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I. INTRODUCTION AND TERMINOLOGY

Prolonged care of eggs or offspring is a common feature of vertebrate reproduction. Parental care takes diverse forms, and presumably has evolved independently many times (e.g., Gross and Shine, 1981). Although parental care is exhibited by only a minority of reptilian species, these include a diverse array of lizards, snakes and crocodylians. The present chapter (a) reviews the occurrence and nature of reptilian parental care and (b) poses and tests hypotheses on the selective forces responsible for the evolution of such behavior. The only previous comprehensive reviews of reptilian parental care are those of Noble and Mason (1933) on squamates and of Cott (1971) on crocodylians.

I define "parental care" as any form of postovipositional parental behavior; that is, any action of the parent after oviposition or parturition, that increases the chances of survival of the offspring. This definition differs from the concept of "parental investment" (Trivers, 1972), which (a) includes investment prior to oviposition, and (b) is restricted to behavior that decreases the probable survivorship or future fecundity of the parent. This latter condition is difficult to verify empirically and hard to apply to certain cases. For example, if the "costs" of a female guarding her eggs are independent of the number of eggs guarded, the addition of more eggs would not increase the mother's "parental investment"; however, her behavior towards those additional eggs clearly would qualify as "parental care."

Parental care may be divided conveniently into two major categories: care of the eggs and care of the young. Care of the eggs is widespread but uncommon in reptiles, and generally consists of the parent remaining with the eggs for some time after oviposition (Figs. 1,2). This behavior usually is termed "egg-brooding" or "egg-guarding." However, although protection against predators is probably the major advantage conferred by the parent's presence (see below), actual defense against predators has been witnessed only rarely. Hence, the terms "nest-guarding" and "egg-guarding" should be applied only to species in which active nest defense has been observed. Cases in which the parent remains with the eggs, but without documentation of nest defense, may be termed "nest attendance" or "egg attendance" (Tryon, 1979). Finally, the term "egg-brooding" may be restricted to species in which the female facilitates incubation by raising nest temperatures above ambient (Campbell and Quinn, 1975). I prefer this terminology to the proposal (Groves, 1982) that the term "egg-brooding" should be reserved for species that actively manipulate their eggs.

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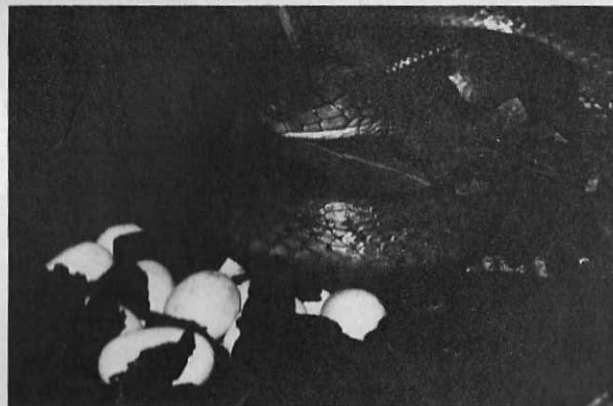


Fig. 1. *Ophiophagus hannah*. King cobra within a nest containing a clutch of eggs. As far as is known, these snakes do not raise the temperature of the clutch. (Photo courtesy of the New York Zoological Society ©).

II. THE OCCURRENCE OF PARENTAL CARE

A. Taxa Reported to Show Parental Care

1. TESTUDINES

Parental care is rare or absent in turtles; apparently the only record is that of Hodsdon and Pearson (1943), who described maternal behavior in the Bahamian emydid *Pseudemys malonci*. According to these authors (and see Oliver, 1955), the female turtles returned to their nest sites immediately before hatching and dug away hard-packed soil above the nest-chambers so that the hatchlings could emerge successfully. Freshwater turtles have attracted considerable ecological study since the time of Hodsdon and Pearson's observations, and if maternal behavior of the type described above is a general phenomenon, it is surprising that it has not been noted by other workers.

2. CROCODYLIANS

In contrast to the turtles, parental care is common (possibly ubiquitous) among crocodilians (Table I). Descriptions of crocodilian nest defense may be found in the works of Pliny and Aristotle (and see



Fig. 2. Uncovered nests. (A) *Ophisaurus apodus*. Female coiled around clutch. (B) *Elgaria multicarinata*. Multidutch nest with several females. (Photo courtesy of B. Langerwerf.)

TABLE I
Crocodilian Taxa Reported to Show Parental Care

Species	Form of parental care					Authority
	Attends nest	Defends nest	Opens nest	Carries young	Defends young	
<i>Alligator mississippiensis</i>	♀	♀	♀	♀	♀	Clarke, 1888; Devenish, 1893; Reese, 1907; McIlhenny, 1934; Joanen, 1970; Joanen and McNease, 1970, 1980; Kushlan, 1973; Fogarty, 1974; Herzog, 1975; Ogden, 1976; Metzen, 1977; Goodwin and Marion, 1978; Kushlan and Kushlan, 1980; Dietz and Hines, 1980; Kushlan and Simon, 1981
<i>Caiman crocodilus</i>	♀	♀, ♂	♀, ♂	♂(?)	♀, ♂	Alvarez del Toro, 1969, 1974; Staton and Dixon, 1977; Gorzula, 1978; Staton, 1978
<i>C. yacare</i>	♀	-	♀	-	♀	Crawshaw and Schaller, 1980
<i>Crocodylus acutus</i>	♀	♀	♀	♀	♀	Descourtilz, 1809; Brehm, 1885; Ogden and Singletary 1973; Ogden, 1978; Dugan et al., 1981
<i>C. cataphractus</i>	♀	-	♀	-	-	Waiukuwait, 1982
<i>C. intermedius</i>	♀	-	-	-	-	Medem, 1958
<i>C. johnsoni</i>	♀	♀(?)	♀	♀	-	Worrell, 1952; Compton, 1981
<i>C. moreletii</i>	♀	-	♀	♀	♀, ♂	Hunt, 1974, 1975
<i>C. niloticus</i>	♀	♀	♀, ♂	♀, ♂	♀, ♂	Pliny (trs. Holland, 1601); Aristotle (trs. Creswell, 1862); Vansleb, 1678; Pitman, 1930, 1941; Chadwick, 1931; Cott, 1961, 1971; Modha, 1967; Pooley, 1969, 1974, 1976, 1977; Hadley, 1969; Pooley and Gans, 1976
<i>C. novaeguineae</i>	♀	♀	♀	♀, ♂	♂	Neill, 1946; J. W. Lang, pers. comm.
<i>C. palustris</i>	♀	♀	♀	-	♀, ♂	Waytialingham, 1880; Deraniyagala, 1939; Dharmakumarsinji, 1947; David, 1970; Whitaker and Whitaker, 1977, 1978

TABLE I (Continued)

Species	Form of parental care					Authority
	Attends nest	Defends nest	Opens nest	Carries young	Defends young	
<i>C. porosus</i>	♀	♀	♀	♀	♀, ♂	Boake, 1870; Shelford, 1916; Deraniyagala, 1939; Loveridge, 1946; Robinson, 1948; Neill, 1971; Webb, 1977; Biswas, 1977; Webb et al., 1977; Bustard and Choudhury, 1980; Bustard and Kar, 1981; Magnusson, 1980; Jelden, 1981; Bustard and Maharana, 1982; Choudhury and Bustard, 1979; Acharjyo and Mishra, 1981
<i>Gavialis gangeticus</i>	♀	♀	♀	♀	♀	Whitaker and Whitaker, 1977b; Singh and Bustard, 1977; Bustard, 1980; Basu and Bustard, 1981; Bustard and Singh, 1981
<i>Melanosuchus niger</i>	No(?)	♀	(?)	-	♀	Hartwig, 1873; Medem, 1971
<i>Osteoleaemus tetraspis</i>	♀	♀	♀	♀, ♂	-	Schmidt, 1919; Cansdale, 1955; Tryon, 1980
<i>Palaeosuchus pulchrosus</i>	♀	♀	-	-	-	Medem, 1958
<i>P. trigonatus</i>	-	-	Yes	-	-	Magnusson et al., 1985

Table indicates sex of parent reported to care for young. A dash indicates that parental care is not reported.

discussion by Böhme, 1977), and more recent scholars have documented parental behavior in virtually every crocodilian species studied in detail.

Although the frequency of nest attendance and active nest defense varies interspecifically, and even intraspecifically (references in Table I), the broad outlines of parental care are similar in all crocodilians for which data are available. The pattern is quite different from that described in any squamate reptile. The female parent remains in the vicinity of the nest after laying, or returns to it at intervals. Potential predators on the eggs may or may not be attacked; species that are not egg predators are ignored (e.g., Modha, 1967; Cott, 1971; Dietz and Jackson, 1979). The female opens the nest at the time of hatching, and

carries full-term eggs and newly-hatched young to the water (Pooley, 1977). The young remain in a group for days or weeks and are actively defended by the adults. If attacked, even older juveniles will give "distress calls" that will initiate aggressive behavior from adult crocodylians toward the attacker (e.g., Hunt, 1974, 1975). Parental behaviors, such as nest-guarding and nest-opening, are probably universal among present-day crocodylians (Greer, 1971; Kushlan and Simon, 1981).

3. SQUAMATES

Postovipositional parental behavior by squamate reptiles can take many forms, of which the simplest is concealment of eggs immediately after oviposition. Oviparous squamates generally lay eggs in places with appropriate conditions of temperature and humidity (Muth, 1980) and away from the attention of egg predators (see Packard and Packard, this volume). Several species of lizards manipulate their eggs after oviposition, presumably to place them into suitable microhabitats. This behavior has been reported in lacertids (Hilzheimer, 1910), iguanids (Gordon, 1960; Smith et al., 1972; Tokarz and Jones, 1979; Jones and Guillette, 1982), scincids (Noble and Mason, 1933), agamids (Asana, 1941), and gekkonids (Nettman and Rykena, 1979; *Phyllurus platurus*, Shine, pers. obs.). Presumably such behavior is widespread among reptiles.

