PARENTAL BEHAVIOR BY VIPERS

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ABSTRACT: Field studies, laboratory experiments, and phylogenetic analyses show that parental behavior by vipers is more interesting than previously realized. Telemetered *Crotalus molossus* fasted from winter dormancy through late summer birthing and attendance of neonates then resumed hunting. Birth sites were rodent burrows or rock outcrops, maternal behavior varied from exposed contact with offspring and increased defensiveness to hidden presence, and littermates sometimes basked together. Neonates shed ca. 10 days after birth, and a female closely observed postnatal ecdysis. Six mothers of nine litters departed birth sites a mean of 1.4 days after the neonates shed. Twenty-five free-living female *Sistrurus miliarius* remained with their young during the post-birth ecdysis cycle. When separated by size-selective barriers under three experimental conditions, 59 captive *S. miliarius* returned to their litters and neonates returned to their mothers. Attending captive female *S. miliarius* were more defensive against a natural predator than before birth or after neonatal ecdysis. Adults of 14 species in eight crotaline genera remain with eggs during incubation, those of 19 species in four genera remain with their young for several days after birth, and thus a total of 33 species in 12 genera exhibit parental care. Rarity or absence in outgroups suggests that the origins of crotaline pits, defensive caudal sound production, and attendance of neonates are historically correlated. Alternatively, parental behavior appeared earlier in the evolution of snakes or even anguimorphs and later was elaborated or lost in many lineages. Pitvipers probably protect their eggs and/or offspring from predators, and aggregation might enhance thermoregulation and retard water loss by neonates. Tongue-flicking among littermates and mothers might facilitate chemically-mediated social mechanisms. Physiological control mechanisms, ecological consequences, variable timing of neonatal ecdysis, and individual, population, and taxonomic variation in parental behavior by snakes warrant further studies.

INTRODUCTION

A few quotes anticipate both the complexity of our topic and the conclusions of this chapter:

"*The statement is frequently made in the literature that the mother snake leaves the young at birth, but [I have assembled] considerable evidence that … females of* Agkistrodon *… [contortrix] and* Crotalus horridus *… remain with the young for several days.*" (Anderson, 1942:215)

"*Service (1902) has written, 'I have year after year seen adders* [Vipera berus] *lying around their mother. As they glide out of sight beneath her she invariably lowers her head.' It is a common statement that the Adder takes no interest in her family, but snakes in captivity are not always good guides on points of behaviour. The parental instinct is developed in many snakes.*" (Smith, 1951:259)

"*I once found a total of 22* [Agkistrodon contortrix *and* Crotalus horridus] *… in a six-foot hollow log. Here a mother copperhead had her young in one end of the log and a mother rattler had hers at the opposite end…. The log was a veritable nursery.*" (Oliver, 1955:147)

" *…there is no final evidence that young rattlers stay with their mothers for more than a day or so at most; if they are found together there is no proof that the young rattlers are more than a few days old or that their propinquity is caused by other than use of a common refuge.*" (Klauber, 1956:737)

" *…two adult female* [Agkistrodon piscivorus] *were found with 13 newborn young nearby … This incident was so striking that I regard it as guarding behavior ….Aggregation prior to and following birth could have survival value in repelling predators who could more easily cope with a lone female, even though the tendency may have originated in some egg-guarding oviparous … [Old World pitviper].*" (Wharton, 1966a:154–155)

"*Obviously, reptiles are unlikely to teach us much about the hormonal control of parental care.*" (Moore and Lindzey, 1992:77)

Vipers have played surprisingly little role in elucidating the ecological and evolutionary significance of parental care (reviews in Clutton-Brock, 1991; Rosenblatt and Snowdon, 1996) despite 19th century observations by John James Audubon (Klauber, 1956), a few moderately detailed field accounts (e.g., Pope, 1935; Dunkle and Smith, 1937; Price, 1988), and explicit claims that maternal attendance of young is not coincidental (e. g., Anderson, 1942; Smith, 1951; Wharton, 1966a). Instead, discussions of parental care

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by non-avian reptiles have scarcely mentioned those snakes (Tinkle and Gibbons, 1977; Shine, 1988; de Fraitpont et al., 1996; Gans, 1996; but see Graves and Duvall, 1995), perhaps reflecting a skeptical presumption (e.g., Klauber, 1956) that parent-offspring aggregations are simply incidental to recent birth and non-adaptive. Controlled studies have been limited to a descriptive account of egg-guarding by captive Malayan Pitvipers (*Calloselasma rhodostoma*, York and Burghardt, 1988), and a field investigation of defensive behavior and maternal attendance in Prairie Rattlesnakes (*Crotalus v. viridis*, Graves, 1989).

Definitions of parental care range from virtually any investment in offspring fitness (e.g., nest building, provision of yolk, Clutton-Brock, 1991; timing of parturition, Olsson and Shine, 1998) to specific actions of a parent after oviposition or parturition that increase survivorship of the young (Shine, 1988). We prefer the latter definition, because it focuses on behavior and measurable benefits, and herein we often use the less conclusive term parental attendance, acknowledging a lack of direct proof that remaining with their eggs and/or young increases fitness for free-living vipers. We will show that attendance of eggs and/or offspring by pitvipers (Crotalinae) is far more widespread and interesting than previously realized. First, we summarize long-term field studies of telemetered female Black-tailed Rattlesnakes (*Crotalus molossus*) and their young, and report laboratory experiments on parent-offspring interactions and response to a natural predator by Pygmy Rattlesnakes (*Sistrurus miliarius*). Next, we review parental attendance by other pitvipers and successive outgroups. We recount specific observations because the details are important to our conclusions, some information comes from unpublished or obscure sources, and previous reviews and secondary citations sometimes have proved misleading. Finally, we explore the ecological and evolutionary implications of parental care in vipers, and conclude that they offer exciting prospects for further field and laboratory studies.

PARENTAL CARE BY BLACK-TAILED RATTLESNAKES (*Crotalus molossus*)
Background

Dunkle and Smith (1937:14; see Smith, 2001) caught several female Mexican Black-tailed Rattlesnakes (*C. m. nigrescens*) with their broods, " ... sometimes accompanied by an adult male." The snakes were beneath or near a ledge at the rim of a steep canyon; adults were sunning themselves near retreats, whereas the young were in cavities under the rocks. "The first specimens were discovered when a female began rattling from … near the edge of a large rock. She immediately took refuge…. The sixteen young in the depression formed by the base of the rock began scattering in all directions." A rattling and noticeably thin female Northern Black-tailed Rattlesnake (*C. m. molossus*) twice approached Savary (1999) to less than 2 m, then retreated under a ledge 3–4 m distant, where she joined several obviously pre-molt neonates (eyes opaque). One young rattlesnake crawled in his direction, was overtaken by the female and pressed down briefly with her neck, after which both snakes retreated into the crevice. On subsequent daily visits the number of visible babies decreased and one or two shed skins appeared. By the fourth day there were no snakes in the crevice, and Savary checked the site during several subsequent summers without encountering any snakes. A captive *C. m. molossus* basked outside of a hide box until birth, then remained with her young in the refuge and "…exhibited great care not to … slide on top of them. Neonates shed from seven to 10 days after birth … [they were] removed on the eighth day, and the female remained inside the hide box … for a day longer…." (Gaulden, 2000:17–18).

Beginning in 1988, Hardy and Greene have logged at least 3,271 encounters with 49 telemetered *C. m. molossus*, over periods for each individual ranging from a few days to more than nine years. The primary goals have been to assemble a detailed behavioral inventory for that species as part of an effort to understand the ecological and evolutionary diversification of vipers (e.g., Greene, 1992, 1997), and to publish an extensively illustrated, monographic account of its biology (for a synopsis, see Hardy and Greene, 1999a). Here we present observations of six females, based on 744 encounters during a total of nine pregnancies and attendance of young, and conducted from mid-July of the year they mated through post-parturition and onset of winter dormancy the following year. Individual males, females and their litters, and neonates are indicated by numbers or numbers separated by a dash (e.g., M28 refers to male 28, F21-1 refers to female 21 and/or her first litter, and N3 to the third neonate observed during a particular encounter with a litter).

Methods

Our study site is in the eastern foothills of the Chiricahua Mountains, ca. 6.3 km west of Portal on the road to Paradise, Cochise Co., Arizona (Plate 11b).

Ranging in elevation from 1550 to 1800 m, the generally open, rocky slopes support Ocotillo (*Fouquieria splendens*), Whitethorn Acacia (*Acacia neovernicosa*), several kinds of cacti, and other plants typical of upland Chihuahuan Desertscrub. Arizona Sycamores (*Platanus wrightii*) and other shade trees border Silver Creek, an intermittent stream that drains the canyon, and some of the larger side ravines harbor Madrean Evergreen Woodland (see Brown, 1994).

Because pitvipers (and probably many other snakes) might be traumatized by manual restraint (Wharton, 1966b; Brown, 1993), we took care to gently capture our animals with snake hooks, a bag stick, and plastic tubes; they were never pinned nor manually restrained. Size measurements, close examination, and transmitter implantation were done under inhalation anesthesia (for methods see Reinert, 1992; Hardy and Greene, 1999b, 2000). Following processing, individuals were returned to their exact capture sites, usually within 24 h of capture. Whenever possible we minimized disruption of females and their offspring (e.g., by approaching them slowly and low on the horizon, so as not to cast shadows). Distances between major landmarks were measured with optical rangefinders, and those values were used to visually estimate others.

From mid-July until after females and their progeny had dispersed, we usually checked birth sites once per day. We observed from a distance of 2–5 m with close-focusing binoculars, and recorded behavior with written narratives, 35 mm still photography, and occasionally a video camera. In 1998 and 2000, 25 of 26 neonates in six litters were gently captured and PIT-tagged (Camper and Dixon, 1988) for individual identification and future study, and most were immediately returned to their mothers. Among those neonates, a total of six from litters F21-2 and F21-3 were implanted with transmitters and returned to their birth site the following day. Surgical recovery thus coincided with maternal attendance, and telemetered neonates dispersed at about the same time as their siblings (we will report our observations on neonatal *C. molossus* elsewhere). Our research activities at times clearly influenced snake behavior, but even the effects of direct intervention were evidently short-term. We surgically corrected a transmitter problem for F21 (posterior migration with partial extrusion) on 6 June, midway in her 1998 gestation. She subsequently moved 5 m, returned to her original site five days later, and on 31 July gave birth to the largest litter and neonates with the largest mass in our sample.

Field Observations

Individual *C. molossus* at our Chiricahua study site typically use individual winter refuges within rock outcrops and emerge from inactivity in late March or early April. Mating is concentrated during the early wet season, from late July until early September. Based on timing of mating and studies of other pitvipers, including other species of rattlesnakes, mated females of *C. molossus* presumably show obligatory long-term sperm storage through winter dormancy, with ovulation and fertilization occurring in late spring (Schuett, 1992). Parturition and attendance of neonates by their mothers occur in July. Based on direct observations and visible prey lumps, snakes feed from late March until late November or early December, the onset of winter inactivity. For example, F21 had palpable feces and was accompanied by M28 when first captured on 11 September 1994; she had an obvious meal swelling on 29 October, was in her winter refuge by 27 November and still there the following 3 February, had left that site by 18 March, and gave birth to litter F21-1 ca. 19 July 1995. She was accompanied by three different males on 1 October 1995, 20 July 1996, and 14 August 1996; copulated on 30 July 1997 with M27, prior to litter F21-2 in 1998; and copulated on 12 August 12 1999 with M26, prior to litter F21-3 in 2000. Over a period of six years her three litters were likely sired by at least three different males. Over the course of nine reproductive episodes by six females, we observed them visited 1–5 times (total of 13) by nine different males during the mating season of the previous year. We recorded copulation by females four times in the years prior to litters F21-2, F21-3, F29-1, and F34-1, and at other times we observed the six females courted or accompanied by but not copulating with nine males.

