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BIBLIOGRAPHIC INFORMATION

Call Number:
Title: Reproductive biology and phylogeny of snakes /
ISBN: 9781578087013 (hardcover)
Imprint: Enfield, NH : Science Publishers ; Boca Raton, FL : Marketed and distributed by CRC Press, c2011.
Series: Reproductive biology and phylogeny ; v. 9.
Article Author: Stahlschmidt, Zachary
Article Title: Parental care in snakes.
Date: 2010
Pages: 673-702
Verified: <TN:126282><ODYSSEY:141.165.185.57/ILL> OCLC

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Parental Care in Snakes

Zachary R. Stahlschmidt and Dale F. DeNardo

18.1 INTRODUCTION

Broadly defined, parental care refers to any non-genetic contribution by a parent that appears likely to increase the fitness of its offspring (modified from Clutton-Brock 1991). This includes behavioral and physiological traits that occur before, during, and after parition (used to collectively define oviposition and parturition, Smith 1975). Similar to other components of life history, parental care is characterized by tradeoffs, including the classic concept of parent-offspring tradeoffs, as well intra-offspring tradeoffs, which result from different offspring needs requiring conflicting parental behaviors.

Despite these tradeoffs, parental care can provide considerable selective advantages. Thus, parental care, particularly parental attendance of eggs or offspring, is remarkably widespread across the animal kingdom (Clutton-Brock 1991). Despite its costs to future reproductive success, nest-attending parents can increase their current reproductive success by reducing embryonic predation (frogs, Townsend 1986), improving egg water balance (skinks, Somma and Fawcett 1989), thermoregulating embryos (bumblebees, Heinrich 1979), promoting embryonic respiration (fish, Lissaker and Kvarnemo 2006), reducing pathogen infiltration of eggs (crickets, West and Alexander 1963), and provisioning offspring with food (birds, Clutton-Brock 1991). Further, female-only parental care is the predominant mode of care in internally fertilizing vertebrates (e.g., reptiles and mammals, Clutton-Brock 1991) including species within major taxa in which external fertilization predominates (i.e., fish and amphibians, Gross and Shine 1981), as well as terrestrial arthropods (Zeh and Smith 1985). In this broad context, post-paritive parental care (i.e., care provided after oviposition or parturition) in snakes may be particularly relevant as it is overwhelmingly represented by female-only parental attendance. While this chapter emphasizes post-paritive parental care in snakes, it also summarize

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pre-paritive parental care for completeness. This chapter concludes also highlights python egg brooding, because of the preponderance of data in this taxon relative to other snakes groups. We conclude with suggestions for future directions in the study of snake parental care.

18.2 PRE-PARITIVE PARENTAL CARE

Non-genetic parental contributions to offspring fitness begin well before parition, and such early forms of parental care are widespread among vertebrates, including snakes. The influence of pre-paritive parental care in snakes is often profound and encompasses multiple variables important to offspring development and quality. Thus, for simplicity, we review the dynamics of snake pre-paritive care in relation to two well-studied developmental variables, energy balance and thermoregulation. We then follow with a discussion on the oviparity-viviparity continuum before summarizing nest site selection in snakes.

18.2.1 Energy Balance

While a ubiquitous requirement regardless of taxon or reproductive mode, energy investment for embryonic development is a significant form of parental care as the extent of investment can vary and affect future reproductive success (Clutton-Brock 1991). Most notably, females must provide their offspring with sufficient energy reserves to allow for development at least until parition. However, the source and timing of these nutrients can vary. In lecithotrophy, nutrients are invested prior to fertilization in the form of follicular yolk, whereas matrotrophy refers to the provisioning of nutrients post-fertilization via another mechanism (e.g., placenta or uterine secretions) (Wourms 1981). While all energy provisioning to offspring by reptiles is pre-paritive, the majority of nutrient utilization by oviparous offspring occurs post-paritively. Moreover, energy provided pre-paritively typically exceeds that required to support development until hatching (e.g., Ji et al. 1997a; Speake et al. 2003). Prior to hatching, offspring absorb excess nutrients to support neonatal maintenance and growth, which enhances neonate survival (Ji et al. 1997a, b, 1999).

Energy stores in neonatal reptiles consist of two forms, residual yolk and stored lipids in adipose tissue. The partitioning of energy reserves between residual yolk and adipose tissue probably reflects the relative advantages of these two sites for the neonate. Mobilization of fats from adipose tissue is very rapid, whereas yolk provides a more versatile store as it contains lipids, protein, vitamins, and minerals (Speake et al. 2003). In general, hatchling snakes contain more residual yolk than do hatchling lizards (snakes: 11–25% and lizards: 0–12% of the total hatchling dry mass, Cai et al. 2007), and this energy resource may confer an adaptive advantage. For example, residual yolk and fat bodies in hatchling Water Pythons (Liasis fuscus) make up approximately 10% and 30%, respectively, of the

initial egg lipids (Speake et al. 2003), and these substantial reserves enable these neonates to survive for several weeks without feeding (Bedford and Christian 2001). As with other hatchling phenotype variables, abiotic factors can affect the amounts of residual yolk and stored lipid (e.g., incubation temperature in the Bullsnake (Pituophis catenifer sayi, Gutzke and Packard 1987). However, in this same study, hydric conditions of the incubation environment did not have an effect on energy reserves at hatching. Less is known about residual yolk content of viviparous offspring. However, neonatal Red-backed Ratsnakes (Elaphe rufodorsata) had a total lipid content of 22% (Xiang 1995), which is similar to that of oviparous snakes.

While macronutrients receive the vast majority of scientific interest, yolk contains other components that affect offspring fitness among reptiles. A few of these components including minerals (Ji et al. 1997a, b, 1999), immunoglobins (Hassl 2005a, b), antioxidants (reviewed in Thompson and Speake 2004), and defensive toxins (Hutchinson et al. 2008) have received some attention in snakes. However, their adaptive significance, provisioning dynamics, and phylogenetic context are poorly understood.

18.2.2 Thermoregulation

Thermal sensitivity is a nearly universal feature of biochemical processes; thus, temperature influences many facets of an organism's life (Huey and Kingsolver 1989; Hochachka and Somero 2002). Effects related to temperature begin during embryogenesis. In fact, temperature has been shown to affect snake developmental rate, hatching success, and offspring phenotype (Burger and Zappalorti 1988; Deeming and Ferguson 1991; O'Donnell and Arnold 2005; Webb et al. 2006). Furthermore, the effects of developmental temperature can have long-lasting consequences on individual growth, developmental stability, and fitness (Shine 2004; Webb et al. 2006). Thus, snakes have developed multiple parental strategies to reduce potentially deleterious environmental impacts on their progeny. Although ectothermic vertebrates produce negligible metabolic heat, they can promote thermal regulation of their developing offspring. Notable pre-paritive parental thermoregulatory strategies include behavioral thermoregulation and temperature-based selection of nest sites (Tu and Hutchison 1994; Charland 1995; Shine 1995; Shine and Harlow 1996; Chiaraviglio 2006). Despite their benefits to offspring, reproduction-related shifts in behavioral thermoregulation likely incur fitness-related costs to mothers similar to other forms of parental care (e.g., increased energy requirements due to temperature-induced elevations in metabolism result in increased risk of maternal predation, Bonnet et al. 2002; Ladyman et al. 2003).