More complex, or at least longer-term, parental care is shown by many species. Among the squamates, at least 103 species have been reported to have one or both parents remain with the eggs after oviposition (Table II). These species include a taxonomically diverse array of lizards and snakes. Unfortunately, some of the cases listed in Table II are poorly documented; at least 15 of the 103 examples depend upon single observations of adults found near eggs. Undoubtedly, some of the cases do not indicate parental care, but may be coincidental or reflect incipient oophagy or discovery of a female with a recently oviposited clutch. The force of this objection is diminished by the consistency with which the adult is reported to be coiled around the eggs rather than merely close to them, but nonetheless these reports should be regarded with caution. I once found a small snake (*Unechis gouldi*) only a few centimeters from four eggs under a piece of tin; the obvious inference would have been parental care, except that the snake species is viviparous, and the eggs were those of an agamid lizard.

Records of parental care for the Varanidae are particularly difficult to evaluate. No well-documented case is available, but at least three anecdotal reports are suggestive. For example, Cogger (1967:60) notes that "on several occasions when adult goannas have been disturbed at

TABLE II
Squamate Taxa in Which the Female Parent Has Been Reported to Remain With the Eggs After Oviposition

Family	Species	Authority
Lizards		
Anguinae	<i>Diploglossus delasagra</i>	Barbour and Ramsden, 1919; Greer, 1967
	<i>D. bilobatus</i>	Taylor, 1956; Fitch, 1970
	<i>Gerrhonotus tlocephalus</i>	Greene and Dial, 1966; Tinkle and Gibbons, 1977
	<i>Elgaria multicarinatus</i>	Langerwerf, 1981
	<i>Ophisaurus apodus</i>	Langerwerf, 1981
	<i>O. attenuatus</i>	Fitch, 1970
	<i>O. gracilis</i>	Daniel, 1983
	<i>O. harti</i>	Smith, 1935
	<i>O. ventralis</i>	Noble and Mason, 1933; Vinegar, 1968; Mount, 1975
Iguanidae	<i>Amblyrhynchus cristatus</i>	Carpenter, 1966; Eibl-Eibesfeldt, 1966; Trillmich, 1979
	<i>Brachylophus fasciatus</i>	Cogger, 1974; Gibbons and Watkins, 1982
	<i>B. vitiensis</i>	Gibbons and Watkins, 1982
	<i>Conolophus pallidus</i>	Christian and Tracy, 1982
	<i>C. subcristatus</i>	Werner, 1982
	<i>Cyclura carinata</i>	Iverson, 1979
	<i>C. stepheneri</i> (= <i>C. cornuta</i>)	Wiewandt, 1977, 1979
	<i>C. cyclura</i>	Carey, 1975
	<i>C. nubila</i>	Shaw, 1954
	<i>Iguana iguana</i>	Rand, 1968; Alvarez del Toro, 1972; Rand and Rand, 1976; Wiewandt, 1982
Scincidae	<i>Emoia cyanura</i> (?)	Fitch, 1970
	<i>Eumeces anthracinus</i>	Smith, 1946; Dowling, 1950; Collins, 1974
	<i>E. brevilineatus</i>	Werler, 1951
	<i>E. callicephalus</i>	Campbell and Simmons, 1961
	<i>E. chinensis</i>	Wang, 1966
	<i>E. egregius</i>	Mount, 1963
	<i>E. elegans</i>	Mell, 1929; Hikida, 1981

(Continued)

TABLE II (Continued)

Family	Species	Authority
Lizards (Continued)		
Scincidae	<i>E. fasciatus</i>	Ruthven, 1911; Dunn, 1920; Blanchard, 1922; Smith, 1882; Brimley, 1904; Ditmars, 1904; Brady, 1927; Burt, 1928; Corrington, 1929; Klots, 1930; Cagle, 1940; Fitch, 1954; Strecker, 1908; Allard, 1909; Hurter, 1911; McCauley, 1939, 1945; Bishop, 1926; Evans and Roecker, 1951; Minton, 1972; Cooper et al., 1983
	<i>E. inexpectatus</i>	Duellman and Schwartz, 1958
	<i>E. laticeps</i>	Smith, 1946; Martof, 1956; Vitt and Cooper, 1985
	<i>E. laticutatus</i>	Hikida, 1981
	<i>E. multivirgatus</i>	Gehlbach, 1965; Van Devender and Van Devender, 1975
	<i>E. obsoletus</i>	Smith, 1946; Evans, 1959; Fitch, 1955, 1970; Hall, 1971
	<i>E. okadae</i>	Hikida, 1975; Hasegawa, 1984
	<i>E. oshimensis</i>	Toyama, 1975
	<i>E. quadrilineatus</i>	Mell, 1929
	<i>E. "pekinensis" (= xanthi)</i>	Mell, 1929
	<i>E. septentrionalis</i>	Breckenridge, 1943; Smith, 1946
	<i>E. skiltonianus</i>	Tanner, 1943, 1957; Smith, 1946
	<i>E. stinsoni</i> (?)	Taylor, 1935
	<i>E. tetragrammus</i>	Behler and King, 1979
	<i>E. xanthi</i>	Schmidt, 1927; Taylor, 1935
	<i>Neoseps reynoldsi</i>	Telford, 1959
Teiidae	<i>Tupinambis teguixin</i>	Krieg, 1925
Varanidae	<i>Varanus mitchelli</i> (?)	G. Gow, pers. comm.
	<i>V. salvator</i> (?)	Biswas and Kar, 1981
	<i>V. varius</i> (?)	Cogger, 1967

TABLE II (Continued)

Family	Species	Authority
Snakes		
Boidae	<i>Aspidites melanocephalus</i>	Boos, 1979; Barker, 1981; Charles et al., 1985
	<i>Chondropython viridis</i>	Kratzer, 1962; Mackay, 1973; Walsh, 1979; Switak, 1975
	<i>Liasis albertisii</i>	Ross, 1978
	<i>L. amethystinus</i>	Pope, 1961; Boos, 1979; Charles et al., 1985
	<i>L. boa</i>	Barker, 1981
	<i>L. childreni</i>	Ross, 1973; Dunn, 1979a; Barker, 1981
	<i>L. fuscus</i>	Kinghorn, 1956; Ross, 1978; Boos, 1979; Shine, pers. obs.
	<i>L. mackloti</i>	Ross and Larman, 1977; Barker, 1981
	<i>Morelia bredli</i>	Gow, 1981
	<i>M. spilotes</i>	Cogger and Holmes, 1960; Boos, 1979; Harlow and Grigg, 1983; Charles et al., 1983
	<i>Python curtus</i>	Noble, 1935; Pope, 1961; Vinegar et al., 1970
	<i>P. molurus</i>	Lamarre-Picquot, 1835, 1842; Valenciennes, 1841; Forbes, 1881; Abercromby, 1913; Wall, 1921; Stemmler-Morath, 1956; Pope, 1961; Hutchinson et al., 1966; Yadav, 1967; Vinegar et al., 1970; Wagner, 1973, 1976; Van Mierop and Barnard, 1976, 1978. Achariyo and Misra, 1976; Coborn, 1975; Foekema, 1975
	<i>P. regius</i>	Logan, 1973; Pitman, 1938; Walsh, 1979; Boos, 1979; Schivre, 1972; Van Mierop and Bessette, 1981

TABLE II (Continued)

Family	Species	Authority
Snakes (Continued)		
Boidae	<i>P. reticulatus</i>	Wray, 1862; Wall, 1926; Lederer, 1944; Pope, 1961; Taylor, 1965; Vinegar et al., 1970; Honegger, 1970; La Panouse and Pellier, 1973; Hediger, 1968; Müller, 1970
	<i>P. sebae</i>	Sclater, 1862; FitzSimons, 1930; Benedict, 1932; Pitman, 1938; Broadley, 1959; Dowling, 1960; Pope, 1961; Schutte, 1970; Vinegar et al., 1970; Dunn, 1979b; Schmidt, 1973
	<i>P. timoriensis</i>	Murphy et al., 1981; Barker, 1981
Colubridae	<i>Amphiesma mairii</i>	J. Bredl, pers. comm.
	<i>A. stolata</i>	Wall, 1921; Mell, 1929
	<i>Cemaphora coccinea</i>	Ditmars, 1942
	<i>Elaphe climacophora</i>	Fukada, 1965
	<i>E. guttata</i>	D. Kent, pers. comm.
	<i>E. obsoleta</i>	Oliver, 1955; Medsger, 1919
	<i>E. quadrivirgata</i>	Fukada, 1965
	<i>Farancia abacura</i>	Meade, 1940; Goldstein, 1941; Riemer, 1957; Ashton and Ashton, 1981
	<i>F. erythrogramma</i> (?)	Ashton and Ashton, 1981
	<i>Heterodon platyrhinos</i> (?)	Hahn, 1909
	<i>Lampropeltis triangulum</i>	Babcock, 1929; Ditmars, 1942; Minton and Minton, 1973; G. Marsec, pers. comm.
	<i>Lycodon aulicus</i>	Smith, 1943
	<i>L. striatus</i> (?)	Wall, 1921
	<i>Natrix natrix</i>	Gallwey, 1932; Smith, 1973
	<i>Ophedrys vernalis</i> (?)	Blanchard, 1933
	<i>Opisthotropis latouchi</i> (?)	Pope, 1935
	<i>Pituophis melanoleucus</i> (?)	Carl, 1944

TABLE II (Continued)