Upon spring emergence, non-reproductive females moved to individual hunting ranges of previous years, ca. 200–1000 m from their winter sites, whereas those that had mated the previous summer usually settled at individual sites for gestation and birth, 15–150 m ($\bar{x}$ = 61 m) from their respective winter sites. From spring emergence until birth, a period of about four months, each reproductive female occupied an area of ca. 1.5 m² (see below for an exception). Six birth sites were excavations under boulders, two were in rock outcrops, and one was in an abandoned mammal burrow. All sites had dirt floors and east-, southeast-, or west-facing entrances (Plate 11b). The single site used by F21-2 and F21-3, and another used by F24-1 were probably made by Rock Squirrels (*Spermophilus variegatus*),

based on hole size for the former and a sighting at the latter; other birth sites probably were excavated by Harris' Antelope Squirrels, (*Ammospermophilus harrisii*), based on hole size, habitat, and lack of White-throated Woodrat (*Neotoma albigula*) nest litter.

Females might assess alternative shelters, then re-use or change birth sites. F21 was under a small granite boulder with south-facing entrance (probably hot in summer), 20 m southeast of her winter site on 18 March 1995; was under a larger rock 5 m further south from 13 May to 11 June; and on 24 June was 2.5 m north under a rock shelter she occupied through birth ca. 19 July and subsequent attendance of neonates. F21 used two winter sites, 100 and 150 m from her first and second birth sites, during the five years prior to her third pregnancy. In November 1999, while moving to a winter site and prior to the year of her third litter, she passed within a few m of her first birth site. At that point the previous refuge had filled with dirt, presumably due to weathering and lack of rodent excavations. F21 then entered a new winter site, 25 m from her second birthing site, and the following spring used the same nearby shelter for her third litter. The following November she returned to an earlier winter site, 150 m from the birth sites for her second and third litters. F24 changed winter sites after her first litter, perhaps in response to chronic presence of Gray Foxes (*Urocyon cinereoargenteus*) and Rock Squirrels near the birth site, and following three non-reproductive years she joined F30 for gestation and birth at a new site (see below).

After cool nights in early spring, reproductive *C. molossus* typically basked in the early morning, sometimes with only the posterior portion of the body exposed to the sun and the remainder in shelter, and by mid- or late-morning they withdrew out of sight, presumably for the remainder of the day and night. We did not see pregnant females basking outside of their shelters during warmer late spring and summer weather, nor did we observe food lumps, so females might not have fed during gestation or attendance of neonates. However, aside from the possibility of small meals that were not externally visible, lack of feeding might only reflect low probability of encountering prey at a particular birth site rather than lack of motivation to hunt and eat. Nine times we observed two attending females in postures typical of ambush hunting by *C. molossus* (i.e., tight, circular coils with tail hidden, neck in an S-posture, and head resting on an outer coil).

Parturition is roughly coincident with the onset of summer rains, but only two of nine births were asso-ciated with rain during the previous seven days. Three times we saw a female obviously pregnant on one day and with neonates the next, yielding exact birth dates of 25–31 July; subtracting 10 days from the first appearance of neonatal sheds (see below), we estimated birth dates for six other litters as 5–28 July (thus for nine litters, $\bar{x}$ = 20 July). Unusually heavy rain in June 2000, may have led to early births of litters F21-3, F24-2, and F30-1; excluding them, six other birth dates were after the more typically late July onset of summer rains ($\bar{x}$ = 26 July).

F29, F30, F31, and F34 each produced one litter during the study, F24 delivered two litters with a non-reproductive interval of three years, and F21 delivered three litters with non-reproductive intervals of one and two years. The nine litters consisted of 2–6 neonates ($\bar{x}$ = 3.9). Females departed from birth sites from one day prior to five days after neonatal ecdysis ($\bar{x}$ = 1.4 days), ca. 11–12 days after parturition, then moved to their usual summer ranges and began ambush hunting. Neonates in three litters for which we knew birth dates shed their skins after 9–12 days ($\bar{x}$ = 10.1, N = 5). As judged against counts of young seen at birth sites, we found 71% of the neonates' shed skins, shortly before or after they had dispersed, and all but one of them were within or very near the birth site entrance. One neonate of F29-1 was freshly shed and coiled under a small plant, next to a freshly shed skin and ca. 1.5 m from the birth site.

We saw female *C. molossus* on 40 (57%), neonates on 44 (63%), and females with babies on 25 (36%) of our 70 post-parturition visits to birth sites. Compared to non-reproductive adults, neonates, and especially their mothers, seemed wary and sometimes moved back into birth site shelters when we approached closely. Often within seconds of one snake seeking refuge, all others disappeared into the cavity. F21-1 and F29-1 usually basked at the entrance of their birth sites, often in physical contact with one or more neonates; we never observed F21-2, F24-1, and F34-1 post-parturition at birth sites, but on each visit we tele-metrically confirmed their presence. Exposed female *C. molossus* remained stationary 31 of 40 (76%) times that we recorded their reactions to our approach within 2 m. These females usually remained quiet, but once F21-2 rattled briefly from inside her birth site, and once F31-1 rattled briefly and remained visible at the shelter entrance. Neonates sometimes basked in the early morning, separately or in loose piles of two or more snakes. They were usually within 25 cm from the shelter at the boundary of sun and shade, but twice

one was in full sun, ca. 80 cm from its birth site entrance. Neonates sometimes were still when a sibling crawled against or over them, and sometimes moved slowly a short distance away when thus touched; they remained exposed 29 of 40 (73%) times that we approached within 2 m.

Circumstances permitted sustained observations of two females and their litters, yielding the following behavioral details for early, middle, and final stages of maternal attendance (see color photographs in Greene, 1997:26; Plate 11a herein). On 26 July 1996, within 24–36 h of birth, two neonates in litter F24-1 emerged from an abandoned squirrel burrow at 1048 h. They elevated ca. one-third of their bodies, tongue-flicked repeatedly, then retreated out of sight at 1050 h. A neonate with distinctive head markings re-emerged, tongue-flicked repeatedly, and paused in sun at the entrance with head turned acutely into a loose coil at 1058 h; it raised its head, tongue-flicked, and slowly uncoiled into the burrow at 1107 h.

On 23 July 1995, ca. four days post-parturition, F21-1 was in grass near her birth site at 0705 h, and five neonates crawled from the entrance, over her body, and into grass between 0740–0835 h. The young snakes were stacked three or four deep on the female at 0936 h; one retreated into the entrance at 1020 h, she shifted coils when a neonate crawled over her head at 1048 h, and the remaining snakes were together in shade at 1052 h. On 24 July, F21-1 emerged partly and immediately retreated as one of us (DLH) approached to 5 m, at 0702 h. Her neonates emerged and coiled, three at the birth site entrance and three in nearby grass, between 0730–0815 h; they crawled with slow forward movements of a few head lengths at a time, and flicked their tongues in short volleys ca. 1/sec. On 25 July, F21-1 was in nearby grass with one neonate lying next to her from 1000–1050 h; four other young were partly extended from the entrance, with 20–30% of their bodies exposed to sun. On 26 July, F21-1 and a neonate immediately retreated into the birth site when DLH approached to 5 m at 0902 h, but three or four neonates were coiled in the entrance at 0924 h and did not move when two Red-tailed Hawks (*Buteo jamaicensis*) circled overhead for 5–10 sec.

On 27 July 1995, ca. nine days post-parturition, F21-1 was lying in grass as a neonate emerged, pushed skin off its snout against the rocky birth site entrance, bumped the female's rattle, and withdrew from sight at 1643 h. A neonate emerged slowly with skin rolled back to mid-body at 1712 h, crawled into grass and completed shedding at 1720 h, then turned

in a wide arc toward the entrance and its shed skin. F21-1 closely approached the shed skin without tongue-flicking, while the neonate coiled and uncoiled at the entrance, then retreated out of sight at 1726 h. A freshly shed neonate emerged and circled in front of the mother at 1744 h, then crawled onto her coils and remained still at 1747 h.

The next morning, F21-1 was again in grass with head outstretched toward the birth site, facing two shed skins (from N1 and N2) that extended in parallel from the entrance, at 0725 h. Individual N3 appeared and pushed it's head against the rock, then against its mother's face at 0800 h; she withdrew into grass and N3, now with skin rolled back over its eyes, retreated into the birth site at 0805 h. F21-1 had crawled slowly into the birth site by 0811 h. N3 again appeared briefly in the entrance with shed skin over its head at 0813 h, re-emerged with skin rolled to midbody and was accompanied by N4, and the latter pushed its head against the ground at 0825 h. N3 retreated into the birth site, dragging its skin, at 0829 h. A freshly shed, presumably N3 rapidly crawled from the entrance to nearby grass and shade at 0834 h, encountered N4 with shed skin one-third back from its head, and retreated into the birth site at 0839 h. N4 crawled in a circle across dirt and the other two sheds, then completed shedding and entered the birth site at 0845 h.

One apparent pregnancy is not included in the above summaries because no neonates or shed skins were found; thus we cannot be certain that F39 gave birth. She had copulated for at least 22 h the previous year, mass was 543 g (typical of pregnant females) on 31 March 2000, when she was captured 5 m from her winter site and implanted with a new transmitter, and on that date she had four easily palpatable, enlarged follicles. After release at the capture site, F39 moved to a south-facing rodent excavation in limestone boulders 25 m from her winter site, remained there until 19 July, and over four days moved 400 m to her typical summer hunting range. She weighed 385 g, typical of females immediately post-parturition, when she was found hunting on August 1, an estimated 12 days after having given birth.

Two sets of observations show that females may interact with one another while one or both are reproductive. First, a 586 g, non-pregnant F38 was initially captured as she crawled within 0.5 m of F29-1 and two neonates at their birth site. After transmitter implantation and release, F38 remained in that birth site for at least eight days, including four days after F29 had departed and young were no longer visibly

present. F29 and F38 shared a refuge that next winter, 75 m from the birth site, after which both transmitters failed and the snakes were lost from our study (among other snakes in our study, only M9 and M11 shared a winter site). Second, F24-1 moved to a new winter site in November 1996, perhaps due to presence of Gray Foxes near her birth site that year, and on 17 March 2000, she moved 15 m to join F30-1 at the latter's winter site. They remained there together until 8 May, when F30-1 moved to a birth site and F24-2 continued gestating at F30-1's winter site. F24-2 joined F30-1 at the latter's gestation site on 27 June, where they both gave birth ca. 9 July. The following November, each female returned from her summer hunting range to a separate refuge that had been used the previous winter.

