A CATEGORIZATION AND BIBLIOGRAPHIC SURVEY
OF PARENTAL BEHAVIOR IN
LEPIDOSAURIAN REPTILES

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INTRODUCTION

Parental behavior is a significant aspect of the life history of a wide variety of animal taxa. Parental behavior is common to the vertebrate classes Osteichthyes (Blumer, 1979, 1982; Perrone and Zaret, 1979; Baylis, 1981; Gittleman, 1981; Gross and Sargent, 1985), Amphibia (McDiarmid, 1978; Wells, 1981; Nussbaum, 1985; Duellman and Trueb, 1986), and universal within the Aves (Kendeigh, 1952; Skutch, 1957, 1976; Welty, 1982; Silver et al., 1985) and Mammalia (Kleiman and Malcolm, 1981; Dewsbury, 1985; Kleiman, 1985; Malcolm, 1985). In contrast, relatively few reptiles exhibit parental behavior (Tinkle and Gibbons, 1977; Shine and Bull, 1979; Shine, 1985, 1988). Parental behavior is common in living crocodilians (Greer, 1970, 1971; Lang, 1987; Shine, 1988) and also may have been common in extinct archosaurs (Horner and Makela, 1979; Coombs, 1982; Horner, 1982, 1984, 1987; Horner and Gorman, 1988) and cynodonts (Graves and Duvall, 1983; Duvall, 1986). Accounts of parental behavior in four turtle species (Gopherus agassizii: Barrett and Humphrey, 1986; G. flavomarginatus: Carr, 1952; Janulaw and Appleton cited in Morafka, 1982; Appleton, 1986; Ernst and Barbour, 1989; Manouria emys: Louwman, 1982; McKeown et al., 1982; Trachemys stejnegeri malonei: Hodsdon and Pearson, 1943) are remarkable, because turtles generally lack any form of parental behavior (Shine, 1988; Ernst and Barbour, 1989). The purpose of this review is to survey the various categories of parental behavior reported for lepidosaurians (lizards, snakes, amphibiaenians and a rhychocephalian) and to provide an extensive bibliography as a guide to current and future researchers.

The phrase "parental care" refers to all nongametic and postfertilization contributions of parents to the survival of their offspring (Wittenburger, 1981; Blumer, 1982) and is construed by some (Williams, 1966; Baylis, 1981; Keenleyside, 1981; Gross and Sargent, 1985; Congdon, 1989; Spotila and O'Connor, 1989) to include viviparity and other physiological contributions. I use the phrase "parental behavior" to limit the scope of this survey to all behavioral contributions by the parent to offspring survival after oviposition or parturition. Behaviors associated exclusively with oviposition and nest construction are not included in this survey; they are probably common to most oviparous lepidosaurians (Hahn, 1909; Hilzheimer, 1910; Blanchard, 1933; Carl, 1944; Carpenter, 1966; Platt, 1969; Rand and Rand, 1976; Duvall et al., 1979; Jones and Guillette, 1982; Green and Pauley, 1987).

The term "brooding" describes behaviors of the parent while attending the nest and progeny (sensu Somma, 1988; also see Pope, 1961; Peters, 1964; Carpenter and Ferguson, 1977). Thus, brooding does not include territorial, nest-site defense wherein the parent remains at a distance from the nest, and not in or on the nest or progeny, as seen in some iguanine and gekkonid lizards, and the tuatara.
HISTORICAL ASPECTS

The oldest conceivable documentation of parental behavior in a lepidosaurian is in the book of Isaiah, 34:15 (McDowell et al., 1982) written some time between 745-350 BC (Asimov, 1968). In this account, the Hebrew word "lilith," at one time interpreted as an owl (Strong, 1961; Asimov, 1968), is referred to as the "arrow snake." This vernacular name may have referred to the bold Eryx jaculus (Topsell, 1608; White, 1954). Since E. jaculus is viviparous, the snake reputed to "lay eggs and hatch, and gather them under her shadow" (McDowell et al., 1982) may refer to an oviparous snake or be erroneous, if not simply a fable.

Much of the pre-Twentieth century natural history literature indicates that many authors believed parental behavior was universal in snakes (Aristotle, [d. 322 BC]; Nicander of Colophon [135-133? BC]; Gesneri, 1551-1587; Topsell, 1608; Chateaubriand, 1827; Sundowner, 1895, 1902). The Second Voyage of Sinbad the Seaman, written in the 8th century AD (Burton, 1885-1888), is an example of early fiction that mentions a giant snake (undoubtedly a python) brooding its eggs. The "cockatrice" or "basilisk" was reputed to brood her eggs (Gesneri, 1551-1587; Topsell, 1608). It is likely that this mythical beast was a fantastical description of a cobra, either Ophiophagus hannah or a species of Naja (White, 1954; also see descriptions by Pliny the Elder, [d. AD 79]; Gesneri, 1551-1587; Topsell, 1608). Similarily, brooding was attributed to the "asp" (= Naja haje?) and the "dipsas" (= Bungarus sp.?; White, 1954) by Nicander. Modern documentation confirms that these taxa brood their eggs (Table VI).

Snakes have long been credited with the ability to swallow their young to protect them from danger (Topsell, 1608; Carver, 1778; Mease, 1807; Holmes, 1823; Hunter, 1824; Chateaubriand, 1827; Gosse, 1851; Rivers, 1874; Stanley, 1972; Burroughs, 1908; Meek, 1946). Earliest accounts of this behavior are found in hieroglyphics attributed to the ancient Egyptians circa 2300 BC (Speck, 1923). So prevalent was (and still is!) this belief, that it was incorporated into early fiction, including the pre-Elizabethian poem, The Faerie Queene (Spenser, 1590). This alleged behavior, attributed not only to snakes but also to the lizard, Lacerta vivipara (Hopley, 1882), has been reviewed and discussed by numerous authors for more than 300 years (Browne, 1646; White, 1787; Hopley, 1882; Noble, 1921; Speck, 1921, 1923; Schmidt, 1929; Ditmars and Bridges, 1937; Angel, 1950; Klauber, 1972; Russell, 1983; Shine, 1988). Despite many inquiries into the plausibility of this behavior, no scientific evidence exists for its occurrence (Klauber, 1972; Shine, 1988).

Among saurians, Scincus scincus was reputed to care for its eggs and young (Gesneri, 1551-1587; Topsell, 1608), but no modern observations support this contention (Table V). Hoy (1883) suggested that all lizards brooded their eggs. In all likelihood, his statement is based upon observations of Ophisaurus attenuatus and Eumeces septentrionalis; these are the only egg-brooding lizards that he actually observed (Hoy, 1883). The suggestion that an amphisbaenian broods its eggs (Gesneri, 1551-1587; Topsell, 1608; Aldrovandi, 1640; reviewed in Druce, 1910), has not been verified.
CATEGORIES OF PARENTAL BEHAVIOR

The various categories of parental behavior, as reported in the
literature, are listed below. The symbol in parentheses identifies the
categories used in Tables I and II. The literature sources are provided in
Tables V and VI.