Family	Species	Authority
Snakes (Continued)		
Colubridae	<i>Psammophylax rhombeatus</i>	FitzSimons, 1962; Le Roux, 1964; Bourquin, 1970; Visser, 1971; Broadley, 1977
	<i>P. tritaeniatus</i> (?)	Sweeney, 1961; but see Broadley, 1977
	<i>P. variabilis</i>	Broadley, 1977
	<i>Ptyas korros</i>	Mell, 1929
	<i>P. mucosus</i>	Wall, 1907, 1921; Mell, 1929; Pope, 1935
	<i>Rhabdophis subminiatus</i>	Mell, 1929
	<i>Xenochrophis piscator</i>	Mell, 1929; Abercromby, 1913
Elapidae	<i>Bungarus caeruleus</i>	Smith, 1943; Wall, 1921
	<i>B. candidus</i>	Mell, 1929
	<i>B. ceylonicus</i>	Green, 1905; Wall, 1921
	<i>B. fasciatus</i>	Mell, 1929; Pope, 1935; Smith, 1943
	<i>Calliophis maculiceps</i> (?)	Frith, 1977
	<i>Demansia papuensis</i> (?)	Parker, 1982
	<i>Laticauda colubrina</i>	Smedley, 1931; Neill, 1964; Taylor, 1965; but see Dunson, 1975
	<i>Micrurus corallinus</i>	Mole, 1924
	<i>M. fulvius</i>	Campbell, 1973
	<i>Naja naja</i>	Wall, 1921; Mell, 1929; Smith, 1937; Kopstein, 1938; Smith, 1943; Tweedie, 1957; Petzold, 1968; Campbell and Quinn, 1975
	<i>N. melanoleuca</i>	Tryon, 1979
	<i>Ophiophagus hannah</i>	W. Smith, 1935; H. Smith, 1936; Mustill, 1936; M. Smith, 1943; Oliver, 1956; Leakey, 1969; Shaw and Shebbeare, 1931
	<i>Pseudechis butleri</i> (?)	Fitzgerald and Mengden, 1987
	<i>Pseudonaja textilis</i> (?)	Fleay, 1943; R. Wells, pers. comm.; J. Edwards, pers. comm.

(Continued)

TABLE II (Continued)

Family	Species	Authority
Snakes (Continued)		
Leptotyphlopidae	<i>Leptotyphlops dulcis</i>	Hibbard, 1964
Typhlopidae	<i>Rhinotyphlops caecus</i>	Bogert, 1940; but see Erasmus and Branch, 1983
	<i>Rhamphotyphlops braminus</i> (?)	Mell, 1929
Viperidae	<i>Causus rhombeatus</i> (?)	Sweeney, 1961; Broadley, 1983
	<i>Calloselasma rhodostoma</i>	Smith, 1915, 1943; Tweedie, 1957; Leakey, 1969
	<i>Lachesis muta</i>	Mole, 1924
	<i>Trimeresurus monticola</i>	Leigh, 1910; Pope, 1935

A question mark indicates that the data are anecdotal and possibly unreliable.

termite mounds, newborn young have been found emerging. This suggests that the female may remain near the nest until the young are ready to hatch, at which time she makes a new tunnel to release the young." In each case, the species involved was *Varanus varius* (H. Cogger, pers. comm.). On two separate occasions, a captive female *Varanus mitchelli* was found with the tail coiled around the eggs (G. Gow, pers. comm.). Parental care is suggested by the behavior of a female *Varanus salvator* that remained at the nest site for several days after oviposition (Biswas and Kar, 1981). A less reliable account of possible parental care in varanids, probably a case of misinterpreted egg predation, has been reported by Berney (1936).

Parental care in squamates may be divided into four major categories, the first three of which deal with care of the eggs rather than the offspring: (1) female buries eggs and defends nest site briefly against conspecific females; (2) female coils around eggs, defends them against predators and warms them by shivering thermogenesis; (3) female remains with eggs after oviposition and may defend them against predation or pathogens; (4) female aids newly born or newly hatched young.

1. Nest-site defense against conspecific females is widespread in iguaine lizards (Table II) but has not been reported in any other squamate group. In some cases, the nest site is defended even prior to

TABLE III
Shivering Thermogenesis in Brooding Female Pythons:
Disagreements in the Literature

Species	Shivering thermogenesis	
	Occurs	Does not occur
<i>Aspidites melanocephalus</i>	Boos, 1979; Charles et al., 1983	Murphy et al., 1981
<i>Liasis amethystinus</i>	Boos, 1979	Charles et al., 1983
<i>L. mackloti</i>	Charles et al., 1985	Ross and Larman, 1977
<i>Morelia spilotes</i>	Harlow and Grigg, 1983	Charles et al., 1985
<i>Python curtus</i>	Vinegar et al., 1970	Noble, 1935
<i>P. regius</i>	Pitman, 1974; Logan, 1973	Van Mierop and Bessette, 1981
<i>P. reticulatus</i>	Hediger, 1968; Müller, 1970	Honegger, 1970; La Panouse and Pellier, 1973; Pitman, 1974; Vinegar et al., 1970
<i>P. sebae</i>	Benedict, 1932; Noble, 1935	Vinegar et al., 1970; Pitman, 1974

oviposition (Wiewandt, 1982). The intensity of nest site defense varies considerably among species, and even among geographic areas within a species. Some of this variability may be attributed to the physical condition of the females: only animals in good condition can engage in vigorous nest defense (Wiewandt, 1982; references in Table II).

2. Egg brooding (shivering thermogenesis) has been recorded only in pythons (Table II; Fig. 3). The female coils tightly around the clutch, so that the eggs are completely hidden. In at least some species, rhythmic muscular contractions of the mother's body produce sufficient heat to maintain a relatively high and constant temperature in the egg mass. This phenomenon has been described in *Aspidites melanocephalus*, *Chondropython viridis*, *Liasis amethystinus*, *L. mackloti*, *Morelia spilotes*, *Python curtus*, *P. reticulatus*, and *P. sebae* (references in Table II), and may be universal within the pythons.

Certainly the pythons known to show shivering thermogenesis cover a broad taxonomic range, including small as well as large species, and exclusively tropical as well as temperate-zone taxa. Although several authors (especially Vinegar et al., 1970) have stressed that only some python species utilize shivering thermogenesis, the evidence for interspecific differences in such behavior is weak. Commonly, studies of the same species by different workers are contradictory with respect to whether or not shivering thermogenesis is exhibited (Table III). These

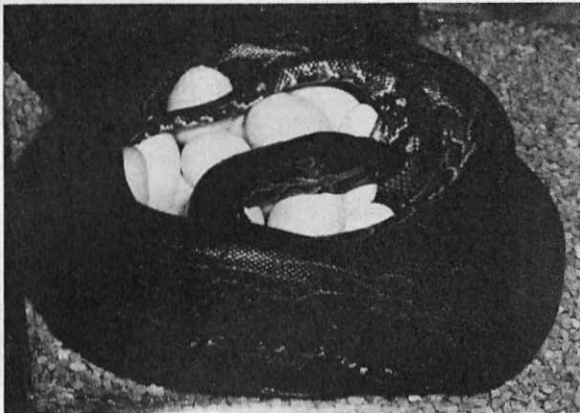


Fig. 3. *Python sebae*. Python coiled around a clutch of eggs and contracting its muscles at a regular rate, thus raising the temperature of body and clutch. (Photo courtesy of the New York Zoological Society ©).

disagreements are due to several factors, including (a) the type of evidence used (e.g. temperature measurement versus presence of muscular twitching), (b) the temperature-dependence of shivering thermogenesis (if the room is warm, no shivering is observed), (c) the difficulties in interpreting slight temperature differences between the egg mass and ambient, because of the great thermal inertia of these large reptiles (e.g., Cogger and Holmes, 1960), and (d) the low sample sizes (often only one or two animals). Some python species may not utilize metabolic heat production during brooding but convincing data are currently unavailable.

The maintenance of high temperatures during incubation undoubtedly quickens embryonic development (e.g., Joshi, 1967) and also may increase embryonic survivorship. Python embryos develop normally only at high temperatures (approximately 30°C), and are much more stenothermic in this regard than embryos of most other squamates (Joshi, 1967; Vinegar, 1973; Harlow and Grigg, 1984). One hypothesis is that maternal brooding is an adaptation to this embryonic thermal sensitivity (Vinegar, 1973). However, distinguishing cause and effect is difficult in such a correlation. Equally plausibly, the embryonic sensitivity may have evolved because of maternal brooding rather than vice versa. If the eggs

are always kept warm by the brooding female, selection to maintain embryonic tolerance of low temperature would be weak or absent. An additional hypothesis is that maternal thermogenesis allows pythons to reproduce successfully under colder climatic conditions than would otherwise be possible (Harlow and Grigg, 1984).

The apparent restriction of shivering thermogenesis to pythons might be a function of their massively developed lateral musculature. Presumably, most reptiles would lack the physiological ability for sustained muscular contraction and hence, significant metabolic heat production. The substantial increase in metabolic rate of brooding female pythons (Hutchinson et al., 1966; Van Mierop and Barnard, 1976, 1978; Harlow and Grigg, 1984) means that maternal care in these snakes confers a massive energetic cost. Curiously, this group has not followed the boines in evolving viviparity, a strategy allowing egg temperatures to be raised by maternal behavioral (rather than physiological) thermoregulation. One reason may be that an egg-retaining female python could not subdue prey by constriction, because of the risk of damaging the eggs. An egg-brooding female would not face this restriction.

3. The most widespread form of squamate parental care consists of the female remaining with the eggs after oviposition. Her presence presumably serves some function, which has rarely been demonstrated. Functions documented in some species include defense against predators, and regulation of egg temperature or moisture levels (discussed further in Section III.A). Many of the reported cases of egg-attending (Table II) are likely to be invalid inferences, because they are based on single observations of adults with eggs. Nonetheless, the consistency with which this behavior has been reported in particular species clearly indicates that egg-attendance is widespread in squamates (Table II).