PARENTAL CARE BY PYGMY RATTLESNAKES (*Sistrurus miliarius*)

Background

A female Carolina Pygmy Rattlesnake (*S. m. miliarius*) and four neonates with prebuttons (i.e., postnatal ecdysis had not occurred) were found under a fallen wooden gate, two adults and three young were found under a log, and two adults with five young were found under a board; the sexes of the latter four adults were not determined, but in each pair one snake was emaciated (perhaps implying recent parturition, Palmer and Williamson, 1971). A captive pregnant female Dusky Pygmy Rattlesnake (*S. m. barbouri*) was "…very aggressive … [and after birth] defended her offspring. When disturbed, the young hid behind her … the mother rattled and tried to bite…." (Verkerk, 1987). Six females were found in the field with neonates that "…appeared to have been born in the last two d[ays], because the birth sites were usually found nearby with wet birth membranes, and because the neonates had not yet shed their skin for the first time" (Farrell et al., 1995:23).

We (PM, JS, and TF) made additional field observations on maternal associations from 1992–1998, as part of a long-term field study of *S. m. barbouri*, involving frequent censuses of several populations in western Volusia Co., Florida (see Farrell et al., 1995; May et al., 1996). Twenty-five aggregated litters were found from 1992–1997, neonates were in contact or within a few centimeters of their siblings, and a post-parturient female was found with 23 of these litters. Mean litter size was 5.96 young (SE = 0.323), compared with a mean of 5.76 (SE = 0.175) for 135 litters born in captivity. Only 2 of 25 field litters included neonates that had completed their post-natal shed (1 of

4 in one litter, 2 of 4 in the other). Females attending litters were typically not aggressive when they were collected, although when we approached closely their neonates usually fled under cover while the adult remained motionless. Inspired by these observations, we capitalized on the local abundance of *S. miliarius* by using four laboratory experiments to address two key questions about maternal attendance: 1) When separated by selectively permeable barriers, will females re-aggregate with their newborn young and vice versa, as proposed by Butler et al. (1995)? 2) Do females change their response to a natural predator while attending their neonates, as implied by some of the anecdotes reviewed herein and as demonstrated by Graves (1989) for free-living *C. viridis*?

Methods

We collected pregnant *S. miliarius* in July and August, maintained them in field enclosures under conditions approximating those in which they were initially found, and checked daily for parturition (for details on caging, see Farrell et al., 1995). In 1997, all mothers with litters born in captivity and those found in the field (total of 31 litters) were randomly assigned to one of two treatments. "Moveable mother" (MM) and "moveable babies" (MB) trials used selective barriers that allowed the female or her litter to move into a section of the terrarium containing the other. Using 11 females and their litters in the summer of 1998 and 17 females and their litters in 1999, we replicated "mother's choice" (MC) trials to determine if females would attend their offspring given more alternative locations than in MM trials. In all treatments, female and neonates were monitored at 1 hr after setup (typically between 1500–1800 h), and then once each morning (0800–1000 h) and afternoon (1800–2000 h) until all neonates in a litter had completed their post-natal shed. Females and their offspring were maintained in captivity until neonates had completed post-natal ecdysis then released at the adult's capture site. After each mother and her litter were released, the terraria were cleaned, and the sand and leaf-litter replaced. Terraria were maintained in a screened, shaded room at ambient temperature and humidity, and were placed in a variety of orientations to prevent positional biases.

MM trials were performed in glass terraria (L60 x W30 x H40 cm), each separated by a cardboard partition into two compartments. We cut an 8 x 10 cm rectangular opening medially in the partition, 18 cm above the terrarium floor. Both sides of the terrarium

were covered to about 1cm with sand and then leaves; each side contained identical water dishes and shelter tubes. Before the mother was placed on one side, 2–3 neonates from her litter were dragged from the sand, up the surface of the partition, to the hole and through to the other side of the terrarium to create an odor trail. Next, the entire litter was placed in the compartment opposite the side with the odor trail, and the female was placed in the other compartment. The height of the opening allowed the adult female to cross sides, but precluded movement by the neonates.

MB trials used glass terraria (L75 x W30 x H30 cm) partitioned into three approximately equal compartments; each end was prepared as in the MM treatments, and the middle compartment contained a PVC tube (5.5 cm in diameter) connecting the two end compartments. The tube was drilled at one end with five pairs of holes to accommodate five nails which, when inserted, produced a 0.75 cm grating. This allowed movement of neonates through the tube, while precluding passage by the female. Before the neonates were placed in one of the end compartments, the female was coaxed through the tube to create an odor trail. After passage, nails were inserted to prevent movement of the female back into the tube and the neonates were placed in the opposite compartment.

MC trials used glass terraria (L75 x W30 x H30 cm), each separated by four plywood partitions into five equal compartments. Walls separating the central compartments from the four edge compartments were 18 cm above the floor of the terrarium so that mothers, but not offspring, could cross these barriers. The wall separating the two compartments on each side extended to the terrarium top, so that mothers could not move from one edge compartment to another without first entering the central area. All compartments were covered to about 1 cm with sand and then leaf-litter; the four edge compartments contained identical water dishes and shelter tubes. Before the mother was placed in the central compartment, 2–3 neonates from her litter were dragged from there across the sand and against one of the walls to create an odor trail. We then placed the entire litter in the edge compartment to which the odor trail led and the female in the central compartment.

To determine if non-reproductive and post-parturient female *S. miliarius* would respond differently to a naturalistic threat, we experimentally exposed them to live Southern Black Racers (*Coluber constrictor priapus*), a common, nonvenomous snake that eats *S. miliarius* at the study site (Printiss, 1994;

P. May and T. Farrell, unpublished). We found pregnant and non-reproductive *S. miliarius* by visual searches from mid-July to mid-August of 1998, then recorded their snout-vent lengths (SVL), determined reproductive status by palpation, and randomly placed a pregnant and a non-reproductive rattlesnake in adjacent enclosures separated by a partition. For staged confrontations, we attached the test *C. constrictor* to a clear length of rigid plastic, 80 cm long and "<" in cross section (each side of the "<" was 1 cm wide). Five Velcro® strips secured the *C. constrictor* to the holder, so that only the anterior 10 cm of the snake could move freely.

We introduced a *C. constrictor* into the enclosure ca. 10–12 cm from the adult *S. miliarius*, then recorded the female rattlesnake's behavior as "response" (body bridging, recoiling, puffing up body, any head movement, rattling, and striking, but not including tongue-flicking) or "no response" (sitting with body motionless). We classified female response as 1) directed movement toward the *C. constrictor* (not including striking), or 2) striking. We did Trial 1 the morning after paired snakes were placed in the enclosures by approaching each snake individually with either a "large" (SVL 80.9 cm) or a "small" (SVL 67.6 cm) *C. constrictor*. We inspected the enclosures for parturition each morning thereafter, and ran Trial 2 on the paired individuals the day the pregnant member of the set gave birth by following the same procedure as above. To test for significant differences in behavior between pregnant and non-reproductive females before and after the former gave birth, we scored them for: 1) a response vs no response, 2) strike vs no strike, and 3) movement toward vs no movement toward the *C. constrictor*.

Results and Conclusions

In the MM experiments, 12 of 16 females crossed the barrier, thereby significantly associating with their neonates (binomial test, $P = 0.038$); eight females moved to the side containing the neonates without moving again for the duration of the experiments. Females crossed the barrier between compartments 23 times; 18 of these crosses were in the direction of the neonates. Females and litters were kept under observation for a mean of 4.25 days (SE = 0.39), not including the first afternoon and evening. Seven females crossed the barrier within one hour after being placed in the terraria. The proportion of females in association with their neonates increased steadily with time through the third morning after birth, when over 70% of females were in association with their

Table 1. Behavior of female *Sistrurus miliarius barbouri* in trial 1 (prior to parturition).

Behavior	Pregnant	Non-reproductive	*P*-value
% Responding	50	58	NS
% Striking	0	8	NS
% Directed movement	0	0	NS

neonates (Fig. 1). There was no significant difference between weight/SVL of females that moved to their neonates and females that did not move groups ("move," $\overline{x}$ = 1.26 ± 0.068, "no move," $\overline{x}$ = 1.29 ± 0.056, F = 0.05, P = 0.83), suggesting no influence of relative body mass on tendency to move.

In the MB experiments, mothers and litters were observed for a mean of 4.13 days (SE = 0.336), excluding the first afternoon and evening. Neonates accumulated over time in the compartment with the mother, reaching a maximum of 84.5% of babies by the third afternoon (Fig. 2). Mean proportion of neonates with the mother was calculated as the average of the proportion of neonates within individual litters with the mother. We compared neonates distribution against the null hypothesis that half of them would be in each compartment, using a one-sample *t*-test with Bonferroni correction for multiple tests in SYSTAT (Wilkinson, 1997). The mean proportion of neonates with their mother did not differ significantly from 0.5 in the first three time periods (one hour – t = –1.129, P = 0.245; first p.m. – t = 0.550, P = 0.591; first a.m. – t = 0.239, P = 0.815), but thereafter, significantly more than half of the neonates were with their mother in all except one period (second p.m. – t = 2.2375, P = 0.034; second a.m. – t = 2.232, P = 0.044; third p.m. – t = 5.701, P < 0.0001; third a.m. – t = 1.578, P = 0.141; fourth p.m. – t = 2.948, P = 0.015; fourth a.m. – t = 2.473, P = 0.033; fifth p.m. – t = 7.039, P < 0.0001; fifth a.m. – t = 10.786, P < 0.001; sixth p.m. – t = 8.148, P = 0.004). In the MC experiment, mothers were significantly more likely to be with their litters than not in three of the last four observation periods (binomial tests with probability that a mother would be with her offspring by chance set at 0.25; Fig. 3).

Of nine female *S. miliarius* whose behavior was noted when collected with their neonates from the enclosures in which they gave birth, three struck when confronted by a gloved hand, while six retreated or remained motionless. During Trial 1, 50% of the pregnant females and 58% of the non-reproductive
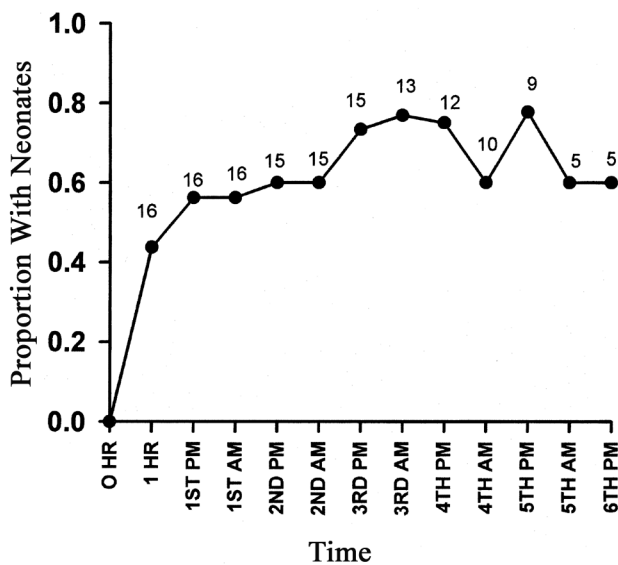

Fig. 1. Mean proportion of post-parturient female *Sistrurus miliarius* in association with their litters in the MM experiment. Numbers above each point indicate sample size for that mean.
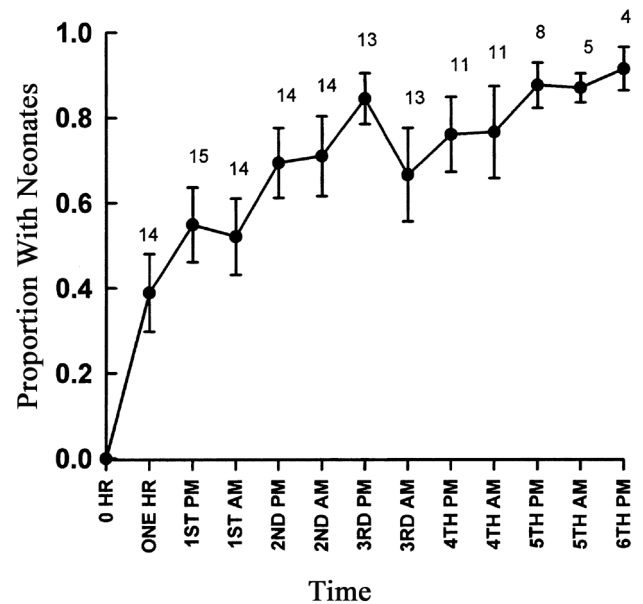

Fig. 2. Mean proportion of neonatal *Sistrurus miliarius* in association with their mother in the MB experiment. Error bars indicate ±1 SE. Numbers above each point indicate sample size (number of litters) for that mean.

