RESORPTION OF OVIDUCTAL EGGS AND EMBRYOS IN SQUAMATE REPTILES

DANIEL G. BLACKBURN

Department of Biology, Life Sciences Center, Trinity College, Hartford, CT 06106, USA

Among squamate reptiles, gravid females are frequently said to be able to resorb infertile and malformed eggs from their oviducts. This pattern, if it existed, would allow females to recycle nutrients from abortive attempts at reproduction, and to increase lifetime reproductive potential by modulating reproductive effort according to environmental circumstances. However, a review of the literature reveals that evidence for oviductal egg resorption is weak, and does not preclude other fates for abortive eggs (egg retention or expulsion). Furthermore, for the oviduct to resorb eggs would require that it have the functional properties of the digestive tract, properties that may be incompatible with its several reproductive functions. Future work should not assume oviductal egg resorption in squamates without definitive evidence that the eggs are not simply aborted or retained by females following absorption of water.

INTRODUCTION

In literature dating back to the late 1800s, female lizards and snakes have been said to be able to resorb eggs and embryos from their oviducts under conditions of physiological stress and infertility. Theoretically, such resorption could be an ideal way for a female to minimize loss of nutrients during failed attempts at reproduction, and to control reproduction in such a way as to maximize lifetime reproductive potential. However, as discussed below, evidence for resorption is weak, and several reasons exist to question whether specific squamates actually resorb oviductal eggs, as opposed to aborting them. The purpose of this review is to explore the question of whether squamates can resorb their eggs and embryos, and to encourage individuals with experience in herpetoculture to share evidence bearing on egg resorption in particular species. This issue is of functional, theoretical, and evolutionary significance, and has practical implications for the maintenance and breeding of squamates in captivity.

THEORETICAL ADVANTAGES OF EGG RESORPTION

An ability to resorb eggs and embryos could offer important benefits to female squamates. In typical oviparous squamates, the developing eggs spend about 20-40% of the total developmental period in the oviducts, prior to being laid (Shine, 1983; Blackburn, 1995). Therefore, an opportunity for resorption could exist in egg-layers, as well as in viviparous forms, which retain their eggs to term. By resorbing infertile and malformed eggs, a female could recycle the nutrients that she has invested in her eggs, and thereby enhance her own future survival and reproduction. In oviparous squamates, most or all of the nutrients invested into eggs are in the form of the ovulated yolk, and a similar situation exists in most live-bearing species. In viviparous lizards and snakes, small amounts of organic and inorganic ions are provided to the embryos by the oviduct after ovulation (Panigel, 1956; Hoffman,

1970a; Thompson, 1977, 1982; Stewart, 1989; Stewart et al., 1990). However, as shown by these and other studies (Thompson, 1981; Stewart & Castillo, 1984), the yolk typically provides most of the nutrients for development. Therefore, given that most of female nutrient investment into the prospective neonate occurs at the time of ovulation in both oviparous and viviparous forms, a female that could resorb the yolk or the developing embryo could achieve considerable savings of energy and nutrients.

A second potential advantage of egg resorption is that it would allow females to minimize the physical burden imposed by inviable eggs. Gravidity tends to handicap locomotory ability in female squamates (e.g., Vitt & Congdon, 1978; Shine, 1980; Seigel et al., 1987; Cooper et al., 1990; Sinervo et al., 1991; also see Schwarzkopf, 1993). Moreover, in some snake species, females do not feed during pregnancy (Shine, 1980), probably because gravidity inhibits passage of food down the posterior gastrointestinal tract. Therefore, by carrying a clutch of inviable eggs, a female would be decreasing her ability to feed, thermoregulate, and escape from predators, with no compensatory advantages.

Thirdly, inviable eggs block the oviducts and would prevent future attempts at reproduction if not removed. The squamate uterus is a thin tube that, in repose, is much smaller in diameter than a single egg. An egg lodged in the uterus could block eggs from subsequent ovulations from being transported through the oviducts, and might well prevent sperm from ascending the tract to the site of fertilization. Resorption of inviable eggs would be an ideal way for females to free up the oviducts for subsequent reproductive attempts.

