

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 169

**The Evolution of
Parental Care
in Salamanders**

by

Ronald A. Nussbaum
Museum of Zoology
and Division of Biological Sciences
The University of Michigan
Ann Arbor, Michigan 48109-1079

Ann Arbor
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
August 5, 1985

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 169

ROBERT RUSH MILLER, EDITOR
MARY JOANNE CATTERALL, ASSISTANT EDITOR

The publications of the Museum of Zoology, University of Michigan consist of two series—the Occasional Papers and the Miscellaneous Publications. Both series were founded by Dr. Bryant Walker, Mr. Bradshaw H. Swales, and Dr. W. W. Newcomb.

The Occasional Papers, publication of which was begun in 1913, serve as a medium for original studies based principally upon the collections in the Museum. They are issued separately. When a sufficient number of pages has been printed to make a volume, a title page, table of contents, and an index are supplied to libraries and individuals on the mailing list for the series.

The Miscellaneous Publications, which include papers on field and museum techniques, monographic studies, and other contributions not within the scope of the Occasional Papers, are published separately. It is not intended that they be grouped into volumes. Each number has a title page and, when necessary, a table of contents.

A complete list of publications on Birds, Fishes, Insects, Mammals, Mollusks, and Reptiles and Amphibians is available. Address inquiries to the Director, Museum of Zoology, Ann Arbor, Michigan 48109-1079.

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 169

**The Evolution of
Parental Care
in Salamanders**

by

Ronald A. Nussbaum
Museum of Zoology
and Division of Biological Sciences
The University of Michigan
Ann Arbor, Michigan 48109-1079

Ann Arbor
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
August 5, 1985

ABSTRACT

Nussbaum, Ronald A. 1985. *The evolution of parental care in salamanders*. Misc. Publ. Mus. Zool. Univ. Michigan, 169:1-50, figs. 1-4.—The occurrence of parental care (embryo guarding) among salamanders (Amphibia: Caudata) is reviewed. The presence or absence of parental care in salamanders is correlated with three reproductive modes that were recognized by previous authors. Two modes exist among species that have indirect development and breed in the aquatic environment. Salamanders of one group, lentic-breeders, normally have (1) relatively large clutches of small eggs, (2) short embryonic periods, (3) small hatchlings, (4) exposed nest sites, and (5) no parental care. Salamanders of the second group, lotic-breeders, usually have (1) relatively small clutches of large eggs, (2) long embryonic periods, (3) large hatchlings, (4) hidden nest sites, and (5) parental care. The third, or terrestrial-mode, consists of species that deposit small clutches of large eggs in hidden, terrestrial nests. The embryos of terrestrial breeders have long embryonic periods and direct development (no aquatic larval stage), and the embryos are usually attended by the female parent. Salamanders of the terrestrial-mode evolved from lotic breeding ancestors that already had large eggs, hidden nests, and parental care. Therefore, the terrestrial-mode need not be considered in an analysis of the origin of parental care in salamanders.

It is argued that lentic and lotic environments are fundamentally different in trophic structure, and that this difference is ultimately responsible for the presence or absence of parental care in salamanders. Lentic environments are characterized by blooms of zooplankton during the spring when the small hatchlings of lentic breeding salamanders appear, and the hatchlings are dependent on the zooplankton for food. Lotic environments are virtually devoid of zooplankton, and the prey (aquatic insects and other benthos) available to hatchling salamanders in streams occurs in much larger sizes more evenly distributed in abundance across time. Selection will adjust the size of hatchlings, through egg size selection, for maximum utilization of available food in their respective environments. In the lentic environment, small eggs are sufficient to yield the relatively small hatchlings needed to harvest the abundant zooplankton, and an increase in egg size, at the cost of reduced clutch size, would not significantly increase the amount of food available to hatchlings in lentic habitats. In lotic environments, large eggs are needed to yield large hatchlings capable of capturing and ingesting the larger, scarcer prey. Large eggs carry the costs of reduced clutch size and longer embryonic period. A longer embryonic period results in greater total embryonic mortality unless the embryonic death rate is reduced. Selection for hidden nests and embryo guarding as means of reducing embryonic death rate may be a consequence of the evolution of large eggs.

Either the female or the male cares; there are no certain cases of biparental care in salamanders. It is argued that the sex that chooses the oviposition site will be the care-giving sex among salamanders. The evolution of the salamander spermatophore was the crucial step that allowed courtship sites and oviposition sites to be separated in space and time, and the sequestering of spermatophores from courtship sites by females determined that females of such species would be the care-giving sex.