4. Parental care of offspring rather than of eggs is remarkably rare in reptiles, perhaps because the mother and neonates are rarely in close proximity. One exception involves egg-attending (or guarding or brooding-) species in which the female often is present at hatching. In at least one such species (*Eumeces obsoletus*), a female was observed to help the young hatch, and later "groom" the offspring (Evans, 1959). Even more remarkable is the observation (unfortunately uncorroborated) of newly-hatched *Python molurus* returning to their empty eggshells at night, with the mother then coiling around them and heating them by shivering thermogenesis (Döflein, 1932; cited in La Panouse and Pellier, 1973). An aborigine from Mudginberri Station (Alligator Rivers region, tropical Australia) suggested that female water pythons (*Liasis fuscus*) "took the babies down to the water and taught them how to swim" (R. Lambeck, pers. comm.).

If the scarcity of posthatching parental care in squamates is due to the lack of physical association between mother and young in most oviparous forms, this problem is overcome in viviparous squamates, which comprise approximately one-fifth of all species of lizards and snakes (Shine, 1985). Observations of viviparous females at parturition confirm that mothers in some squamate species may stimulate the young to emerge from their membranous sacs by pushing with the snout, or may actually tear open the membranes themselves. This occurs in xantusiid lizards (Cowles, 1944; Miller, 1954), scincid lizards (Niekisch, 1975; Rebouças-Spieker and Vanzolini, 1978; Shine, pers. obs. for *Sphenomorphus quoyii*), and boid snakes (Groves, 1981).

However, mothers apparently do not open the fetal membranes at birth in viviparous iguanid, diploglossid, or lacertid lizards (Rebouças-Spieker and Vanzolini, 1978). In some colubrid and boid snakes, the mother ingests dead young and birth debris after the living young have emerged from their membranes (Neill and Allen, 1962; Rieppel, 1970; Groves, 1981; Holmstrom and Behler, 1981). A similar phenomenon occurs in oviparous reptiles, the mothers of which ingest spoiled eggs (e.g., crocodylians: Kushlan and Simon, 1981; squamates: Groves, 1982). Such behavior has been interpreted as parental care, because (a) it may prevent fungal infection spreading to other eggs, and (b) it may prevent odors attracting predators (Groves, 1982). Alternatively, rotting eggs may have a different odor than healthy eggs, and the females may mistake them for food items (R. B. Huey, pers. comm.).

One further form of squamate parental care, which has received great publicity, is the alleged ability of female snakes to swallow their young for protection when danger threatens. The first published reference to this behavior comes from the Egyptians at about 2500 B.C. (Speck, 1923), whereas the first reference in the English language is in Spenser's "The Faerie Queene" (1590). The story has been applied to many species, especially to viviparous forms, and often to species that have been observed in detail by other workers who have failed to report the same phenomenon (e.g., *Bothrops neuwiedi*: Schupp, 1913; Melgarejo, 1977). The extensive literature on the subject has been summarized and evaluated multiple times (Noble, 1921; Ortenburger, 1930; Schmidt, 1929; Angel, 1950; Rose, 1962; Klauber, 1972). The consensus is that no satisfactory evidence of the phenomenon has ever been produced. The stories seem unlikely to be true because (a) the behavior has never been reported in captivity or from field observations of scientists; (b) undigested young have never been discovered in stomachs of snakes dissected for dietary studies; (c) offspring are probably unable to survive for significant periods inside the stomach of the mother (e.g., Klauber, 1972). Nevertheless, the occurrence of mouth-brooding and transport of

young in cichlid fishes and crocodylians, as well as the recent discovery of gastric brooding in an Australian frog (Corben et al., 1974), suggest that gastric protection of young in snakes is not impossible. Nonetheless, reliable data are totally lacking.

Other popular tales concerning reptilian parental care include the mother snake nourishing the young inside her stomach (Rivers, 1874; Stanley, 1897; Burroughs, 1908), the mother rattlesnake crooning (by rattling mildly) to her newborn young (Crites, 1952), and the mother rattlesnake caring for her young until they are well-grown, and then finding suitable home sites for them (Meek, 1946). Charming as these stories are, their validity seems doubtful.

Although the present review is concerned only with living reptiles, parental care also may have been shown in a variety of groups that are now extinct (e.g., Coombs, 1982; Horner, 1984).

B. Taxonomic Biases

1. GENERAL

The incidence of reptilian parental care is not distributed randomly among different taxonomic groups. This taxonomic bias is evident at the levels of order, suborder, family, and genus.

2. COMPARISONS AMONG ORDERS

The three orders of living reptiles are only distantly related to each other, having been evolving as separate lineages for almost 300 million years (e.g., Romer, 1966). This long divergence has resulted in great differences among the living orders in morphology and, as shown by the present review, in the frequency and form of parental care. Parental behavior appears universal in crocodylians (and in their relatives, the birds) but seems to be lacking in testudines. Parental care is seen in many squamate taxa, but has been described in only about 2% of all oviparous squamate species (7% of oviparous genera). Of course, many species have yet to be examined in this regard.

3. COMPARISONS BETWEEN SUBORDERS

Among the squamate suborders, parental care is unknown in amphisbaenians (possibly because of a paucity of field data), rare in lizards (recorded in 41 of approximately 3000 oviparous species, or 1.3%), and more common in snakes (47 of 1700 species, or 2.8%). If each species is treated as an independent data point (see Ridley, 1983, for a critique of this assumption), the proportion of oviparous species recorded to show parental care is significantly lower in lizards than in snakes (2×2 table, 1 d.f., $\chi^2 = 18.5$, $p < 0.001$). However, this may

The remaining case of parental care is in *Elaphe obsoleta* at Jacob's Creek, Pennsylvania (Medsger, 1919). The eggs were buried in an old sawdust pile, and the two "parent" snakes remained on, in, or near the pile for at least 3 weeks. At one point, "Mr. Medsger secured a fork, and at a depth of twelve inches dug up 44 eggs of the pilot snake. The male snake was coiled around the eggs" (Medsger, 1919:28). Mr. Medsger's talk on this subject was illustrated by photographs, so there seems no reason to doubt his observations. However, his means of sexing the adult snakes may have been in error. The reported clutch size is very high; usual clutches for this species are 7-12 eggs (Fitch, 1970), and communal oviposition has been recorded (Lynch, 1966). Hence, the clutch was probably a communal one, and the two snakes observed by Medsger may both have been females. Further observations on reproduction of this relatively common snake would be of interest.

III. HYPOTHESES ON THE EVOLUTION OF PARENTAL CARE

A. Cost-Benefit Models

1. GENERAL

The selective forces responsible for the evolution of reptilian parental care may be investigated by an analysis of the possible "costs" and "benefits" of such behavior. Thus, the fitness (lifetime reproductive success) of a hypothetical reptile showing parental care is compared to that of an otherwise identical animal not showing care, and the ecological conditions or species characteristics conferring a higher fitness to the former individual are considered.

As described in theoretical models for the evolution of viviparity (Shine, 1985), the primary "costs" of parental care are likely to be decrements in the food intake, survivorship, or subsequent fecundity of the parent. Remaining with the eggs may increase vulnerability of the parent to predators, depending on the site chosen and on whether the eggs have an odor detectable to predators. Remaining with the eggs certainly is likely to reduce the feeding opportunities of the parents. This in turn may prevent the accumulation of energy required for production of a second clutch. In males, restriction to the nest site and guarding of young may reduce opportunities for further copulation.

The "benefit" of parental care presumably is to increase offspring fitness, either by increasing survivorship of embryos and hatchlings or by accelerating embryogenesis so that hatching occurs at a favorable time. The increase in offspring survivorship could result from parental protection against many potential sources of mortality (e.g., predation,

desiccation, flooding, and fungal attack). These factors are considered in more detail below.

2. BENEFITS OF PARENTAL CARE

Table V summarizes published hypotheses and available evidence on the functions (benefits) of reptilian parental care. Several of these presumed benefits may be valid, and indeed any single case of parental care may well have evolved for a variety of reasons. The common observations that females are particularly aggressive during the defense of nests (Table V) suggests that deterring predators is a major function of parental care. This phenomenon is particularly striking in cases in which the individual reptile, or the species to which it belongs, is generally nonaggressive (e.g., *Bungarus*, *Laticauda*, *Naja naja*, *Python regius*; Table V). However, many nest-attending females are not aggressive: females of several pythons and crocodylians, as well as those of *Ophisaurus apodus*, *O. ventralis*, *Naja melanoleuca*, and *Ophiophagus hannah*, have all been reported to be relatively quiescent (in some cases, almost comatose) while attending eggs (Barker, 1981; Cott, 1971; Langerwerf, 1981; Noble and Mason, 1933; Tryon, 1979; Oliver, 1956). Nonetheless, it cannot be claimed unambiguously that any of these changes in maternal behavior (e.g., increased or decreased levels of aggression) are adaptations to parental care. The behavior of the parents could alternatively be interpreted as a direct response to a changed thermal environment, endocrine modifications associated with oviposition, the physiological stress of oviposition, or some other factor. This does not mean that the behavior of the parent fails to protect the eggs, but merely that it may be a direct consequence of the physiology of the parent rather than an adaptation per se.

Although the studies cited in Table V show that females may actively defend their eggs against potential predators, the only work to compare predation rates on defended versus undefended clutches is that of Metzén (1977), who studied 110 nests of *Alligator* in the Okfenokee swamp. Most nests (96) were not defended by females, and almost all of these nests (92, or 96%) were destroyed by predators, especially bears. However, in 14 actively-defended nests, predation was rare (four nests destroyed, or 29%).