A fourth potential benefit of egg resorption comes from consideration of life history theory (Stearns, 1992). If a female could resorb eggs under conditions of physiological stress, she could modulate reproduction after ovulation, according to changing environmental circumstances. If conditions were unsuitable (or simply less than ideal) for reproduction, a

female could resorb her reproductive investment and wait until conditions improved to reproduce. Unsuitable conditions could be reflected in unseasonal climatic change, depletion of maternal fat reserves, or food scarcity. A viviparous female that could not resorb or otherwise get rid of her eggs would be "locked in" to pregnancy, carrying the embryos until they were finally born, even at the expense of her own survival. This consideration may be less significant for typical oviparous squamates; given the smaller proportion of the developmental period that eggs reside in the oviducts, the opportunity for females to modulate reproductive investment after ovulation would necessarily be less than in viviparous forms. In the latter, gestation length ranges from several weeks to about a year, depending on the species (Tinkle & Gibbons, 1977; Blackburn & Vitt, 1992); therefore, environmental conditions could change markedly between the period of ovulation and parturition. Consequently, from this standpoint, we would expect the capability of egg and embryo resorption to be particularly advantageous to viviparous species.

DO FEMALE SQUAMATES RESORB OVIDUCTAL EGGS?

An ability to resorb eggs while they are still in the oviducts clearly could have important advantages for female squamates. The question remains, however, as to whether females are able to accomplish such resorption. Uterine resorption of embryos is well known to occur among eutherian mammals, notably certain rodents (Brambell, 1948; MacFarlane et al., 1957; Low, 1978; Gosling, 1986; Westlin et al., 1995). However, evidence for egg resorption among squamates is less clear.

Uterine egg resorption has been inferred for particular species of both lizards and snakes (e.g., Mingazzini, 1892; Domini, 1928; Jacobi, 1936; Clausen, 1940; Kasturirangan, 1951; Parameswaran, 1962; Bustard, 1966; Hoffman, 1970b; Yaron, 1972), based on three separate lines of evidence. First, such inferences sometimes are based on observations of oviductal eggs that have stopped developing, or that show no evidence of fertilization. Indeed, abortive or infertile eggs have been reported in the oviducts of numerous squamate species (Giacomini, 1891; Giersberg, 1923; Blanchard, 1925; ten Cate-Hoedemaker, 1933; Jacobi, 1936; Parker, 1940; Neill & Boyles, 1957; Parameswaran, 1962; Badir, 1967, 1968; Hoffman, 1970b; Shine, 1977; Powell and Russell, 1991; Gregory et al., 1992; Farrell et al., 1995).

Such observations do not offer *prima facie* evidence of egg resorption, in absence of signs that the oviduct takes up egg components. Non-developing eggs could simply be retained in the oviducts, with or without subsequent expulsion. In the viviparous garter snake, *Thamnophis sirtalis*, for example, Hoffman (1970b) found that upon emergence in the spring, the snakes

contained oviductal embryos and adnexae that had been retained from the preceding summer. This also occurs in oviparous species. For example, a female *Diadophis* was reported to retain a fertilized, dead egg for some months (Blanchard, 1925), and a female *Elaphe climacophora* reportedly retained an oviductal egg for more than 16 months (Watanabe et al., 1989). Thus, inviable eggs may be retained in the oviducts, rather than being actively resorbed, even though such retention may have detrimental affects on subsequent reproduction.

Alternatively, malformed or infertile eggs could eventually be expelled by the oviducts and extruded via the cloaca. Squamates are routinely reported to deposit infertile and abnormal eggs, including both oviparous species (e.g., Rollinat, 1904; Neill & Boyles, 1957; Fitch, 1970; Campbell & Quinn, 1975; Dyrkacz, 1977; Murphy et al., 1978) and viviparous species (Jacobi, 1936; Branch, 1973; Branson & Baker, 1974; Mitchell, 1976; Ji, 1995; Ronne, 1996). For example, a captive *Elaphe longissima* female was observed to deposit inviable, deformed eggs of subnormal size; the eggs were not laid as a clutch, but extruded at the rate of one or two a day as the snake crawled around the cage (Lotzke, 1975). In an analysis of 162 *Thamnophis sirtalis* that had been captured and then maintained in captivity, Gregory et al. (1992) found that about a quarter of the deposited litters included fully-developed but dead young; another quarter contained one or more undeveloped eggs or young. Interestingly, snout vent length of the live and dead neonates did not differ statistically. Data reported by Ji (1995) on the viviparous *E. rufodorsata* indicate that infertile eggs extruded at the end of gestation do not differ from oviductal eggs collected months earlier, in terms of lipid content or caloric value. One would expect a decline in both parameters if organic components were being resorbed.