Key words: *Salamanders, Amphibia, Caudata, parental care, mating systems, evolution.*

CONTENTS

	PAGE
INTRODUCTION.....	1
OCCURRENCE OF PARENTAL CARE IN SALAMANDERS.....	2
FUNCTION OF PARENTAL CARE.....	6
ORIGIN OF PARENTAL CARE IN SALAMANDERS.....	7
TROPHIC STRUCTURE OF LENTIC AND LOTIC WATERS.....	8
FEEDING ECOLOGY OF LARVAL SALAMANDERS.....	9
Feeding Behavior.....	9
Feeding Apparatus.....	9
Food Habits.....	10
Food Size.....	12
Food Size-Body Size Relationship.....	12
EGG SIZE AND HATCHLING SIZE.....	13
EGG SIZE AND EMBRYONIC PERIOD.....	15
CONSEQUENCES OF PROLONGED EMBRYONIC PERIOD.....	20
LACK OF PARENTAL CARE AMONG LENTIC-BREEDING SALAMANDERS.....	22
ADAPTIVE SIGNIFICANCE OF EGG SIZE.....	23
PARENTAL CARE AND EGG SIZE.....	27
PARENTAL CARE AND MATING SYSTEMS IN SALAMANDERS.....	28
Models of Mate Desertion.....	28
Phylogeny and Parental Care in Salamanders.....	29
Modes of Fertilization.....	30
Mating Systems of Salamanders.....	30
Mate Desertion and Parental Care in Salamanders.....	35
SUMMARY.....	38
ACKNOWLEDGMENTS.....	39
LITERATURE CITED.....	39
APPENDIX.....	50

ILLUSTRATIONS

FIGURE		PAGE
1	Gill arches and rakers of <i>Ambystoma tigrinum</i> and <i>Dicamptodon copei</i>	11
2	Scatter plot of egg size and embryo length when they begin feeding	16
3	Scatter plot of egg size and length of embryonic period	17
4	Survival rate of embryos of <i>Hynobius nebulosus</i>	21

TABLES

TABLE		PAGE
1	Salamanders with parental care among species with aquatic nest sites	3
2	Number of gill rakers of larval salamanders	10
3	Relationship between body size and food size for <i>Rhyacotriton olympicus</i>	14
4	Developmental data for salamanders	18
5	Nest site temperatures	25
6	Mating modes of salamanders	31

INTRODUCTION

We have to avoid being misled by the assumption that the cost of Genesis is measured by the number of the young produced, instead of being measured, as it is, by the weight of nutrition abstracted to form the young, *plus* the weight consumed in caring for them. (Herbert Spencer, 1867, *The Principles of Biology*, vol. II, p. 415)

Whether a species of animal produces many offspring of which it takes no care or a few of which it takes much care—that is, whether its reproductive surplus is laid out wholly in germs or partly in germs and partly in labour on their behalf—must have been decided by that moulding of constitution to conditions, slowly effected through the more frequent preservation of descendants from those whose reproductive habits were best adapted to the circumstances of the species. (Ibid, p. 472)

Herbert Spencer's "Laws of Multiplication" are now largely overlooked or ignored. But, many of his highly original insights including his views on the interplay of reproductive effort, parental investment, sexual asymmetry, and parental care, are active topics of investigation by today's evolutionary ecologists. Spencer was prescient enough to cast parental care into a cost/benefit framework. He realized, for instance, that parental care represents an investment in current offspring that subtracts from the parent's ability to produce additional offspring and from the parent's ability to sustain its own life. Thus, in Spencer's view, parental care is a costly activity that is expected to evolve only under special and potentially predictable circumstances.

Since Spencer's time, interest in evolutionary aspects of parental investment was sporadic until Williams (1966, 1975), Trivers (1972), and others expanded and reformulated Spencer's ideas into cogent and testable models. Galvanized largely by Trivers' (1972) work, ecologists produced a plethora of papers over the past decade that deal with many aspects of parental care.

Parental care is nearly uniformly present in birds and mammals. Among the "lower" vertebrates, parental care is rare in reptiles, but is relatively common among amphibians and fishes. The latter two groups are ideal for the comparative study of parental care because in them (1) the occurrence of parental care cuts across phylogenetic lineages, (2) groups with external and internal fertilization are included, and (3) a wide variety of mating systems exists.