Although the discussion of maternal thermoregulation and its resulting benefits to the offspring is often restricted to viviparous species, oviparous squamates (lizards and snakes) provide similar pre-paritive parental care to their embryos for at least part of development. Unlike what is seen in

other reptiles, at least one-fourth of embryonic development in oviparous squamates is completed in the oviduct prior to oviposition (Shine 1983; Blackburn 1985; Andrews 2004). Such intra-oviductal development allows oviparous squamates to behaviorally regulate the thermal conditions experienced by the embryos during a significant proportion of early development. Shine (2006) recently proposed a pre-adaptation hypothesis, according to which modified maternal thermoregulation observed in viviparous species would be an extension of a pre-existing behavior in oviparous species. An experimental study on the Eastern Three-lined Skink (*Bassiana duperreyi*) suggests that maternal thermophily before oviposition influences the developmental rate as well as the phenotypic traits of offspring (Shine 2006). This hypothesis is likely applicable to snakes, as basking is more frequent, body temperature higher, and/or body temperature is less variable in gravid female Montpellier Snakes (*Malpolon monspessulanus*, Blazquez 1995), *Liasis fuscus* (Shine and Madsen 1996), Ratsnakes (*Pantherophis obsoletus* complex, Blouin-Demers and Weatherhead 2001), and Children's Pythons (*Antaresia childreni*, Lourdais et al. 2008), but see Isaac and Gregory (2004) for an instance of lower and more variable body temperature in gravid Grass Snakes (*Natrix natrix*).

18.2.3 Costs and Benefits along the Oviparity-Viviparity Continuum

Reproductive mode influences the degree to which females regulate the developmental environment of their offspring. Viviparity within squamates has evolved on more than 100 occasions (Blackburn 1985; Shine 1985), and the selective force responsible for these repeated transitions is probably linked to improved developmental conditions (Shine 1995). Comparative analyses by Shine (1985) have demonstrated that the transitions to viviparity have primarily occurred in cold climates where maternal thermoregulation benefits incubation temperature. This supports a "cold climate hypothesis" for the evolution of viviparity (Mell 1929; Weekes 1933; Sergeev 1940). However, to address the presence of large numbers of viviparous species in the tropics, Shine (1995) proposed a more broad "maternal manipulation hypothesis" whereby females enhance fitness-relevant phenotypic traits of their offspring by manipulating thermal conditions of the developmental environment (Shine 1995). This latter hypothesis incorporates the ability of females to maintain a different and or more stable developmental temperature regardless of climate, and thus explains the existence of viviparity in tropical climates. In support of the maternal manipulation hypothesis, female body temperature has been shown to be higher, less variable, or both during reproduction in a diverse group of viviparous snakes, including the Northern Pacific Rattlesnake (*Crotalus oreganus oreganus*, Gier et al. 1989), Prairie Rattlesnake (*Crotalus viridis*, Charland and Gregory 1990; Graves and Duvall 1995), Diamond-backed Watersnake (*Nerodia rhombifer*, Tu and Hutchison 1994), Terrestrial and Common Gartersnake (*Thamnophis elegans* and *Thamnophis sirtalis*, Charland 1995),

Northern Watersnake (*Nerodia sipedon*, Brown and Weatherhead 2000), Aspic Viper (*Vipera aspis*, Ladyman et al. 2003), Northern Death Adder (*Acanthophis praelongus*, Webb et al. 2006), and Argentine Boa Constrictor (*Boa constrictor occidentalis*, Chiaraviglio 2006).

While improved developmental conditions were likely a common driving force for the evolution of viviparity, viviparity itself should be considered a reproductive mode rather than a form of pre-paritive parental care (contra Clutton-Brock 1991; Gans 1996). This is not to discount the importance that reproductive mode has on pre-paritive parental care. As discussed previously, maternal thermoregulation is an important pre-paritive parental behavior of snakes. Although this behavior occurs in both oviparous and viviparous species, the duration of this behavior is greatly influenced by reproductive mode. While viviparous species can use behavioral thermoregulation to regulate the developmental environment throughout development, this parental behavior is only available for the first one-quarter to one-third of development in oviparous species.

Similarly, viviparity also influences female provisioning to offspring. In species where some degree of matrotrophy exists, viviparity provides females with an extended opportunity to provide energy and other nutrients to offspring. While not discussed earlier, water is also a critical material provided to offspring (reviewed in Belinsky et al. 2004). While all females must make some degree of water investment into their offspring, the parchment or elastic, ectohydric shell typical of all oviparous snakes allows for water absorption from the environment and thus may reduce water investment demands on the female (at least in moist nest environments) (reviewed in Belinsky et al. 2004). In contrast, viviparity requires females to invest the full allotment of water required for offspring development. While likely more hydrically demanding, viviparity provides the offspring greater independence from environmental hydric conditions. Thus, hydroregulation is likely another form of pre-paritive parental care that is affected by mode of reproduction.

Beyond its effects on provisioning offspring and regulating the developmental environment, viviparity also impacts other aspects of life history. Viviparity may reduce predatory risk to the developing offspring but may exacerbate the predatory risk of the female as a result (Bonnet et al. 2002; Ladyman et al. 2003). Lastly, because viviparity reduces the demands for the environment to provide a suitable developmental environment, choice of parition site may be less critical in viviparous species, although see the following discussion on nest site selection.

18.2.4 Nest Site Selection

Nest site selection is an important form of pre-paritive parental care as post-oviposition nest conditions influence the developmental environment in the majority of snakes studied. For example, the magnitude or variability of nest temperature has been shown to affect offspring phenotypic traits

associated with fitness in a diverse group of snakes including the Pinesnake (*Pituophis melanoleucus*, Burger 1998), Bullsnake (*Pituophis catenifer sayi*, Gutzke and Packard 1987), Eastern Racer (*Coluber constrictor*, Burger 1990), Eastern Kingsnake (*Lampropeltis getula*, Burger 1990), *Liasis fuscus* (Shine *et al.* 1997), Chinese Cobra (*Naja atra*, Ji and Du 2001), Five-pace Pit Viper (*Deinagkistrodon acutus*, Lin *et al.* 2005), Keelback Snake (*Tropidonophis mairii*, Brown and Shine 2006), and Ratsnakes (*Pantherophis obsoletus* complex, Patterson and Blouin-Demers 2008). Further, the hydric characteristics of the nest (i.e., nest humidity or the water content/potential of nest substrate) affect offspring phenotype in *P. catenifer sayi* (Gutzke and Packard 1987), the Rough Greensnakes (*Opheodrys aestivus*, Plummer and Snell 1988), *T. mairii* (Brown and Shine 2006), and Children's Python (*Antaresia childreni*, Lourdais *et al.* 2007).

