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PARENTAL BEHAVIOR IN ANGUID LIZARDS

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ABSTRACT: Among 21 species for which information is available (out of ca. 100 extant species), three diploglossines, five gerrhonotines, and six anguines attend their eggs during incubation, implying that parental behavior might be synapomorphic for the more inclusive clade Anguinae. A captive *Gerrhonotus infernalis* attended her clutch for 62 days, occasionally left it to feed and defecate, and did not pursue prey in the presence of her neonates. Viviparous *Barisia imbricata*, *Elgaria coerulea*, and *Mesaspis moreleti* consume extraembryonic debris and sometimes assist with birth; viviparous *M. monticolus* and *Diploglossus fasciatus* (mode of reproduction unknown) likely attend their neonates; and parental behavior is perhaps absent in viviparous *Anguis fragilis* and *Ophiodes*. Meager circumstantial evidence suggests that chemical cues influence those activities in anguids, and that thermoregulation, defense of eggs and/or young, and hygienic removal of spoiled eggs or birth debris are among the ecological advantages of their parental behavior. Viviparity has evolved at least four times within Anguinae, consistent with theoretical expectations that live birth is favored in egg-guarding taxa. These diverse lizards thus show much promise for studies of specialized parental investment in ectothermic vertebrates.

KEY WORDS: Squamata, Anguinae, Parental Care, Behavioral Homology

INTRODUCTION

Parental behavior, defined as specific actions of a parent after oviposition or parturition that increase survivorship of the young, has traditionally been regarded as absent in most reptiles other than archosaurs (Shine, 1988; Greene, 1999; Somma, 2003). Nevertheless, the most recent surveys for pitvipers (Greene *et al.*, 2002) and more generally for lepidosaurs (Somma, 2003) imply that it may be more widespread and diverse among lizards and snakes than previously believed. Our purposes here are to review evidence for parental behavior in anguid lizards, to present new observations for several species, and to discuss the ecological, ethological, and evolutionary implications of those findings. We show that this behavior is substantially more complex in anguids than heretofore reported, as was also the case for pitvipers (Greene *et al.*, 2002), and we corroborate Shine's (1988) tentative conclusion that it is a derived trait for Anguinae. These lizards often do well in captivity (e.g., Langerwerf, 1981; Solórzano, 2001) and may be "unusually intelligent" (Fitch 1935), and thus our findings imply that they offer diverse possibilities for more detailed studies of parental activities in reptiles.

Anguinae (galliwasps, alligator lizards, glass lizards, and their relatives) is a small but morphological-

ly diverse, relatively ancient clade of generally insectivorous squamates, within which limblessness and viviparity have evolved repeatedly (Shine, 1985; Blackburn, 1999; Macey *et al.*, 1999; Wiens and Slingsluff, 2001). Average adult snout-vent lengths (SVL) of extant species range from 7 cm in *Gerrhonotus parvus* (Banda *et al.*, 2005) to 50 cm in *Ophisaurus apodus*. Morphological and molecular phylogenetic analyses agree on the monophyly of three main subclades of anguids, encompassing about 100 species assigned to 12-15 genera (Wiens and Slingsluff, 2001; Pianka and Vitt, 2003; Conroy *et al.*, 2005), and we summarize evidence for parental behavior within that taxonomic framework. We refer readers to Somma (2003) for an extensive literature survey and confine our citations here to new references and earlier ones that provide particular details for anguids.

Parental behavior in diploglossines

Diploglossines (sometimes known as galliwasps) are found in Mexico, Central and South America, and the West Indies; unlike gerrhonotines and most anguine anguids, diploglossines lack ventrolateral grooves and those with well-developed limbs superficially resemble skinks (Scincidae). Cuban *Diploglossus delasagra nigropunctatus* (= *D. nigropunctatus*, Thomas and

Hedges, 1998) and the mainland *D. bilobatus*, *D. lessonae*, and *D. monotropis* are oviparous (Fitch, 1970; Vitt, 1985). Viviparity occurs in the Mexican *D. enneagrammus*, *D. legnotus*, and *D. rozellae* (Canseco-Márquez *et al.*, 2004); in the West Indian *Celestus costatus*, *C. crusculus*, *C. curtissi*, *C. stenurus*, *D. pleei*, *D. warreni*, *Sauresia sepsoides*, and *Wetmorena haetiana*; and in at least two species of near-limbless South American *Ophiodes* (Greer, 1967; Schwartz and Henderson, 1991; Pizzato, 2005).