Coil around brood (C): The attendant parent remains coiled around or covers
the brood with its body, presumably creating a physical buffer or barrier
between progeny and the external environment. This is the most common form of
parental behavior.

Nest constructed and maintained (NC): A burrow or brood chamber is
constructed by the parent and maintained while attending progeny. Although
this usually involves digging a depression or burrow in the substrate,
Ophiophagus hannah is known to maintain a relatively complex nest chamber
constructed from surrounding vegetation (Wasey, 1892; Oliver, 1956; Leakey,

Defense of brood (D): Progeny are aggressively defended by parent in the
presence of conspecifics or heterospecifics.

Passive protection (PP): Neonatal vipers may accrue protection from the
venomous female, without her exhibiting any overt signs of aggressive behavior
(i.e., Crotalus horridus: W. Martin, pers. comm.).

Thermoregulation (T): Attendant parent uses its body to maintain a relatively
constant incubation temperature for developing eggs. Most, perhaps all,
pythonines are able to become low-grade endotherms while brooding through
"shivering thermogenesis," thereby raising the temperature of the female's
body and developing eggs above that of ambient conditions (Vinegar et al.,
1970; Harlow and Grigg, 1984; Shine, 1988). However, it has been suggested
that shivering thermogenesis is not practiced by all species of pythons
(Vinegar et al., 1970; Ellis and Chappell, 1987; but see [Orlov], 1986; Shine,
1988). It is also possible that an attendant parent could (1) provide a
passive thermal barrier between eggs and the external environment with its
body or (2) bask in the sun and transfer radiantly absorbed heat from its body
to its eggs (Medsger, 1919, 1932; Noble and Mason, 1933; Cogger and Holmes,
1960). Python eggs, of at least two species, that are not brooded, and
subsequently incubated at lower temperatures, take longer to hatch and exhibit
a higher rate of developmental anomalies (Vinegar, 1973, 1974; Branch and
Patterson, 1975).

Hydroregulation (H): Even though is has never been demonstrated
experimentally, hydroregulation has been inferred from some squamates (Fitch,
1954; Somma, 1985b; Bels and Van den Sande, 1986; [Orlov], 1986; York and
Burghardt, 1988; Somma, 1989b; Somma and Fawcett, 1989). In addition, tenuous
evidence suggests that two species of snakes wet their bodies with water and
then lay over the eggs, thereby reducing desiccation (Elaphe obsoleta: J.
Lombard, pers. comm.; Trimeresurus wiiroli: Mehrtens, 1987).
False brooding (FB): Many species of pythons continue to brood when their clutches are removed prior to hatching (T. Miller, pers. comm.), and a Python molurus has brooded without ovipositing (J. S. Foster, pers. comm.). The nongravid female P. m. bivittatus housed with two gravid conspecifics brooded when the gravid females oviposited and brooded their eggs. This "false brooding" consisted of the python laying in a conical coil and exhibiting shivering thermogenesis (J. S. Foster, pers. comm.; Somma, pers. observ.).

Oophagy (OO): The parent eats eggs or aborted ova. This is a form of parental behavior because it may prevent microbial infection of viable, healthy eggs from adjacent infected eggs (Groves, 1982; Somma, 1989a) or prevent detection of progeny by predators using olfaction (i.e., detection of chemical cues released from rotting eggs or aborted ova) to locate food (Tinkle and Gibbons, 1977; Groves, 1982; Shine, 1988). Earliest observations of this behavior may be found in Hindu scriptures dating back to 600 BC (Rao, 1957).

Removal of nonviable eggs from nest (RE): Nonviable eggs are removed from the nest, presumably at a safe distance from viable eggs. This behavior has been reported only in Python molurus (Griehl, 1982) and perhaps occurs in Gerrhonotus liocephalus (Greene cited in Tinkle and Gibbons, 1977).

Parental care of neonates (CN): A parent remains with and expresses parental behavior toward neonates after hatching or parturition.

Neonates assisted during hatching or parturition (AN): Attending parent assists neonates from eggs, extraembryonic membranes or nest chamber. In Eumeces obsoletus and E. septentrionalis, the mother licks amniotic fluid from neonates' bodies after hatching (Evans, 1959; Somma, 1987c).

Manipulation or retrieval of eggs (ME): Eggs are manipulated within the nest or moved to a new nest site. Eggs that have been removed from the nest may also be retrieved.

Communal care of eggs (CC): Eggs may be deposited in a communal clutch and attended by several unrelated parents. In some situations, this behavior could be interpreted as alloparental care (Banks and Schwaner, 1984; Somma, 1987a).

Neonatal feeding facilitated (FN): A brooding female E. obsoletus avoided taking food items in deference to its young, waiting for them to finish before she fed (Evans, 1959). This behavior has not been observed in other reptiles.

Normally does not exhibit parental behavior (NPB): Parental behavior has been reported (sometimes reliably) for individuals of species that normally abandon their progeny.

Details unknown (DU): Details of parental behavior are not known or not reported.

Reliability uncertain (RU): Reliability of report regarded as uncertain or possibly unreliable due to paucity of information provided or observed by the author.
Erroneous documentation (E): Report considered unsubstantiated due to inadequate information for a species normally lacking parental behavior.

DISCUSSION

Over 6140 extant species of lepidosaurian reptiles are currently recognized (Bellairs, 1986); of these, parental behavior has been reported for 210 species. Only 148 species (82 lizards, 65 snakes, and Sphenodon) are represented by reliable documentation or approximately 2.4% of all lepidosaurs (Table III). These species represent 17 families, excluding the unsubstantiated documentation for the Hydrophiidae, Typhlopidae and the unidentified amphisbaenid family (Tables I, II, III). Parental behavior is common in Eumeces, Phelsuma, Uromastix, anguids, xantusiids, iguanines, oviparous boids, southeast-Asian elapids, oviparous viperids, Elaphe, Farancia, and Psammophylax (Tables I and II). In most species (96%) parental behavior is entirely maternal; however, paternal and biparental behavior have been confirmed (Table IV).

The literature in this survey (Tables V and VI) demonstrates a paucity of experimentally obtained data on parental behavior in lepidosaurs (but see Noble and Mason, 1933; Hutchison et al., 1966; Vinegar et al., 1970; Van Mierop and Barnard, 1976a, 1978; Hasegawa, 1985, Somma, 1985b; [Orlov], 1986; Ellis and Chappell, 1987; York and Burghardt, 1988; Graves, 1989; Somma and Fawcett, 1989; Vitt and Cooper, 1989; Guillette et al., in review). The majority of the literature is descriptive or anecdotal, and the adaptive functions of this life history trait remain largely conjectural. Furthermore, the only ecological/evolutionary analysis devoted solely to parental behavior in reptiles is provided by Shine (1988; see Lillywhite, 1988).