Recent reviews (Baylis, 1981; Blumer, 1979; McDiarmid, 1978; Perrone and Zaret, 1979; Ridley, 1978; Wells, 1977, 1981) of parental care in lower vertebrates were focused on factors that may determine whether care is given by the male, the female, or by both parents. Less attention was given

to factors that may determine whether care is given at all. Maynard Smith (1977) recognized that desertion by both parents is expected if neither parent can increase its lifetime reproductive output by investment beyond fertilization, but the extreme generality of this concept limits its value. Ridley (1978) explicitly ignored the question of factors that select for parental care. Perrone and Zaret (1979) hypothesized that the absence of brood care in fishes should occur in the absence of predators, because the main function of brood care in fishes is to protect the embryos and hatchlings from being eaten. However, it is difficult to imagine predator-free environments, and there are alternative methods for non-guarding fishes to protect their offspring from predators (e.g., egg-burying in salmonids, egg-scattering in clupeids and elopids).

There is little doubt that parental care among lower vertebrates evolved at least partly in response to egg predation and/or egg cannibalism. But, predation is only one of a constellation of secondary factors likely to be involved in the evolution of parental care. At least as far as salamanders are concerned, there appears to be a more general explanation. I will argue that with few exceptions parental care among salamanders evolved as a consequence of the radically different trophic structures of lentic (pond/lake) and lotic (stream) environments.

In this paper, I summarize the literature on parental care in salamanders and present data that support the lentic-lotic hypothesis. I also discuss the issue of male versus female care among salamanders in regard to the theory of mating systems.

OCCURRENCE OF PARENTAL CARE IN SALAMANDERS

Aspects of parental care in salamanders were reviewed by Forester (1979), Ridley (1978), Ryan (1977), Salthe (1969), Salthe and Mecham (1974) and Wells (1977). None of these reviews directly addresses the issue of the origin of parental care in salamanders, and only Ridley (1978) and Wells (1977) comment (briefly) on parental behavior in relation to the mating systems of this group.

Parental care in salamanders is limited to attendance of embryos within egg capsules. Posthatchlings may derive some parental protection if they remain in the nest for a brief period, but parental care ends when the offspring leave the nest to begin feeding. Either there is no parental care or the male or the female engages in parental care. There are no certain cases of biparental care in salamanders in nature, although there are conflicting reports for captive *Proteus anguinus* (male cares, Vandel and Bouillon, 1959; female cares, Durand and Vandel, 1968; usually the female but sometimes the male cares, Briegleb, 1962; biparental, Durand and Bouillon, 1964). Some species may have variable patterns of parental care (footnotes, Appendix I), but natural observations for most species are so few

that one cannot be sure whether a variable pattern exists, or whether the observations are faulty.

Nest sites of salamanders are of three general kinds (Dunn, 1923, 1926; Noble, 1927). Eggs may be deposited in ponds or lakes (lentic sites), in streams (lotic sites), or on land.

Among salamanders with aquatic nests, parental care is reported in 18 species of 12 genera and six families (Table 1). Sixteen of these 18 species typically breed in streams. One of the two exceptions, *Hynobius nebulosus*, breeds in ponds or lakes. However, parental care in *H. nebulosus* is of doubtful occurrence for four reasons. Firstly, Thorn's (1962, 1967) reports

TABLE 1
SALAMANDERS WITH PARENTAL CARE (EGG GUARDING)
AMONG SPECIES WITH AQUATIC NEST SITES

Taxa	Fertilization	Parental Sex	Breeding Habitat
Hynobiidae			
<i>Hynobius kimurai</i> ¹	external	male	lotic
<i>Hynobius naevius</i> ¹	external	male	lotic
<i>Hynobius nebulosus</i> ² (? , see text)	external	male	lentic
Cryptobranchidae			
<i>Andrias japonicus</i> ³	external	male	lotic
<i>Cryptobranchus alleganiensis</i> ⁴	external	male	lotic
Ambystomatidae			
<i>Dicamptodon copei</i> ⁵	internal	female	lotic
<i>Dicamptodon ensatus</i> ⁶	internal	female	lotic
Proteidae			
<i>Necturus maculosus</i> ⁷⁻⁸	internal	female	lotic/lentic
<i>Proteus anguinus</i> ⁹⁻¹²	internal	female and/or male (see text)	lotic (subterranean)
Plethodontidae			
<i>Desmognathus monticola</i> ¹³	internal	female	lotic
<i>Desmognathus quadramaculatus</i> ¹³	internal	female	lotic
<i>Desmognathus welleri</i> ¹⁴	internal	female	lotic
<i>Eurycea bislineata</i> ¹⁵	internal	female	lotic
<i>Eurycea longicauda</i> ¹⁶	internal	female	lotic
<i>Gyrinophilus porphyriticus</i> ¹⁷⁻¹⁸	internal	female	lotic
<i>Leurognathus marmoratus</i> ¹⁹	internal	female	lotic
<i>Pseudotriton montanus</i> ²⁰⁻²¹	internal	female	lotic
Sirenidae			
<i>Siren intermedia</i> ²²⁻²⁴	?	female	lentic