Not unexpectedly, some snakes demonstrate adaptive nest site selection in response to abiotic factors, particularly hydric conditions (e.g., *Opheodrys aestivus*, Plummer and Snell 1988; *Tropidonophis mairii*, Brown and Shine 2006). The physical characteristics of the nest may also influence adaptive nest site selection as gravid *Pituophis melanoleucus* choose nest sites with soft soil in minimally shaded locations (potentially due to these sites' favorable thermal or hydric properties) (Burger and Zappalorti 1986). However, "perfect" nest site selection may not be possible in some instances. For example, free-ranging *Liasis fuscus* choose between nest sites that are thermally favorable but vulnerable to predation, or nest sites that are thermally poor but minimally vulnerable to predation (Madsen and Shine 1999). Also, the co-variation between soil temperature and water content due to depth (i.e., deeper nests are cooler but moister) may force female snakes to navigate a temperature-hydration tradeoff in some systems.

Biotic factors may also influence nest site selection decisions. Many snakes reportedly nest communally, including the Texas Threadsnake (*Leptotyphlops* [=*Rena*] *dulcis*, Hibbard 1964) Copperheads (*Agkistrodon contortrix*, Palmer and Braswell 1995), and at least 13 species of colubrids (reviewed in Swain and Smith 1978; Doody *et al.* 2009). To our knowledge, its significance has not been tested in snakes; yet, communal nesting reduces nest-clutch water flux and results in larger, faster offspring in scincid lizards (Radder and Shine 2007). Physical remains of successful prior incubation (e.g., eggshells) also influences nest site selection in some snakes (i.e., *Opheodrys aestivus*, Plummer 1981; *Pituophis melanoleucus*, Burger and Zappalorti 1992; *Tropidinophis mairii*, Brown and Shine 2005). In particular, some female snakes have a tendency to choose nest sites that they themselves had either hatched from or used in the past, including *O. aestivus* (Plummer 1981), *P. melanoleucus* (Burger and Zappalorti 1992), *T. mairii* (Brown and Shine 2007), *Liasis fuscus* (Madsen and Shine 1999), and the Western Whip Snake (*Hierophis viridiflavus*, Filippi *et al.* 2007). Although nest site selection related to chemosensory cues may be generally adaptive, it does not seem to be "perfect" in all cases. For example, *T. mairii* are just as likely to oviposit in the nest of an egg predator (Slatey-grey Snake,

Stegonotus cucullatus) as they are to oviposit in the nest of a conspecific (Brown and Shine 2005). Clearly, the roles of biotic (e.g., chemosensory) cues in snake nest site selection need to be investigated in more depth.

Additionally, some snakes reportedly construct or excavate sites prior to oviposition, and such nest site manipulation is often related to other types of parental behavior. For example, gravid *Pituophis melanoleucus* excavate nest substrate prior to oviposition and choose soft, sandy nest sites that are easier to excavate than sites obstructed by roots (Burger and Zappalorti 1986). Further, biparental nest excavation has been reported in cobras (reviewed in Somma 2003a). Notably, the notion of bi-parental care in snakes has traditionally been viewed with skepticism due to conflicting results (Shine 1988). However, if the reports are accurate, this combination may persist because parents are more likely to invest in additional parental behaviors if the parent-specific costs of care are reduced, or parents may be under selection to enhance the developmental environment (e.g., thermal or hydric properties of the nest) as much as possible if they choose to invest in nest-attending behaviors. The latter hypothesis appears to be the case for female Diamond Pythons (*Morelia spilota spilota*) as they construct insulated incubation mounds before investing heavily into thermogenic egg brooding behavior (Slip and Shine 1988). Thus, nest site manipulation in snakes may be due to physical constraints (e.g., the feasibility of substrate excavation), the mediation of parent-offspring tradeoffs (e.g., substantial increase of offspring benefits at minimal cost to the parent[s]), or both.

18.3 POST-PARITIVE PARENTAL CARE

Oftentimes, discussion of parental care is limited to events that occur after parturition or oviposition (e.g., Greene *et al.* 2002; Somma 2003a). Such post-paritive parental care is a major component of reproductive strategies in both birds and mammals. In fact, it has been proposed that the ability to provide parental care was the primary driving force for the independent evolution of endothermy in both birds and mammals (Farmer 2000; Koteja 2000). Post-paritive parental care is also common in some ectotherm lineages, including fish, salamanders, and crocodilians. While post-paritive parental care is not as widespread among snakes as pre-paritive care, it has been documented in a relatively diverse number of snakes and even appears to be ubiquitous in some groups. This section provides an overview of parental care among snakes, but in no way attempts to be an all inclusive review. Extremely comprehensive works on post-paritive parental care in non-crocodilian reptiles and viperid snakes are provided in the exceptional works by Somma (2003a, b, c) and Greene *et al.* (2002), respectively.

In most snake families, post-paritive parental care has been documented only sporadically or not at all. Generally, details of parental provisioning are limited and, although sometimes speculated, the functional costs and benefits of parental care mostly remain unexplored. Most commonly,

post-paritive parental care entails the female remaining with her clutch or neonates for some period of time after parition, and the duration of attendance greatly varies among species and even within species. Such behavior is reportedly uncommon in Boidae, Colubridae, and Leptotyphlopidae, common but not ubiquitous in Elapidae, but appears to be ubiquitous or nearly so in the Pythonidae and Crotalinae (Fitch 1970; Somma 2003a, b, c, d).

18.3.1 Care of Eggs

Variable terminology has been devoted to describing reptilian egg care, including (but not limited to): "brood defended", "coil around brood", "egg attendance", "egg brooding", "egg guarding", "false brooding", "nest attendance", "nest guarding", "passive protection" (Shine 1988; Somma 1988, 2003a). After reviewing the literature, Somma (1988) and Blackburn (1994) conclude that it is best to follow Peters (1964) as well as Carpenter and Ferguson (1977) in defining "brooding" as any situation where the female remains with the eggs after oviposition. However, "brooding" has also been used as a subset of such situations to identify only those cases where the egg attendance provides thermoregulatory benefits (Campbell and Quinn 1975; Lillywhite 2008). Because the vast majority of the reports of snakes remaining with their eggs after oviposition provide little to no empirical evidence of function, we opt to describe this behaviorial trait as "egg attendance" because this term has no history in the literature of suggesting a functional role. We limit our use of "brooding" to those instances of egg attendance where physiological benefits have been documented. In doing so, our use of brooding is in line with both the broader (e.g., Peters 1964; Carpenter and Ferguson 1977) and more specific (e.g., Campbell and Quinn 1975) definitions, and thus avoids confusion.

Reports of egg attendance are numerous, particularly within the Colubridae, Elapidae, Pythonidae, and Crotalinae, and have been thoroughly reviewed by Fitch (1970), Shine (1988), and Somma (2003a, b, c). However, as noted by these authors, many of the reports within the Colubridae and Elapidae are anecdotal observations based on small sample sizes (e.g., Forest Cobra [*Naja melanoleuca*], Haagner 1990, N = 1; Blue Beauty Snake [*Orthriophis taeniura*], Humphrey 2000, N = 1), found in nonrefereed publications (e.g., Eastern Milksnake [*Lampropeltis triangulum triangulum*], Winstel 1991), not primary observations (e.g., Rainbow Snake [*Farancia erytrogramma*], Mitchell 1994; *Naja atra*, Spitting Cobra [*Naja siamensis*], Monocled Cobra [*Naja kaouthia*], Lim Leong Keng and Lee Tat-Mong 1989), or some combination thereof. Further, the details of primary accounts are often insufficient. As one of many examples, Winstel (1991) wrote the following regarding *L. t. triangulum*: "Females typically remained with the eggs." Such wording may have referred to the proportion of females who remained with their eggs or the amount of time females spent with their eggs. Further, the spatial relationship between the attending female and her eggs is unclear.