An alternative threat to eggs may come from their being dug up by other nesting females. This has been reported to occur in sea turtles (Carr, 1967) and presumably is the selective force favoring nest-site defense in iguanine lizards (Table V). Suitable nesting areas are rare in some habitats occupied by these lizards, so that disturbance of an earlier clutch by an ovipositing female is frequent. In these species, nests are defended only until the end of the egg-laying season. A similar situation

TABLE V
"Beneficial" of Parental Care: Hypotheses and Evidence

Benefit	Species	Evidence	Authority	
1. Deter potential egg predators	<i>Elysiya multicarinatus</i>	♀ Aggressive to humans	Langerwerf, 1981	
	<i>Eumeces egregius</i>	♀ Aggressive to potential predators	Mount, 1963	
	<i>E. fasciatus</i>	♀ Aggressive to potential predators	Noble and Mason, 1933	
	<i>E. laticeps</i>	♀ Aggressive to potential predators	Noble and Mason, 1933	
	<i>Tupinambis teguixin</i>	♀ Aggressive to humans	Kreig, 1925	
	<i>Brachylophus fasciatus</i>	♀ Aggressive to humans	Gibbons and Watkins, 1982	
	<i>Liasis albertisii</i>	♀ Aggressive to humans	Ross and Larman, 1977	
	<i>Morone spilotes</i>	♀ Aggressive to humans	Charles et al., 1983	
	<i>Python regius</i>	♀ Aggressive to humans	Van Mierop and Bessette, 1981	
	<i>Natrix natrix</i>	♀ Aggressive to humans	Gallwey, 1932	
2. Prevent disturbance to nest by other ovipositing females	<i>Bungarus caudatus</i>	♀ Aggressive to humans	Meil, 1929	
	<i>Laticauda colubrina</i>	♀ Aggressive to humans	Jennison, 1931; Campbell and Quinn, 1975	
	<i>Naja naja</i>	♀ Aggressive to humans	McLillemy, 1934; Dietz and Jackson, 1979	
	<i>Alligator mississippiensis</i>	♀ Aggressive to potential predators, humans	Jackson, 1979	
	<i>Crocodylus acutus</i>	♀ Presence reduces egg predation	Mezzen, 1977	
	<i>C. niloticus</i>	♀ Aggressive to potential predators	Dagan et al., 1981	
	<i>C. palustris</i>	♀ Aggressive to potential predators, humans	Morha, 1967; Cott, 1971	
	<i>C. porosus</i>	♀ Aggressive to potential predators, humans	Dharmakumarsinhji, 1947; Anon, 1982	
	<i>Gerrhonotus garinotus</i>	♀ Aggressive to humans	Cott, 1971; Biswas, 1977; Acharjyo and Mishra, 1981; Bustard and Choudhury, 1980; Bustard and Kar, 1981; Bustard and Maharana, 1982	
	3. Provide additional heat to speed embryonic development	<i>Alligator mississippiensis</i>	♀ Attacks conspecifics if they attempt to excavate nest	Bustard and Singh, 1981
<i>Gerrhonotus garinotus</i>		♀ Stops turtles digging into nest	References in Table II	
4. Regulate egg temperatures		<i>Alligator mississippiensis</i>	♀ Stops turtles digging into nest	Dietz and Jackson, 1979
		<i>Eumeces fasciatus</i>	♀ Produces heat by "shivering"	References in Tables II, V
		<i>Eumeces fasciatus</i>	♀ Basks, returns to eggs	Noble and Mason, 1933, but see Fitch, 1954
		<i>Python regius</i>	♀ Basks, returns to eggs	Van Mierop and Bessette, 1981
		<i>Morone spilotes</i>	♀ Basks, returns to eggs	Harlow and Grigg, 1984; Charles et al., 1985
		<i>Elaphis obsoleta</i>	Parents bask, return to eggs	McGee, 1919
		<i>Ophisaurus ventralis</i>	♀ Adjusts depth to which eggs are buried	Vinegar, 1968
		<i>Eumeces fasciatus</i>	♀ Adjusts depth to which eggs are buried	Fitch, 1954
	<i>Crocodylus porosus</i>	♀ Lies on nest on sunny day	Deraniyagala, 1959	
	<i>Eumeces fasciatus</i>	♀ Moves eggs from flooded burrows	Fitch, 1954	
5. Prevent eggs drowning	<i>Ophisotritus latirostris</i>	Nest site is vulnerable to flooding	Fitch, 1970	
	<i>Eumeces fasciatus</i>	♀ Urinates on nest	Fitch, 1954	
	<i>Crocodylus palustris</i>	♀ Urinates on nest	Whitaker and Whitaker, 1977b	
	<i>C. niloticus</i>	Guarded nest is damp	Pooley, 1976	
	<i>C. porosus</i>	Guarded nest is damp	Webb et al., 1977	
	<i>Eumeces fasciatus</i>	♀ Eats spoiled eggs	McCauley, 1945; Groves, 1982	
	<i>Gerrhonotus illocephalus</i>	♀ Eats eggs	Trinkle and Gibbons, 1977	
	<i>Ophisaurus attenuatus</i>	♀ Eats eggs	Fitch, 1970	
	<i>Pseudemys maloni</i>	♀ Opens nest at hatching time	Hodsdon and Pearson, 1943	
	<i>Varanus varus</i>	♀ In vicinity of nest at hatching time	Cogger, 1967	
6. Provide moisture for eggs	Probably all crocodylians	♀ Returns to nest	References in Table I	
	<i>Iguana iguana</i>	♀ Returns to nest daily, makes repairs	Alvarez del Toro, 1972	
	<i>Ophiophagus hannah</i>	♀ Recovers exposed eggs	Oliver, 1956	
	Many crocodylians	Adults respond to alarm call	References in Table II	
	<i>Eumeces fasciatus</i>	♀ Turns eggs; unattended eggs rot	Fitch, 1954	
	7. Eat or remove spoiled eggs; to deter fungal attack or discovery by predators	<i>Eumeces fasciatus</i>	♀ Eats spoiled eggs	References in Tables II, V
		<i>Gerrhonotus illocephalus</i>	♀ Eats eggs	Fitch, 1954
		<i>Ophisaurus attenuatus</i>	♀ Eats eggs	Vinegar, 1968
		<i>Crocodylus porosus</i>	♀ Lies on nest on sunny day	Fitch, 1954
		<i>Eumeces fasciatus</i>	♀ Moves eggs from flooded burrows	Fitch, 1954
<i>Ophisotritus latirostris</i>		Nest site is vulnerable to flooding	Fitch, 1970	
<i>Eumeces fasciatus</i>		♀ Urinates on nest	Fitch, 1954	
<i>Crocodylus palustris</i>		♀ Urinates on nest	Whitaker and Whitaker, 1977b	
<i>C. niloticus</i>		Guarded nest is damp	Pooley, 1976	
<i>C. porosus</i>		Guarded nest is damp	Webb et al., 1977	
8. Open nest to enable hatchlings to emerge	<i>Eumeces fasciatus</i>	♀ Eats spoiled eggs	McCauley, 1945; Groves, 1982	
	<i>Gerrhonotus illocephalus</i>	♀ Eats eggs	Trinkle and Gibbons, 1977	
	<i>Ophisaurus attenuatus</i>	♀ Eats eggs	Fitch, 1970	
	<i>Pseudemys maloni</i>	♀ Opens nest at hatching time	Hodsdon and Pearson, 1943	
	<i>Varanus varus</i>	♀ In vicinity of nest at hatching time	Cogger, 1967	
	Probably all crocodylians	♀ Returns to nest	References in Table I	
	<i>Iguana iguana</i>	♀ Returns to nest daily, makes repairs	Alvarez del Toro, 1972	
	<i>Ophiophagus hannah</i>	♀ Recovers exposed eggs	Oliver, 1956	
	Many crocodylians	Adults respond to alarm call	References in Table II	
	<i>Eumeces fasciatus</i>	♀ Turns eggs; unattended eggs rot	Fitch, 1954	
9. Keep eggs covered and hidden	<i>Eumeces fasciatus</i>	♀ Produces heat by "shivering"	References in Tables II, V	
	<i>Eumeces fasciatus</i>	♀ Basks, returns to eggs	Noble and Mason, 1933, but see Fitch, 1954	
	<i>Python regius</i>	♀ Basks, returns to eggs	Van Mierop and Bessette, 1981	
	<i>Morone spilotes</i>	♀ Basks, returns to eggs	Harlow and Grigg, 1984; Charles et al., 1985	
	<i>Elaphis obsoleta</i>	Parents bask, return to eggs	McGee, 1919	
	<i>Ophisaurus ventralis</i>	♀ Adjusts depth to which eggs are buried	Vinegar, 1968	
	<i>Eumeces fasciatus</i>	♀ Adjusts depth to which eggs are buried	Fitch, 1954	
	<i>Crocodylus porosus</i>	♀ Lies on nest on sunny day	Deraniyagala, 1959	
	<i>Eumeces fasciatus</i>	♀ Moves eggs from flooded burrows	Fitch, 1954	
	<i>Ophisotritus latirostris</i>	Nest site is vulnerable to flooding	Fitch, 1970	
10. Deter predators of hatchlings	<i>Eumeces fasciatus</i>	♀ Urinates on nest	Fitch, 1954	
	<i>Crocodylus palustris</i>	♀ Urinates on nest	Whitaker and Whitaker, 1977b	
	<i>C. niloticus</i>	Guarded nest is damp	Pooley, 1976	
	<i>C. porosus</i>	Guarded nest is damp	Webb et al., 1977	
	<i>Eumeces fasciatus</i>	♀ Eats spoiled eggs	McCauley, 1945; Groves, 1982	
	<i>Gerrhonotus illocephalus</i>	♀ Eats eggs	Trinkle and Gibbons, 1977	
	<i>Ophisaurus attenuatus</i>	♀ Eats eggs	Fitch, 1970	
	<i>Pseudemys maloni</i>	♀ Opens nest at hatching time	Hodsdon and Pearson, 1943	
	<i>Varanus varus</i>	♀ In vicinity of nest at hatching time	Cogger, 1967	
	Probably all crocodylians	♀ Returns to nest	References in Table I	
11. Turn eggs to prevent growth of mould	<i>Iguana iguana</i>	♀ Returns to nest daily, makes repairs	Alvarez del Toro, 1972	
	<i>Ophiophagus hannah</i>	♀ Recovers exposed eggs	Oliver, 1956	
	Many crocodylians	Adults respond to alarm call	References in Table II	
	<i>Eumeces fasciatus</i>	♀ Turns eggs; unattended eggs rot	Fitch, 1954	

occurs in *Alligator*. Turtles attempting to nest on their nest mounds may disturb their eggs and nest-attending female *Alligator* attack them under such circumstances (Dietz and Jackson, 1979).