Five female Costa Rican *Diploglossus bilobatus* have been found accompanying eggs, usually under logs (Taylor, 1956; Fitch, 1970; Savage, 2002), and among them one was photographed loosely coiled with her feet and chin resting on at least six eggs (Savage, 2002:Plate 323). A male *D. nigropunctatus* was “under a stone... lying over five eggs and when disturbed made no effort to escape, simply hiding his head as if for protection” (Barbour and Ramsden, 1919:176), and a female that was curled around eggs under a piece of rotting wood had been with them for at least several days (Barbour and Shreve, 1937). Shine (1988) erroneously cited Taylor (1956) for egg attendance by a female *D. nigropunctatus* (actually reported by Barbour and Shreve, 1937) and therefore expressed doubts about the sex of Barbour and Ramsden’s animal; given the subtlety of externally sexing diploglossines (Thomas and Hedges, 1998), Ramsden’s matter-of-fact comment suggests instead that he indeed confirmed that the attending lizard was a male. A captive Costa Rican *D. monotropis* coiled around her newly laid eggs under a water dish, and “greeted every attempt to remove them with an open mouth and threatening posture” (Solórzano, 2001; the eggs were incubated separately from the female).

Mode of reproduction is unknown for *Diploglossus fasciatus*, but a female and four young were found together on a newly felled tree in Brazil (Marques and Sazima, 2003), implying that post-hatching or postnatal attendance occurs in this species (see Greene *et al.*, 2002, for comments on the unlikelihood that such associations simply reflect very recent birth). Observations of birthing by a South American glass lizard (*Ophiodes* sp.) included no mention of postnatal parental behavior, although the female pressed her cloacal region against a loop of her tail, implying attention to the emerging young beyond the peristaltic contractions inherent in parturition (Rocha-Barbosa *et al.*, 1991, see Pizzato, 2005 for comments on species identification).

Parental behavior in gerrhonotines

Previous Studies – Gerrhonotines (known in English as alligator lizards) are widespread in western North America and Central America. *Elgaria kingii*, *E. multicaudata*, *E. panamintina*, *Gerrhonotus infernalis*, *G. lugoi*, and *G. ophiurus* are oviparous, whereas *E. coerulea* and evidently all species of *Abronia*, *Barisia*, and *Mesaspis* are viviparous (Fitch, 1970; Shine, 1985). Nothing is known about the reproductive biology of *Coloptychon*.

A female *Elgaria kingii* was found “with 12 eggs in the process of hatching from a horizontal crevice, suggesting the possibility of parental care” (Degenhardt *et al.*, 1996:246). Three captive females of *E. multicaudata* jointly constructed a nest cavity in soil under a flat stone and accompanied their clutches, totaling at least 21 eggs; the cavity was large enough that females could move around the clutches, and in response to a human intruder they “became very aggressive and constantly tried to bite” (Langerwerf, 1981).

Two female *Gerrhonotus infernalis* were coiled with eggs in a heavily wooded limestone outcrop in Texas, USA. (Greene and Dial, 1966), and a captive female ate spoiled eggs from within her attended clutch (Tinkle and Gibbons, 1977). A captive female *G. lugoi* from Coahuila, México, “remained coiled around the eggs” for an unstated period of time, after which the clutch was removed for incubation (Lazcano *et al.*, 1993). A female *G. ophiurus* was under a rock with eggs in tropical deciduous forest in San Luis Potosí, México; she made no attempt to escape, had not consumed a dry egg that was among the 10 in her clutch, and the subsequent incubation period in captivity implied that she had attended the eggs for ca. two weeks prior to capture (Mendoza Quijano and Schmidt-Balardo, 1995). Another female *G. ophiurus* was under a rock with about 15 eggs in desert habitat in Puebla, México (UTA R4715; C. J. Franklin, pers. comm.).

According to Guillette and Hotton (1986:243), females of *Barisia imbricata*, *Elgaria coerulea*, and *Mesaspis moreleti* “assist the young in breaking from the amniotic sac after birth, and eating the remnants of the sac”. After the birth of each neonate in five litters of *B. imbricata* from México, “the mother tongue-licked it and ate the extraembryonic membranes. Two of these females... subsequently ate the nonviable eggs and the dead neonates” from among the live offspring

(Martínez Torres, 1999:165). There “appears to be some parental care by females [of Costa Rican *M. monticolus*], since groups of young are often found in close association with the presumed mother (plate 328)” (Savage, 2002:534).