Table 2. Behavior of female *Sistrurus miliarius barbouri* in trial 2 (following parturition). * = significant.

Behavior	Postpartum	Non-reproductive	*P*-value
% Responding	83	33	0.019*
% Striking	25	0	0.217
% Directed movement	50	0	0.014*

females responded in some manner, as described above in methods. None of these pregnant snakes struck, while 8% (1 of 12) of the non-reproductive females did. In Trial 1, aside from strikes, no snakes moved toward the *C. constrictor* and there was no significant difference between the 12 pregnant and 12 non-reproductive females for any of the three behavioral comparisons (Fisher exact test, *P* = 1.00; Table 1). In Trial 2 pregnant females responded to the stimulus more often after parturition than did non-reproductive snakes (83% vs 33%, *P* = 0.0194), insignificantly more post-parturient females than non-reproductive females struck at the *C. constrictor* (25% vs 0%, *P* = 0.2174), and post-parturient females moved toward the *C. constrictor* significantly more often than did non-reproductive females (50% vs 0%, *P* = 0.0137; Table 2). In several cases of active defense, a mother followed the *C. constrictor* and chased it out of the enclosure, after which she returned to the neonates; when the *C. constrictor* was replaced in or on top of the enclosure, the mother once again chased the intruder until it was no longer visible to her.

The mean SVL of pregnant snakes was 46.5cm, significantly longer than the mean SVL of 41.9 cm for non-reproductive females (*t* = 2.28; *df* = 19; *P* = 0.035; included all 12 pregnant females but only 10 non-reproductive females, because we did not record SVL for two of the latter). During Trial 1, there was no significant difference between the behavior of the two groups; during Trial 2, post-parturient mothers responded significantly more frequently, but those responding were not necessarily the larger snakes. There was no apparent correlation between size of attending female and response to the predator, in that as many small mothers as large mothers exhibited active defense; the same number of mothers exhibited active defense against the large *C. constrictor* as against the smaller individual predator.

PARENTAL CARE BY OTHER PITVIPERS AND OUTGROUP TAXA
Oviparous Old World Pitvipers
A captive female *C. rhodostoma* coiled about her newly laid eggs and "…in her own sluggish way … strongly resented any interference …"; after 41 days of incubation, when the snake was inadvertently dislodged by a falling branch, she left the clutch, ate a mouse and shed her skin, then returned to the eggs (Smith, 1915:788). Three field-collected clutches of *C. rhodostoma* were sheltered but not covered, each of them accompanied by an adult female (Leakey, 1969; his photograph shows the snake loosely coiled upon the eggs, in grass). Deuve (1970) stated that a male and female remain with the eggs until they hatch, the female close to them in a cavity. An attending captive female *C. rhodostoma* had no effect on the temperature of her clutch, but as humidity decreased and increased she shifted coils to expose less or more of the eggs, respectively; that snake and another incubating female responded to tactile disturbance by body bridging, a typical crotaline defensive posture (York and Burghardt, 1988). Gloyd and Conant (1990:384–385) summarized several additional records of this species
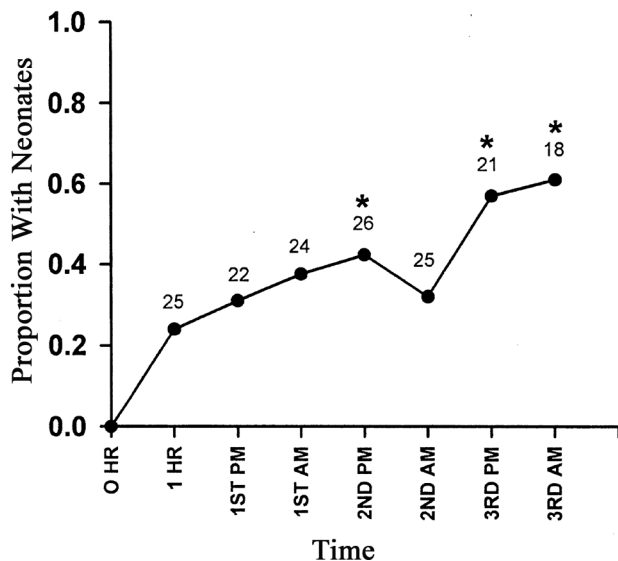

Fig. 3. The proportion of post-parturient female *Sistrurus miliarius* in the same section as their litters in the MC experiment. Numbers above each point indicate sample size. Proportions that show statistical significant deviations from random choice (25% of mothers with offspring) are labeled with an asterisk.

remaining with eggs throughout incubation, including a captive female that changed from "notably aggressive" to "calm" after oviposition, during which she responded to touch only by body bridging.

A Mountain Pitviper (*Ovophis monticola*) remained with her eggs for four days after discovery, within a pile of shredded bamboo, and two other females coiled with their eggs were dug up from tea gardens; these snakes are "rather sluggish and disinclined to strike except when guarding eggs" (Leigh, 1910; Pope, 1935:415). Two captive female *O. monticola* stayed on their clutches for several days, out of total incubation periods of 38–42 days (Orlov, 1997), and according to Manthey and Grossmann (1997) a male and female remained with the eggs until hatching. A captive Hime-Habu Pitviper (*O. okinavensis*) coiled around her clutch (Koba et al., 1970:Fig. 8).

Several observations from captivity confirm that female Hundred-pace Pitvipers (*Deinagkistrodon acutus*) coil around their eggs throughout incubation, and in one instance a female was restless and aggressive before oviposition but calm thereafter (Fleck, 1987; Gloyd and Conant, 1990:401). The Mangshan Pitviper (*Ermia mangshanensis*) lays 13–21 eggs; two adults and 21 juveniles were found together in a "snakeden" (Zhao and Chen, 1990, translated and cited in David and Tong, 1997:12). Female Habus (*Protobothrops flavoviridis*) lay their eggs in cavities in earth and coil around them, sometimes throughout incubation (Yoshida, 1989; Mishima et al., 1999). Three female Kaulback's Pitvipers (*P. kaulbacki*) were "…on guard over their eggs… in holes in the ground"; evidently they had remained with their clutches throughout incubation, as the third nest began to hatch "on the same day" (M. A. Smith, 1940:486). Female Chinese Habus (*P. mucrosquamatus*) have been found in nature with their eggs (Lue et al., 1999), female Bornean Pitvipers (*Trimeresurus borneensis*) encircle their eggs until hatching (Manthey and Grossmann, 1997), and captive female Philippine Pitvipers (*T. flavomaculatus*) coiled around their eggs (Klusmeyer and Fausten, 1994).

Oviparous New World Pitvipers

Oviparous New World pitvipers include the Bushmasters (*Lachesis*) and perhaps a single species of *Bothrops*. One captive female South American Bushmaster (*L. muta*) observed in 1903 provided the earliest observations of a viperid attending eggs (Mole, 1924), and another captive coiled around her clutch after oviposition and resisted removal of the eggs (Boyer et al., 1989). Ripa (1994a, b, 1999) found a *L. muta* coiled around her eggs in the burrow of a Paca (*Agouti paca*); his captive Black-headed Bushmasters (*L. melanocephala*) and Central American Bushmasters (*L. stenophrys*) formed beehive-like, stacked coils around their eggs during oviposition and remained as such throughout incubation. Two of Ripa's female *L. melanocephala* persisted for 77 days in stacked coils while their eggs were artificially incubated elsewhere, whereas a female *L. stenophrys* removed from her eggs and their former substrate ceased guarding. Behavior of his captive female Bushmasters during and subsequent to oviposition varied from unusually defensive to "docile" (Ripa, 1994a, b, 1999). "Considerable anecdotal information [suggests that the Colombian Lancehead, (*B. colombianus*)]… is an egg layer and egg brooder…." (Campbell and Lamar, 1992:8).

Rattlesnakes

Van Hyning (1931), Meek (1946), and Wright and Wright (1957) each found a large Eastern Diamond-backed Rattlesnake (*Crotalus adamanteus*) with 15–18 neonates in or near a Gopher Tortoise (*Gopherus polyphemus*) burrow. The last two reports specifically involved adult females with the young. An adult *C. adamanteus*, presumed to be a female, was found with a total of 10 neonates at Cumberland Island National Seashore, Georgia, on 14–15 September 1973, and that female retreated under boards when approached but did not appear otherwise disturbed by human observers. The neonates had obvious umbilical scars and cloudy eyes, implying they had not shed their natal skins (J. Cadle, in litt.). Butler et al. (1995) reported seven instances of litter attendance by unsexed adult *C. adamanteus*, including three at a tortoise burrow and one in a stump hole. The latter authors documented adults staying with babies until the latter shed, neonate dispersal within hours or a few days of first ecdysis, a tendency of aggregated neonates to retreat intruders, and wariness by an attending adult.

Audubon's journals for 1849–1850 referred to an adult and babies of what were presumably Western Diamond-backed Rattlesnakes (*Crotalus atrox*), together in a hole (Klauber, 1956). In Arizona, an adult female of that species was coiled under a rock within several cm of three groups totaling eight young (Gloyd, 1937). In New Mexico another female *C. atrox* gave birth in the vicinity of a pitfall can trap,

then remained there with the young for at least six days until after neonatal ecdysis. The adult was not especially defensive toward an intruding human, and some of the young repeatedly approached the mother snake or the can trap when disturbed (Price, 1988).

Martin (1992) summarized numerous accounts of attendance of neonates by Timber Rattlesnakes (*Crotalus horridus*; see Anderson, 1942; Swanson, 1952; Oliver, 1955; Brown and MacLean, 1983; Reinert and Zappalorti, 1988), and later added additional records for this widespread species (Martin, 1996, this volume). He found a female within 1 m of 215 of 278 groups of neonates, and at least some of the latter were pre-molt; neonates were wary, and a quick movement by one resulted in others retreating to cover (Martin, 1992). Other generalizations from the literature are that females remain near young but are not particularly defensive, and that mother-offspring associations end about the same time as postnatal ecdysis. Experiments (Brown and MacLean, 1983) and telemetrically facilitated field observations (Reinert and Zappalorti, 1988) demonstrated that neonate *C. horridus* follow scent trails of conspecifics to winter aggregation sites.