As anyone with experience with captive breeding of viviparous squamates knows, extrusion of inviable eggs occurs with great frequency; to breeders they are known as "slugs". In my laboratory, we have frequently observed extruded yolky material in the sandy substrate in my breeding colony of *Chalcides ocellatus*, and recently found small amounts of extruded yolk, surrounded by shell membrane, from captive *Thamnophis* whose oviducts were found shortly thereafter to contain unfertilized eggs. Similarly, we have seen captive *Elaphe gutatta* extrude a small amount of unshelled yolk material prior to oviposition of a normal clutch. Extruded yolk material is easy to overlook, and can dry quickly under a heat lamp or in a sandy substrate. The incidence of infertile eggs, in captive squamates at least, can be high in both oviparous and viviparous species (McEachern, 1991; Ronne, 1996). One must question why infertile eggs are deposited if resorption can occur in the species in question.

A second line of evidence that has been invoked as evidence of egg resorption comes from observations of

oviducts containing eggs that are shrunken and mis-shapen (e.g., Kasturirangan, 1951). Jacobi (1936, p. 415) published a photograph of the oviducts of the pregnant viviparous slow-worm *Anguis fragilis* in which a single "Abortivei" was considerably smaller than the adjacent normal eggs. Similarly, Domini (1928) illustrated oviducts of the viviparous skink *Chalcides chalcides*, in which eggs were sufficiently misshapen and shrivelled as to suggest loss of egg material. Blanchard (1925) described a female *Diadophis punctatus* with a retained oviductal egg that appeared somewhat shrunken and hardened in the centre. In his comprehensive work on the viviparous garter snake *Thamnophis sirtalis*, Hoffman (1970*b*) found that half of the pregnant females contained at least one abnormal or developmentally-arrested embryo. The abnormal young were described as being partly mineralized or in a semi-liquified state "apparently indicative of active resorption".

Such observations are suggestive of egg dehydration and necrosis, and perhaps uptake of water by the surrounding uterine tissues. However, observations of dehydrated, abortive uterine eggs do not indicate that the organic components of the eggs and embryos are digested and absorbed by the oviducts, rather than being expelled after water extraction. In fact, in observations of pregnant female *C. chalcides* that contained both normal and degenerating eggs, Domini (1928) found that the decomposing eggs may not disappear from the oviducts until parturition. Likewise, Ronne (1996) described expulsion of dehydrated yolks during parturition of normal young in captive boas.

Definitive evidence of uterine resorption could be provided by histological examination of abortive uterine egg sites. From microscopic study, Mingazzini (1892) inferred that tissues of the oviduct might resorb such eggs in the Mediterranean skink *Chalcides chalcides*, but offered no supportive evidence. Subsequent researchers inferred that captive females of this species resorb their embryos when food is not available (Domini, 1928; Jacobi, 1936), based on observations of oviductal eggs in arrested stages of development. This species is of particular interest from a reproductive standpoint, because it is so highly placentotrophic; females ovulate small (3 mm) eggs and during the three month gestation, provide most of the nutrients for development by placental membranes whose complexity rivals that of therian mammals (Blackburn, 1993*a*; Blackburn & Callard, 1997). Domini (1928) examined purported uterine resorption sites in two female *C. chalcides*, and described degenerative necrosis of the embryos in some detail. However, his study fell short of offering specific evidence that products of embryo degeneration are taken up by the uterus. In a recent study in my laboratory, we examined a number of abortive egg sites in this species, and found no evidence that egg components are either digested or absorbed by the uterus (Blackburn *et al.*, 1998). The pregnant females

had been obtained through a trans-oceanic shipment, and upon arrival, laparotomy revealed malformed and possibly degenerating oviductal eggs. Our histological examination revealed that the eggs were undergoing dehydration and dissolution, and were in the process of being extruded down the oviducts following absorption of water; in some cases such extrusion was occurring while the embryos were still developing.