ACKNOWLEDGEMENTS

Obtaining the literature for this survey would have been impossible without the superlative library skills of J. Mundell, L. Valentine and the late M. Covault (Interlibrary Loan Department, University Library, University of Nebraska at Omaha), D. Beaubien, B. Gilbert and K. Harmon (Interlibrary Loan Department, Marston Science Library, University of Florida), and S. Tergas (Interlibrary Loan Department, Main Library West, University of Florida). I am also grateful those who provided or informed me of important references; they are E. J. Bredin, R. L. Burke, D. B. Carter, B. Clark, P. A. Cochran, H. Ehmann, D. Ferraro, L. A. Fitzgerald, J. S. Foster, H. W. Greene, L. J. Guillette, Jr., A. Hagedorn, T. Heaton-Jones, K. Horikoshi, T. R. Johnson, G. Kattan, J. W. Lang, J. F. Lokke, S. A. Minton, Jr., L. D. Moehn, J. C. Murphy, L. Nico, J. G. Robinson, H. M. Smith, N. M. Somma, S. F. Somma, S. Stewart and S. J. Walsh. I wish to thank all of the individuals who allowed me to cite their unpublished observations as personal communications.

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The cover illustration depicts a female *Eumeces s. septentrionalis* from Nebraska brooding eggs. I thank John F. Lokke for creating the original artwork from which the illustration was copied.

**TABLE I**

Distribution of parental behavior in lizards, amphisbaenians and a rhynchocephalian

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Type of parental behavior</th>
<th>Oviparous or viviparous</th>
<th>Maternal, paternal or biparental</th>
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<td>Agamidae</td>
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<tr>
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<tr>
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<tr>
<td>Anguidae</td>
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<tr>
<td><em>Barisia imbricata</em></td>
<td>AN</td>
<td>V</td>
<td>M</td>
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<tr>
<td><em>Diploglossus bilobatus</em></td>
<td>C</td>
<td>0</td>
<td>M</td>
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<tr>
<td>D. <em>delasagra</em></td>
<td>C</td>
<td>0</td>
<td>P</td>
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<tr>
<td>Elgaria coerulae</td>
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<tr>
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**Iguanidae**

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**Lacertidae**

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<td><strong>Lampropeltis getula phyllodes</strong></td>
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<td><strong>Lampropeltis getula vitticeps</strong></td>
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**Scincidae**

<table>
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<th>Species / Genus</th>
<th>D, NPB?</th>
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<th>M</th>
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<tr>
<td><strong>Calyptotis scutirostrum</strong></td>
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<td><strong>Coruia zebra</strong></td>
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<td><strong>Cyclosadina pseudornata</strong></td>
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<td><strong>Egernia cunninghami</strong></td>
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<tr>
<td><strong>E. striata</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>E. whitii</strong></td>
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<td></td>
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</tr>
<tr>
<td><strong>E. cyanura</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Bemeces anthracinus</strong></td>
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<tr>
<td><strong>E. callicephalus</strong></td>
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<td></td>
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</tr>
<tr>
<td><strong>E. chinensis</strong></td>
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<td></td>
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</tr>
<tr>
<td><strong>E. cophi</strong></td>
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<td></td>
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</tr>
<tr>
<td><strong>E. engregius</strong></td>
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<tr>
<td><strong>E. elegans</strong></td>
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<td><strong>E. fasciatus</strong></td>
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<td><strong>E. inexpectatus</strong></td>
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<td><strong>E. laticeps</strong></td>
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<td><strong>E. laticotus</strong></td>
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<td><strong>E. lynx</strong></td>
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<tr>
<td><strong>E. multivirgatus</strong></td>
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</tr>
<tr>
<td><strong>E. obsolatus</strong></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

*Note: Some species have multiple distributions marked by commas.*
E. okadae C, NC, OO, ME, CC 0 M
E. oshimensis DU 0 M
E. parviauricularatus CN 0 M
E. quadrilineatus DU 0 M
E. schneiderii C 0 M
E. septentrionalis C, D, NC, H, ME, CN, CC, OO, AN 0 M
E. skiltonianus C, D, NC, ME, CN? 0 M
E. stimsoni RU, DU 0 M
E. tetragrannus C 0 M
E. xanthi C 0 M
Lampropholis mustelina ME, NC 0 M
Leioliopisma otagense AN V M
L. smithi AN V M
L. zia ME, NC 0 M
Mabuya capensis AN V M
M. macrorhyncha AN V M
M. macularia RU, DU 0 M
Neoseps reynoldsi C 0 M
Scincus scincus E?, CN 0 M
Sphenomorphus quoyii AN V M
Tiliqua rugosa AN V M

Teiidae
Tupinambis teguixin C, D, CN?, NC, AN? 0 M
T. rufescens NC, D? 0 M

Varanidae
Varanus gouldii E, AN 0 ?
V. griseus RU, DU 0 M
V. komodoensis RU, AN, NPB? 0 M
V. mitchelli RU, C 0 M
V. salvator RU, D?, NPB 0 M
V. varius AN 0 M

Xantusiidae
Xantusia henshawi AN V M
X. vigilis AN V M

Trogonophidae or Amphibsaenidae (?)
`Amphisbaina' RU, C 0 M
(= unidentified species)

Sphenodontidae
Sphenodon punctatus D 0 M

*One instance of viviparity in E. callicephalus has been reported by Taylor (1985).
**TABLE II**

DISTRIBUTION OF PARENTAL BEHAVIOR IN SNAKES

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Type of parental behavior</th>
<th>Oviparous or viviparous</th>
<th>Maternal, paternal or biparental</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Boa</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aspidites melanocephalus</td>
<td>C, T</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>Boa constrictor</td>
<td>RU, C, D, NPB</td>
<td>V</td>
<td>M</td>
</tr>
<tr>
<td>Casarea dussemieri</td>
<td>RU, C</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>Chondropython viridis</td>
<td>C, T, D, H</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>Epicrates cenchria</td>
<td>AN, OO, D, CN</td>
<td>V</td>
<td>M</td>
</tr>
<tr>
<td>E. striatus</td>
<td>OO</td>
<td>V</td>
<td>M</td>
</tr>
<tr>
<td>E. subflavus</td>
<td>E, C</td>
<td>V*</td>
<td>M</td>
</tr>
<tr>
<td>Eunectes murinus</td>
<td>AN, OO</td>
<td>V</td>
<td>M</td>
</tr>
<tr>
<td>E. notaeus</td>
<td>AN, OO</td>
<td>V</td>
<td>M</td>
</tr>
<tr>
<td>Lisias albertisii</td>
<td>C, D, T</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>L. boa</td>
<td>C</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>L. childreni</td>
<td>C</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>L. fuscus</td>
<td>C, T, D, H</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>L. olivaceus</td>
<td>C</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>L. papauanus</td>
<td>C, T</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>L. perthensis</td>
<td>C</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>Morelia amethistina</td>
<td>C, T, CC</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>M. breedi</td>
<td>C</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>M. spliotato</td>
<td>C, T, H, D, NC</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>Python anchietae</td>
<td>C, T</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>P. curtus</td>
<td>C, T</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>P. molurus</td>
<td>C, T, D, FB, RE, CN?, H?, ME</td>
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<td>P. regius</td>
<td>C, T, D, H, ME</td>
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<tr>
<td>P. reticulatus</td>
<td>C, T?, D</td>
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<td>M</td>
</tr>
<tr>
<td>P. sebae</td>
<td>C, T?, D, ME, RE</td>
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<tr>
<td>P. timoriensis</td>
<td>C, T</td>
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<td>M</td>
</tr>
<tr>
<td>'Lilith'or'arrow snake' (= Eryx jaculus?)</td>
<td>E?, C</td>
<td>V</td>
<td>M</td>
</tr>
</tbody>
</table>