Additional Observations on Egg-guarding – A female *Gerrhonotus infernalis* (SVL ca. 13 cm) was collected March 14, 2004, in Bexar County, Texas, USA, and maintained for educational purposes in a 75-liter terrarium. She subsequently appeared gravid (lateral grooves expanded, even while she was immobile and undisturbed) and on April 11 an artificial plastic “nest cavity” was placed in the back right corner of the terrarium. The cavity was 15 cm in diameter and 10 cm deep, and contained fine gravel to a depth of 3 cm; a 3 cm access hole was cut in the container wall, just above gravel level, and water was added so that the gravel was always discolored to a depth of 1-2 cm. A tight-fitting clear plastic lid was taped to the container to minimize desiccation, and a second, movable opaque plastic lid placed on top of the first permitted minimally obtrusive access for photography and observations.

The female had not laid eggs when checked at 0800 hrs on May 8, 2004. At 1400 hrs on May 9 she was loosely coiled over 19 eggs on the gravel surface, at the back of the nest cavity (Fig. 1). She had not previously reacted defensively to handling, but when gently grasped and lifted so that the clutch could be examined, the female inflated, opened her mouth, and hissed. Domestic crickets and roaches were usually available in the terrarium, and at 1334 hrs on May 11 she was eating a cricket about 20 cm from the nest with her tail extended back into it; by 1338 hrs she was looped back facing the nest entrance and evidently basking in sunlight from a nearby window; at 1413 hrs she licked her lips as if she'd eaten again; and at 1434 hrs she slowly entered the nest and coiled around the eggs. Fecal pellets were occasionally found in the terrarium, always in the farthest corner from the nest. On June 2 the sand under the eggs was a few mm lower and darker (wetter?) relative to the rest of the substrate; when the observer briefly poked a finger through the cavity entrance, the female drew her head and neck back, opened her mouth slightly, and quickly flicked her tongue.

Beginning June 20 the female frequently lingered outside the nest entrance, on June 25 scaly black-and-

white patterns were visible through the eggshells, and on June 29 movement was seen through one egg. No hatchlings were visible at 1200 hrs on July 11 (63-64 days after oviposition), but at 1749 hrs the female was in the cavity and a single hatchling was present next to a slit eggshell; at 2130 hrs she was in the cavity, a single hatchling was at the opposite end of the terrarium, and there were three slit shells, the other hatchlings presumably under substrate paper in the terrarium. At 0745 hrs on July 12 there were four clumped empty eggshells, and lizard snouts were visible through slits in four other clumped eggs; the adult female was 8-10 cm outside the cavity and facing its opening. The female was emerging from the cavity at 1745 hrs, inside it with snout in the opening at 2135 hrs, and thereafter outside the nest container; she sometimes made digging and climbing movements with her forelegs in the terrarium corners, and exhibited no obvious interactions with or attraction to the young.

Over the next three days neonates emerged from the eggs, then within minutes or hours left the cavity; they reacted to nearby movements of an observer by fleeing under substrate papers, and exhibited no response to each other or the adult other than an occasional tongue-flick. The adult lizard refused to eat crickets placed near her in the terrarium but immediately seized one that was offered after she had been lifted to a nearby desk. At 1500 hrs on July 15 the terrarium was dismantled, revealing 19 seemingly healthy neonates and 16 empty eggshells.

Additional Observations on Post-natal Parental Behavior – Guillette and Hotton's (1986:243) reference to postnatal parental attention to neonates by *Mesaspis moreleti* was based on previously unpublished observations by H.W.G. of a captive female (SVL ca. 9 cm) from Guatemala. She was confined in a small plastic terrarium with a fine gravel substrate, gave birth during daylight hours to seven offspring, and immediately approached each newborn by way of a tight right turn back toward her vent. Five neonates broke free of their enclosing membranes by vigorous axial bending within seconds of parturition and the female poked the other two once or twice, after which they flexed and broke free of their membranes. The adult female consumed the fluids and membranes associated with each of the neonates within minutes after they were born (Fig. 2).



Figure 1: Captive female Texas Alligator Lizard (*Gerrhonotus infernalis*), leaving nest chamber while neonates are hatching (see text for details).

A female *Barisia imbricata* (SVL ca. 10 cm) from the Sierra Fría, Aguascalientes, México, was maintained for educational purposes and gave birth to 18 neonates, after which we attempted to provide a captive context in which she might choose to avoid or aggregate with her neonates. Their container consisted of a 30 x 30 x 30 cm plastic box divided by 10 cm cardboard walls into quadrants, out of which we incorrectly assumed the neonates could not climb; each quadrant contained a small water dish. The quadrants initially contained the female and either no neonates, three neonates, six neonates, or nine neonates. We began observations at 1321 hrs on the day after birth and photographed the box at 30-minute intervals over a period of ten hours, for a total of 21 observations. Within one hour of being placed in the box, a neonate climbed in with the female and returned to its original quadrant, and the female subsequently entered the quadrant with six neonates. She was in a quadrant with neonates in 19 of 21 photographs, and in those containing six or nine young for 18 of them; she was thus with her litter significantly more often than expected by chance ($X^2 = 12.33$, $p < 0.05$). One or more neonates lay on the female in eight photographs, and once she stood high over one. Our observations imply a tendency by the female to actively associate with her litter, and raise the possibility (cf. Kaufman *et al.*, 1996) that she attempted to do so with the largest available number of offspring.