However, some reports within the Colubridae and Elapidae are more reliable and insightful. Female Skaapstekers (*Psammophylax rhombeatus* and *Psammophylax variabilis*) reportedly coil around their eggs for up to six weeks (reviewed in Broadley 1977). Similarly, despite being in a non-refereed publication, picture evidence supports claims that *Orthriophis taeniura* may remain with their clutch until hatching, only leaving the clutch periodically to drink (Humphrey 2000). Furthermore, a single account of egg attendance within the Leptotyphlopidae is of special interest because this family is ancestral among snakes (Greene 1997; Slowinski and Lawson 2002), and the egg attendance was associated with communal nesting (i.e., multiple egg-attending females were found in close proximity of each other) (Texas Threadsnake, [*Leptotyphlops* {=Rena} *dulcis*], Hibbard 1964).

It is unclear whether the sporadic reports of egg attendance within the Colubridae, Elapidae, and Leptotyphlopidae accurately reflect that the behavior is relatively uncommon in these lineages or whether it reflects a need for a much more expansive exploration into this phenomenon among these and other lineages. Despite the relatively secretive nature of snakes, especially during parition, egg attendance has been documented widely among the Pythonidae, oviparous Afro-Asian Elapidae, and the Crotalinae (Wall 1921; Pope 1935; Smith 1943; Fitch 1970; Shine 1988; Greene *et al.* 2002; Somma 2003a, b, c).

Egg attendance has been documented in every species of python (Somma 2003a, b; Weigel pers. com.), and the behavior is atypical from that of most other reports of snake egg attendance in that the females tightly coil around their clutch. In fact, female pythons coil so effectively around their clutches that oftentimes the eggs are barely visible, if at all (Fig. 18.1). As there is a considerable and growing body of literature on post-paritive parental care in pythons, we will discuss python parental care more in-depth in a later section.
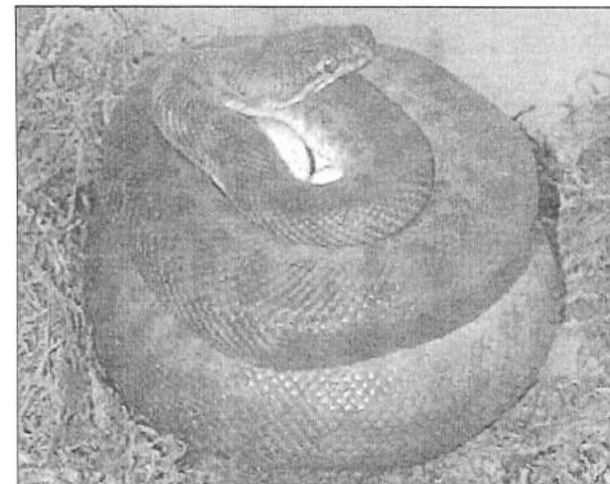

Fig. 18.1 A female Children's Python (*Antaresia childreni*) in a tightly coiled egg brooding posture.

Although not documented in all oviparous species of the diverse Crotalinae, egg attendance has been widely documented in this group including in the few existing oviparous New World pit vipers and numerous Old World pit vipers (reviewed in Greene *et al.* 2002). In some cases, the egg attendance was atypically tight, much like that seen in pythons (Ripa 1994). As a result of its wide occurrence within the Crotalinae, egg attendance likely originated at or prior to the origin of the ancestral oviparous crotaline at least 23 mya (Greene *et al.* 2002). Interestingly, while pit vipers are members of the Viperidae, egg attendance in the Viperinae (the other sub-family of the viperids) is extremely rare. The only report of egg attendance in a viperine snake is in the primitive Rhombic Night Adder (*Causus rhombeatus*), which coils around its eggs throughout incubation (FitzSimons 1912). Why egg attendance is so prevalent in Pythonidae and Crotalinae is unclear, as these groups are both phylogenetically and ecological quite distinct from each other. It has been theorized that parental care should characterize organisms that are especially capable of defense (Shine 1988), and most pythons and pit vipers clearly have such abilities. However, such theory does not explain the prevalence of post-paritive parental care in the more diminutive python species, and, more importantly, the lack of post-paritive parental care in the viperines (Greene *et al.* 2002).

Of interest but yet unknown relevance is the fact that both the Pythonidae and Crotalinae possess heat-sensing organs, an otherwise uncommon trait among snakes (but also present in some Boidae). While it has been postulated that female pythons use their heat-sensing organs to monitor clutch temperature (G. Schuett in Kend 1997), there is no evidence that elucidates whether these organs enabled the evolution of this relatively complex post-paritive parental care, evolved as a result of existing post-paritive parental care, or function completely independent of post-paritive parental.

18.3.2 Care of Neonates

Akin to egg attendance in oviparous species, neonate attendance has been reported in some viviparous snakes. While there are sporadic reports of neonate attendance with limited detail in other snake taxa (see Somma 2003a for review), neonate attendance is most prevalent and best described in the Crotalinae (see Greene *et al.* 2002 for a thorough review). This distinction may in some part reflect a greater attention of scientists toward pit vipers. Yet, it is worth noting that neonate attendance has been documented in 17 species of North American crotalines, but there are no documented accounts of attendance in any of the 36 species of viviparous natricine snakes in the United States (Greene *et al.* 2002).

Neonate attendance appears nearly or completely ubiquitous among temperate viviparous crotalines, but it is absent in tropical viviparous crotalines. Accordingly, the Neotropical Rattlesnake (*Crotalus durissus*) is the lone rattlesnake species with a lowland tropical distribution and the only rattlesnake known to lack neonate attendance. Similar to the pattern in the prevalence of egg attendance, offspring attendance has not been convincingly documented in the Viperinae, despite being common in the Crotalinae. While neonate attendance has been alleged in the Adder (*Vipera berus*), it has not been observed by numerous researchers who are highly experienced with this species (Greene *et al.* 2002).

In viviparous pit vipers, neonate attendance seems to consistently last from parturition until the first ecdysis (i.e., skin shedding) of the neonates, which is about one to two weeks post-parturition for most species. Coincidently, neonates of *Crotalus durissus*, the lone rattlesnake species where neonate attendance has not been documented, shed within 24 hours after birth (Reinert, reported in Greene *et al.* 2002). While the female and neonates might move around the oviposition site (e.g., emerge from and retreat into a subterranean refuge), females and their litters do not depart from the oviposition site until after neonatal ecdysis wherein each individual departs on its own (reviewed in Greene *et al.* 2002).

Post-paritive care is apparently a common component of reproductive behavior among pit vipers regardless of reproductive mode. As hatchling snakes also show a neonatal ecdysis typically several days after emergence, it is interesting to consider whether egg-attending female snakes show pre-ecdysis neonatal attendance. Field observations of egg-attending females also attending newly hatched offspring has been recorded in the Southern African Rock Python (*Python natalensis*, Alexander 2004; Alexander and Marais 2007) and the Malayan Pit Viper (*Calloselasma rhodostoma*, Hill *et al.* 2006). Whether or not the existence of a short-term interaction with newly hatched neonates is common in these species, let alone other egg-attending species, is unknown.