The only other major function of reptilian parental care is likely to be its effect on the thermal environment of the eggs (Packard and Packard, this volume). Egg temperatures may be modified by (a) the parent adjusting the depth at which the eggs are laid beneath the soil surface (Fitch, 1954; Vinegar, 1968); (b) the parent basking and then returning to the eggs (Medsger, 1919; Noble and Mason, 1933, but see Fitch, 1954; also Harlow and Grigg, 1984, for *Morelia*); or (c) the parent producing heat metabolically to warm the eggs. The last of these alternatives is employed commonly by boid snakes; shivering thermogenesis has been reported in at least nine species (see above).

Apart from benefits accruing from defense against predators or disturbance, and from thermoregulation, other functions of parental care have only been hypothesized rather than demonstrated (Table V). Most seem intuitively reasonable, but are likely to be important only in a restricted number of cases. Other hypotheses seem invalid; for example, Coborn's (1975) explanations for "shivering" in brooding pythons are that this behavior (1) promotes circulation of air around the eggs, (2) increases maternal circulation, and (3) is a maternal reaction to the presence of eggs between the coils. Undoubtedly, the posthatching parental care of crocodylians protects offspring from predatory attacks (e.g., Hunt, 1974, 1975). The parent-offspring bond in crocodylians also may enable the parents to "teach" specific behavior patterns to their offspring, but no data are available to test this hypothesis.

3. COSTS OF PARENTAL CARE

By staying with the eggs after oviposition, the adult reptile may forego opportunities for feeding. This in turn may reduce energy intake to the point that production of a subsequent clutch of eggs is delayed. Alternatively, a lower growth rate may depress subsequent fecundity. In either case, the reproductive success of the animal is reduced. A more direct "cost" of parental care may be a decrement in survivorship, due to increased exposure to predators or other hazards. This might be likely if parental care occurs in a habitat different from that normally occupied by adults, or if predators can detect eggs more easily than they detect adults. The high metabolic expenditure of brooding pythons, which raise metabolic rate to warm the eggs, is another clear "cost" of parental care.

A reduced food intake, often a total cessation of feeding, has been documented in several egg-attending species both in the field and in captivity (Table VI). Observations of captive specimens indicate that

TABLE VI
"Costs" of Parental Care: Hypotheses and Evidence

Cost	Species	Evidence	Authority	
1. Reduction of food intake	<i>Eumeces egregius</i>	♀ Remains with eggs constantly	Mount, 1963	
	<i>E. fasciatus</i>	♀ Remains with eggs constantly	Fitch, 1954	
	<i>E. obsoletus</i>	♀ Remains with eggs constantly	Fitch, 1955	
	<i>E. obsoletus</i>	♀ Remains with eggs constantly	Hasegawa, 1984	
	<i>E. septentrionalis</i>	♀ Remains with eggs constantly	Breckenridge, 1943	
	<i>Ophisaurus attenuatus</i>	Empty stomachs in egg-attending ♀	Fitch, 1970	
	<i>Opheophagus hannah</i>	Empty stomachs in nest-attending ♀	Leakey, 1969	
	<i>Morelia spilotes</i>	Captive ♀ refuse food	Shine, 1980	
	<i>Python molurus</i>	Captive ♀ refuse food	Taylor, 1965; Van Mierop and Barnard, 1978	
	<i>P. reticulatus</i>	Captive ♀ refuse food	La Panouze and Pellier, 1973	
	<i>P. regius</i>	Captive ♀ refuse food	Boos, 1979; Ross, 1978; Van Mierop and Besette, 1981	
	<i>P. schwe</i>	Captive ♀ refuse food	FitzSimons, 1930	
	<i>Aspidites melanoccephalus</i>	Captive ♀ refuse food	Charles et al., 1985	
	<i>Liasis amethystinus</i>	Captive ♀ refuse food	Charles et al., 1985	
	<i>Crocodylus niloticus</i>	Empty stomachs in nest-attending ♀	Pitman, 1930; Pooley, 1977; Cott, 1971	
	2. Reduction of subsequent fecundity	<i>C. porosus</i>	Empty stomachs in nest-attending ♀	Deraniyagala, 1939; Choudhury and Bustard, 1979; Bustard and Maharana, 1982
		<i>Python reticulatus</i>	♀ Breeds less often than annually	Fitch, 1970
<i>Morelia spilotes</i>		♀ Breeds less often than annually	Harlow and Grigg, 1984	
<i>Eumeces obsoletus</i>		♀ Breeds less often than annually	Fitch, 1970	
<i>Alligator mississippiensis</i>		♀ Breeds less often than annually	Neill, 1971	

inattention during this period is due to a specific disinclination to feed rather than a lack of encounters with suitable prey. Apart from the cases cited in Table VI, many other reports of nest attendance refer to the constant presence of the female with the eggs. Presumably, food intake is reduced in most or all of these species. Egg-attending females often are reported as appearing emaciated by the time that parental care terminates (e.g., Mell, 1929). Interspecific differences may occur in fidelity to the nest; females of some species regularly leave the eggs and forage, whereas those of other species never do so (Mell, 1929). However, specific data on this point are lacking. Females remaining with eggs potentially could obtain considerable quantities of food by consuming potential egg-predators attracted to the nest (Tinkle and Gibbons, 1977). Again, data are lacking.

A reduced food intake probably is common, but not universal, in egg-attending females (e.g., Ross, 1978; Boos, 1979). The same situation occurs with other reproductive modes in reptiles; for example, food intake is reduced during gestation in many, but not all, viviparous species (Shine, 1980).

Without direct experimental manipulation (such as removal of clutches), longer-term costs of parental care are difficult to assess. The hypothesized delay in subsequent reproduction is supported by long intervals (greater than 1 year) among successive clutches in at least four egg-attending species of reptiles (Table VI). Indeed, a strong correlation has been demonstrated both for reptiles and amphibians, among low frequencies of reproduction and "accessory costs", such as parental care, viviparity, and long breeding migrations (Bull and Shine, 1979). Low reproductive frequencies are common in taxa that do have such "costs." However, this correlation may not reflect the fact that parental care confers a high cost per se, but rather that the cost is relatively independent of fecundity. For example, the reduction in food intake of a brooding female python probably is independent of the number of eggs she is brooding. Under these circumstances, calculations suggest that infrequent reproduction, in each case with the production of a large clutch, will be the optimal life-history strategy (Bull and Shine, 1979). A recent study of *Eumeces okadae* (Hasegawa, 1984) confirmed that postovipositional weight loss of egg-attending females was not correlated with their fecundity.

Although the egg-attending species with low frequencies of reproduction (Table VI) provide circumstantial evidence in support of "costs" of parental care, the opposite extreme also occurs; many egg-attending species, especially those from tropical areas, have been reported or suggested to produce more than a single clutch per year. These include *Gerrhonotus liocephalus*, *Elgaria multicarinatus*, *Tupinambis teguixin*, *Rhab-*

dophis subminiatus, *Xenochrophis piscator*, *Cemophora coccinea*, *Lycodon aulicus*, *Pituophis melanoleucus*, *Ptyas korros*, and *P. mucosus* (data and references in Fitch, 1970). However, these records may be based on females that have lost or abandoned their first clutch (Fitch, 1970).

4. CONCLUSION

Overall, the available data are consistent with hypothesized "benefits" and "costs" of parental care, but are generally circumstantial in nature. The only direct demonstration of the effectiveness of parental care in increasing egg survivorship comes from a study of *Alligator* (Metzen, 1977). Good quantitative estimates of costs of parental care are lacking. These inadequacies in the available data are regrettable, because studies to measure the relevant variables are entirely feasible. Experimental manipulations could provide measurements both of the benefits of parental care (what is the survivorship of attended and unattended eggs?) and its associated costs (what are the differences in food intake, growth rate, and in the time of subsequent reproduction, between those females that are attending eggs and females of which the clutches of eggs have been removed?). Sample manipulations might involve (a) removal of part or all of the clutch of an egg-attending female, and (b) removal of the female from the clutch. Studies on parental care in salamanders (e.g., Tilley, 1973; Huheey and Brandon, 1975; Forester, 1979a, b), frogs (e.g., Taigen et al., 1984), and insects (e.g., Tallamy and Denno, 1982) have progressed much further in this respect, than have those on reptiles.

B. Intermediate Stages in the Evolution of Parental Care

The vast majority of reptilian species do not show any form of parental care, but a small minority have been reported to remain with the eggs after oviposition (Tables I, II). In most cases, the parent is believed to remain with the clutch for the entire duration of incubation, and only to leave after the eggs have hatched. This situation raises the question of intermediate stages in the evolution of parental care. Presumably, a species without egg-attending behavior does not give rise by a single mutation to individuals that remain with eggs throughout development. Instead, the two more likely scenarios are as follows.

1. The female remains with the eggs for only a short time after oviposition and then leaves. This could occur if the female was "exhausted" by oviposition. Given the chance association between parent and eggs, selection could then favor "parental" behavior (e.g., defense against predators) and ultimately prolonged nest-attendance (Noble, 1931). The feasibility of short-term egg attendance as an intermediate stage towards prolonged parental care is supported by records of short-

term egg attendance in several squamate species (e.g., Gallwey, 1932; Fukada, 1959). Unfortunately, many cases of this phenomenon have been reported in captive animals, even in species known to attend eggs throughout incubation in the wild state (e.g., FitzSimons, 1930; Boos, 1979). This suggests that nest desertion in captivity may be an artifact arising from human disturbance. Variation in the duration of nest defense in iguanine lizards may reflect maternal condition; emaciated females defend nests only briefly, then leave to feed (Wiewandt, 1982).