¹Tago, 1931; ²Thorn, 1962, 1967; ³Tago, 1929; ⁴Smith, 1907; ⁵Nussbaum et al., 1983; ⁶Nussbaum, 1969a; ⁷Eycleshymer, 1906; ⁸Bishop, 1926; ⁹Vandel and Bouillon, 1959; ¹⁰Durand and Vandel, 1968; ¹¹Briegleb, 1962; ¹²Durand and Bouillon, 1964; ¹³Pope, 1924; ¹⁴Barbour, 1971; ¹⁵Wood, 1951, 1953a; ¹⁶Franz, 1964; ¹⁷Bishop, 1924; ¹⁸Organ, 1961; ¹⁹Martof, 1962; ²⁰Brimley, 1939-43; ²¹Goin, 1947; ²²Noble and Marshall, 1932; ²³Hubbs, 1962; ²⁴Godley, 1983.

of paternal care in this species were based on observations of animals breeding in aquaria; secondly, a biologist familiar with *H. nebulosus* in the field stated that parental care does not occur in this species (Kunitomo, 1910); thirdly, a recent study (Kusano, 1980) of egg survivorship of *H. nebulosus* based on 650 egg sacs observed in nature makes no mention of parental care (Kusano, op. cit., reported that the mean length of the egg stage was 56.2, 38.3, and 45.4 days for 3 consecutive years, and that the mean duration of males in the pond was 19.7, 10.2, and 15.4 days for the same three years. Females deserted the pond soon after ovipositing.); and fourthly, where known, other species of *Hynobius* that breed in lentic habitats do not have parental care (Tago, 1931).

The second exceptional species, *Siren intermedia*, is also problematic in that there are few observations of parental care in this form, its eggs are large for a lentic breeder, and some systematists believe that sirenids are not salamanders. Noble and Marshall (1932) reported that a "boy" saw an adult *S. intermedia* of unknown sex "glide away from the mud" containing eggs of this species taken from a pond. Hubbs (1962) stated that "several" nests were observed in the mud and vegetation on the bottoms of fish hatchery ponds and that one adult (sex unreported) *S. intermedia* was found in each nest "accompanying more than 100 eggs or larvae." Godley (1983) reported a female in attendance of each of two nests in a water hyacinth community in a canal. Although these observations are few, it seems likely that some form of egg-guarding occurs in this species. The two other species of Sirenidae, *Siren lacertina* and *Pseudobranchius striatus*, probably do not have parental care because their eggs are scattered singly or in small groups, a behavior that is incompatible with parental care, and because no adults were observed near eggs of these species in the few reported cases (Goin, 1947; Netting and Goin, 1942; Noble, 1930; Noble and Richards, 1932). Oviposited eggs of *S. intermedia* average 3.0 mm diameter (Noble and Marshall, 1932). This is the largest egg size reported for a lentic-breeding salamander (compare data for lentic-breeding species in Table 4; all *Ambystoma*, all Salamandridae except *Euproctus asper*). Eggs of this size are usually found only among terrestrial- and lotic-breeding species. Larger eggs require more time to develop, and, as argued below, longer embryonic developmental periods may select for parental care in salamanders. Therefore, *S. intermedia* fits the model developed below, except that it is a lentic-breeder with large eggs. There is no obvious reason why *S. intermedia* should have larger eggs than other lentic-breeders, but it could be related to specialized feeding habits of hatchlings. Sirenids are paedomorphic, highly specialized, fully aquatic amphibians with many unique anatomical, behavioral, and biochemical characteristics that set them far apart from salamanders (Cope, 1889; Goin et al., 1978). Most recent treatments (e.g., Brame, 1967; Estes, 1981; Gorham, 1974; Milner, 1983; Naylor, 1980) include sirenids within the salamander order Caudata, but their phylogenetic position is far from certain.