In southern Arizona, two female Banded Rock Rattlesnakes (*Crotalus lepidus klauberi*) were among rocks with pre-shed neonates (H. Greene, unpublished; G. Schuett and R. Repp, pers. comm.). A female *C. l. maculosus* "…on a southeastern facing rock outcrop ... [had] eleven young coiled or draped about her" (Armstrong and Murphy, 1979:25–26). On 7 June, 2002, in the Sierra Fria, Aguascalientes, Mexico a pile of neonate *C. lepidus* basked in front of a hole under a deep-seated rock ca. 90 cm in diameter and 20 cm thick. They retreated as we approached to within 1 m, and excavation revealed seven neonates in a horizontal tunnel ca. 7 cm wide and at least 90 cm long; on moist soil within the tunnel we also found several acorns (from rodent activity?), a tarantula, and fragments of shed skin from a snake the size of an adult *C. lepidus*. The neonates had pre-buttons and one of them shed within four hours of discovery (H. Greene and J. Sigala-Rodríguez, unpublished).

In Cochise County, Arizona, an adult female Mojave Rattlesnake (*Crotalus scutulatus*) remained with neonates for several days, after which only small shed skins were found at the site (B. Tomberlin, pers. comm.). Another Cochise County adult *C. scutulatus* was in immediate contact with four young at the entrance of a Banner-tailed Kangaroo Rat's (*Dipodomys spectabilis*) burrow (J. Brown, pers.

comm.). In 1998, R. Reiserer (in litt.), J. Redwine, and J. Whorley made detailed observations on two telemetered *C. scutulatus* in San Bernardino Co., California. One female gave birth prior to 24 August to eight offspring, the expected number based on an earlier ultrasound examination. At 1220 h, R. Reiserer was examining soil at the entrance of a rodent burrow when the obviously thin rattlesnake rapidly approached him from within the tunnel, then retreated out of sight as he moved away. At 1746 h, as he repaired an encircling drift fence 2.5 m from the birth site, the female again approached him, he retreated, and she returned to the burrow. Over the next few days, the female emerged about an hour before sunset and basked briefly just outside the burrow, but no neonates accompanied her. On 29 August, eight of the neonates were moving on the surface or coiled in vegetation near the birth site and their mother was crawling 15 m outside of the fence. Excavation of the burrow revealed eight shed neonate skins as well as part of an adult's shed skin, and on 5 September, the mother was "…much less skittish than ever before." Another female gave birth while concealed in a rodent burrow, between 1–5 September, and a neonate partially emerged on the latter date. Two neonates with opaque eyes basked just inside the burrow entrance on 6 September, and neonates were seen daily at the entrance for the next two days. On 9 September, at 0039 h, the female crawled away from the birth site, and just outside the birth site four neonates were captured on 10 September and two on 11 September, matching an earlier ultrasound count of six embryos. Subsequent excavation of the birth site revealed six intertwined shed skins.

Graves and Duvall (1995) summarized numerous accounts of maternal attendance by *C. v. viridis* from several localities (see Klauber, 1956; Cunningham et al., 1996). Judging from detailed studies in Wyoming, pregnant females rely primarily on crypsis and escape, whereas those attending neonates react with warning displays and offensive strikes in the face of experimental predator confrontations. Mothers remain near their litters for ca. 14 days after birth, until after natal ecdysis, and prior to their first winter young snakes follow conspecific scent trails to winter sites (Duvall et al., 1985; Graves et al., 1986; Graves, 1989; Graves and Duvall, 1995). In Nebraska, a telemetered male *C. v. viridis* accompanied a pregnant female and was at the same site, 10 days later, with two post-parturient females and 31 pre-shed neonates (Holycross and Fawcett, 2002). At Natural Bridges National

Monument, Utah, a *C. v. viridis* left her birth site, an overhang in a rocky canyon, after two days of attendance, and her six neonates remained there and shed 9–10 days after parturition (T. Persons, *in litt.*). Three female Northern Pacific Rattlesnakes (*C. v. oreganus*) in British Columbia, obviously post-parturient, were separately encountered with 4–5 pre-shed neonates (M. Charland, *in litt.*).

Female Mojave Desert Sidewinders (*Crotalus c. cerastes*) in San Bernardino Co., California, remain in rodent burrows with their young until after neonatal ecdysis (R. Reiserer, pers. comm., details to be published elsewhere). Five newborn young were found with a Guerreran Small-headed Rattlesnake (*C. intermedius omiltemanus*; Armstrong and Murphy, 1979; J. Campbell, pers. comm.). In Riverside County, California, a telemetered adult female Southwestern Speckled Rattlesnake (*Crotalus mitchellii pyrrhus*) was visible with 5–6 neonates for several days, in the early morning and at dusk, outside a crevice at the base of a slope; neonates positioned themselves within and beside the female's coils or crawled over her, and they dispersed before she left the site (D. Greenberg, pers. comm.). A basking female Mexican Lance-headed Rattlesnake (*C. polystictus*) withdrew into a "rodent burrow in a grassy bank above a stream through a cornfield," where excavation revealed that she was accompanied by six young (McCranie and Wilson, 2001:34; J. McCranie, pers. comm.).; L. Porras (pers. comm.) surprised an adult female *C. polystictus* and two young at the mouth of a burrow in Jalisco, and as he began catching them an adult male of that species crawled rapidly over his hand and into the hole. A female Mexican Dusky Rattlesnake (*C. triseriatus*) was in "partially cleared pine-oak forest under a log...with six newborn young" (Armstrong and Murphy, 1979:58). In the Huachuca Mountains, several female Arizona Ridge-nosed Rattlesnakes (*C. w. willardi*) were under small rocks with their litters (F. Wilson, D. Hardy Sr., and H. Greene, unpublished; J. Bowler pers. comm.), and a female Chihuahuan Ridge-nosed Rattlesnake (*C. w. silus*) was found with neonates (Tanner, 1985; W. Tanner, pers. comm.).

A female Western Massasauga (*Sistrurus catenatus tergeminus*) occupied a rockpile with 11 neonates that were in pre-shed condition (Greene and Oliver, 1965). An adult Eastern Massasauga (*S. c. catenatus*) was found with five neonates, and the latter shed within a few days of capture (Swanson, 1930); several other post-parturient females were found basking with neonates for several days (Reinert and Kodrich, 1982; Johnson, 2000).

In contrast to our observations on *C. molossus*, nine telemetered, free-living Aruba Island Rattlesnakes (*C. durissus unicolor*) immediately moved 20–60 m following parturition and were not seen with their offspring, although on each of three occasions, after exhaustive searching, a single, post-shed neonate was found between the sites where its mother was last seen pregnant, and next seen post-parturient. Seven captive-born litters shed their skins within 6–24 hours of birth (H. Reinert, *in litt.*).

Other Viviparous Pitvipers

Wall (1903:98–99) found an adult Yangtze Mamushi (*Gloydius blomhoffii siniticus*) "…lying together … with twelve young," all evidently killed by a human. A female Caucasian Pitviper (*G. intermedius caucasicus*) "…had five young nearby" (Ataev, 1985, translated and cited by Gloyd and Conant, 1990:355).

A. G. Smith (1940:79) located a female Northern Copperhead (*Agkistrodon contortrix mokasen*) and seven young under a log, and was uncertain whether the litter was born that day. Several female Osage Copperheads (*A. c. phaeogaster*) have been found with their young in the field; in one case young remained with the female for at least a day, and members of three litters shed within two days of capture, implying that they remained with the female a few days after birth (Anderson, 1942; Oliver, 1955; Fitch, 1960). Pregnant animals were "noticeably more docile … but … after the birth of their litters … became irritable and would vibrate their tails in response to any disturbance …" (Fitch, 1960:178). A female Southern Copperhead (*A. c. contortrix*) and four young found under a log were still there when checked a day later (Kennedy, 1964). Two Florida Cottonmouths (*A. piscivorus conanti*) were found with 13 neonates, and remained in the vicinity while the young snakes were caught; another attending female was with six "milky-eyed young" that were at least four days old (Wharton, 1966a:154). Another large female and seven neonates were encountered twice over a period of three days, lying in front of a hollow chamber of mud, vegetation, and cypress knees; the snakes retreated into the chamber when disturbed, and the adult repeatedly approached the observers when a neonate was lifted on a snake hook (Walters and Card, 1996).

Viperines and More Distant Outgroups

Rhombic Night Adders (*Causus rhombeatus*) coil around their eggs immediately after oviposition and remain with them throughout incubation unless repeatedly disturbed (FitzSimons, 1912). Some authors have claimed that Adders (*Vipera berus*) aggregate with their young for up to several days after birth, and that the young seek cover under the female when approached closely. Neonates often shed their skin within one or two days after birth (Smith, 1951; Street, 1979). Conversely, several experienced researchers at the conference on which this volume is based have not observed female *V. berus* attending their young (S. Anderson, C. Andrén, T. Madsen, and R. Thorpe, pers. comm.).

Maternal attendance of eggs is widespread in elapids and pythonids, and occurs in at least a few colubrids and scolecophidians (Shine, 1988; Somma, 1990; Greer, 1997). Field anecdotes suggest maternal attendance and defense of young by *Boa constrictor* (Greene, 1997), and a captive of that species nudged young with her neck "to get them moving" (Ronne, 1996:34). Among living lizards that are basal to snakes, some female anguids and scincids attend their eggs and/or offspring (Somma, 1990; Mendoza Quijano and Bellardo, 1995; Lanham and Bull, 2000), and some female varanids liberate their young from sealed nests at the time of hatching (Carter, 1999). Parental care among archosaurs and tetrapods more distantly related to vipers has been reviewed elsewhere (McKitrick, 1992; Crump, 1996; Clark et al., 1999; Greene, 1999).

BEHAVIORAL VARIATION AND PHYLOGENETIC ANALYISIS

Behavioral Character Description

Ideally, behavior can be characterized in terms of kinematic profiles, stimulus control, and several contextual variables (Drummond, 1981), as well underlying physiological control mechanisms (Bass, 1998). At present, however, the most broadly applicable description of parental behavior in vipers is simply sustained proximity to eggs and/or young, a response that may last for several weeks after oviposition (e.g., 60–77 days in *Lachesis*, Ripa, 1994a, 1994b) or ca. 10 days after birth (e.g., several species of *Crotalus*). That some oviparous crotalines attend their eggs throughout incubation has not been controversial, although no one has documented whether those females remain with their young after hatching (as perhaps implied by first shed at an age of ca. 10 days

in *C. rhodostoma* [Chanhome, 1998] and 15 days in *L. stenophrys* [D. Hardy, Sr., unpublished]). Conversely, herpetologists usually have been reluctant to attribute parental care to adult pitvipers found in the field with newborn young, perhaps because observations were brief and alternative explanations seem plausible (Klauber, 1956). Finneran (1953), for example, suggested that female *A. contortrix* and neonates might coincidentally remain at thermally favorable sites previously selected by the adults. Butler et al. (1995) proposed that most females and young of *C. adamanteus* might disperse immediately after birth, such that infrequently observed aggregations are more easily detected but abnormal; they also noted that the mother's presence might result only from fatigue and physiological stress associated with birth.