**Colubridae**

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Type of parental behavior</th>
<th>Oviparous or viviparous</th>
<th>Maternal, paternal or biparental</th>
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<tbody>
<tr>
<td>Ahaetulla nasuta</td>
<td>OO</td>
<td>V</td>
<td>M</td>
</tr>
<tr>
<td>Amphiasma stolata</td>
<td>C</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>Atretium schistosum</td>
<td>RU, C</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>Cemophora cocinea</td>
<td>E, C, OO</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>Cerberus rynchops</td>
<td>RU, CN</td>
<td>V</td>
<td>M</td>
</tr>
<tr>
<td>Clelia clelia</td>
<td>C, H?</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>Coronella austriaca</td>
<td>RU, CN</td>
<td>V</td>
<td>M</td>
</tr>
<tr>
<td>Diadophis punctatus</td>
<td>C, NPB, CC?</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>Elaphe climacophora</td>
<td>C</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>E. flavolineata</td>
<td>C</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>E. guttata</td>
<td>RU, C, NPB</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>E. obsoleta</td>
<td>C, D, H2, NPB, CC?</td>
<td>0</td>
<td>M, B?</td>
</tr>
<tr>
<td>E. quadrivirgata</td>
<td>C, D</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>E. quatuorlineata</td>
<td>RU, C, NPB</td>
<td>0</td>
<td>M</td>
</tr>
<tr>
<td>E. schrenki</td>
<td>RU, C</td>
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<td>Species</td>
<td>Characteristics</td>
<td>Notation</td>
<td>Source</td>
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<td>---------------------------------</td>
<td>-----------------</td>
<td>----------</td>
<td>--------</td>
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<tr>
<td>Farancia abacura</td>
<td></td>
<td>C, NC, CN?</td>
<td>M</td>
</tr>
<tr>
<td>E. erythrogramma</td>
<td>RU, C</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Heterodon platirhinos</td>
<td>E, C, D</td>
<td></td>
<td>M</td>
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<tr>
<td>Hydrodynastes gigas</td>
<td>RU, C</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Lampropeltis triangulum</td>
<td>RU**, C, NPB</td>
<td></td>
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</tr>
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<td>Lycodon aulicus</td>
<td>RU, C</td>
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<td>M</td>
</tr>
<tr>
<td>L. striatus</td>
<td>RU, C</td>
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</tr>
<tr>
<td>Masticophus flagellum</td>
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<td></td>
<td>B</td>
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<td>Natrix natrix</td>
<td>C, D, NPB</td>
<td></td>
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</tr>
<tr>
<td>Oligodon taeniolatus</td>
<td>RU, C</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Opisthotropis latouchii</td>
<td>C, H?</td>
<td></td>
<td>M</td>
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<tr>
<td>Pituophis catenifer</td>
<td>E, C, D</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Psammophylax rhombeatus</td>
<td>C, CC</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>P. tritaeniatus</td>
<td>C</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>P. variabilis</td>
<td></td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Ptyas korros</td>
<td>RU, C</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>P. mucusos</td>
<td>C</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Rhabdophis subminiata</td>
<td>C</td>
<td></td>
<td>M</td>
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<tr>
<td>Sinonatrix percarinata</td>
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<td></td>
<td>M</td>
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<tr>
<td>Tropidonophis mairii</td>
<td>C</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Xenochrophis piscator</td>
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Elapidae

<table>
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<th>Characteristics</th>
<th>Notation</th>
<th>Source</th>
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<tbody>
<tr>
<td>Bungarus caeruleus</td>
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<td>M</td>
</tr>
<tr>
<td>B. candidus</td>
<td></td>
<td>C</td>
<td>M</td>
</tr>
<tr>
<td>B. oeylonicus</td>
<td>C, CC?, NC, CN?</td>
<td></td>
<td>B?</td>
</tr>
<tr>
<td>B. fasciatuss</td>
<td>C, CN?</td>
<td></td>
<td>M, B?</td>
</tr>
<tr>
<td>'Dipsas' (= Bungarus sp.)</td>
<td>RU, CN?</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Calliophis maculiceps</td>
<td>RU, D?</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Demansia papuensis</td>
<td>RU, DU</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Micrurus fulvius</td>
<td>RU, C, NPB</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>M. psyches</td>
<td>RU, DU</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Naja melanoleuca</td>
<td>C</td>
<td></td>
<td>M, B?</td>
</tr>
<tr>
<td>N. naja</td>
<td>C, D, NC, OO</td>
<td></td>
<td>M, B</td>
</tr>
<tr>
<td>N. nigricollis</td>
<td>RU, DU</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>'Asp' (= Naja haje?)</td>
<td>RU, D</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Ophiophagus hannah</td>
<td>C, NC</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>'Cockatrice'or 'basilisk'</td>
<td></td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>(= Ophiophagus hannah or Naja sp.)</td>
<td>RU, C</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>Pseudechis butleri</td>
<td>RU, C, D</td>
<td></td>
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</tr>
<tr>
<td>Pseudonaja textilis</td>
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Hydrophiidae

<table>
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<th>Characteristics</th>
<th>Notation</th>
<th>Source</th>
</tr>
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<tbody>
<tr>
<td>Pelamis platurus</td>
<td>E, CN, C</td>
<td>V</td>
<td>M</td>
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</table>

Laticaudidae

<table>
<thead>
<tr>
<th>Species</th>
<th>Characteristics</th>
<th>Notation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laticauda colubrina</td>
<td>C, D, CN?</td>
<td></td>
<td>M</td>
</tr>
<tr>
<td>L. semifasciata</td>
<td>RU, DU</td>
<td></td>
<td>?</td>
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</table>

Leptotyphlopidae

<table>
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<tr>
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<th>Characteristics</th>
<th>Notation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leptotyphlops dulcis</td>
<td>C</td>
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<td>M</td>
</tr>
<tr>
<td>L. humilis</td>
<td>E?, C</td>
<td></td>
<td>M</td>
</tr>
</tbody>
</table>
Typhlopidae
Ramphotyphlops braminus  RU, C, NPB  O  M
Rhinotyphlops caecus  RU, DU  O  M

Viperidae
Agkistrodon contortrix  RU, CN, D  V  M
A. piscivorus  RU, CN, D?  V  M
Calloselasma rhodostoma  C, H, D  O  M
Causus rhombeatus  C  O  M
Crotalus sp.  RU, CN  V  M
C. adamanteus  E?, CN, D  V  M
C. atrox  CN, PP  V  M
C. horridus  CN, PP  V  M
C. viridis  CN, D, PP  V  M
Deinagkistrodon acutus  C  O  M
Lachesis muta  C, D  O  M
Porthidium nummifer  RU, CN  V  M
Sistrurus catenatus  RU, CN  V  M
Trimeresurus kaulbacki  DU, D?  O  M
T. monticola  C, D  O  M
T. okinavensis  C, D  O (V)  M
T. wotii  C, H?  O  M
Vipera aspis  RU, CN, PP?  V  M
V. berus  CN, PP  V  M

*This species is viviparous (Lynn and Grant, 1940), not oviparous as reported by Gosse (1851). Perhaps Gosse confused an oviparous colubrid for E. subflavus.