Figure 2: Female Mayan Alligator Lizard (*Mesaspis moreleti*), consuming embryonic fluids and membranes immediately after parturition (note her optical fixation on the neonate, extended tongue, and birth membranes with blood vessel being drawn into the female's mouth).

Parental behavior in anguines

Anguines are unusually elongate and either lack limbs or have tiny remnants of hind legs. Holarctic glass lizards (*Ophisaurus*) are found in Eurasia and eastern North America, whereas the Slow Worm (*Anguis fragilis*) is restricted to Eurasia. *Ophisaurus apodus*, *O. attenuatus*, *O. compressus*, *O. gracilis*, *O. harti*, and *O. ventralis* are oviparous (Fitch, 1970; Bartlett, 1985), and females of each of those species remain with their incubating eggs (Somma, 2003).

Captive *Ophisaurus apodus* females tightly coiled around their clutches soon after oviposition, exhibited no defensive behavior in response to a person removing the eggs to an incubator, and in one instance remained at the site for a week thereafter (Bischoff, 1974; Langerwerf, 1981). A natural nest of *O. attenuatus* in Tennessee, USA, was in a depression in soil under a wooden cover board (Gerald, 2005), whereas four others in Kansas, USA, were in cavities beneath flat rocks and in abandoned tunnels of small mammals (Fitch, 1989). In North Carolina, USA, a natural nest of *O. attenuatus* was a few cm beneath the surface of sandy soil, whereas of 11 nests of *O. ventralis*, eight were “in shallow depressions in slightly moist soil under logs or similar shelter,” one was buried a few cm deep in an old sawdust pile, one was under a clump of grass, and one was in a rotten pine stump (Palmer and Braswell, 1995). Female *O. attenuatus* (Gerald, 2005) and *O. ventralis* (Vinegar, 1968) can raise egg temperatures 0.5–1.5°C above

ambient, but do not bite in defense of their eggs against mammalian intruders (Noble and Mason, 1933; Fitch, 1989; Gerald, 2005). Attending female *O. attenuatus* sometimes eat one or more eggs in their clutches (Fitch, 1989; Mitchell and Groves, 1993).

The widespread, often common *Anguis fragilis* is viviparous and judging from the extensive literature on this species, neonates liberate themselves from birth membranes and females do not exhibit parental behavior (e.g., Dely, 1981; Petzold, 1982; Somma, 2003). However, captive females in England “coiled with their young in a hollow on the day of birth, with much tongue flicking between female and young each time they encountered each other... after the first day, females often used the hollows while the young generally dispersed into the grass and compost, although one or two... coiled with them at times... females [were also found] under refugia in the field with up to three young, but they tended to be scattered under the refugia and rarely coiled up together. The captive born young were released with their mother at the refuge where she had been captured... [and often turned up] under the same refuge that autumn “ (A. Riddell, pers. comm.). These observations suggest that *A. fragilis* females might actively attend their young, but do not exclude the possibility of parents and offspring passively sharing a favorable refuge.

Behavioral variation and a preliminary phylogenetic assessment

Ideally, behavior can be characterized in terms of kinematic profiles, stimulus control, and several contextual variables, as well as underlying ontogenetic and physiological mechanisms (Drummond, 1981; Bass, 1998; Greene, 1999). Presence of parental behavior is based on single observations for several species of anguids and thus might be suspect (Shine, 1988), so we emphasize that multiple records, usually from multiple localities and by multiple observers, are available for diploglossines (*Diploglossus bilobatus*, *D. nigropunctatus*), gerrhonotines (*Barisia imbricata*, *Elgaria multicarinata*, *Gerrhonotus infernalis*, *G. ophiurus*, *Mesaspis monticolus*), and anguines (*Ophisaurus apodus*, *O. attenuatus*, and *O. ventralis*). Confirming the absence of parental behavior without direct observations is difficult (Crump, 1996; Somma, 2003), as emphasized here by the seemingly well-studied *Anguis fragilis*. Available data show that pa-

rental behavior is usually or always performed only by female anguids, but there is as yet little basis for characterizing individual and taxonomic variation in nest site selection, attendance postures, and other activities. Instead, the most broadly applicable descriptions at present of parental behavior by these lizards are simply (i) absence, by which we mean reports of oviposition or parturition have not mentioned any such activities; (ii) sustained proximity to eggs, a response that may last for several weeks after oviposition (e.g., 62 days in our *Gerrhonotus infernalis*); and (iii) consumption of birthing debris and/or sustained proximity to neonates (for perhaps up to several days).