2. The female leaves the eggs after oviposition, but returns to them regularly because they are located under a favored refuge. This intermittent proximity of parent and eggs provides the opportunity for selection to favor "parental" behavior, and perhaps leads eventually to more persistent nest attendance. We do not know how commonly this phenomenon occurs in nature, although Mell (1929) suggests that there is a continuum among species from intermittent to constant egg attenders.

Both pathways may well have been involved in the evolution of parental care, as is suggested by the apparent occurrence of both putative "intermediate stages" in modern reptiles. However, such strategies in modern reptiles may be secondary modifications of prolonged nest attendance, and not intermediates in the evolution of this trait.

C. Factors Increasing the Benefits of Parental Care

1. PREDICTION

If the primary benefit of parental care is an increase in egg survivorship, then parental care should evolve most readily in situations in which it has a large effect on survival of the eggs. This may occur in species or environments in which the attending parents are unusually successful at reducing mortality rates of eggs, either because of the abilities of the parents, or the high susceptibility of the unprotected eggs.

2. EXPOSED VERSUS HIDDEN NEST SITES

Eggs that are laid under superficial cover on the surface of the ground, rather than being deeply buried, may be particularly vulnerable to predation. Hence, parental care might evolve more readily in species that do not bury their eggs (Noble and Mason, 1933). This hypothesis has been used to explain the presence of parental care in *Tupinambis teguixin*, and its absence in the synonymous *T. nigropunctatus*, which oviposits inside termite mounds (Noble and Mason, 1933; but see Goeldi, 1902 and Riley et al., 1985, who report that *T. teguixin* oviposits

in termitaria). However, the argument can be generalized to predict that parental care should be more common in snakes, which typically do not bury their eggs (probably because of the lack of limbs with which to excavate a nest-hole) than in lizards, which typically dig nest-holes. For the same reason, parental care should be more common in limbless (nonburrowing) lizards than in species with fully-developed limbs.

Data presented earlier support the prediction that parental care is more common in snakes than in lizards (3% of oviparous species versus 1%) and has evolved more often in the former group (15 origins in 11 families versus 5 origins in 15 families). Limblessness has evolved many times among lizards, but is shown by only a small proportion of taxa (Gans, 1975). Hence, the parental care of the limbless *Ophisaurus* offers further, although weak, support for the hypothesis that limblessness favors the evolution of parental care.

3. ABILITY OF PARENTS TO DEFEND EGGS

If a major benefit of parental care is the repulsion of potential egg-predators, then parental care should evolve most often in species in which the parent is capable of deterring predators. This is most likely to be true of large and of venomous species. No such trend is evident among the lizards, except for *Tupinambis* and the tentative records for *Varanus*.

However, in snakes there is a strong bias for such parental care in large and venomous species. The only major taxon in which parental care is common (probably universal) is the Pythoninae, and this group contains the largest oviparous snakes of the world. Parental care also occurs in 4 of the 8 oviparous genera of the Viperidae (50%) and 7 of the 17 oviparous genera of the Elapidae (41%). In contrast, the much larger (>200 genera) Colubridae, which consists primarily of nonvenomous (or less venomous) species, shows parental care less commonly (15 genera, or 7.5%). Several of the colubrids reported to show parental care are unusually large (e.g., *Elaphe*, *Farancia*, *Ptyas*), or belong to the minority of venomous forms within the family (e.g., *Psammodromus*, *Rhabdophis*). The prevalence of parental care in crocodylians—most of which are large and formidable—also is consistent with the prediction that this behavior should be shown most frequently by groups in which parents are well able to defend their eggs. Interestingly, many taxa of marine invertebrates show the opposite trend; parental care is most common in the smaller species of marine invertebrates (Strathmann and Strathmann, 1982). Nonetheless, extended parental care may also be common in highly venomous forms (e.g., *Haplochaena*, *Chironex*; Sutherland, 1983).

4. LIMITED AVAILABILITY OF NEST SITES

If nest sites are scarce relative to the number of nesting females, older nests may be excavated and destroyed by new arrivals. This situation has been described in sea turtles (e.g., Carr, 1967) and island populations of iguanine lizards (Rand and Rand, 1976; Wiewandt, 1982). Active defense of nest sites by postovipositional females is common in iguanines (references in Table II). Intraspecific variations in intensity of iguanine nest defense are correlated with the degree to which suitable nest sites are available, and the ease of digging burrows (Wiewandt, 1982). The selective advantage of parental care in this situation is increased by the relatively synchronous nesting of the population; thus even brief nest defense is effective.

Although these arguments are consistent with the behavior seen in iguanines, they are unlikely to be of general importance because scarcity of suitable nesting sites may be a rare phenomenon. The only parallels to iguanine nest defense may be in alligators, in which the nest-guarding female prevents ovipositing turtles from digging into the nest mound (Dietz and Jackson, 1979), and tuataras, in which resting females defend nesting sites against other females (M. Thompson, pers. comm.).

D. Factors Reducing the Costs of Parental Care

1. PREDICTION

If the major "costs" of parental care are a reduction in food intake, probable survivorship, or subsequent fecundity of the reproducing female, then parental care would be expected to evolve most often in species and environments in which such costs were minor or insignificant.

2. SELECTION FOR "RISKY" LIFE-HISTORY STRATEGIES

Life-history theory predicts that small, short-lived species are more likely to pursue "risky" reproductive strategies than are large, long-lived ones (Williams, 1966). Although parental care was suggested to be "risky," a test on fishes revealed no clear trend for more parental care in smaller species, possibly because the smaller species were not capable of deterring egg-predators (Williams, 1966). Similarly, a compilation of data on 49 species of lizards showed a trend reverse to that predicted; parental care was more common in late-maturing species (5 of 14, or 36%) than in those that matured early (2 of 35, or 6%) (Tinkle, 1969). This contradiction has been explained by suggesting that parental care is not as "risky" as it appears; "lizards that practice it usually remain with their

eggs in a well-hidden site in which they may be less exposed to dangers than a female that does not tend her eggs" (Tinkle, 1969:505). Indeed, following a general discussion of the evolution of lizard life histories, Tinkle (1969) predicted that parental care will generally be found in long-lived iteroparous species, especially those with a short, annual breeding season.

To the degree that large body size is correlated with late attainment of maturity (Williams, 1966; Dunham, Miles, and Reznick, this volume), the trend for parental care in large reptiles (see previous section) is consistent with Tinkle's (1969) prediction. However, it is consistent also with the hypothesis that parental care by small species is ineffective against predators, or the alternative hypothesis that in small species, parents themselves are too vulnerable to predation to permit the evolution of parental care. Certainly, the data on reptiles (Table II) are inconsistent with the prediction that parental care will be most common in small, short-lived species (Williams, 1966).

3. FREQUENCY OF REPRODUCTION

Egg-attending reduces food intake of the reproducing female (Table VI), and thus may delay the time at which a subsequent clutch can be produced. Hence, parental care is likely to evolve in species that produce only a single clutch of eggs per year. The costs of remaining with the eggs may be independent of the number of eggs guarded, whereas the benefits increase with the number of eggs. Hence, parental care might be more likely to evolve in species that produce large but infrequent clutches rather than in those that produce small and frequent clutches. Both hypotheses predict that parental care should be most common in species that produce clutches only once a year or less often. Data on lizards support the prediction (Tinkle, 1969), although there are some puzzling cases of multiple-clutching, egg-attending species (see previous section on "costs"). The correlation between parental care and extremely low frequencies of reproduction (Bull and Shine, 1979) also is consistent with this prediction, but is open to the other interpretations discussed earlier.

Because the annual production of multiple clutches is common only in the tropics (Dunham, Miles, and Reznick, this volume), parental care should typify temperate rather than tropical species (Tinkle, 1969). The available data are biased by the concentration of scientific study in the temperate zone, but even so, the prediction is refuted; parental care is widespread in tropical reptiles (Tables I, II). The reptilian subfamilies in which parental care is most common (Iguaninae, Pythoninae, Al-

ligatorinae, Crocodylinae) are all primarily tropical groups. Overall, the predicted bias toward temperate-zone species is conspicuously lacking.

4. SUITABILITY OF HABITAT FOR CLUTCH ATTENDANCE

Parental care might be unlikely to evolve whenever eggs are laid in a habitat different from that usually occupied by the adult. In such a situation, the parent may be unusually susceptible to predation or physiological stress. This hypothesis suggests that parental care should be rare in aquatic or arboreal species. It is an obvious explanation for the lack of testudinian parental care, but is unconvincing because (a) many turtles are terrestrial; and (b) many other aquatic reptiles show parental care (e.g., crocodylians, laticaudid sea snakes).

5. HARSH AND UNPREDICTABLE ENVIRONMENT

Prolonged attendance on the clutch might be most likely to be favored in environments in which resources for the adult, at about the time of egg deposition, become increasingly scarce or unpredictable so that searching for such resources becomes a high-risk endeavor (Tinkle and Gibbons, 1977). Under these circumstances, parental care might strongly benefit egg survivorship while conferring only a minor cost on the opportunities of the adult for future reproduction. This hypothesis predicts that parental care will most often be found in environments in which resources for adults are limited at the time of egg deposition (Tinkle and Gibbons, 1977). The prediction is difficult to test, but seems inconsistent with the strong taxonomic bias in the distribution of reptilian parental care. If specific environmental variables are important, one might expect to see parental care restricted to particular habitat types rather than to all species within a given taxon (e.g., *Eumeces*). However, available data are insufficient to convincingly refute the prediction.

6. BRIEF INCUBATION PERIODS

Parental care might be associated with brief incubation periods for three reasons:

(1) The "costs" of remaining with the eggs depend upon the incubation period: if the eggs hatch soon after oviposition, the female is burdened only briefly by egg attendance.

(2) Natural selection may favor prolonged oviducal retention of eggs in species with parental care, because the costs of this retention may be no higher than the costs of parental care (Shine and Bull, 1979). In

contrast, species without parental care are less likely to evolve egg retention; in this case, the physical burdening of the gravid female imposes too high a cost on survivorship and subsequent fecundity.