Three lines of evidence imply that Anderson (1942) and Wharton (1966a) were correct, that parental attendance of young is biologically significant for several species of pitvipers. First, coincidence is an unlikely explanation because parent-offspring associations have been reported repeatedly in crotalines and yet have not been reported for so many other frequently encountered species of snakes. For example, females of 17 species of North American crotalines have been found with their young in the field, sometimes repeatedly, but evidently no one has recorded maternal attendance for any of the ca. 36 species of viviparous natricine snakes in the United States—some of which are terrestrial, relatively large, abundant, and well studied (e.g., Wright and Wright, 1957; Fitch, 1965; Shine, 1988; Rossman et al., 1996). Second, extensive field observations of *C. horridus*, *C. molossus*, *C. scutulatus*, *C. viridis*, and *S. miliarius*, as well as anecdotes for at least six other species of pitvipers, show that females attend young for several days, until or shortly after neonatal ecdysis and regardless of the exact interval between birth and shedding (aggregations of the young in captivity, exclusive of a female, also cease after first ecdysis in *C. viridis*; Graves et al., 1986). H. Reinert's (in litt.) studies provide the important counter observations that immediately after birth free-living female *C. d. unicolor* abandon their offspring, and that the neonates shed immediately. Third, our laboratory experiments confirm that attending *S. miliarius* are attracted to their young and vice versa, prior to the first neonatal ecdysis, and that females change their response to a predator during attendance.

Confirming the lack of parental attendance in a particular snake species is of course difficult in the absence of direct observations. There are apparently

no reports of parental attendance of eggs or young by viperines other than *C. rhombeatus* and possibly *V. berus*, respectively, or by any viviparous tropical pitvipers. With the exception of Reinert's studies of *C. d. unicolor* (described above), however, little evidence indicates that any of those snakes do not exhibit parental care. Three broods of *Trimeresurus macrolepis* were found at the base of bamboo clumps; "…on danger approaching, the young hurry back to the protection of the leaves … I never found an adult accompanying [them]" (Hutton, 1949:459). Jumping Pitvipers (*Atropoides nummifer*; R. Queen, pers. comm.), Picado's Pitvipers (*A. picadoi*; R. Aymerich, pers. comm.), Side-striped Palm-pitvipers (*Bothriechis lateralis*; W. Lamar, pers. comm.), and several species of Brazilian lanceheads (*Bothrops* spp.; S. Sant'Anna, pers. comm.) shed within hours of birth, suggesting that those Neotropical crotalines also lack parental attendance. Conversely, Eyelash Pitvipers (*Bothriechis schlegelii*) shed their skins 5–7 days after birth (Antonio, 1980), raising the possibility that at least one species of viviparous Neotropical crotaline attends its young.

There is as yet little basis for characterizing postural variation among attending oviparous viperids, or for comparing their behavior with that of egg attending pythonids and colubroids. Published illustrations show a single body loop or loose coils encircling eggs, sometimes with the head over part of a clutch as if ready to strike, for *C. rhombeatus* (FitzSimons, 1912), *C. rhodostoma* (Smith, 1915; Leakey's [1969] photo shows a tight, not obviously pre-strike coil overlapping about half of the clutch from one side), *O. monticola* (Pope, 1935), and *O. okinavensis* (Koba et al., 1970). Attending female *Lachesis* encompass their eggs with coils stacked like a beehive (Ripa, 1994a, 1994b).

We know next-to-nothing about sensory and physiological mechanisms that control parental care in vipers, although circumstantial evidence implies that chemical cues are important for initiating and maintaining maternal attendance. A captive *C. rhodostoma* attempted to coil on another female and her eggs, 16 days before the intruder laid her own clutch (York and Burghardt, 1988), and female *Lachesis* of two species did or did not continue attendance behavior, depending on whether eggs or the snakes themselves were removed to another site, respectively (Ripa, 1994a, b). G. Schuett (in litt.) has indicated to us that shedding in squamates is likely associated with thyroid function, and because a mother pitviper's departure from the birth site coincides with postnatal ecdysis, changes in the neonatal thyroid system probably affect skin chemistry and thereby influence her response. Furthermore, because female *C. atrox* show only a short-lived but highly elevated spike for corticosterone, beginning 24 h before and ending within hours after parturition, and no elevation in sex steroid levels during that period, those hormones are probably not involved in controlling maternal attendance (G. Schuett, unpublished).

Most reports of parental attendance by pitvipers seemingly involve a single female with (presumably her) young. With the exception of one *C. polystictus* and one *C. viridis*, only vague reports for *C. rhodostoma*, *C. molossus*, and *O. monticola* have mentioned males found with neonates. Aggregations of multiple females with young are known for *A. contortrix*, *A. piscivorus*, *C. horridus*, *C. molossus*, and *C. viridis*. Two pairs of *S. miliarius* with young each involved only one emaciated (presumably post-parturient) adult, such that the other adult might have been a male, a pre-parturient female, or a non-reproductive female (Palmer and Williamson, 1971). Although those groupings might reflect only a shortage of appropriate basking sites, the interactions we observed among female *C. molossus* and theoretical considerations (Graves and Duvall, 1995) imply more complex, adaptive explanations. Curiously, whereas communal gestation is well documented in several crotalines and communal oviposition occurs in diverse other snakes (Graves and Duvall 1995), the latter is not recorded for oviparous pitvipers.

Our review indicates that the behavior of attending female pitvipers and perhaps their young varies among species and/or individuals. Oviposition sites can be in burrows (*Lachesis, Protobothrops*), within piles of vegetation (*O. monticola*), or exposed on the surface (*C. rhodostoma*); birthing sites include burrows made by tortoises, rodents, and perhaps other mammals (*A. piscivorus, C. adamanteus, C. atrox, C. cerastes, C. molossus, C. polystictus, C. scutulatus*), under rocks or within rock piles (*C. horridus, C. lepidus, C. mitchellii, C. molossus, C. viridis, C. willardi, S. catenatus*), and under or within timber (*A. contortrix, C. horridus, C. triseriatus, S. miliarius*). As Graves et al. (1986) noted, particular birthing sites might facilitate thermoregulation and escape from predators, and those sites typically are disjunct from winter refuges and foraging areas.

Captive *C. rhodostoma* regulate relative humidity around their eggs and respond to disturbance by defensive body-bridging movements; females of *C.*

rhodostoma and three species of *Lachesis* accompanying their eggs vary in temperament from unusually defensive to "calm" or even "docile." In the field, attending females of *O. monticola* and *A. contortrix* seem more prone to strike than at other times, while those of *D. acutus*, *C. adamanteus*, *C. atrox,* and *C. horridus* appear passive or at least not especially defensive. Free-living female *C. viridis* and captive female *S. miliarius* become more prone to active defense during attendance of neonates, an attending female *C. scutulatus* twice approached a nearby human, and the responses of free-living female *C., molossus* attending their young range from advancing and rattling at an intruder to not emerging from their birth refuges. Female *C. molossus* and their young experience mutual tongue-flicking and tactile contacts; one female visually fixated on one of her neonates as it shed, and another physically restrained a neonate that began to crawl toward an approaching human.

Phylogenetic Analysis

In addition to a survey of variation in the taxa of interest and in their outgroups, an historical analysis of any character requires a phylogenetic hypothesis for the groups under study and a method for reconstructing ancestral attributes (e.g., Larson and Losos, 1996; Greene, 1999). Accordingly, we used the software MacClade (Maddison and Maddison, 1992) and the information summarized above to map parental care on cladograms, parsimoniously reconstruct ancestral behavioral states, and thereby infer evolutionary transformations. Our analysis is necessarily preliminary because of missing information for many taxa and incomplete resolution of phylogenetic relationships at several levels.

As reviewed above, certain control mechanisms, attendance by multiple females and/or a male, particular behavioral responses, and other attributes are reported or implied for one or more species of vipers, but they have not been documented at higher levels of taxonomic generality. We therefore conducted a phylogenetic analysis of "presence" or "absence" of parental attendance as the only comparison justified by available evidence, treated those states as unordered, and assumed that transitions between them were equally probable. We have confirmed presence of that behavior for 33 species in 14 genera of viperids, including at geographically disparate localities for several widespread species (e.g., *A. controtrix*, *C. horridus*, *C. molossus, C. scutulatus*, *C. viridis*). We can confirm absence for two species in two genera,

yielding information on presence or absence of parental care for only about 14% percent of 230 species and 40% percent of 35 genera (David and Ineich, 1999; McDiarmid et al., 1999). There are so many unscored taxa in Viperidae, however, that for this exploratory analysis we scored lineages for parental attendance based on evidence for one or more species in each group. For example, we scored all *Gloydius* as present based on reports of parental attendance for two species in that clade. All Neotropical pitvipers except *B. colombianus* and *Lachesis* were scored as absent, based on no records despite substantial fieldwork, (e.g., Solórzano and Cerdas, 1989; Martins and Oliveira, 1999) and several reports of immediate post-natal ecdysis. *Hypnale*, *Tropidolaemus*, and viviparous *Trimeresurus* were scored as absent based on direct evidence for *T. macrolepis* and lack of records for the others (but see below). For heuristic purposes we alternatively coded parental attendance as absent in *Azemiops feae*, other snakes, and other reptiles (there are no records for the former and it varies from absent to ubiquitous among subclades of the latter two groups), or as unknown in *A. feae* and variably present in outgroup snakes and anguimorphs.

We provisionally based phylogenetic hypotheses for vipers and relevant outgroups on Knight and Mindel (1994), Kraus et al. (1996), Cullings et al. (1997), Kraus and Brown (1998), Lee (1998), Parkinson et al. (2002), Vidal et al. (1999), Parkinson et al. (2000), Malhotra and Thorpe (2000), and Lenk et al. (2001). Briefly stated, available evidence implies an Old World origin for Viperidae, including Crotalinae, and a paraphyletic Old World radiation of crotalines and a single, monophyletic invasion of the New World. Finally, it appears there was an initial divergence of New World crotalines into a predominantly temperate North American clade (*Agkistrodon* plus rattlesnakes) and a tropical Middle and South American clade (all others). We used Klauber's (1972) phylogenetic tree for rattlesnakes, because molecular systematic approaches have thus far not conclusively resolved basal lineages and all studies place *C. durissus*, the one rattlesnake with a substantially lowland tropical distribution and the only one known to lack parental care, nested well within that clade (Murphy et al., this volume; K. Zamudio et al., unpublished). The taxonomic occurrence of reproductive modes and of tropical versus temperate distributions is indicated in Figure 4 as a context for interpreting parental behavior.