In addition to a survey of variation in the taxa of interest, an evolutionary historical analysis of any organismal attribute requires a phylogenetic hypothesis, a method for reconstructing ancestral branch states (see Frost *et al.*, 2006:25, for “branch” versus “node” in this context), and specification of at least two outgroups for comparison (Brooks and McLennan, 2002). We provisionally based relationships within Anguinae (Fig. 3) on Wiens and Slingluff (2001) and Conroy *et al.* (2005), and we initially excluded the problematic *Anniella* (see below). The first and second outgroups for Anguinae within Anguimorpha remain uncertain, but suggested taxa always include Xenosauridae, Shinisauridae, Helodermatidae, and Varanidae (cf. Wiens and Slingluff, 2001; Lee, 2005), the first two of which are viviparous (Shine, 1985) and for most species of which (with a few likely exceptions among varanids) there have been no observations of parental behavior (Somma, 2003). Accordingly we coded two unspecified outgroups for Anguinae as “absent,” subject to certain caveats discussed below; treated absence, egg attendance, and post-parturient hygienic activities and/or aggregation as three unordered states; and assumed that transitions among those states were equally probable. We then used the software MacClade (Maddison and Maddison, 2000) and information summarized above to map behavioral variables on a cladogram, parsimoniously reconstruct their ancestral branch states and thereby infer evolutionary transformations, and examine the impact of alternative character codings and phylogenetic topologies on inferences about the evolution of parental behavior.

The following generalizations follow from our analysis, with the qualification that nothing is known for about 80% of anguid species and these conclusions are correspondingly tentative (see Fig. 3):