**Female L. triangulum remain coiled around their eggs for a brief period after oviposition in order to compress them into an adherent mass before abandoning them (McCauley, 1945; Green and Pauley, 1987). This may account for the considerable number of references (Table VI) suggesting that this species broods its eggs.

*There is an unverified report of viviparity in P. regius (Anonymous, 1941).

**TABLE III

Summary of the number of species and genera exhibiting parental behavior within lepidosaurian taxa (based on Tables I and II)

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Number* of genera</th>
<th>Number* of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Squamata</td>
<td>107 (69)</td>
<td>209 (147)</td>
</tr>
<tr>
<td>Amphibia</td>
<td>1 (0)</td>
<td>1 (0)</td>
</tr>
<tr>
<td>T. eosgona or Amphibiousidae (?)</td>
<td>1 (0)</td>
<td>1 (0)</td>
</tr>
<tr>
<td>Sauria</td>
<td>48 (36)</td>
<td>104 (82)</td>
</tr>
<tr>
<td>Agamidae</td>
<td>3 (1)</td>
<td>4 (2)</td>
</tr>
<tr>
<td>Anguidae</td>
<td>6 (6)</td>
<td>13 (13)</td>
</tr>
<tr>
<td>Family</td>
<td>Number of species</td>
<td>Percent of total</td>
</tr>
<tr>
<td>---------------</td>
<td>-------------------</td>
<td>------------------</td>
</tr>
<tr>
<td>Cordylidae</td>
<td>1 (1)</td>
<td>2 (2)</td>
</tr>
<tr>
<td>Gekkonidae</td>
<td>11 (7)</td>
<td>18 (13)</td>
</tr>
<tr>
<td>Iguanidae</td>
<td>9 (6)</td>
<td>14 (11)</td>
</tr>
<tr>
<td>Lacertidae</td>
<td>2 (1)</td>
<td>2 (1)</td>
</tr>
<tr>
<td>Scincidae</td>
<td>13 (11)</td>
<td>41 (35)</td>
</tr>
<tr>
<td>Teiidae</td>
<td>1 (1)</td>
<td>2 (2)</td>
</tr>
<tr>
<td>Varanidae</td>
<td>1 (1)</td>
<td>6 (1)</td>
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<tr>
<td>Xantusilidae</td>
<td>1 (1)</td>
<td>2 (2)</td>
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<td>Serpentes</td>
<td>58 (33)</td>
<td>104 (65)</td>
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<td>Boidae</td>
<td>10 (7)</td>
<td>28 (24)</td>
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<td>Colubridae</td>
<td>25 (14)</td>
<td>36 (20)</td>
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<td>Elapidae</td>
<td>8 (3)</td>
<td>14 (7)</td>
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<tr>
<td>Hydrophiidae</td>
<td>1 (0)</td>
<td>1 (0)</td>
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<td>Laticaudidae</td>
<td>1 (1)</td>
<td>2 (1)</td>
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<tr>
<td>Leptotyphlopidae</td>
<td>1 (1)</td>
<td>2 (1)</td>
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<tr>
<td>Typhlopidae</td>
<td>2 (0)</td>
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<tr>
<td>Viperidae</td>
<td>10 (7)</td>
<td>19 (12)</td>
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<td>Sphenodontidae</td>
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*Number in parentheses represents actual total when erroneous and uncertain accounts are deleted from analysis (see Tables I and II).

**TABLE IV**

Prevalence of maternal, paternal and biparental behavior in lepidosaurians

<table>
<thead>
<tr>
<th>Parent exhibiting behavior</th>
<th>Number* of species</th>
<th>Percent* of total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maternal only</td>
<td>193 (142)</td>
<td>92.0 (96)</td>
</tr>
<tr>
<td>Paternal only</td>
<td>1 (1)</td>
<td>0.5 (0.7)</td>
</tr>
<tr>
<td>Biparental only</td>
<td>7 (2)</td>
<td>3.0 (1.3)</td>
</tr>
<tr>
<td>Maternal and bipartental</td>
<td>4 (1)</td>
<td>2.0 (0.7)</td>
</tr>
<tr>
<td>Paternal or maternal</td>
<td>2 (2)</td>
<td>1.0 (1.3)</td>
</tr>
<tr>
<td>Sex of parent unknown</td>
<td>3 (0)</td>
<td>1.5 (0)</td>
</tr>
</tbody>
</table>