Jacobi (1936) examined four abortive egg sites in *Anguis fragilis* histologically. In one of these four sites, he found what he considered to be possible evidence of uterine egg resorption, in the form of a few tiny granules in the connective tissue below the uterine epithelium. While recognizing that the granules were much smaller than yolk droplets of the vitellus, Jacobi (1936) tentatively suggested that they might represent products of yolk digestion. However, the granules were not observed in other "resorbing" females, and Jacobi's (1936) diagram does not rule out the likelihood that they simply represent mast cell granules. Mast cells are common in reproductive tissues of squamates, including the oviduct (Jones *et al.*, 1975; Uribe *et al.*, 1988), and I have observed them in both intact and degranulated condition in abortive egg sites of *Chalcides chalcides*.

In sum, the studies cited above have not demonstrated that female squamates can or do resorb eggs from their oviducts. These studies do not of course preclude the possibility that such absorption occurs, but as discussed below, one can use them to derive criteria for recognition of such resorption.

EVOLUTIONARY CONSIDERATIONS

Given the paucity of evidence that egg and embryo resorption occur among squamates, are we correct in presuming that such a pattern would be advantageous? Probably - after all, selective pressures represent only one factor that affects evolutionary change. Natural selection requires both sufficient time in which to operate and appropriate heritable variation to be present, and the latter may be affected by constraints imposed by disparate functions. For the uterus to undertake egg resorption would require that it be able to accomplish large-scale extracellular digestion of macromolecules, epithelial absorption of the products of such digestion, intracellular breakdown, and finally, export of the products of digestion to the connective tissue where it could be taken up by macrophages or transported away by the circulatory system. Large-scale digestion, secretion and absorption requires enlarged (i.e. columnar) epithelial cells for housing the organelles accomplishing these functions; however, the uterus is adapted in part for physiological exchange with the developing egg, which requires a thinned epithelium. Incompatibility of these functions could constrain a role in digestion, even given sufficient time and strong selective pressures.

As for the temporal parameter, it is useful to keep in mind that egg resorption would probably be most advantageous to viviparous forms. Viviparity in squamates tends to be a relatively recent phenomenon; of the more than 100 origins of viviparity that have been identified among squamates (Blackburn, 1992; Shine, 1985), most have occurred at sub-generic levels, and many appear to be Pliocene or Pleistocene events (Blackburn, 1995). We can only speculate whether this period of time has been sufficient for selection to have conferred upon the uterus the functional attributes of an intestine.

Furthermore, oviductal egg resorption is not the only way for females to recycle nutrients from inviable eggs. Various species of viviparous snakes reportedly eat infertile eggs and dead babies (Ronne, 1996). Captive female *Lepidodactylus lugubris* (Gekkonidae) kept on a poor diet produce deformed eggs with thin shells, which they usually eat upon oviposition (Seufer, 1985). Similarly, female *Phelsuma* kept on a diet deficient in calcium eat their oviposited eggs (Osadnik, 1984). If this pattern is widespread among squamates, recycling of nutrients may offer less of an advantage to oviductal resorption than would otherwise be the case.

Embryo resorption has been widely documented among eutherian mammals (Brambell, 1948; Low, 1978); have these animals not been subjected to the same functional and temporal constraints as squamates? In fact not, because mammalian viviparity dates to the Mesozoic (Lillegraven, 1979; Blackburn, 1993*b*), and the structure of the eutherian uterus is fundamentally different from that of squamate reptiles. The uterine lining in eutherians forms a thick, glandular endometrium, and the implanting blastocyst penetrates the epithelium in most species, often taking up a position deep in the connective tissue (Luckett, 1977; Mossman, 1987). There, under conditions of resorption, embryonic tissues are susceptible to attack by macrophages and cells of the immune system. In contrast, the squamate uterus during pregnancy is a very thin-walled tube with but a thin layer of connective tissue, and no true implantation occurs. Further, no definitive evidence exists that the uterine epithelium is eroded during pregnancy in any squamate species (Blackburn, 1993*c*); thus embryonic tissues are not directly exposed to phagocytic cells of the uterine connective tissue.