Bearing in mind the uncertainties detailed above, we used MacClade to examine the impact of alterna-
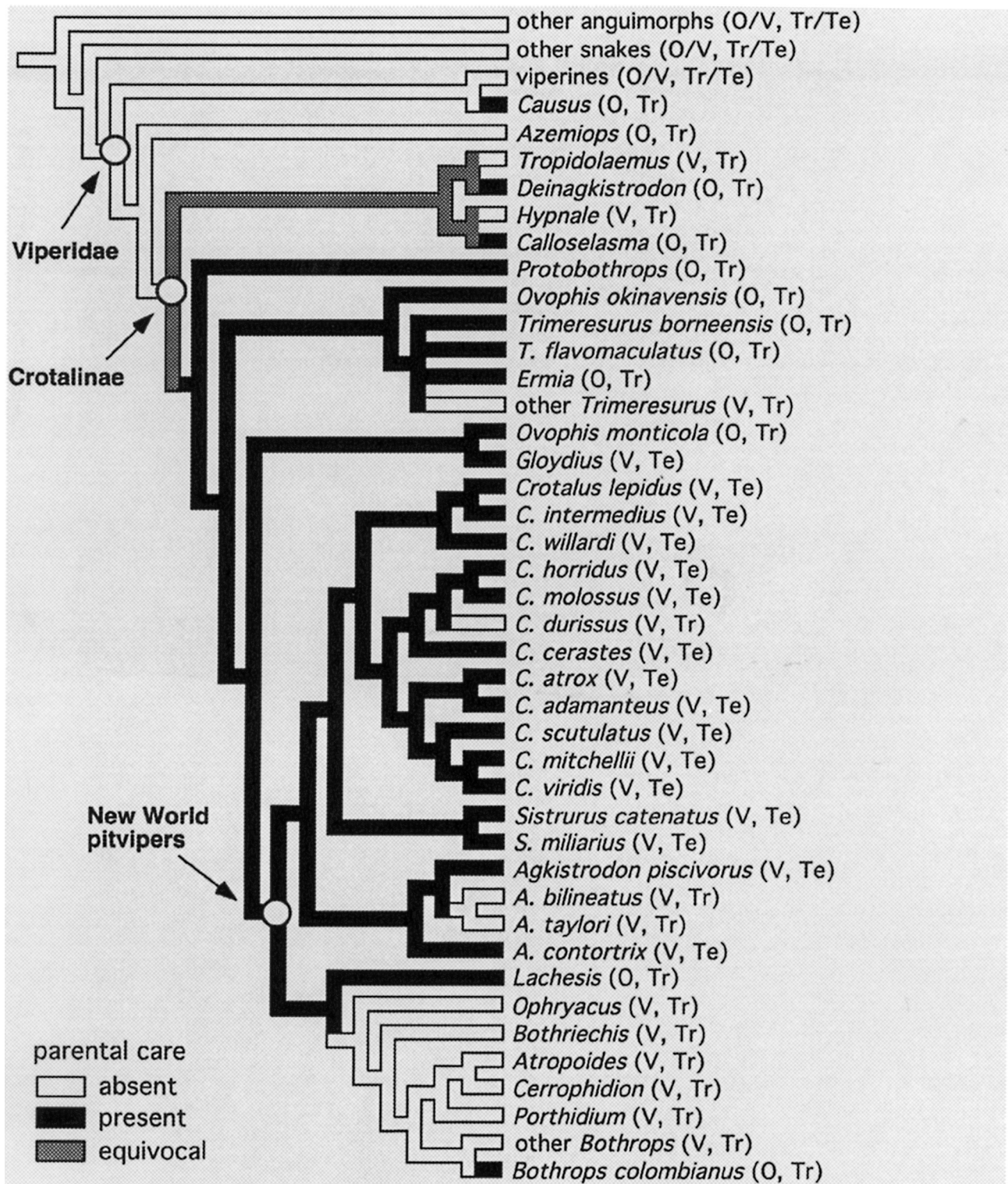
Fig. 4. A tentative scenario for the evolution of parental attendance in pitvipers and several outgroup taxa, based on the assumptions that *Causus* is the sister taxon to other viperines, *Lachesis* is basal to other Neotropical pitvipers, and parental attendance is absent or independently derived within outgroups to Crotalinae. Abbreviations indicate mode of reproduction (O = oviparous, V = viviparous, O/V = polymorphic for a taxon) and distribution (Tr = tropical, Te = temperate, Tr/Te = polymorphic for a taxon).

tive character coding and phylogenetic topologies on inferences about the evolution of parental care in vipers. Four tentative generalizations follow from our analysis:

(i) McClade reconstructed the nodal state for pitvipers as ambiguous because parental care was scored absent in the viviparous sister taxa of two egg-guarding species in a basal tropical crotaline clade (Fig. 4). Absence in at least three other viviparous tropical pitviper lineages (see below), however, suggests that loss might also have independently occurred twice within that primitively egg-guarding, *Calloselasma-Deinagkistrodon* clade, in the ancestors of *Hypnale* and *Tropidolaemus*. Alternatively, because neonates of *Hypnale hypnale* first shed 7–10 days after birth (De Silva and Toriba, 1984), perhaps females do attend their young. In either case, parental attendance would reconstruct as a synapomorphy for pitvipers within Viperidae (Fig. 4); however, if that behavior proves to be widespread in viperines and/or near outgroups, the level at which it is inferred to be derived will be more inclusive than Crotalinae.

(ii) Parental attendance of young by viviparous temperate pitvipers arose at least once within an Old World tropical egg-attending clade, in the ancestor of *Gloydius*. Whether temperate New World viviparous crotalines retained neonatal attendance from a viviparous common ancestor with *Gloydius* or independently evolved it from an egg-guarding New World common ancestor with *Lachesis* is ambiguous, given uncertainties about the phylogenetic placement of the latter.

(iii) Parental attendance probably has been lost several times in viviparous tropical pitviper lineages: in the ancestors of *C. durissus*, *Hypnale*, and *Tropidolaemus*; at least once in *Trimeresurus*; and in the ancestor of all or most Neotropical crotalines. This conclusion could be contradicted by direct evidence of parental attendance in viviparous tropical crotalines.

(iv) Oviparity and/or egg attendance could be parsimoniously interpreted as reversals if *B. colombianus* and/or *Lachesis* are in fact nested within groups that lack those traits. That conclusion would be contradicted by strong evidence for more basal placement of those taxa (Fig. 4), or by independent evidence that reversal to oviparity and maternal attendance are unlikely, such that *B. colombianus* and/or *Lachesis* probably retain primitive states despite their phylogenetic relationships. In any case, retention of egg guarding in those snakes and other tropical oviparous taxa (e.g., *Causus*, *Calloselasma*, *Protobothrops*) provides an intriguing contrast to repeated loss of neonate attendance by viviparous tropical pitvipers.

DISCUSSION
Ecological Consequences

Understanding the maintenance of a particular behavior in a population entails an analysis of ecological consequences, with the working expectation that benefits must exceed costs for natural selection to favor a trait. The response of female crotalines to intruders can vary within populations (e.g., *C. molossus*, *C. viridis*, *S. miliarius*), and maternal attendance was exhibited by only ca. 50% of females in a laboratory colony of an elapid, the Shield-nosed Cobra (*Aspidelaps scutatus*, Haagner and Morgan, 1992), thus confirming that individual variation in parental care by snakes can be susceptible to selection. Shine's (1988) scholarly analysis forms the basis for the following brief consideration of benefits and costs of parental attendance of young by vipers (see also Clutton-Brock, 1991; Rosenblatt and Snowdon, 1996; Agrawal et al., 2001).

Venomous snakes are at least occasionally eaten by a wide range of predators, despite their potential for deadly retaliation against an adversary (e.g., Klauber, 1956; Greene, 1988). Furthermore, mortality often may be relatively heaviest on young snakes, and perhaps especially so for venomous species that are generally well defended as adults (Fitch, 1949; Klauber, 1956; Greene, 1988; Bonnet et al., 1999). Neonates might be especially vulnerable as a result of their small size and inexperience, and the newborn young of *A. contortrix* (Fitch, 1960) and *C. atrox* seem "…uncharacteristically unresponsive to threatening external stimuli" (Price, 1988:372). During their natal shed cycle, the young snakes' vision is presumably hampered by development of their new spectacles (Price, 1988), and perhaps the pits of newborn crotalines also are functionally compromised prior to shedding. Moreover, although aggregation might provide physiological advantages for neonates (Graves et al., 1986; Graves and Duvall, 1995), it could increase visibility to predators and endanger a female's entire reproductive output for one or more years (Price, 1988); discovery of a litter might even be facilitated "when birthing scents are strong" (Butler et al., 1995:197).

Known or potential predators on *C. molossus* at Greene and Hardy's Arizona study site include the Sonoran Whipsnake (*Masticophis bilineatus*, Enderson,1999; G. Middendorf, pers. comm.), *B. jamaicensis* and other raptors, Loggerhead Shrike (*Lanius ludovicianus*, Chapman and Casto, 1972), Roadrunner (*Geococcyx californicus*), Collared Peccary (*Pecari tajacu*), Ringtail (*Bassariscus astutus*,

Mead and Van Devender, 1981), White-nosed Coati (*Nasua narica*), *U. cinereoargenteus*, Coyote (*Canis latrans*), Black Bear (*Ursus americanus*), Bobcat (*Lynx rufus*), Puma (*Puma concolor*), and perhaps Jaguar (*Panthera onca*; for felid predation on large adult *Crotalus*, see Armstrong and Murphy, 1979:14). Known or potential predators of *S. miliarius* at May, Sciturro, and Farrell's Florida study site include *C. constrictor* (Printiss, 1994), Scarlet Kingsnake (*Lampropeltis triangulum elapsoides*), several species of birds (e.g., hawks, owls, herons, crows), Northern Raccoon (*Procyon lotor*), and Nine-banded Armadillo (*Dasypus novemcinctus*).

Given diverse potential enemies that sometimes specifically avoid venomous snakes (Greene, 1988; Pough, 1988; Beckers et al., 1996), as well as increased defensiveness by attending females of *S. miliarius* and certain other crotalines, the most likely way in which vipers protect their eggs and/or young is through their presence and in some cases antipredatory behavior. Variation in defensive responses among maternally attending crotalines might therefore reflect regional- or even birth site-specific predation pressures. Also, presence of an egg guarding female might prevent incidental destruction by armadillos, rodents, or other previous inhabitants of underground refuges (Ripa, 1994a, b), and the cryptic coloration of an attending *C. rhodostoma* probably conceals otherwise exposed eggs (York and Burghardt, 1988). Observations of several species of attending pitvipers are consistent with the suggestion by Butler et al. (1995) that retreat from an intruder by mothers and their aggregated neonates might be socially facilitated.

There are several other potential benefits of parental care, none of them necessarily exclusive of an antipredator role. Mammal burrows might provide stable microclimates (see Kay and Whitford, 1978) for incubating eggs (e.g., *Lachesis*, Ripa, 1994a, b) and neonate aggregation might be advantageous in terms of thermoregulation and water regulation (Finneran, 1953; Duvall et al., 1985; Graves et al., 1986; Graves and Duvall, 1995); in such cases parental attendance might enhance or facilitate the physiological advantages, as well as protect eggs that would not have been as exposed had they been buried rather than placed in a burrow. Aggregation also might facilitate trail following to a den by neonates of *C. horridus* (Brown and Maclean, 1983; Reinert and Zappalorti, 1988), *C. viridis* (Graves et al., 1986), and other pitvipers, as well as promote incest avoidance and other aspects of social behavior (Graves and

Duvall, 1995). Although those and other social advantages might seem less likely for *C. adamanteus* and other species that do not den communally (Butler et al., 1995), young *C. horridus* in New Jersey do follow adults to individual winter refuges (Reinert and Zappalorti, 1988).

The general lack of paternal attendance in vipers conforms to theoretical predictions about which sex and what species should care for young (Shine, 1988). Male parental care should be selected against when paternity is uncertain and males are not otherwise likely to be near their offspring at birth, both conditions consistent with the apparent lack of paternal care in pitvipers (for alternative explanations of males accompanying post-parturient females see Holycross and Fawcett, 2002). In fact, multiple paternity occurs in some snakes (Schuett, 1992; McCracken et al., 1999). We documented visits by multiple males to individual female *C. molossus*, and female viperids typically give birth at specific sites that often are removed from areas used by other members of the population (e.g., *C. molossus*; see also Martin, 1992; Duvall et al., 1995). Biparental care might be advantageous in cases where two parents are more effective than one, as for example with mobile young, but that circumstance seemingly does not apply to venomous viviparous snakes. A more likely benefit of biparental care would be increased deterrence toward a predator provided by presence of more than one adult venomous snake. From a benefits/costs perspective, females should be more likely to care because of their certainty of maternity and proximity to their eggs and/or young, as is the case in all viperids with some form of parental attendance.