*Number in parentheses represents actual value when erroneous and uncertain sources are deleted from analysis.
<table>
<thead>
<tr>
<th>Taxa</th>
<th>Sources</th>
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<tr>
<td><strong>Agamidae</strong></td>
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<tr>
<td>Leiolepis belliana</td>
<td>Boulenger, 1903</td>
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<tr>
<td>Phrynocephalus sp.</td>
<td>Bertin and Burton, 1967</td>
</tr>
<tr>
<td>Uromastix aegyptius</td>
<td>Mendelssohn and Bouskila, 1989; H. Mendelssohn, pers. comm.</td>
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<td>U. ornatus</td>
<td>Mendelssohn and Bouskila, 1989; G. Perry, pers. comm.; H. Mendelssohn, pers. comm.</td>
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<td><strong>Anguidae</strong></td>
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<tr>
<td>Barisia imbricata</td>
<td>Guillette and Hotton, 1986</td>
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<tr>
<td>Diploglossus bilobatus</td>
<td>Taylor, 1956</td>
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<tr>
<td>D. delasagra</td>
<td>Barbour and Ramsden, 1919</td>
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<tr>
<td>Elgaria coerulea</td>
<td>Stewart in Guillette and Hotton, 1986, and pers. comm.</td>
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<td>Gerrhonotus liocephalus</td>
<td>Greene and Dial, 1966; Greene in Tinkle and Gibbons, 1977</td>
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<tr>
<td>Mesaspis moreleti</td>
<td>Greene in Guillette and Hotton, 1986</td>
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<tr>
<td>Ophisaurus apodus</td>
<td>Petzold, 1971; Langerwerf, 1981, 1984; Claffey and Johnson, 1982a, b; Huff, 1985</td>
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<tr>
<td>O. compressus</td>
<td>Bartlett, 1985</td>
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<tr>
<td>O. gracilis</td>
<td>Wall, 1908; Smith, 1935; Jayaram, 1974; Daniel, 1983</td>
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<tr>
<td>O. harti</td>
<td>Pope, 1929, 1955</td>
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<tr>
<td>O. ventralis</td>
<td>Noble and Mason, 1932, 1933; Telford, 1952; Vinegar, 1968; Villiard, 1969; Mount, 1975; Somma, pers. observ.</td>
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<td><strong>Cordylidae</strong></td>
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<td>Cordylus cataphractus</td>
<td>Branch, 1988; S. Jacobs, pers. comm.</td>
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<td>C. giganteus</td>
<td>Patterson and Bannister, 1987; S. Jacobs, pers. comm.</td>
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<td><strong>Gekkonidae</strong></td>
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<td>Ailuronyx sechellensis</td>
<td>High, [1976]; Miller, 1980; McKeown and Miller, 1985; Slavens, 1987</td>
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<tr>
<td>Chondrodactylus angulifer</td>
<td>Miller, 1983a</td>
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<td>Eublepharis macularis</td>
<td>Miller, 1980</td>
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<td>G. petricolus</td>
<td>Zaworski, 1987a, b</td>
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<td>G. smithii</td>
<td>Tho and Ho, 1979</td>
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<td>Hemidactylus turcicus</td>
<td>Somma, pers. obs.</td>
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<td>Hemiphyllodactylus typus</td>
<td>Eijsden, 1978</td>
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<td>Naultinus grayi</td>
<td>Robb, 1980; J. Fawcett, pers. comm.</td>
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Phelsuma borbonica  Miller, 1982
P. dubia  Osadnik, 1984
P. flavigularis  Osadnik, 1984
P. lineata  Osadnik, 1984
P. madagascariensis  Osadnik, 1984; Rösler, 1988
P. standlingi  Digney and Tytle, 1983
Phylodactylus lanei  Z. Uribe, pers. comm.; A. Ramírez, pers. comm.
Phychozoon lionotum  Waitkus, 1983; Tytle et al., 1987
Teratoscincus scincus  Miller, 1983b

Iguanidae
Amblyrhynchus cristatus  Heller, 1903; Eibl-Eibesfeldt, 1966; Trillmich, 1979; Fitch, 1982; Dellinger, 1989
Brachylophus fasciatus  Cogger, 1974; Gibbons and Watkins, 1982
B. vitiensis  Gibbons and Watkins, 1982; Gibbons, 1984/85
Conolophus pallidus  Christian and Tracy, 1982
C. subcristatus  Werner, 1982
Crotaphytus collaris  Burt and Hoyle, 1934
Cyclura carinata  Iverson, 1977, 1979
C. cornuta  Shaw, 1969; Wiewandt, 1977, 1979; Boylan, 1984
C. cychliura  Carey, 1975
C. nubila  Shaw, 1954; Crutchfield, 1982, 1986; Thompson in Blair, 1983a, b
Iguana iguana  Alvarez del Toro, 1960; Mertens, 1960; Wiewandt, 1982; Ellison, 1985
Phrynosoma douglassi  Lockwood, 1883
Sauromalus varius  Lawler and Jarchow, 1986; Lawler in Gilbert, 1987; Castillo S., 1989
Sceloporus undulatus  Hay, 1892

Lacertidae
Acanthodactylus scutellatus  G. Perry, pers. comm.
Lacerta viridis  Mertens, 1960; Burton and Burton, 1984

Scincidae
Calyptotis scutirostrum  Ehmann, 1988
Cyclodina pseudornata  J. Fawcett, pers. comm.
Egernia cunninghami  Niekisch, 1975, 1980; Zimmermann, 1986
E. striata  Pianka and Giles, 1982
E. whitii  McPhee, 1979
Emoia cyanura  J. Fitch in Fitch, 1970
Eumeces anthracinus  Clausen, 1938; Dowling, 1950; Hamilton, 1958; Anderson, 1965; Cooper et al., 1973; Collins, 1975
E. callicephalus  Campbell and Simmons, 1961; Zweifel, 1962;
E. chinensis  [Wang, 1966]
E. copei  L. Guillette, pers. comm.
E. egregius  Hamilton and Pollack, 1958; Mount, 1961, 1963;
Somma, pers. observ.
E. elegans  
E. fasciatus*  
E. Inexpectatus  
E. laticeps  
E. latiscutatus  
E. lynxe  
E. multivirgatus  
E. obsoletus  
E. okadae  
E. oshimensis  
E. parviauriculatus  
E. quadrilineatus  
E. schneiderii  
E. septentrionalis

Mell, 1929; Hikida, 1981

Smith, 1946; Duellman and Schwartz, 1958; Hamilton, 1958; Molchos, 1971; Loop and Scoville, 1972; Mount, 1975; Vitt and Cooper, 1986; Dundee and Rossman, 1989; Somma, pers. observ.

Hurter, 1911; Noble and Mason, 1932, 1933; Taylor, 1935; Cook, 1943; McClellan et al., 1943; Mansuetl, 1948; Martof, 1956; Smith, 1961; Mount, 1975; Johnson, 1979; Moehn, 1980; Schuette, 1980; Ashton and Ashton, 1985; Cooper and Vitt, 1985; Hammond, 1985; Vitt and Cooper, 1985a, b, 1989; Green and Pauley, 1987; Johnson, 1987; Meshaka et al., 1988; Somma, pers. observ.

Sengoku, 1979; Hikida, 1981; [Mathui, 1985]
L. Guillette, pers. comm.
Gehlbach, 1965; Van Devender and Van Devender, 1975; A. Aquino, pers. comm.; J. Lynch, pers. comm.
Toyama, 1975
Tanner, 1987, and pers. comm.
Mell, 1929
Zimmermann, 1986
E. skiltonianus  
E. stimsoni  
E. tetragrammus  
E. xanthi  
Lamproophilis mustelina  
Leiopopisma otagense  
L. smithii  
L. zia  
Mabuya capensis  
M. macrorhyncha  
M. macularia  
Neoseps reynoldsi  
Sphenomorphus quoyi  
Scincus scincus  
Tiliqua rugosa  

Telidae  
Tupinambis teguixin  
T. rufescens  

Varanidae  
Varanus gouldii  
V. griseus  
V. komodoensis  
V. mitchelli  
V. salvator  
V. varius  

Xantusiidae  
Xantusia henshawi  
X. vigilis  

Trogonophidae or Amphisbaenidae (?)  
'Amphisbaina' (= species?)  

