and G. Naulleau. 2002. Reproduction in a typical capital breeder: Cost, currencies and complications in the Asp Viper (*Vipera aspis*). *Ecology* 83:2124–2135.
- Burns, C., A. Ramos, and A. Muchlinski. 1996. Fever response in North American snakes. *Journal of Herpetology* 30:133–139.
- Farmer, C. 2000. Parental care: Key to understanding endothermy and other convergent features in birds and mammals. *American Naturalist* 155:326–334.
- Fox, C.W., and M.E. Czesak. 2000. Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology* 45:341–369.
- Fox, S.F. 1975. Natural selection on morphological phenotypes of the lizard *Uta stansburiana*. *Evolution* 29:95–107.
- Harlow, P., and G. Grigg. 1984. Shivering thermogenesis in a brooding Diamond Python, *Python spilotes spilotes*. *Copeia* 1984:959–965.
- Hutchison, V.H., H.G. Dowling, and A. Vinegar. 1966. Thermoregulation in a brooding female Indian Python, *Python molurus bivittatus*. *Science* 151:694–696.
- Ladyman, M., X. Bonnet, O. Lourdais, D. Bradshaw, and G. Naulleau. 2003. Gestation, thermoregulation and metabolism in a viviparous snake, *Vipera aspis*: Evidence for fecundity-independent costs. *Physiological and Biochemical Zoology* 76:497–510.
- Lorion, S., D.F. DeNardo, R. Gorelick, and O. Lourdais. 2012. Maternal influences on early development: Preferred temperature prior to oviposition hastens embryogenesis and enhances offspring traits in the Children's Python (*Antaresia childreni*). *Journal of Experimental Biology* 215:1346–1353.
- Lourdais, O., F. Brischoux, D.F. DeNardo, and R. Shine. 2004. Protein catabolism in pregnant snakes (*Epicrates cenchria maurus* Boidae) compromises musculature and performance after reproduction. *Journal of Comparative Physiology B* 174:383–391.
- Lourdais, O., T. Hoffman, and D.F. DeNardo. 2007. Maternal brooding in the Children's Python (*Antaresia childreni*) promotes egg water balance. *Journal of Comparative Physiology B* 177:569–577.
- Lourdais, O., B. Heulin, and D.F. DeNardo. 2008. Thermoregulation during gravidity in the Children's Python (*Antaresia childreni*): A test of the preadaptation hypothesis for maternal thermophily in snakes. *Biological Journal of the Linnean Society* 93:499–508.
- Lourdais, O., S. Lorion, and D.F. DeNardo. 2012. Structural and performance costs of reproduction in a pure capital breeder, the children's python, *Antaresia childreni*. *Physiological and Biochemical Zoology*. In press.
- Lysenko, S., and J.E. Gillis. 1980. The effects of ingestive status on the thermoregulatory behavior of *Thamnophis sirtalis sirtalis* and *Thamnophis sirtalis parietalis*. *Journal of Herpetology* 14:155–159.
- Madsen, T., and R. Shine. 1998. Quantity or quality? Determinants of maternal reproductive success in tropical pythons (*Liasis fuscus*). *Proceedings of the Royal Society of London B* 265:1521–1525.
- Madsen, T., and R. Shine. 1999. Life history consequences of nest-site variation in tropical pythons (*Liasis fuscus*). *Ecology* 80:989–997.
- Madsen, T., and R. Shine. 2000. Energy versus risk: Costs of reproduction in free-ranging pythons in tropical Australia. *Austral Ecology* 25:670–675.
- Marshall, D.J., and T. Uller. 2007. When is a maternal effect adaptive? *Oikos* 116:1957–1963.
- Pearson, D., R. Shine, and A. Williams. 2003. Thermal biology of large snakes in cool climates: A radio-telemetric study of Carpet Pythons (*Morelia spilota imbricata*) in south-western Australia. *Journal of Thermal Biology* 28:117–131.
- Rawlings, L.H., D.L. Rabowsky, S.C. Donnellan, and M.N. Hutchison. 2008. Python phylogenetics: Inference from morphology and mitochondrial DNA. *Biological Journal of the Linnean Society* 93:603–619.
- Rock, J., and A. Cree. 2003. Intraspecific variation in the effect of temperature on pregnancy in the viviparous gecko *Hoplodactylus maculatus*. *Herpetologica* 59:8–22.
- Ross, R.A., and G. Marzec. 1990. The Reproductive Husbandry of Pythons and Boas. Institute for Herpetological Research, USA.
- Schwarzkopf, L., and R.M. Andrews. 2012. Are moms manipulative or just selfish? Evaluating the “maternal manipulation hypothesis” and implications for life-history studies of reptiles. *Herpetologica* 68:147–159.
- Shine, R. 1983. Reptilian reproductive modes: The oviparity–viviparity continuum. *Herpetologica* 39:1–8.
- Shine, R. 1995. A new hypothesis for the evolution of viviparity in reptiles. *American Naturalist* 145:809–823.
- Shine, R. 2006. Is increased maternal basking an adaptation or a pre-adaptation to viviparity in lizards? *Journal of Experimental Zoology* 305A:524–535.