An inability to feed might not be a substantial cost of parental care, although some females are obviously hungry and yet unlikely to capture prey while gestating and attending eggs or young (for an excellent review of hypophagia in gestating snakes, see Gregory et al., 1999). Among 362 pregnant *C. viridis*, only eight spring-captured snakes had food in their stomachs (Macartney and Gregory, 1988), and some egg-attending captive pitvipers accept food provided on forceps (*T. flavomaculatus*, Klusmeyer and Fausten, 1994) or even leave their clutches briefly to feed (*C. rhodostoma*, Smith, 1915). Pregnant and attending female *C. molossus* in nature are highly sedentary for about four months and thus unlikely even to encounter their rodent prey, but they infrequently adopt ambush postures while gestating and typically move immediately to hunting areas after the young disperse. Pregnant

female *C. horridus* never adopt ambush postures (Reinert et al., 1984). On the other hand, a *C. lepidus* (University of Kansas Museum of Natural History, KU 52000) with well-developed embryos has a relatively large *Sceloporus* sp. in its stomach, implying that a female *C. lepidus* might ambush lizards (often abundant in the habitat of that species) that pass by its birthing site, and some other snakes do feed while gestating (Graves and Duvall, 1995). In any case, mass loss by pregnant *C. v. oreganus*, between emergence from hibernation and parturition, averaged only 6.1% (Macartney and Gregory, 1988), and an additional 10 days of fasting during attendance of neonates likely would not affect future fecundity in pitvipers that reproduce less than once annually (Price, 1988; Butler et al., 1995) Note, however, that variation in the duration of egg attendance by Water Pythons (*Liasis fuscus*) dramatically influences female survivorship (Madsen and Shine, 1999).

Widespread presence of maternal attendance in pitvipers conforms to a theoretical prediction that parental care should characterize organisms that are especially capable of defense (Shine, 1988), but existing theory does not explain the apparent near restriction of that behavior to crotalines within a larger clade of venomous snakes. Perhaps the costs of parental care are such that it is more likely feasible as part of a confrontational syndrome, a suite of pitviper innovations that also included infrared imaging organs (the better to assess enemies), aposematic sound production by the specialized tail tip, and increased reliance on camouflage and active defense rather than flight (Greene, 1992, 1997). We do not understand why delayed neonatal ecdysis (as opposed to shedding immediately after birth, typical of many snakes and some tropical crotalines) is associated with maternal attendance in temperate viviparous crotalines, but time to first shed is positively correlated with hatchling size in Australian pythons (Greer, 1997), so perhaps comparative studies of viperid life histories will inspire a solution to that mystery.

Evolutionary History

Wharton (1966a) speculated that egg-guarding by Old World pitvipers was the evolutionary precursor of maternal attendance of neonates by *A. piscivorus*, whereas Butler et al. (1995) conjectured that short-term exhaustion from birth, resulting in incidental protection of young snakes, might have occurred prior to more sustained parental behavior such as they described for *C. adamanteus*. Our phylogenetic analysis

corroborates Wharton's hypothesis, in that taxa exhibiting maternal attendance of neonates are nested within Crotalinae, the basal-most lineages of which attend their eggs during incubation (Fig. 4). As such, parental attendance is homologous for pitvipers (and perhaps a more inclusive group), implying that it originated at or prior to origin of the ancestral oviparous crotaline, at least 23 mya (Greene, 1992, 1997; Ivanov, 1999; Szyndlar and Rage, this volume). During the diversification of pitvipers, egg attendance apparently has been transformed to neonatal attendance in one or more viviparous lineages, and subsequently lost in several more highly nested, Neotropical taxa. Protection of eggs and/or young from predators is perhaps the most widespread consequence of maternal attendance in crotalines and therefore a likely historical adaptive role, but we cannot exclude the possibility that ancestral parental pitvipers increased offspring survivorship due to one or more of the other advantages discussed above. In any case, crotalines provide one and likely several evolutionary events that corroborate the hypothesis that viviparity should arise within clades characterized by maternal care of eggs (Shine and Bull, 1979; Shine and Lee, 1999).

Some alternatives for parental care as a shared-derived behavioral trait for Crotalinae deserve future scrutiny. First, maternal attendance might be an older, retained primitive attribute in pitvipers, given its presence in at least one near outgroup (*C. rhombeatus*) and in more distantly related macrostomatans (e.g., various elapids and pythonids, *B. constrictor*; see Shine, 1988; Somma, 1990; Haagner and Morgan, 1992; Greer, 1997), as well as successively more basal scolecophidians (Shine 1988), varanids (Carter 1999), anguids (Langerwerf, 1981; Mendoza Quijano and Bellardo, 1995), and scincids (e.g., Lanham and Bull, 2001). Given the late- to early Mesozoic fossils of those viper outgroups (e.g., basal macrostomatan snakes, Tchernov et al., 2000; varanids, Pepin, 1999), maternal attendance in their common ancestor might well be at least 100 million years old. However, as Rieppel and Zaher (2000) emphasized, accurate characterization of particular phenotypes is critical to phylogenetic reconstruction, and the older and more different two attributes the less likely they are homologous (references in Greene, 1999). Other possible explanations for the apparent sporadic occurrence of maternal attendance in vipers (and snakes generally) include homoplasy within that clade, latent homology (implying re-expression of

maternal attendance, Greene, 1999), and phenotypic plasticity (Madsen and Shine, 1999). Of course, given a paucity of detailed field studies to date, many more species of snakes might eventually prove to attend their eggs and/or young.

The putative homology of parental attendance for Crotalinae might explain an apparent paradox, that a specific defensive behavior elicited by chemical cues from an exclusively New World predator, body-bridging against kingsnakes (*Lampropeltis*) by some North American pitvipers (e.g., *Agkistrodon*, *Crotalus*, Carpenter and Gillingham, 1975; Weldon and Burghardt, 1979; Gutzke et al., 1993), is also exhibited by at least one Old World species. In nature, a body-bridging response by a guarding female *C. rhodostoma* (elicited in captives by York and Burghardt, 1988) would perhaps be directed at kukrisnakes (*Oligodon*), a widespread Asian colubrid clade of reptile egg-eaters (Coleman et al., 1993). Body-bridging against kingsnakes by New World crotalines thus would be exaptive, having evolved in their Asian ancestors as an adaptive response to egg predation and later co-opted for defense against predators on adult pitvipers.

Additional Problems and Prospects

Parental attendance is widespread among pitvipers, and the many unanswered questions about this behavior offer rich avenues for future studies. We know almost nothing about the significance of individual, population, and taxonomic variation—we have only tantalizing hints regarding stimulus control and adaptive roles. Do oviparous crotalines remain with their offspring throughout the neonatal shed cycle, or abandon them immediately after hatching? How might hormonal cycles, shedding behavior, and skin chemistry cause mothers to abandon birth sites and resume hunting? Do mothers recognize their own young among those from another female, do neonates recognize their mothers among several aggregating adults, and what stimuli control recognition and attraction (see Graves et al., 1986)? How might parental responses be affected by such factors as age and health status, experience, the size and quality of a litter, severity of a particular predation threat, and local ecological conditions (Clutton-Brock, 1991; Madsen and Shine, 1999; Agrawal et al., 2001; Ghalambor and Martin, 2001)? Of what significance, if any, are interactions among siblings and their mothers for the future behavior of all concerned?

Our studies of *C. molossus* and *S. miliarius* underscore claims that snakes are appropriate subjects for diverse field and laboratory research (Seigel, 1993; Beaupre and Duvall, 1998; Shine and Bonnet, 2000). Female pitvipers and their young may be accessible for detailed observations and even controlled manipulations in nature (a generally uncommon situation for non-avian reptiles, see Burghardt, 1978; Burghardt et al., 1978; Burghardt and Layne, 1995), such that studies of crotalines have great potential for elucidating behavioral development. Some squamate eggs and/or neonates can be maintained with a parent in captivity (e.g., Smith, 1915; Noble and Mason, 1933; York and Fleck, 1987; Burghardt, 1988; Klusmeyer and Faustin, 1994), and thus descriptive aspects of parental care in crotalines could be studied in laboratory colonies, zoos, and the private collections of herpetoculturists. In terms of experimental approaches, maternal attendance has a well-defined endpoint (neonatal ecdysis and dispersal) and is not confounded by lactation or other types of food provisioning, so if chronic blood sampling proved feasible (see Schuett et al., 1997; Bonnet et al., this volume), hardy pitvipers (e.g., *A. contortrix*, *A. piscivorus*) might serve as excellent models for investigating the endocrine control of parental care.

While emphasizing the importance of research on parental care in vipers, in terms of both scientific progress and knowledge-enhanced appreciation of these animals (Greene, 1997, 1999; Greene and Campbell, 1992), we also strongly endorse techniques that minimize stress to individuals and populations in studies of snake biology. For example, protocols for secure caging, anesthesia, tubing, and other indirect management options can minimize trauma to the snakes as well as reduce risks to an investigator working with venomous species (e.g., Altimari, 1998; Hardy and Greene, 1999b, 2000; Waters et al., 1999). Naturalistic approaches to captive conditions likewise are advisable in terms of both good science and humane animal care (Burghardt, 1998a). And while field manipulations could justifiably be used to assess the fitness consequences of parental presence or absence, because they might expose litters to increased predation and deprive neonates of significant interactions with their mothers and siblings, the methodology and ethics of such studies should be carefully considered in advance (for a cogent discussion, see Emlen, 1993).

Finally, because parental care and various other surprising behaviors are more prevalent among non-archosaurian reptiles than previously recognized (e.g., see for turtles Barrett and Humphrey, 1986; Iverson,

1990; Burghardt, 1998b), the lives of these animals are likely far more complex than even herpetologists have imagined. Recall, for example, the demonstration of self-recognition and spatial memory in rattlesnakes by Chiszar et al. (1991) and Burghardt's (1996) assessment of the "private experience" of various colubrids. Consider that a "family" exists when "offspring continue to interact into adulthood with their parents" (Emlen, 1997:229), perhaps exemplified by high genetic relatedness among individuals of *C. horridus* sharing a den (Bushar et al., 1998). As a counter example, Black Ratsnakes (*Elaphe o. obsoleta*) are not characterized by family-like population genetic structure, although they too use communal winter sites and are broadly sympatric with *C. horridus* in eastern North America (Lougheed et al., 1999). Given the potential complexity and diversity of snake behavior, do female pitvipers ever behave as helpers (Emlen, 1997) or engage in intraspecific brood parasitism (Zink, 2000)? Does parental attendance of neonates result in indirect genetic effects (Wolf et al., 1998)? Culture, however difficult to define, typically implies transmission of information across generations (McGrew, 2001), so is that term applicable to initial location of dens by young-of-the-year *C. horridus* (Reinert and Zappalorti, 1988) and *C. viridis* (Graves et al., 1986) that follow chemical trails left by adult conspecifics? At this point we are about as far out on a limb as an island pitviper awaiting migrant song birds, but clearly research on snakes has much to offer for understanding fundamental issues in behavioral and evolutionary biology.

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