The paucity of evidence for oviductal resorption of eggs in squamates does not preclude resorption of eggs that have lodged in the peritoneal cavity. Ectopic embryos have been observed in several squamates (Matthews, 1955, 1965), including, for example, members of the snake genera *Vipera* (Bellairs, 1949), *Coluber* (Minton 1949), *Nerodia* (Neill, 1948) and *Thamnophis* (Neill, 1948; Hoffman, 1970*b*), and the lizard genus *Lacerta* (Dufaure, 1964; Poyntz, 1965). Shine (1977) observed ectopic eggs in females of the Australian snake genera *Pseudechis*, *Notechis*, and

Austrelaps, which he inferred were undergoing resorption. Resorption of ectopic eggs may well occur, since they would be exposed to the motile macrophages, mast cells, and lymphocytes of the peritoneal cavity.

The scarcity of evidence for oviductal resorption of entire uterine eggs also does not preclude uptake by the uterine epithelium of water-soluble organic molecules derived from oviductal eggs. If in fact water is resorbed from abortive eggs, it would be surprising if no such uptake occurred whatsoever. The question remains, however, whether such uptake represents a significant proportion of the yolk lipoproteins, and why egg masses are extruded by female squamates if such uptake is substantial.

FUTURE STUDY

The issue of whether any female squamates can resorb abortive uterine eggs is resolvable with further descriptive and experimental study. Definitive evidence for such resorption could be offered by histological study of abortive egg sites, studies of uterine uptake of labelled molecules incorporated into the eggs, or observations that rule out extrusion of the products of egg decomposition via the cloaca. Conversely, long-term retention of inviable eggs and cloacal extrusion of yolk masses offer evidence against egg resorption. Unfortunately, reports of yolk extrusion and possible egg resorption are less likely to show up in the primary scientific literature than in journals and magazines on reptilian herpetoculture. In fact, individuals with experience in reptile breeding are likely to encounter useful evidence relevant to the issues discussed herein, and could well suggest species as probable candidates for studies of egg resorption. One goal of the present paper is to encourage individuals with such experience to share their information with academic researchers who could benefit from their knowledge.

ACKNOWLEDGMENTS

REFERENCES

Badir, N. (1967). Some observations on the technique of deluteinization in pregnant viviparous lizard *Chalcides ocellatus* in the light of the naturally occurring embryonic mortality. *Anat. Anz.* **121** (8), 468-473.

Badir, N. (1968). The effect of population density on the embryonic mortality in the viviparous lizard *Chalcides*

ocellatus (Forsk.). *Anat. Anz.* **122** (8), 11-14.

Bellairs, A. d'A. (1949). Ectopic embryos in *Vipera berus*. *Brit. J. Herpetol.* **1949**, 55.

Blackburn, D. G. (1992). Convergent evolution of viviparity, matrotrophy, and specializations for fetal nutrition in reptiles and other vertebrates. *Amer. Zool.* **32**, 313-321.

Blackburn, D. G. (1993*a*). Histology of the late-stage placentae of the matrotrophic skink *Chalcides chalcides* (Lacertilia: Scincidae). *J. Morphol.* **216**, 179-195.

Blackburn, D. G. (1993*b*). Lactation: historical patterns and potential for manipulation. *J. Dairy Sci.* **76**, 3195-3212.

Blackburn, D. G. (1993*c*). Chorioallantoic placentation in squamate reptiles: structure, function, development, and evolution. *J. Exper. Zool.* **266**, 414-430.

Blackburn, D. G. (1995). Saltationist and punctuated equilibrium models for the evolution of viviparity and placentation. *J. Theor. Biol.* **174**, 199-216.

Blackburn, D. G. & Callard, I. P. (1997). Morphogenesis of the placental membranes in the viviparous, placentotrophic lizard *Chalcides chalcides* (Squamata: Scincidae). *J. Morphol.* **232**, 35-55.

Blackburn, D. G. & Vitt, L. J. (1992). Reproduction in viviparous South American lizards of the genus *Mabuya*. In *Reproductive Biology of South American Vertebrates: Aquatic and Terrestrial,* 150-164. Hamlett, W. (Ed.). New York: Springer-Verlag.

Blackburn, D. G., Kleis-San Francisco, S. & Callard, I. P. (1998). Histology of abortive eggs sites in the uterus of a viviparous, placentotrophic lizard, the skink *Chalcides chalcides. J. Morphol.* **235**, 97-108.