- Shine, R. 2012. Manipulative mothers and selective forces: The effects of reproduction on thermoregulation in reptiles. *Herpetologica* 68:289–298.
- Shine, R., and S.J. Downes. 1999. Can pregnant lizards adjust their offspring phenotypes to environmental conditions? *Oecologia* 119:1–8.
- Shine, R., T.R.L. Madsen, M.J. Elphick, and P.S. Harlow. 1997. The influence of nest temperatures and maternal brooding on hatchling phenotypes of water pythons. *Ecology* 78:1713–1721.
- Sinervo, B., and P. Doughty. 1996. Interactive effects of offspring size and timing of reproduction on offspring reproduction: Experimental, maternal, and quantitative genetic aspects. *Evolution* 50:1314–1327.
- Slip, D.J., and R. Shine. 1988. Reptilian endothermy: A field study of thermoregulation by brooding pythons. *Journal of Zoology (London)* 216:367–378.
- Speake, B.K., M.B. Thompson, F.E. Thacker, and G.S. Bedford. 2003. Distribution of lipids from the yolk to the tissues during development of the Water Python (*Liasis fuscus*). *Journal of Comparative Physiology B* 173:541–547.
- Stahlschmidt, Z.R., and D.F. DeNardo. 2008. Alternating egg brooding behaviors create and modulate a hypoxic developmental micro-environment in Children's Pythons (*Antaresia childreni*). *Journal of Experimental Biology* 211:1535–1540.
- Stahlschmidt, Z.R., and D.F. DeNardo. 2009a. Effect of nest temperature on egg-brooding behavior, metabolism, and clutch-nest thermal relations in Children's Pythons (*Antaresia childreni*). *Physiology and Behavior* 98:302–306.
- Stahlschmidt, Z.R., and D.F. DeNardo. 2009b. Obligate costs of parental care to offspring: Egg-brooding induced hypoxia creates smaller, slower, and weaker python offspring. *Biological Journal of the Linnean Society* 98:414–421.
- Stahlschmidt, Z.R., and D.F. DeNardo. 2010a. Parental care in snakes. Pp. 673–702 in R. D. Aldridge, and D. M. Sever (Eds.), *Reproductive Biology and Phylogeny of Snakes*. Science Publishers Inc., USA.
- Stahlschmidt, Z.R., and D.F. DeNardo. 2010b. Parental behavior in pythons is responsive to both the hydric and thermal dynamics of the nest. *Journal of Experimental Biology* 213:1691–1696.
- Stahlschmidt, Z.R., T.C.M. Hoffman, and D.F. DeNardo. 2008. Postural shifts during egg-brooding and their impact on egg water balance in Children's Pythons (*Antaresia childreni*). *Ethology* 114:1113–1121.
- Stahlschmidt, Z.R., J.A. Brashears, and D.F. DeNardo. 2011. The role of temperature and humidity in python nest-site selection. *Animal Behaviour* 81:1077–1081.
- Stahlschmidt, Z.R., R. Shine, and D.F. DeNardo. 2012a. Temporal and spatial complexity of maternal thermoregulation in tropical pythons. *Physiological and Biochemical Zoology* 85:219–230.
- Stahlschmidt, Z.R., R. Shine, and D.F. DeNardo. 2012b. The consequences of alternative parental care tactics in free-ranging pythons (*Liasis fuscus*) in tropical Australia. *Functional Ecology* 26:812–821.
- Touzeau, T., and L.M. Sievert. 1993. Postprandial thermophily in Rough Green Snakes (*Ophedrys aestivus*). *Copeia* 1993:1174–1176.
- Van Mierop, L.H.S., and S.M. Barnard. 1976. Thermoregulation in a brooding female *Python molurus bivittatus* (Serpentes: Boidae). *Copeia* 1976:398–401.
- Van Mierop, L.H.S., and S.M. Barnard. 1978. Further observations on thermogenesis in the brooding female *Python molurus bivittatus* (Serpentes: Boidae). *Copeia* 1978:615–621.
- Vinegar, A. 1973. The effects of temperature on the growth and development of embryos of the Indian Python, *Python molurus* (Reptilia: Serpentes: Boidae). *Copeia* 1973:171–173.
- Vinegar, A., V.H. Hutchison, and H.C. Dowling. 1970. Metabolism, energetics, and thermoregulation during brooding of snakes of genus *Python* (Reptilia, Boidae). *Zoologica* 55:19–48.
- Wapstra, E., T. Uller, G.M. While, M. Olsson, and R. Shine. 2010. Giving offspring a head start in life: Field and experimental evidence for selection on maternal basking behaviour in lizards. *Journal of Evolutionary Biology* 23:651–657.
- Wilson, A.J., J.G. Pilkington, J.M. Pemberton, D.W. Coltman, A.D.J. Overall, K.A. Byrne, and L.E.B. Kruuk. 2005. Selection on mothers and offspring: Whose phenotype is it and does it matter? *Evolution* 59:451–463.

Accepted: 17 May 2012

Associate Editor: Stephen Mullin

Copyright of Herpetologica is the property of Allen Press Publishing Services Inc. and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.