18.3.3 Oophagy

Oophagy and the consumption of stillborn neonates is reportedly widespread among viviparous snakes, including Bimini Island Boas (*Epicrates striatus*, Huff 1980), Rainbow Tree Boas (*E. cenchria*, Groves 1981; Lourdais *et al.* 2005), Green Anacondas (*Eunectes murinus*, Holmstrom and Behler 1981), Amazon Tree Boas (*Corallus hortulanus*, Miller 1983; Jes 1984), Yellow Anacondas (*E. notaeus*, Townson 1985), Egyptian Sand Boas (*Gongylophis colubrinus*, Ross and Marzec 1990), Cantils (*Agkistrodon bilineatus*, Mitchell and Groves 1993), Abaco Island Boas (*Epicrates exsul*, Tolson and Henderson 1993), and Mexican Lance-headed Rattlesnakes (*Crotalus polystictus*, Deloya *et al.* 2009). Oophagy has been hypothesized to reduce chemical cues that could attract predators (Groves 1981; Polis 1981; Shine 1988) or reduce fungal infestation of healthy eggs or neonates (Polis 1981). An alternative hypothesis posits that it may not be a parental care behavior but, rather, function as a means to facilitate post-parturition energy recovery (Lourdais *et al.* 2005). In Iberian Rock Lizards (*Iberolacerta monticola*), the presence of unfertilized eggs did not affect mold proliferation

or clutch predation of viable eggs (Moreira and Barata 2005). Alternatively, research in *E. cenchria* and *C. polystictus* demonstrated that oophagy does help post-parturient females recover otherwise wasted energy (Lourdais *et al.* 2005; Deloya *et al.* 2009). In sum, while there is some evidence that oophagy and the consumption of stillborn neonates in snakes benefits female energy balance, there is not yet any evidence for a benefit to the offspring. Thus, oophagy should likely not be considered a parental care behavior until offspring benefits are verified by further research.

18.3.4 Function of Post-paritive Attendance

Contrary to some literature (e.g., Clutton-Brock 1991; Gardiner 2002), post-paritive parental attendance occurs sporadically across diverse lineages of snakes (Pope 1935; Fitch 1970; Greene *et al.* 2002; Somma 2003a). In fact, post-paritive parental care is the rule, and not the exception, in some lineages (e.g., pythons and pit vipers). Because parental behaviors are generally viewed as adaptive (Clutton-Brock 1991), the benefits to the offspring are assumed to outweigh the costs to the parent. As in Trivers (1974), the dynamics of a parent-offspring tradeoff may be resolved in the context of a benefit:cost model (Fig. 18.2). Parental attendance may be relatively beneficial and, thus, persist for a certain period of time. However, over time the costs may exceed the benefits; thus, attendance should desist at some optimal point in time ($T_{optimal}$) (Fig. 18.2). While the significance of adaptations can be tested in a present context (Reeve and Sherman 1993), data regarding offspring benefits and parental costs derived from post-paritive attendance in snakes are only beginning to accumulate. Unfortunately, the vast majority of reports of post-paritive attendance in non-pythonid snakes are limited to descriptive observations. When focusing
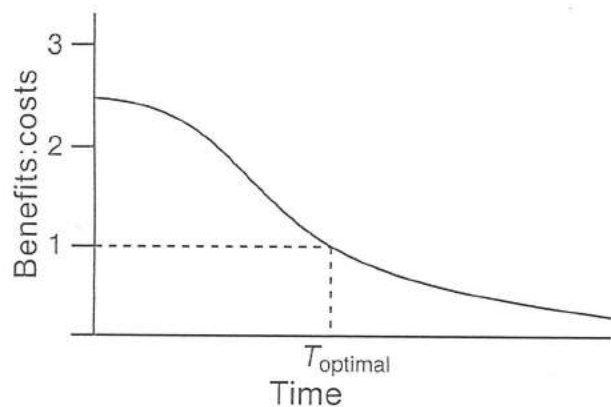

Fig. 18.2 Benefit:cost ratio of offspring attendance as a function of time. Benefits are measured in units of reproductive success to offspring while costs are measured in comparable units of reproductive success to parent's future reproductive success. At some point in time ($T_{optimal}$), the costs begin to outweigh the benefits and offspring attendance should desist. Unfortunately, benefit and cost determination in snake parental care is in its infancy.

on field data, parental attendance has been most extensively described in crotalines. However, despite widespread documentation, there is little empirical data that provides insight into the functional role of attendance in this group of snakes. Yet, several benefits of parental attendance have been postulated.

Neonatal attendance by pit vipers has frequently been referred to as "guarding". While there have been several reports of female pit vipers aggressively defending their offspring, there is an equal number of reports where the female did not appear to be aggressive toward intruders (reviewed in Green *et al.* 2002). However, many potential predators are likely familiar with pit vipers and may choose to avoid them upon detection, regardless of the snake's response to their presence (Greene 1988). Therefore, the mere presence of a female, let alone any anti-predator behavior, might provide substantial protection to the neonates (Greene *et al.* 2002). Oviparous females may deter predation of their eggs not only through protection, but also by using their cryptic coloration to better conceal their white eggs (York and Burghardt 1988). While protection is likely a critical function of parental attendance in pit vipers, empirical data are needed to ascertain the effectiveness of this protection and its importance to reproductive success.

Physiological benefits of parental attendance in pit vipers are even more poorly understood. In the lone assessment of a physiological benefit associated with pit viper egg attendance, there was no evidence that *Calloselasma rhodostoma* provide any thermal benefit to their eggs (York and Burghardt 1988). However, in the same study, females adjusted their coiling behavior in response to laboratory manipulations of humidity. When humidity dropped below 70%, females increased their coverage of the eggs, oftentimes covering them completely. However, field observations of an egg-attending female *C. rhodostoma* revealed only slight variation in the extent to which the female covered her eggs (Hill *et al.* 2006). In that instance, relative humidity never dropped below 70% and the authors estimated egg exposure to never exceed 20%, even during rainfall (Hill *et al.* 2006). Relatedly, the activity patterns and body posture of non-reproductive *C. rhodostoma* were strongly influenced by ambient humidity in a separate field study, suggesting acute hydrosensory abilities (Daltry *et al.* 1998).

Physiological benefits of mother-neonate aggregation in viviparous pit vipers is also unsubstantiated. Transcutaneous water loss is greater prior to a neonate's first ecdysis (Duvall *et al.* 1985; Tu *et al.* 2002). Because attendance predominantly occurs pre-ecdysis, some have suggested a hydroregulatory, and possibly a thermoregulatory, advantage to parental attendance (Finneran 1953; Graves and Duvall 1995). However, quantitative experiments examining the hydroregulatory benefits of offspring attendance are needed before any conclusions can be made. Another possible, but completely untested, benefit of neonatal attendance is that tongue-flicking among the mother and neonates might facilitate chemically-mediated social mechanisms (Greene *et al.* 2002).