Blanchard, F. N. (1925). Eggs and young of the eastern ring-neck snake, *Diadophis punctatus edwardsii. Papers Mich. Acad. Sci. Arts Lett.* **7**, 279-292.

Brambell, F. W. R. (1948). Prenatal mortality in mammals. *Biol. Rev.* **23**, 370-405.

Branch, W. R. (1973). Birth in the mole snake, *Pseudaspis cana. J. Herpetol. Assoc. Africa* **10**, 24-25.

Branson, B. A., & Baker, E. C. (1974). An ecological study of the queen snake, *Regina septemvittata* (Say) in Kentucky. *Tulane Stud. Zool. Bot.* **18**, 153-171.

Bustard, H. R. (1966). Observations on the life history and behavior of *Chameleo bitaeniatus* Fischer. *Herpetologica* **22**, 13-23.

Campbell, J. A. & Quinn, H. R. (1975). Reproduction in a pair of Asiatic cobras, *Naja naja* (Serpentes, Elapidae). *J. Herpetol.* **9**, 229-233.

Clausen, H. J. (1940). Studies on the effect of ovariotomy and hypophysectomy on gestation in snakes. *Endocrinology* **27**, 700-704.

Cooper, W. E., Jr., Vitt, L. J., Hedges, R. & Huey, R. B. (1990). Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): behavioral shift in activity may offset costs of reproduction in an active forager. *Behav. Ecol. Sociobiol.* **27**, 153-157.

Domini, G. (1928). Osservazioni sui riassorbimento degli embrioni nella *Seps chalcides. Arch. zool. ital. (Torino)* **12**: 191-218.

Dufaure, J. P. (1964). Un embryon ectopique chez le lezard vivipare *Lacerta vivipara* Jacquin. *Brit. J. Herpetol.* **3**, 165.

Dyrkacz, S. (1977). The natural history of the eastern milk snake (Reptilia, Serpentes, Colubridae) in a disturbed environment. *J. Herpetol.* **11**, 155-158.

Farrell, T. M., May, P. G. & Pilgrim, M. A. (1995). Reproduction in the rattlesnake, *Sistrurus milliarius barbouri*, in central Florida. *J. Herpetol.* **29**, 21-27.

Fitch, H. S. (1970). Reproductive cycles in lizards and snakes. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* **52**, 1-247.

Giacomini, E. (1891). Materiali per la storia dello svilluppo del *Seps chalcides*. Cuv. Bonap. *Monitore Zool. Ital.* **2**, 179-192, 198-211.

Giersberg, H. (1923). Untersuchungen über Physiologie und Histologie des Eileiters der Reptilien und Vögel; nebst einem Beitrag zur Fasergenese. *Zeitschr. wiss. Zool.* **70**, 1-97.

Gosling, L. M. (1986). Selective abortion of entire litters in the coypu: adaptive control of offspring production in relation to quality and sex. *Amer. Nat.* **127**, 772-775.

Gregory, P. T., Larsen, K. W. & Farr, D. R. (1992). Snake litter size = live young + dead young + yolks. *Herpetol. J.* **2**, 145-146.

Hoffman, L. H. (1970*a*). Placentation in the garter snake, *Thamnophis sirtalis. J. Morphol.* **131**, 57-88.

Hoffman, L. H. (1970*b*). Observations on gestation in the garter snake, *Thamnophis sirtalis sirtalis. Copeia* **1970**, 779-780.

Jacobi, L. (1936). Ovoviviparie bei einheimischen Eidechsen. Vergleichende Untersuchungen an den Eiern und am Ovidukt von *Lacerta agilis, Lacerta vivipara* und *Anguis fragilis. Zeitschr. wiss. Zool.* **148**, 401-464.

Ji, X. (1995). Egg and hatchling components of a viviparous snake, *Elaphe rufodorsata. J. Herpetol.* **29**, 298-300.

Jones, R. E., Tokarz, R. R., Roth, J. J., Platt, J. E. & Collins, A. C. (1976). Mast cell histamine and ovarian follicular growth in the lizard *Anolis carolinensis. J. Exp. Zool.* **193**, 343-352.