(3) Parental care and prolonged uterine retention of eggs are both examples of increased maternal investment, and may be favored by the same selective forces. Hence, they are likely to occur in the same species and the same environments.

A recent review of incubation periods showed "at least an indication that egg-guarding species may have slightly shorter development times than those that do not guard eggs" (Tinkle and Gibbons, 1977:27). More detailed analysis of the data from Tinkle and Gibbons (1977:Table 13) confirms that the mean incubation period of egg-attending species (57.5 days; $n = 39$; $s.d. = 23.2$) is lower than that of nonattending species (74.4 days; $n = 124$, $s.d. = 44.0$), but the variances are so high that the difference fails to reach statistical significance (median test, 1 d.f., $\chi^2 = 0.6$, n.s.). One confounding variable in this test, however, is the trend for parental care in larger species (see earlier); large species tend to have larger eggs, which in turn have longer incubation periods.

An alternative test involves the examination of the embryonic stage of development at oviposition in egg-attending and non-egg-attending species. "Visible embryonic development at oviposition" has been reported more commonly in species with parental care (Shine and Bull, 1979). However, a more recent study, which used objective criteria to stage embryonic development, found that relatively prolonged retention of eggs is the rule rather than the exception in oviparous squamates (Shine, 1983a). No evidence exists to show that uterine retention is more prolonged among egg-attending species (Shine, 1983a).

A recent analysis of parental care in salamanders (Nussbaum, 1985) argues that parental care should evolve in species with long incubation periods; that is, it predicts the reverse of the above-discussed prediction. Nussbaum notes that salamanders with parental care tend to have large eggs, and that such eggs take a long time to develop. From these data, he argues that parental care has evolved to reduce the otherwise high rate of mortality of these slowly-developing embryos. An alternative interpretation of the same data is that natural selection has favored an increase in egg size in species with parental care, because the offspring may thereby be kept for longer in a low-risk situation (protected eggs) rather than as unprotected free-living juveniles (Shine, 1978; the "safe harbor" hypothesis). The association of parental care with large offspring is less clear in reptiles than in many other animal taxa, possibly because of the concentration of most reptilian embryonic mortality to a short postovipositional period (Shine, 1978).

E. Which Sex Should Show Parental Care?

One consistent feature of reptilian parental care (Section II.D) is that involvement by the male is nonexistent (squamates) or relatively minor (crocodilians). In contrast, male parental care is common in amphibians, fishes, and birds (Ridley, 1978). The evolutionary basis for sex differences in the tendency to show parental care has been the subject of several recent discussions (e.g., Trivers, 1972; Ridley, 1978; Perrone and Zaret, 1979; Blumer, 1979; Gross and Shine, 1981; Nussbaum, 1985). Two hypotheses for the selection of parental care have received wide attention:

1. Selection against male parental care, because internal fertilization results in a delay between insemination and oviposition, making the paternity of any given clutch uncertain (unlike the situation in most external fertilization). This low reliability of paternity may select against male parental care in species with internal fertilization (Trivers, 1972), including reptiles (Tinkle and Gibbons, 1977; Perrone and Zaret, 1979).

2. The unlikelihood of selection for male parental care in species with internal fertilization, because the time delay between insemination and oviposition means that a male and his offspring may never be in close proximity (Williams, 1966; Gross and Shine, 1981).

Both of these hypotheses correctly predict that reptilian parental care should be performed by females rather than males. Although the reptilian data therefore do not permit a test between the two hypotheses, the latter (parent-offspring proximity) model seems more accurately to predict the distribution of parental care in teleosts and amphibians (Gross and Shine, 1981). The paternity hypothesis also has been criticized on the grounds of faulty logic (Werren et al., 1980).

An alternative approach is to consider the effects of reproductive activities on the parents. If the female is "exhausted" by oviposition, she may be likely to stay with the eggs until she recovers, protoadapting the species for female parental care (Noble, 1931). However, exactly the opposite prediction is made by Maynard Smith (1977); because the female is exhausted, she has a greater need than the male to recommence feeding as soon as possible. Thus, Maynard Smith predicts that this situation should favor the evolution of male parental care. The reptilian pattern is consistent with the prediction of Noble rather than with that of Maynard Smith, but does not provide strong support for the former hypothesis, because the predominance of maternal care is consistent with several alternative theories.

A related question is why biparental care is virtually unknown in squamates, and probably rare even in crocodylians (Tables I, II). This result is consistent with a general trend for biparental care to be less common in ectotherms than in endothermic vertebrates (Case, 1978; Gross and Shine, 1981). Biparental care may be most likely to evolve when the form of care is such that two parents are much more effective than one; for example, feeding or guarding mobile young, rather than merely guarding eggs (Maynard Smith, 1977; Perrone and Zaret, 1979). This hypothesis predicts that biparental care in reptiles should be restricted to crocodylians (the only group to guard offspring after hatching), and that the contribution of the male should commence only after the eggs hatch. This prediction is strongly supported by data in Table I.

F. Why Is Parental Care Rare in Reptiles?

An analysis of parental care at the familial level reveals major differences among reptiles, teleost fishes, and amphibians in the frequency and form of parental care they exhibit (Table VII). The proportion of families containing care-giving species is highest among amphibians, in terms of parental care by either sex, or overall. Reptiles differ strongly from the other two groups in their low frequency of male parental care (Table VII). This probably reflects the lack of externally-fertilizing reptilian species (see earlier discussion). Although the overall proportion of families showing parental care is similar in fishes and reptiles, this direct comparison is misleading. Most fish species produce pelagic eggs, so that parental care is impossible. The proportion of species showing parental care would be much higher in demersal-spawning teleosts than in reptiles. This difference may be attributable to (a) the high incidence of external fertilization in teleosts, protoadapting for male parental care (Gross and Shine, 1981), and (b) the brief incubation period of teleost eggs, requiring only a short duration of parental care.

Although parental care is proportionally less common among reptiles than among other ectothermic vertebrates, an alternative form of increased parental investment—viviparity—is strikingly more common in reptiles (Table VII). This may reflect two reptilian features: internal fertilization and behavioral thermoregulation. The former protoadapts the species to viviparity (Gross and Shine, 1981), whereas the latter enables rates of embryonic development to be accelerated greatly by uterine retention of eggs (Shine, 1983b). Because parental care of eggs may serve as a protoadaptation to viviparity, the incidence of reptilian parental care may be lowered by a trend for viviparity to evolve in care-giving species (Shine and Bull, 1979; Shine, 1985).

TABLE VII
The Distribution of Parental Care and Viviparity Among Families of Teleost Fishes, Amphibians, and Reptiles

	Teleosts	Amphibians	Reptiles
Number of families for which data available	182	35	43
Number with male parental care (and proportion with male parental care)	63 (.35)	16 (.46)	1 (.02)
Number with female parental care (and proportion)	28 (.15)	17 (.49)	13 (.30)
Number with parental care by either parent (and proportion)	68 (.37)	23 (.66)	13 (.43)
Number with viviparity (and proportion)	11 (.06)	6 (.17)	18 (.42)
Number with parental care and/or viviparity (and proportion)	77 (.42)	25 (.71)	24 (.56)

Data for teleosts and amphibians from Gross and Shine (1981), and references therein.

IV. SUMMARY

1. Parental care in reptiles occurs in at least four different forms: egg-attending (female remains with clutch), egg-guarding (female defends clutch against potential predators), egg-brooding (female keeps clutch temperature above ambient), and the complex parental behavior of crocodylians (including guarding of eggs and young, nest opening, and mouth transport of eggs and young). Parental care in squamates is typically directed towards the eggs rather than the young.

2. Parental care has been reported in over 100 species of reptiles, but many records are inadequate. Parental care is rare or lacking in testudinians, probably universal in crocodylians, and has been reported in approximately 2% of oviparous squamate species.

3. Both the frequency and the form of parental care show a strong taxonomic bias, which may be detected at the level of order, suborder, family, and genus. Despite the overall scarcity of care-giving species

among reptiles, this behavior is abundant (universal?) among a few taxonomic groups (Crocodylia, Iguaninae, Pythoninae, Crotalinae, and the scincine genus *Eumeces*).

4. The strong taxonomic bias in parental care suggests that it has evolved only rarely (once within each such group). A phylogenetic analysis suggests that the number of independent evolutionary origins of reptilian parental care among extant species may be as low as 21 (5 in lizards, 15 in snakes, 1 in crocodylians).

5. All well-documented cases of squamate parental care involve only the female parent. Among crocodylians, nest-guarding is undertaken by the female, but the male may contribute also to subsequent protection of the young. These biases to female parental care of eggs, and biparental care of young, are consistent with patterns observed in teleost fishes and amphibians.

6. Parental care imposes both "benefits" (to egg survivorship) and "costs" (to parental survivorship and subsequent reproduction). Major "benefits" of parental care probably come from deterring either potential egg-predators or conspecific females that otherwise would disturb the nest. In pythons, maternal care also helps to keep the eggs at high and constant temperature throughout incubation. The main "cost" of parental care probably is a reduction in food intake of the reproducing female.

7. This paper attempts to test several hypotheses on the evolution of reptilian parental care. The available data are consistent with predictions that parental care is likely to be shown by: (a) Species utilizing exposed rather than hidden nest sites (i.e., snakes rather than lizards); (b) species in which adults are large (e.g., crocodylians, pythons) and/or venomous (e.g., vipers), and hence able to deter potential predators; (c) species that compete intraspecifically for limited nest sites (iguana lizards); (d) females rather than males because of the low probability that a male will be in close proximity with his offspring; and (e) both parents in species that guard mobile young (crocodylians), because two parents are more effective deterrents than one.

8. The proportion of species with parental care is lower among reptiles than among amphibians or freshwater teleost fishes. This difference reflects the absence of male parental care in squamates, which in turn may be due to internal fertilization. However, the high incidence of viviparity in this group means that increased parental investment (of which parental care is a special case) is a common phenomenon in the Reptilia.

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