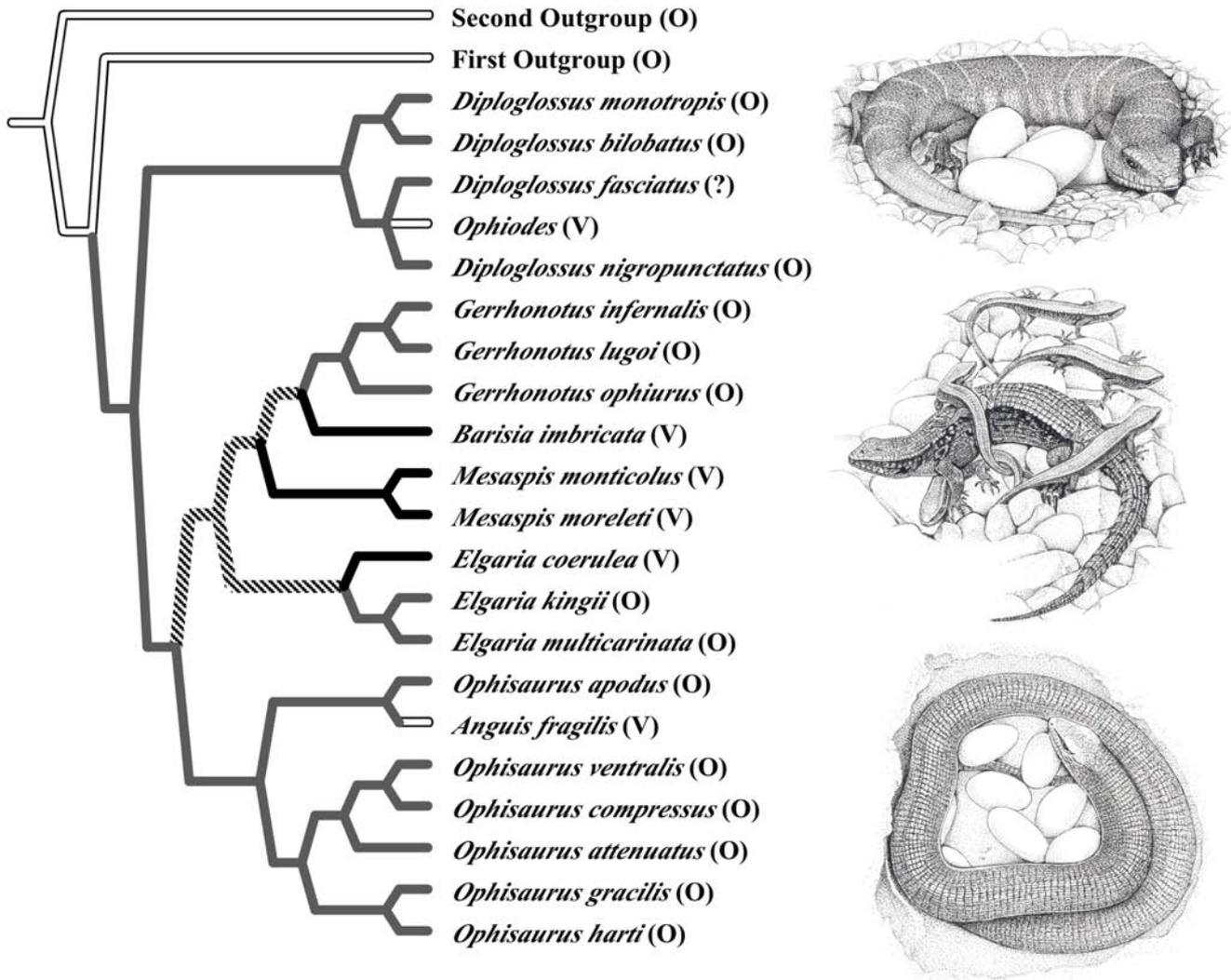


Figure 3: Evolution of parental behavior in Anguinae. Open bars = absence, gray bars = egg attendance, black bars = postnatal hygienic behavior and/or association with neonates, and diagonaled bars = ambiguous; O = oviparous and V = viviparous. Illustrations at right (top to bottom, respectively) are of *Diploglossus monotropis* with eggs (adapted from Solórzano, 2001), *Mesaspis monticolus* with neonates (adapted from Savage, 2002:Plate 328), and *Ophisaurus apodus* with eggs (adapted from Langerwerff, 1984).

(i) Shine (1988) concluded that parental behavior arose once in Anguinae, and our results corroborate his implicit hypothesis that egg attendance is a synapomorphy for a clade defined by inclusion of diploglossines, gerrhonotines, and anguines. Note that we excluded from consideration the viviparous, limbless, western North American *Anniella*, for which parental activities have not been recorded and which has been variously regarded as the sister taxon of diploglossines, as the sister taxon of all other anguines, or as more distantly related to that clade within Anguimorpha (Wiens and Slingluff, 2001; Conroy *et al.*, 2005). The latter two options would not affect our phylogenetic conclusions, but treating *Anniella* as sister to diploglossines and scoring it as lacking paren-

tal behavior results in inferring the branch state for Anguinae as uncertain, such that egg attendance might have arisen independently in diploglossines and in other anguines. Under that topology and if transitions from viviparity to oviparity are indeed unlikely (Blackburn, 1999), such that egg attendance characterized ancestral diploglossines, viviparity would have arisen independently in them and in *Anniella*. If parental activity is in fact widespread in varanids and they are the sister taxon of anguines (neither of which currently seems likely), that behavior might prove to be derived for a more inclusive clade than Anguinae.

(ii) Our MacClade analysis coded the gerrhonotine branch as ambiguously either egg attendance or

postnatal behavior because three of its four basal-most lineages are viviparous. However, if transitions from viviparity to oviparity are unlikely (Blackburn, 1999) and thus egg attendance characterized ancestral gerrhonotines, as many as three evolutionary transitions from egg attendance to postnatal care of neonates are implied for that subclade (in *Barisia imbricata*, *Elgaria coerulea*, and *Mesaspis*). Alternatively, oviparity and egg attendance in *Gerrhonotus* reflects an evolutionary reversal within a clade of viviparous gerrhonotines.

- (iii) Information on parental behavior is lacking for most species of diploglossines and relationships within that subclade are especially problematic (Savage and Lips, 1993; Thomas and Hedges, 1998), but with additional knowledge the diversity of reproductive biology in these lizards might prove especially interesting.
- (iv) Parental attendance might have been lost one or more times in taxa with limbs highly reduced or absent, i.e., *Anguis*, *Ophiodes*, and *Anniella*. Because at least the first two of these taxa are nested deeply within their respective subclades, future observations of parental behavior in them would not affect our other conclusions.

DISCUSSION

More than fifty years ago Niko Tinbergen provided a conceptual framework for ethology, by proposing four questions about animal behavior (Burghardt, 1997): how does it arise in the individual, how is it controlled, what is its ecological significance, and how did it evolve? Recently Burghardt (1997) argued that many non-human organisms also possess some sort of "inner world" and proposed a fifth question, what are the private experiences of animals? Even our limited knowledge of parental behavior in anguids exemplifies the heuristic and integrative framework provided by ethology's five questions, but we know nothing about the development and genetics of parental activities in anguids, and we have only scant circumstantial evidence (Noble and Mason, 1933) that chemical cues play a role in controlling them. Our discussion must therefore focus on the last three questions.