Kasturirangan, L. R. (1951). The allantoplacenta of the sea snake *Hydrophis cyanocinctus* Daudin. *J. Zool. Soc. India* **8**, 277-289.

Lillegraven, J. A. (1979). Reproduction in Mesozoic mammals. In *Mesozoic Mammals: The First Two-Thirds of Mammalian History*, 259-276. Lillegraven, J. A., Kielan-Jaworowska, Z., & Clemens, W. A. (Eds.). Berkeley: University of California Press.

Lotze, H. U. (1975). Zum Paarungsverhalten der Äskulapnatter. *Salamandra* **11**, 67-76.

Low, B. S. (1978). Environmental uncertainty and the

parental strategies of marsupials and placentals. *Amer. Nat.* **112**, 197-213.

Luckett, W. P. (1977). Ontogeny of amniote fetal membranes and their application to phylogeny. In *Major Patterns in Vertebrate Evolution*, 439-516. Hecht, M. K., Goody, P. C. and Hecht, B. M. (Eds.). New York: Plenum Press.

Macfarlane, W. V., Pennycuick, P. R. & Thrift, E. (1957). Resorption and loss of foetuses in rats living at 35C. *J. Physiol., London* **135**, 451-459.

Matthews, L. H. (1955). The evolution of viviparity in vertebrates. In *The Comparative Endocrinology of Vertebrates. Part 1. The Comparative Physiology of Reproduction and the Effects of Sex Hormones in Vertebrates*, 129-148. Jones, I. C. and Eckstein, P. (Eds.). Cambridge: Cambridge Univ Press.

Matthews, L. H. (1965). Ectopic embryos in reptiles. *Brit. J. Herpetol.* **3**, 207.

McEachern, M. J. (1991). *Keeping and breeding corn snakes.* Herpetocultural Library Series, Advanced Vivarium Systems, Lakewide, California.

Mingazzini, P. (1892). L'oolisi della *Seps chalcides. Atti Acc. Lincei* (Rend V) **1**, 41-45.

Minton, S. A. (1949). Ectopic embryo in *Coluber. Herpetologica* **5**, 96.

Mitchell, J. C. (1976). Notes on reproduction in *Storeria dekayi* and *Virginia striatula* from Virginia and North Carolina. *Bull. Maryland Herp. Soc.* **12**, 133-135.

Mossman, H. W. (1987). *Vertebrate Fetal Membranes.* New Brunswick, New Jersey: Rutgers University Press.

Murphy, J. B., Barker, D. G., & Tryon, B. W. (1978). Miscellaneous notes on the reproductive biology of reptiles. 2. Eleven species of the Family Boidae, genera *Candoia, Corallus, Epicrates,* and *Python. J. Herpetol.* **12**, 385-390.

Neill, W. T. (1948). Ectopic embryos in *Natrix* and *Thamnophis. Copeia* **1948**, 139.

Neill, W. T. and J. M. Boyles (1957). The eggs of the crowned snake, *Tantilla coronata. Herpetologica* **13**, 77-78.

Osadnik, G. (1984). An investigation of egg-laying in *Phelsuma* (Reptilia: Sauria: Gekkonidae). *Amphibia-. Reptilia* **5**, 125-134.

Panigel, M. (1956). Contribution a l'étude de l'ovoviviparité chez les reptiles: gestation et parturition chez le lézard vivipare *Zootoca vivipara. Ann. S. Nat. Zool.* **11**, 571-665.

Parameswaran, K.N. (1962). The foetal membranes and placentation of *Enhydris dussumieri* (Smith). *Proc. Indian Acad. Sci. B* **56**, 302-327.

Parker, H. W. (1940). Undescribed anatomical structures and new species of reptiles and amphibians. *Ann. Mag. Nat. Hist.* **5**, 257-274.

Powell, G. L. & Russell, A. P. (1991). Parturition and clutch characteristics of short-horned lizards (*Phrynosoma douglassii brevirostre*) from Alberta. *Can. J. Zool.* **69**, 2759-2764.

Poyntz, S. V. (1965). Living ectopic embryo in common lizard. *Brit. J. Herpetol.* **1965**, 230.