18.3.5 Parental Costs of Post-paritive Care

Parental costs are equally important in understanding the adaptive significance of parental attendance in non-pythonid snakes, but they too are poorly known. Unlike the high energy demands associated with energy provisioning in both birds and mammals (Clutton-Brock 1991), parental attendance in most snakes entails no energy provisioning and minimal activity. However, parental attendance in snakes may lead to a negative energy balance due to lost foraging time (Shine 1988). Attending females have little to no opportunity to actively forage or even select optimal ambush sites. Nonetheless, attending females under captive conditions have been reported to leave their clutch to feed (Gloyd and Conant 1990). In the wild, while attendance and foraging is likely in much greater conflict than it is in captivity, some evidence of feeding in egg-attending females exists (Hill *et al.* 2006). Despite these occurrences of feeding during egg attendance, opportunities to feed are likely considerably reduced; thus, a negative energy balance during attendance is probable. In viviparous pit vipers, where attendance is brief (i.e., 1-2 weeks) and reproduction infrequent (i.e., super-annual), the negative energy balance which might occur during attendance may not significantly affect future fecundity (Price 1988; Butler *et al.* 1995). However, prolonged negative energy balance potentially associated with egg attendance might not be inconsequential.

18.4 PYTHON PARENTAL CARE

Parental care in snakes has been most studied in the Pythonidae. Pre-paritively, female pythons invest heavily into yolk stores that provide vital energy to the offspring during development and post-hatching (Bedford and Christian 2001; Speake *et al.* 2003). Additionally, gravid pythons also alter thermoregulatory behavior to optimize early offspring development (Shine and Madsen 1996; Lourdais *et al.* 2008). While pre-paritive parental care in pythons is similar to that of other snakes, python parental care is deserving of separate attention in this chapter because researchers have gained considerable insight into the functional significance of its post-paritive parental care. As mentioned earlier, egg attendance is ubiquitous among pythons wherein females coil tightly around their eggs as to oftentimes encompass the clutch completely or nearly so (Fig. 18.1).

18.4.1 Thermoregulatory Benefits of Egg Attendance

Python egg attendance can clearly be called brooding as multiple physiological benefits have been documented. Most notably, facultative thermogenesis by egg brooding pythons can raise clutch temperature as much as 7°C above ambient temperature (Vinegar *et al.* 1970). This phenomenon is frequently mentioned in introductory science textbooks and parental care reviews (e.g., Shine 1988; Farmer 2000; Somma 2003a).

However, it has thus far been convincingly documented (i.e., increased metabolic rate or the maintenance of clutch temperature with decreasing nest temperature) in only three species (Burmese Python [*Python bivittatus*], Indian Python [*Python molurus*], Hutchison *et al.* 1966; Vinegar *et al.* 1970; *Morelia spilota spilota*, Harlow and Grigg 1984; Slip and Shine 1988). Facultative thermogenesis has been either disputed or convincingly disproven in at least 10 other python species (Table 18.1). Discrepancies in published observations could be attributed to population variation, individual variation, variation in data collection, or experimental technique. For example, because they are concurrent with endogenous heat production in thermogenic species, coordinated large-scale muscular contraction (i.e., shivering) has been implicated as the mechanism of facultative thermogenesis (Vinegar *et al.* 1970) and used as a proxy for facultative thermogenesis in egg brooding pythons. However, poor correlations between contraction frequency and both oxygen consumption and the clutch-nest temperature gradient suggest that simple observation of muscular contraction during brooding does not provide definitive evidence that a female is sufficiently thermogenic to influence incubation temperature. Furthermore, these poor correlations suggest the possibility that thermogenic pythons may also incorporate non-shivering heat generating processes, such as those seen in birds and mammals (Van Mierop and Barnard 1976, 1978).

Table 18.1 Studies refuting facultative thermogenesis during maternal egg brooding within the Pythonidae

Species	Common name	References
Antaresia childreni	Children's Python	Stahlschmidt and DeNardo 2009a
Aspidites melanocephalus	Black-headed Python	Murphy *et al.* 1981; DeNardo unpublished
A. ramsayi	Woma	DeNardo unpublished
Morelia kinghorni	Scrub Python	Charles *et al.* 1985
M. spilota cheynei	Jungle Carpet Python	DeNardo unpublished
M. viridis	Green Tree Python	DeNardo unpublished
Python brongersmai	Blood Python	Noble 1935
P. regius	Ball Python	Van Mierop and Bessette 1981; Ellis and Chappell 1987
P. reticulatus	Reticulated Python	Honegger 1970; Vinegar *et al.* 1970; La Panouse and Pellier 1973; Pitman 1974
P. natalensis	Southern African Rock Python	Pitman 1974
P. sebae	African Rock Python	Vinegar *et al.* 1970

Although many species of pythons are incapable of significant heat production, they may use other behaviors to enhance the thermal environment around their eggs. For example, free-ranging Black-headed Pythons (*Aspidites melanocephalus*) and *Python natalensis* use heat radiated from the sun or conducted from substrate to warm their clutches (Johnson *et al.* 1975; Alexander 2007). Additionally, egg brooding behavior by

free-ranging pythons is dynamic in that females adjust their posture (i.e., increase tight coiling behavior) to prevent egg cooling (Johnson *et al.* 1975).

Similarly, and in a more controlled environment, *Antaresia childreni* have been documented to spend more time tightly coiled around their eggs during cooling than during warming (Stahlschmidt and DeNardo 2009a, 2010a). Further, the amount of time that females spent tightly coiled during warming significantly affected the temperature gradient between the nest and clutch environment (Tnest-Tclutch gradient) (Stahlschmidt and DeNardo 2009a). Thus, although most female pythons are not facultatively thermogenic, they are likely capable of assessing the Tnest-Tclutch gradient and making behavioral adjustments to enhance the thermal microenvironment of their developing offspring.

The selection for physiological and behavioral traits that enhance egg temperature regulation is likely related to the thermal sensitivity of python embryos. Specifically, python embryos require a relatively high, stable incubation temperature (i.e., 30-33°C) for normal development, and deviations from this narrow range results in a combination of reduced hatching success, developmental rate, growth rate, body size, escape behavior, and willingness to feed (*Python bivittatus*, Vinegar 1973; *Python natalensis*, Branch and Patterson 1975; *Morelia spilota spilota*, Harlow and Grigg 1984; *Liasis fuscus*, Shine *et al.* 1997; *Antaresia childreni*, DeNardo unpublished).