Understanding the maintenance of a particular behavior in a population entails an analysis of ecologi-

cal consequences, with the working expectation that benefits must exceed costs for natural selection to favor the origin and/or maintenance of a trait (see Shine, 1988, for a scholarly overview with emphasis on squamates). From a benefits/costs perspective, females should be more likely to care because of their certainty of maternity and proximity to eggs and/or neonates, as is the case in most or all anguids with some form of parental attendance. Widespread presence of parental behavior in diploglossines and gerrhonotines also conforms to a theoretical prediction that it should characterize organisms that are especially vulnerable to predation on eggs and/or neonates, yet capable of effective defense (Shine, 1988).

Anguids are eaten by a wide range of predators (Greene, 1988; Fitch, 1989) and their clutches might be unusually vulnerable, judging from the relatively reduced limbs of these animals (Wiens and Slingluff, 2001) and their presumably reduced ability to dig less accessible nests, as well as the seemingly high frequency with which natural nests are reported in the literature. Patch-nosed snakes (*Salvadora grahamiae*), for example, feed on lizard eggs (Blair, 1961), are widely sympatric with *Gerrhonotus infernalis*, and both species inhabit limestone outcrops on the Balcones Escarpment of Texas, USA (H. W. Greene, pers. obs.). Diploglossines, gerrhonotines, and many outgroup anguimorphs respond to manual restraint by humans with defensive biting (Vitt, 1985; Greene, 1988), and even a 10-14 cm SVL *G. infernalis* or *Diploglossus fasciatus* can inflict painful, bleeding lacerations on human skin (H. W. Greene, pers. obs.). Females of *D. monotropis* (Solórzano, 2001), *Elgaria multicarinata* (Langerwerf, 1981), and *G. infernalis* (this paper) may be even more defensive when they are accompanying eggs, as is the case in some pitvipers (Greene et al., 2002). Conversely, *Anguis fragilis*, *Ophisaurus attenuatus*, *O. koellikeri*, and *O. ventralis* are not particularly prone to bite in response to human handling, relying instead on locomotor escape, axial bending, tail autotomy, and perhaps death feigning as their primary responses to predators (Greene, 1988, pers. obs.; Fitch, 1989). Given the derived phylogenetic placement of anguines, absence of biting as a defense against predators (of themselves and of their eggs and/or offspring) represents a loss within the larger clade Anguinae.

Numerous other potential benefits might accrue as a result of parental behavior, for none of which is there

experimental evidence that applies to anguids; these advantages include provision of a stable developmental microclimate, hygienic removal of debris and thus prevention of predator detection and/or microbial contamination, crypsis supplied by an overlying parent's color pattern, incest avoidance, and prevention of infanticide (Shine, 1988; Mitchell and Groves, 1993; Greene *et al.*, 2002; Somma, 2003; O'Conner and Shine, 2004). Evidence of a thermoregulatory role for attendance by female *Ophisaurus* is inconclusive (Noble and Mason, 1933; Vinegar, 1968; Gerald, 2005), but Vinegar's (1968) suggestion that they might influence egg temperatures by moving the clutch up and down within a nest bears scrutiny, especially given the regulation of humidity by postural adjustments in some egg-attending female pitvipers (York and Burghardt, 1988).

In terms of the ecological costs of parental care, Fitch (1970, 1989) noted that egg guarding by *Ophisaurus attenuatus* might preclude females from producing and attending more than one clutch per season, and was skeptical of a report implying that female *Gerrhonotus infernalis* could do so. Fitch presumably assumed that parental behavior and feeding are incompatible, whereas observations on captive *G. infernalis* (this paper) and *O. ventralis* (Vinegar, 1968) show that at least if their nests sites are in a prey-rich environment, female anguids might continue to eat throughout clutch attendance.