Rollinat, R. (1904). Observations sur la tendence vers l'ovoviviparité chez quelques Sauriens et Ophidiens de la France centrale. *Mem. Soc. Zool. France* **17**, 30-41.

Ronne, J. (1996). Revelations of a boa breeder. *Reptiles* **4** (11), 24-43.

Schwarzkopf, L. (1993). Costs of reproduction in water skinks. *Ecology* **74**, 1970-1981.

Seigel, R. A., Huggins, M. M & Ford, N. B. (1987). Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia* **73**, 481-485.

Seufer, H. (1985). *Geckos.* Philler, Mindern.

Shine, R. (1977). Reproduction in Australian elapid snakes. II. Female reproductive cycles. *Aust. J. Zool.* **25**, 655-666.

Shine, R. (1980). "Costs" of reproduction in reptiles. *Oecologia* **46**, 92-100.

Shine, R. (1983). Reptilian reproductive modes: the oviparity-viviparity continuum. *Herpetologica* **39**, 1-8.

Shine, R. (1985). The evolution of viviparity in reptiles: an ecological analysis. In *Biology of the Reptilia*, 605-694. Gans, C. & Billet, F. (Eds.). New York: Wiley & Sons.

Sinervo, B., Hedges, R. & Adolph, S. C. (1991). Decreased sprint speed as a cost of reproduction in the lizard *Sceloporus occidentalis*: variation among populations. *J. Exp. Biol.* **155**, 323-336.

Stearns, S. C. (1992). Evolution of life histories. New York: Oxford Univ. Press.

Stewart, J. R. (1989). Facultative placentotrophy and the evolution of squamate placentation: quality of eggs and neonates in *Virginia striatula. Amer. Nat.* **133**, 111-137.

Stewart, J. R. & Castillo, R. E. (1984). Nutritional provision of the yolk of two species of viviparous reptiles. *Physiol. Zool.* **57**, 377-383.

Stewart, J. R., Blackburn, D. G., Baxter, D. C. & Hoffman, L. H. (1990). Nutritional provision to the embryos in *Thamnophis ordinoides* (Squamata: Colubridae), a predominantly lecithotrophic placental reptile. *Physiol. Zool.* **63**, 722-734.

ten Cate-Hoedemaker, N. J. (1933). Beiträge zur Kenntnis der Plazentation bei Haien und Reptilien. B. Die Plazentation von *Seps chalcides. Z. Zellforsch. mikrosk. Anat.* **18**, 299-345.

Thompson, J. (1977). The transfer of amino acids across the placenta of a viviparous lizard, *Sphenomorphus quoyii. Theriogenology* **8**, 158.

Thompson, J. (1981). A study of the sources of nutrients for embryonic development in a viviparous lizard, *Sphenomorphus quoyii. Comp. Biochem. Physiol. A, Comp. Physiol.* **70A**, 509-518.

Thompson, J. (1982). Uptake of inorganic ions from the maternal circulation during development of the embryo of a viviparous lizard, *Sphenomorphus quoyii.*

Comp. Biochem. Physiol. A, Comp. Physiol. **71A**, 107-112.

Tinkle, D. W. & Gibbons, J. W. (1977). The distribution and evolution of viviparity in reptiles. *Misc. Publ. Mus. Zool. Univ. Michigan* **154**, 1-55.

Uribe, M. C. A., Velasco, S. R., Guillette, L. J., Jr., and Estrada, E. F. (1988). Oviduct histology of the lizard, *Ctenosaura pectinata. Copeia* **1988**, 1035-1042.

Vitt, L. J. & Congdon, J. D. (1978). Body shape, reproductive effort, and relative clutch mass. *Amer. Nat.* **112**, 595-608.

Watanabe, M., Toriba, M., Sakai, A. & Hirabayashi, K. (1989). A case of long time retention of egg in oviduct of an albino *Elaphe climacophora. Snake* **21**, 113.

Westlin, L. M., Soley, J. T., van der Merwe, N. J. & van Dyk, Y. J. (1995). Late fetal development and selective resorption in *Saccostomus campestris* (Cricetidae). *Reprod. Fertil. Devel.* **7**, 1177-1184.

Yaron, Z. (1972). Endocrine aspects of gestation in viviparous reptiles. *Gen. Comp. Endocrinol., Suppl.* **3**, 663-674.