Given the thermal sensitivity of python embryos, the question remains: Why are only two python species facultatively thermogenic? Phylogenetically, the three thermogenic pythons, *Python bivittatus*, *Python molurus*, and *Morelia spilota spilota*, are members of two different python clades (i.e., Afro-Asian and Indo-Australian, respectively) that diverged over 45 million years ago (Rawlings *et al.* 2008). Thus, *M. s. spilota* is more closely related to 90% of non-endothermic python species than it is to *P. bivittatus* and *P. molurus*. Alternatively, the variation in thermogenic capability may be explained by morphological variation among python species. Specifically, large snakes have lower surface area to volume ratios, and thus they lose heat at a slower rate relative to smaller snakes. Additionally, larger snakes can store far greater quantities of energy. In support of a morphological basis for the appearance of thermogenesis in pythons, *P. molurus* and *P. bivittatus* are two of five giant python species and can grow to over 5.8 m in length and 90 kg in mass (Mattison 2007). Yet, female *M. s. spilota* are not particularly large (i.e., 182-230 cm snout-vent length, Slip and Shine 1988), and the other three giant species (*Python sebae, P. natalensis*, and *P. reticulatus*) are not thermogenic (Vinegar *et al.* 1970). What might drive the existence of thermogenesis in pythons is an interaction between biogeography and morphology. The distributional ranges of *P. bivittatus*, *P. molurus*, and *M. s. spilota* extend to among the highest known latitudes for any python (Jacobs *et al.* 2009), and definitely higher than all species thus far shown not to be thermogenic. In fact, the range of the moderate sized *M. s. spilota* extends as far south as 37.5°S, the most polar of any python (Rawlinson 1969). In addition to being

thermogenic, this species, unlike most other pythons, is known to build insulated incubation mounds (Slip and Shine 1988). Furthermore, the higher latitudinal distribution of *P. bivittatus* and *P. molurus* relative to the congeneric and similarly sized *P. reticulatus* has been attributed to the presence of thermogenic ability in the former but not the latter (Vinegar *et al.* 1970). In sum, python thermogenesis may only occur in species which live in more thermally challenging environments and can minimize the appreciable costs of endogenous heat production (e.g., large body size in *P. bivittatus* and *P. molurus*, and nest construction in *M. s. spilota*).

18.4.2 The Role of Tradeoffs in the Adaptive Significance of Python Parental Care

Like other parental care systems, python egg brooding represents parent-offspring tradeoffs where the costs to egg brooding females are offset by the benefits to the developing offspring. For example, facultative thermogenesis represents a substantial portion of female energy expenditure during egg brooding at cool temperatures (*Python bivittatus*: 92%, *Morelia spilota spilota*: 95%) (Vinegar *et al.* 1970; Harlow and Grigg 1984). Although the results of one study suggest that maternal costs of egg brooding are minimal (Aubret *et al.* 2005a), other studies demonstrate that egg brooding independent of thermogenesis obligates substantial maternal costs. Egg brooding necessitates lost foraging time and is generally accompanied by anorexia (Madsen and Shine 1999; Aubret *et al.* 2005a). Accordingly, in female *Antaresia childreni* under laboratory conditions, it obligates significant epaxial muscle atrophy and reduces contraction strength (Lourdais and DeNardo unpublished; Stahlschmidt *et al.* unpublished), as well as increases susceptibility to oxidative stress (Stahlschmidt *et al.* unpublished). Under natural conditions, the duration of egg brooding is negatively related to reproductive frequency and post-reproductive maternal body condition in free-ranging *Liasis fuscus* (Madsen and Shine 1999).

While likely to infer some cost to the parent, egg brooding conveys benefits to offspring beyond those associated with thermoregulation. For example, egg brooding duration is negatively related to egg predation in free-ranging *Liasis fuscus* (Madsen and Shine 1999). Further, python eggshells have extremely high water vapor conductance, and eggs can desiccate in conditions as moist as 75% relative humidity when not maternally brooded (Lourdais *et al.* 2007; Stahlschmidt *et al.* 2008). Thus, removal of females from their eggs results in reduced hatching success and altered hatchling phenotypes in Ball Pythons (*Python regius*, Aubret *et al.* 2005b) and 0% hatching success in *Antaresia childreni* under some conditions (Lourdais *et al.* 2007). Using a less extreme manipulation, Aubret *et al.* (2003) showed that experimentally increasing clutch size by 50% prohibited female *P. regius* from fully encompassing their clutch, leading to desiccation of the eggs. As a result, embryos in these "enlarged" clutches were more likely to die before hatching or hatch later.

Although less studied, intra-offspring tradeoffs (i.e., those that reflect competing offspring needs) may be important to parental care dynamics (Stahlschmidt and DeNardo 2009b). For example, *Liasis fuscus* females that nest in thermally superior sites abandon their clutches shortly after oviposition ($\overline{X}$ = 6.5 d), while females that nest in thermally poorer sites brood their clutches for the entire incubation period ($\overline{X}$ = 53.8 d) (Madsen and Shine 1999). Although *L. fuscus* nest site selection mitigates a parent-offspring tradeoff (i.e., thermal benefits to offspring vs. lost foraging time for females), an intra-offspring tradeoff between embryonic temperature and predation also exists. That is, thermally favorable nests are more prone to predation than are thermally poor nests (Madsen and Shine 1999).

Intra-offspring tradeoffs associated with python egg brooding have also been detected at a finer scale of brooding behavior. As stated earlier, egg brooding behavior is dynamic and entails shifts in coiling posture. Broadly, dynamics of egg brooding behavior can be divided between (1) a tight coiling state wherein the female is still and encompassing the clutch completely or nearly so, and (2) a postural adjustment state wherein the female makes small but significant movements and exposure of the eggs to the nest environment increases. These distinct brooding behaviors mediate several intra-offspring tradeoffs. During brooding, females predominately adopt the tightly coiled posture, and this positioning serves as an effective barrier to the exchange of gas and heat between the clutch environment (i.e., the space within the females coils) and the nest environment (i.e., the space immediately outside of the female's coils) (Stahlschmidt and DeNardo 2008, 2009a; Stahlschmidt *et al*. 2008).

While an effective barrier to gas exchange dramatically reduces water loss from the eggs, it also limits the transfer of oxygen and carbon dioxide (Stahlschmidt and DeNardo 2008, Stahlschmidt *et al*. 2008). Female *Antaresia childreni* mediate this intra-offspring tradeoff between embryonic water balance and respiration by periodically performing postural adjustments to facilitate nest-clutch gas (O_2 and H_2O vapor) exchange to benefit respiration at the cost of embryonic water balance (Stahlschmidt and DeNardo 2008, 2009b; Stahlschmidt *et al*. 2008). However, while embryonic oxygen consumption increases dramatically over the course of development, female *A. childreni* do not alter the relative frequency or duration of their postural adjustments, and this results in late-incubation developmental hypoxia that reduces offspring size, speed, and strength (Stahlschmidt and DeNardo 2008, 2009b; Stahlschmidt *et al*. 2008).

While oxygen depletion does not impact the relative frequency which female *Antaresia childreni* utilize tight coiling and postural adjustments, females do respond to other environmental conditions. As described above, females enhance the thermal environment of the eggs by performing more postural adjustments when ambient temperature is increasing than when it is cooling (Stahlschmidt and DeNardo 2009a, 2010a). However, this response to environmental temperature is dependent on the nest's hydric condition. During moderate and high nest humidity treatments (23 and

32 $g\cdot m^{-3}$ H_2O, respectively), females show the previously described reduction in tight coiling during nest warming. However, brooding females in low humidity nest environments (13 $g\cdot m^{-3}$ H_2O) maintain a high frequency of tight coiling even when the nest is warming. Thus, females "choose" embryonic thermoregulation over embryonic water balance in relatively humid nest conditions, but *vice versa* during relatively dry nest conditions (Stahlschmidt and DeNardo 2010a).