Sphenodontidae  
Sphenodon punctatus  

Heller in McClain, 1899**; Van Denburgh, 1922; Woodbury, 1931; Tanner, 1943, 1957  
Taylor, 1935  
Strecker, 1908; Werler, 1951; Behler and King, 1979  
Pope in Schmidt, 1927; Mell, 1929  
Ehmann, 1988  
Smithells in Sharrell, 1966  
J. Fawcett, pers. comm.  
Ehmann, 1988  
Rose, 1929, 1950; FitzSimons, 1943  
Rebouças-Spieker and Vanzolini, 1978  
Daniel, 1983  
Telford, 1959  
Shine, 1988  
Gesneri, 1551-1587; Topsell, 1608  
Mertens, 1960; Hitz, 1983  
Reese, 1922; Krieg, 1925; Fitzgerald et al., 1989, In press  
Fitzgerald et al., 1989, In press  
Berney, 1936  
Auffenberg, 1981  
Lallemant, 1929; Pfeffer, 1959; Auffenberg, 1981  
Gow in Shine, 1988  
Biswa and Kar, 1981  
Shaw, 1949  
Cowles, 1944; Miller, 1954  
Gesneri, 1551-1587; Topsell, 1608; Aldrovandi, 1640  
Thompson, 1988, and in Shine, 1988 and Heaton-Jones, 1989; Guillette et al., in review

*Prior to 1932, Eumeces inexpectatus and E. laticeps were included within the species E. fasciatus (Cope, 1900; Davis, 1968; Steiner, 1986). The fasciatus group was divided into three species by Taylor (1932a, b, 1935); E. fasciatus, E. inexpectatus and E. laticeps. Consequently, some references pertaining to E. fasciatus prior to 1932 may actually refer to either, E. inexpectatus or E. laticeps.
**Identity of species as described in this account is uncertain. This could refer to *Eumeces gilberti*; if so, it is the only record of brooding in this species.**

### TABLE VI

Bibliographic sources for reports of snake parental behavior

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Sources</th>
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<tr>
<td><strong>Boidae</strong></td>
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<td><em>Aspidites melanocephalus</em></td>
<td>Ross, 1978; Boos, 1979; Murphy et al., 1981; Barker, 1982, 1985; Charles et al., 1985</td>
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<tr>
<td><em>Boa constrictor</em></td>
<td>Lanworn, 1972; Wells, 1981</td>
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<td><em>Casarea dussumieri</em></td>
<td>Bloxam, 1984</td>
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<td><em>Epicrates cenchria</em></td>
<td>Boos, 1976; Brunner, 1979; Groves, 1981; Walsh and Davis, 1984</td>
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<td><em>E. striatus</em></td>
<td>Huff, 1980; Slavens, 1987</td>
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<td><em>E. subflavus</em></td>
<td>Gosse, 1851</td>
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<td><em>E. notaeus</em></td>
<td>Holmstrom, 1981; Slavens, 1985, 1988; Townson, 1985</td>
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<td><em>Liasis albertisii</em></td>
<td>Kinghorn, 1956; Johnson, 1975; Ross and Larman, 1977; Ross, 1978; Tarbet, 1984; Slavens, 1986; B. Clark, pers. comm.</td>
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<td><em>L. boa</em></td>
<td>Barker, 1982; Mehrtens, 1987</td>
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<td><em>L. childreni</em></td>
<td>Ross, 1973, 1980a, 1983; Dunn, 1979a; Sheargold, 1979; Barker, 1982; Slavens, 1988</td>
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<td><em>L. fuscus</em></td>
<td>Kinghorn, 1956; Gow, 1976; Ross and Larman, 1977; Ross, 1978, 1980b; Boos, 1979, 1983; McPhee, 1979; Barker, 1982; Weidner in Funk, 1982; Orlow, 1982; Bulian and Broer, 1984; Charles et al., 1985; [Orlov], 1986; Mehtrens, 1987; Shine, 1988</td>
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<td><em>L. olivaceus</em></td>
<td>Kinghorn, 1956</td>
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<td><em>L. papuanus</em></td>
<td>Tryon, 1985; Tryon and Whitehead, 1988</td>
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<td><em>L. perthensis</em></td>
<td>Stafford, 1986</td>
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<td><em>Morelia amethystina</em></td>
<td>Pope, 1961; Ross, 1978; Boos, 1979; McPhee, 1979; Parker, [1982]; Banks and Schwaner, 1984; Charles et al., 1985; Grow, 1987; B. Clark, pers. comm.</td>
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</table>
M. bredli
M. spilota

Python anchietae
P. curtus

P. molurus

P. regius

P. reticulatus

Abbott in Wray, 1862; Köhler, 1907;
Ditmars, 1910; Hilzheimer, 1910;
P. sebae

Günther, 1862; Sclater, 1862; [Günther], 1886; F. FitzSimons, [1912], 1930; Werner, 1930 (in Angel, 1950); Benedict and Mann in Ditmars, 1931; Benedict, 1932; Benedict et al., 1932; Pitman, 1938; Lederer, 1942, 1944, 1956; Broadley, 1959; Anonymous, 1960a,b; Dowling, 1960, 1961; Sweeney, 1961; V. FitzSimons, 1962, 1970; Meyer-Holzapfel, 1969; Schütte, 1970; Vinegar et al., 1970; Munnig Schmidt, 1971, 1973; Patterson, 1974; Branch and Patterson, 1975; Broadley and Cock, 1975a,b; Pienaur et al., 1978; Dunn, 1979b; Slavens, 1985; Trutnau, 1986; Patterson and Bannister, 1987; Branch, 1988; Schleich and Kástle, 1988; Shine, 1988

Murphy et al., 1978; Barker, 1982

Isaiah 34:15, [c. 745-350 BC], (McDowell et al., 1982)

P. timoriensis

'Lilith' or 'arrow snake'

(= Eryx jaculus?)

Colubridae

Ahaetulla nasuta
Amphiesma stolata
Atretium schistosum
Cemophora coccinea
Cerberus rynchops
Clelia clelia
Coronella austriaca
Diadophis punctatus

Elaphe climacophora
E. flavolineata
E. guttata

E. obsoleta

E. quadrivirgata
E. quatuorlineata
E. schrenki
Parancia abacura


Rieppel, 1970
Wall, 1911, 1921; Mell, 1929; Daniel, 1983
Murthy, 1986
Ditmars, 1907
Whitaker, 1978; Trutnau, 1986
Brazil, 1914, and in Roosevelt, 1914
Appleby, 1971
?McCauley, 1945; Cook, 1954; Fowlie, 1965;
?Brodie et al., 1969; Somma, pers. observ.

Fukada, 1965
Kopstein, 1938

Ditmars, 1907; Medsger, 1919, 1932;

Fukada, 1965; Orlow, 1982
Vogel, [1958?]