Three provocative macroevolutionary patterns, each deserving of thorough study in a broader ethological context, imply that shifts in reproductive biology have played important roles in the evolutionary origin and diversification of anguids. First, parental behavior is likely synapomorphic for the lineage and thus innovative with respect to outgroup anguimorphs; viviparity arose multiple times within the primitively egg-attending anguid clade, as predicted by theory (Shine, 1985, 1988; Shine and Lee, 1999). Second, parental behavior toward and/or aggregation with neonates evidently arose with at least one origin of viviparity in Anguinae (on the gerrhonotine branch), as well as independently in other more distantly related squamates (Somma, 2003; for a pioneering phylogenetic perspective, see Rebouças-Spieker and Vanzolini, 1978). Beyond a female's attention to the immediate products of oviposition or parturition, perhaps homologous mechanisms respectively underlay parental behavior in oviparous and viviparous anguids –

female *Gerrhonotus infernalis* (this paper) and *Ophisaurus ventralis* (Vinegar, 1968) eat spoiled eggs and remain with their clutches, activities that are arguably the same as consumption of birth debris, but paradoxically they also avoid their live, newly hatched young. Third, the hypotheses that diploglossines and gerrhonotines potentially suffer increased predation and therefore exhibit increased active defense on eggs and/or juveniles compared to other anguimorphs, whereas anguines have evidently lost biting as a common anti-predator response, also warrant further exploration. Better understanding of these and other phylogenetic patterns will require more detailed observations, especially of additional anguid taxa, as well as careful field and experimental studies (Somma, 2003; for an excellent example of the latter, involving antipredator behavior in snakes, see Glaudas *et al.*, 2006).

Successful incubation of eggs left with female *Gerrhonotus infernalis* (this paper) and *Ophisaurus ventralis* (Noble and Mason, 1933), as well as observations of postnatal parental behavior in captive *Barrisia imbricata* (Martínez Torres, 1999) and *Mesaspis moreleti* (this paper), demonstrate that laboratory research on parental behavior in anguids is feasible. Challenges may include providing microclimatic conditions conducive to incubation and observational protocols that minimize disturbance to attending parents. The demonstration that parental behavior is the norm for an increasing number of squamates and can be facilitated in confinement also raises animal welfare issues, such as whether eggs or offspring produced in captivity should immediately be removed from their mothers.

Finally, a number of recent discoveries contradict traditional notions of nonavian reptiles as behaviorally simple organisms (e.g., quantitative skills and play behavior in varanids [Kaufman *et al.*, 1996; Burghardt *et al.*, 2002], family-like social structure in some lizards and pitvipers [Greene *et al.*, 2002; Fox and Shipman, 2003; Masters and Shine, 2003; Clark, 2004]). We know little about anguid social systems other than that they seemingly lack territoriality (Martins, 1994), have relatively subtle sexual dimorphism (e.g., Fitch, 1989; Vial and Stewart, 1989; Thomas and Hedges, 1998), and might exhibit monogamous mate-tending (Vitt, 1985). Nevertheless, the growing evidence for behavioral complexity in these and other squamates underscores the importance of addressing Burghardt's (1997) fifth question, regarding the private experienc-

es of animals. Recalling Fitch's (1935) comment that alligator lizards might be "unusually intelligent," given the details of egg attendance by *Gerrhonotus infernalis* and viewing a photograph of *Mesaspis moreleti* cleaning her young, is it now reasonable to ask if an-guids are "aware"? And can a female *Barisia imbricata* count?

RESUMEN

De las 21 especies para las que existe información disponible (de un total aproximado de 100 especies vi-vientes), tres diploglossinos, cinco gerrhonotinos, y seis anguinos cuidan sus huevos durante la incubación, lo cual implica que el comportamiento parental puede ser una sinapomorfía para el clado más incluyente de lagartijas Anguidae. Un ejemplar de *Gerrhonotus infernalis* en cautiverio cuidó de sus huevos por 62 días, de-jándolos ocasionalmente para alimentarse y excretar, pero no siguió a sus presas cuando los neonatos esta-ban presentes. Las lagartijas vivíparas *Barisia imbricata*, *Elgaria coerulea*, y *Mesaspis moreleti* consumen los desechos extraembriónicos y ocasionalmente proveen ayuda con el nacimiento; las lagartijas viví-paras *M. monticolus* and *Diploglossus fasciatus*, cuyo modo de reproducción se desconoce, probablemente cuidan de sus crías recién nacidas; y es probable que el comportamiento parental esté ausente en las lagartijas vivíparas *Anguis fragilis* y *Ophiodes*. Evidencias cir-cunstanciales e insuficientes sugieren que las señales químicas influyen en estas actividades en anguidos, y que en esas lagartijas, factores como la termorregu-lación, la defensa de los huevos y/o las crías, y la remoción higiénica de los huevos en descomposición o de los desechos del nacimiento son algunas de las ventajas ecológicas del comportamiento parental. La viviparidad ha evolucionado al menos cuatro veces dentro de Anguidae, de acuerdo con las expectativas teóricas de que la viviparidad es favorecida en taxa que proporcionan cuidados a sus huevos. Estas diversas lagartijas son prometedoras para estudios de inversión parental especializada en vertebrados ectotérmicos.

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