In sum, python egg brooding significantly impacts several critical developmental variables including embryonic predation (Madsen and Shine 1999), thermoregulation (Vinegar *et al*. 1970; Stahlschmidt and DeNardo 2009a), water balance (Aubret *et al*. 2005; Lourdais *et al*. 2007; Stahlschmidt *et al*. 2008), and respiration (Stahlschmidt and DeNardo 2008). Further, python egg brooding behavior is dynamic with females using assessments of environmental conditions to adjust brooding behavior on both large scales (i.e., choosing to abandon or continue brooding the clutch) and fine scales (i.e., altering the frequency and duration of postural shifts during brooding). Whether such parental care complexity is unique to pythons or remaining to be discovered in other taxa remains uncertain.

18.5 FUTURE DIRECTIONS

It has been well established that both pre- and post-paritive parental care are widespread among snakes. Many interesting questions remain regarding pre-paritive care, such as "how is the amount of post-hatching yolk determined" and "how is the yolk's energy allocated to various needs". However, the greatest voids to be filled involve post-paritive parental care, in particular egg and neonate attendance.

18.5.1 Documentation of the Occurrence of Parental Care

Currently, the existence of maternal attendance has been well documented in both Crotalinae and Pythonidae, and to a lesser extent Afro-Asian Elapidae, but other taxa have been poorly explored. By better understanding the true occurrence of parental care among snakes, we might better tease out any phylogenetic, ecological, and perhaps even morphological influences on the evolution of parental behaviors. It is critical that further exploration cover diverse taxa and that documentation be sound and thorough. Documenting parental behavior in the field is extremely challenging, especially when it involves extended observations over time. However, such work will be valuable in understanding traits and conditions that influence parental decisions.

18.5.2 The Ecophysiology of Parental Attendance

Our understanding of the function of parental care and its regulation is in its infancy. While recent work using manipulative experiments has greatly expanded our understanding of both costs and benefits of parental care in

pythons, many unknowns still exist. We are only now beginning to explore the regulation of parental care. What environmental cues do females use to adjust both large- and fine-scale parental decisions? What neural, hormonal, or other chemical cues are used to initiate, maintain, and terminate parental behavior?

To explore these questions and others, it is critical that we continue examining species for which data are most abundant (e.g., *Antaresia childreni*, *Liasis fuscus*, *Python bivittatus*, *Python molurus*, *Python regius*), but also begin to explore other lineages which would provide exceptional comparative data. One such lineage is the pit vipers, where parental attendance in nearly ubiquitous but divided between oviparous species that invest long periods of time in attending their eggs and viviparous species that limit attendance predominantly to the relatively short pre-ecdysis periods. These two parental behaviors, while both falling into the category of parental attendance, likely present considerably different costs to the parents and benefits to the offspring. Regardless, it is of interest to examine whether these behaviors are similarly regulated.

While the lineages where post-paritive parental care is commonplace likely provide the best target for studies, we should not discount the value of comparative assessments of costs, benefits, and regulators of maternal attendance. The Colubridae are a diverse (and likely polyphyletic) group and parental attendance either occurs throughout egg incubation, is limited to the immediate post-paritive period, or is non-existent. What factors drive the selection for these different strategies, and are the regulators of parental care in those species that provide it similar to the regulators in the lineages where parental attendance is the norm? We specifically recommend investigating parental care tradeoffs in species whose parental behaviors have been most frequently observed but mostly unstudied (Somma 2003a, b), including both colubrids (e.g., Taiwan Beauty Snake [*Orthriophis taeniurus friesi*], Mud Snake [*Farancia abacura*], Skaapstekers [*Psammophylax* spp.], Keelbacks [*Xenochrophis* spp.]) and elapids (e.g., Shield-nosed Cobras [*Aspidelaps* spp.], kraits [*Bungarus* spp.], cobras [*Naja* spp.], and King Cobra [*Ophiophagus hannah*]).

18.5.3 Why Do We Care?

Without an accurate understanding of reproductive investment, it is impossible to fully understand reproductive strategies and success. Thus, understanding parental behavior more thoroughly will enable us to better understand the evolution and ecology of snakes. However, the value of a thorough documentation and understanding of parental care and its functions in snakes has much broader significance.

Python egg brooding is already demonstrating its value as a useful and relevant parental care model for a number of reasons. First, python egg brooding represents female-only nest attendance, which is the most widespread mode of parental care across taxa (Gross and Shine 1981; Zeh and Smith 1985; Clutton-Brock 1991). Additionally, it significantly

impacts several critical developmental variables (e.g., embryonic predation, thermoregulation, water balance, and respiration) and obligates maternal costs (e.g., fecundity, body condition, oxidative stress susceptibility). Thus, python egg brooding can be used to examine cost-benefit parent-offspring and intra-offspring tradeoffs of parental care that can elucidate the evolution of parental care across taxa.

Expanding detailed investigations beyond pythons will only increase the value of snakes as valuable contributors to understanding the evolution or parental care. Snakes provide an amazing diversity of parental behaviors. Yet, even in its most complex form, snake parental care is quite amenable to study. While post-paritive parental care by snakes serves to balance multiple tradeoffs, the factors involved (e.g., temperature, water balance, respiration) are easily quantifiable. Furthermore, while attendance behavior is dynamic, behaviors are spatially limited, making uninterrupted monitoring and assessment possible. In addition, several advances in snake captive propagation and the development of technical equipment needed to quantify functional benefits are emerging. Together, there is little reason to allow such a valuable information trove to lie virtually unexplored.

18.6 SUMMARY

Parental care (i.e., any non-genetic contribution by a parent that appears likely to increase the fitness of its offspring) is remarkably widespread across the animal kingdom, including snakes. Here, we summarize parental behavioral and physiological traits in snakes that occur before and after parition (used to collectively define oviposition and parturition).

Pre-paritive parental care is ubiquitous among snakes (and likely all vertebrates), and can include investment of resources into the offspring, behavioral thermoregulation, and nest site selection. Energy, whether provided lecithotrophically or matritrophically, is the resource that has received greatest attention from researchers, but other resources that have been shown to be transferred from female snakes to their offspring include water, minerals, immunoglobulins, antioxidants, and defensive toxins.

Since development is highly sensitive to temperature, numerous snakes have been shown to increase and/or more tightly regulate body temperature pre-parition. Increased female thermoregulatory activity, while beneficial to the developing offspring, can impose metabolic and survival costs on the female. Although reproduction-induced changes in thermoregulation have been most studied in viviparous species, they have also been documented in oviparous specie where up to one third of development can occur prior to oviposition. However, oviparous species must also assure a suitable developmental environment post-parition, and thus nest site selection is a vital component of reproduction in these species.

Post-paritive parental care is much less common among snakes but has been documented in a variety of taxa. Most notable are the ubiquitous egg brooding behavior in pythons and nearly ubiquitous egg/neonate

attendance in pit vipers. While the functional significance of post-paritive parental care is mostly untested in most snakes, there is a growing body of data regarding the functional significance of python egg brooding. Egg brooding by female pythons has been shown to impact embryonic predation, water balance, thermoregulation, and respiration. It is unknown whether the implications of post-paritive parental care in other species are equally or less complex. Clearly, more work is needed to explore the occurrence and functional significance of parental care among a greater diversity of snakes.

18.7 ACKNOWLEDGMENTS

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