Kudryavtsev and Frolov, 1984

Ridgeway, 1883 (in Hay, 1892; Wright and Wright, 1957; Minton, 1972); Meade, 1937, 1940, 1945, 1946; Conant and Downs, 1940;
Farancia erytrogramma
Heterodon platirhinos
Hydrodynastes gigas
Lampropeltis triangulum

Lycodon aulicus
L. striatus
Masticophus flagellum
Matrix natrix

Oligodon taeniolatus
Opisthotropis latouchii
Pituophis catenifer
Psammophylax rhombeatus

P. tritaeniatus

P. variabilis
Ptyas korros
P. mucosus

Rhabdophis subminiata
Sinonatrix percarinata
Tropidonophis mairii
Xenochrophis piscator

Elapidae
Bungarus caeruleus
B. candidus
B. ceylonicus
B. fasciatus

'Dipsas' (= Bungarus sp.?)
Calliophis maculiceps

Demansia papuensis

Goldstein, 1941; Cagle, 1942; Reynolds and Solberg, 1942; Cook, 1954; Riemer, 1957; Tinkle, 1959; Hahn and Wilson, 1966; Crawford, 1984; Mehrtens, 1987; Dundee and Rossman, 1989
Fry in Wright and Wright, 1957; Neill, 1964a; Ashton and Ashton, 1981
Hay, 1892, 1893; Hahn 1909
Vogel 1964
Ditmars, 1907; Noble, 1920; Babcock, 1929;
Anonymous, 1940; Minton, 1972; Minton and Minton, 1973; Marsec in Shine, 1988
Herklots, 1935
Wall, 1921
Meek, 1946
Stradling in Hopley, 1882; Galloway, 1932;
Berridge, 1935; Smith, 1951; Parker, 1963; Appleby, 1971
Daniel, 1983
Pope, 1929
Carl, 1944

F. FitzSimons, [1912]; V. FitzSimons, 1962,
1970; Le Roux, 1964; Bourquin, 1970;
Visser, 1971; De Waal, 1978; Branch,
1981, 1988; Broadley, 1983; Jacobsen,
1985; Trutnau, 1986; Patterson and
Bannister, 1987
Sweeney, 1961; Isemonger, 1968; Branch,
1981; Hedges, 1983; Patterson and
Bannister, 1987
Spawls in Broadley, 1977
Mell, 1929
Wall, 1907, 1921; Mell, 1929; Kopstein,
1938; Daniel, 1983
Mell, 1929

Parker, 1929,
1935

?Sundowner, 1895*, 1902; Bredl in Shine,
1988
Abercromby, 1913; Mell, 1929; Whitaker,
1978; Daniel, 1983; Whitaker and
Whitaker, 1986

Wall, 1921; Daniel, 1983; Whitaker and
Whitaker, 1986
Mell, 1929; Shaw and Shebbeare, 1931;
Soderberg, 1973
Green, 1905
Evans, 1905; Wall, 1921; Mell, 1929;
Soderberg, 1973; Yahya, 1985
Nicander of Colophon [135-133? BC]
Frith, 1977 (also illustrated in Phelps,
1981)

Parker, [1982]
Micrurus fulvius
M. pysches
Naja melanoleuca
N. naja

'Asp' (= Naja haje?)
N. nigricollis
Ophiophagus hannah

'Cockatrice' or 'Basilisk'
(= Ophiophagus hannah or Naja sp.?)
Pseudechis butleri
Pseudonaia textilis

Hydrophiidae
Pelamis platurus

Laticaudidae
Laticauda colubrina
L. semifasciata

Leptotyphlopidae
Leptotyphlops dulcis
L. humilis

Typhlopidae
Rhamphotyphlops braminus
Rhinotyphlops caecus

Viperidae
Agkistrodon contortrix
A. piscivorus
Calloselasma rhodostoma

Campbell, 1973
Mole, 1924
Tryon, 1979; Dowling, 1986
(Appuhamy, 1810) (see Deraniyagala, 1955);
Fayrer, 1870; Kipling, 1894*; Wall, 1921;
Mell, 1929; Jennison, 1931; Kopstein,
1938; Smith, 1943; Simmon, 1944; Tweedie,
1954; Deraniyagala, 1955; Rao, 1957;
Duckett, 1964; Deoras, 1965; Petzold,
1968; Miller, 1970; Campbell and Quinn,
1975, Daniel, 1983; Whitaker and
Whitaker, 1986

Nicander of Colophon [135-133? BC]
Håkansson, 1981
Fayrer, 1870; Nicholson, 1870; Wasey, 1892;
Evans, 1903; Joynson, 1917; Wall, 1924;
Berridge, 1935; Mustill, 1936; Smith,
1936; Oliver, 1956; Leakey, 1969; Ionides
and Leakey in Soderberg, 1973;
Reitinger and Lee, 1978; Daniel, 1983;
Gurung, 1983; Whitaker and Whitaker,
1986; Dattatri, 1987; Mehrtens, 1987;
Shine, 1988

Gesneri, 1551-1587; Topsell, 1608
Fitzgerald and Mengden, 1987
Fleay, 1943; Edwards and Wells in Shine,
1988; Shine, 1989

Bertin and Burton, 1967

Semper, 1881; ?Sundowner, 1895, 1902*;
Smedley, 1931; Neill, 1964b, Taylor, 1965
Herre and Rabor, 1949

Hibbard, 1964
Whitfield, 1983++

Mell, 1929
Bogert, 1940

Anderson, 1942; Fitch, 1960; Kennedy, 1964
Wharton, 1960, 1966
Smith, 1915; 1943; Tweedie, 1954; Leakey,
1969; Campden-Main, 1970; Reitinger and
Lee, 1978; Liat, 1982; York and
Burghardt, 1988; Gloyd and Conant, 1989
Causus rhombeatus
Crotalus sp.
C. adamanteus
C. atrox
C. horridus
C. viridis

Deinagkistrodon acutus
Lachesis muta

Porthidium nummifer
Sistrurus catenatus

Trimeresurus kaulbacki
T. monticola
T. okinavensis
T. wiroti

Vipera aspis
V. berus

F. FitzSimons, [1912]; Woodward, 1933; Sweeney, 1961; Broadley, 1983
Auburn, 1909
Meek, 1946
Price, 1988
Gloyd, 1937; Jackley and Shelton in Klauber, 1972; Duvall et al., 1985; Graves, 1988, 1989
Fleck, 1987
Mole, 1924, and in Ditmars, 1910; Donisthorpe, 1947; Ramsey and Travis, 1960; Wehekind, 1960; Emsley, 1977; Caycedo, 1978; Frieberg, 1982
Picado T., 1931
Obst et al., 1988
Leigh, 1910; Pope, 1929, 1935
?Fukada, 1964; Koba et al., 1970
Mehrtens, 1987
Lanworn, 1972; Naulleau, 1987; Dowling, 1986
Brittain, 1866 (in Hopley, 1882); Service, 1902; Smith, 1951; Appleby, 1971; Street, 1979; Naulleau, 1987

*It is not known what species Sundowner actually observed but T. mairii and L. colubrina seem likely candidates. The credibility of Sundowner's [= Tichborne, H. (sic?)] (1895, 1902) observations are at best questionable, and mostly fabricated (Johnson and Smith, 1985). Nevertheless, it is likely that he also observed Australian pythons (species unspecified) brooding their eggs (Sundowner, 1895, 1902).

+Although a work of fiction, Kipling (1894) was one of the earliest published accounts of brooding in Naja naja (mistakenly referred to as Ophiophagus hannah) in English. He based his story, "Rikki-tikki-tavi," on a personal communication from an anonymous herpetologist (Kipling, 1894).

++Whitfield's (1983) mention of brooding in L. humilis is likely a mistaken reference to Hibbard's (1964) observations on L. dulcis.
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