Lotic-breeders always use hidden (sub-surface) nest sites in contrast to the exposed oviposition sites of lentic-breeders. The nests of about 20

species of stream adapted salamanders have never been reported, presumably in part because the nests are subterranean and difficult to find, but also partly because some species occur in remote regions seldom visited by biologists. The presence or absence of parental care is also unknown in these 20 species, but most are likely to have parental care as predicted by the hypothesis developed in this paper.

Parental care in nature has never been reported (*Siren intermedia* excepted) among salamanders that are primarily lentic-breeders (24 ambystomatids, 14 hynobiids, 34 salamandrids). These salamanders attach eggs singly, in small clumps, or in large clumps to submerged vegetation, stones, and other debris and abandon them.

There is little doubt that among salamanders with aquatic development, those that utilize lotic breeding sites are more likely to evolve parental care than are those that breed in lentic habitats. In addition to parental care and hidden nests, lotic breeders almost invariably have (1) larger eggs, (2) fewer eggs (for equivalent-sized females), (3) longer embryonic periods, and (4) larger hatchlings, compared to lentic-breeders (Dunn, 1923; Noble, 1927, 1931; Salthe, 1969). These four characteristics form an adaptive complex, and all four are expected to vary together.

Salamanders with terrestrial nests (*Ambystoma opacum*, *A. cingulatum*, *Echinotriton andersoni*, amphiumids, numerous plethodontids) normally exhibit maternal care (Appendix I). There is strong evidence that plethodontids with terrestrial nests evolved from lotic-nesting ancestors (Dunn, 1926) that probably already had maternal care. I view maternal care in terrestrially-breeding plethodontids as an ancestral characteristic of that group, and, therefore, fully terrestrial plethodontids need not be considered in a discussion of the origin of parental care in salamanders. Too little is known about the relationships of the specialized amphiumids (1 genus, 3 species) to speculate on the origin of maternal terrestrial brooding in that group, although it can be noted that certain amphiumid characteristics such as reduced tail fin, elongated body, and large and few eggs suggest a lotic ancestry for the group. Terrestrial-nesting with maternal brooding in *Ambystoma opacum* is derived from lentic-nesting, probably without parental care (discussed below), and terrestrial egg-scattering without care in *Ambystoma cingulatum* (Anderson and Williamson, 1976) is also viewed as derived from lentic-nesting without care. *Echinotriton andersoni* is a terrestrial-nesting salamandrid derived from lentic-nesting ancestors. Apparently there is no parental care in *E. andersoni*, but observations are few (Nussbaum and Brodie, 1982; Utsunomiya and Utsunomiya, 1977; Utsunomiya et al., 1978; Y. Utsunomiya, pers. comm.).

Nests and presence or absence of parental care are unreported for 6 genera and about 150 species of fully terrestrial plethodontids. Presumably this reflects the difficulty in observing the hidden nest sites of these forms. Parental (maternal) care is predicted in most of these because it is the ancestral condition among plethodontids and because many are known from dissection to produce few large eggs, reproductive characteristics usually associated with parental care.

FUNCTION OF PARENTAL CARE

Functional aspects of parental care among salamanders are not directly relevant to the theme of this paper. I simply assume that parental care contributes to fitness by increasing embryonic survival; otherwise this behavior would not have evolved. It is useful, however, to summarize the literature on this subject.

It has been argued that attending females of plethodontids with terrestrial development (1) prevent intra- and interspecific oophagy, (2) apply antibiotic skin secretion to their embryos, (3) agitate their embryos to prevent yolk sedimentation, adhesions, and developmental anomalies, and (4) provide moisture to their embryos via the maternal skin and urinary bladder or retard desiccation by covering the embryos.

Tilley (1972) and Forester (1979) removed guarding female *Desmognathus ochrophaeus* from their nests and found that the embryos did not survive. They attributed the loss to predation by other salamanders, mainly conspecifics, and invertebrates. Observations in the laboratory showed that brooding females of *D. ochrophaeus* are aggressive toward intruders and that their inclination to defend and their success in defending their broods depend on the kind of predator involved (Forester, 1978). Similarly, Highton and Savage (1961) reported that female *Plethodon cinereus* that are brooding their embryos in the laboratory will bite and drive away conspecific females. The latter were reported to eat embryos if given the opportunity. Gordon (1952) wrote that brooding females of *Aneides aeneus* will attack moving objects near their nests.

There are numerous suggestions that one of the functions of parental care is to prevent embryonic death caused by pathogens. Both removal of infected embryos by the parent and antibiotic effects of maternal skin secretions have been suggested as possibly important in this regard. Forester (1979) showed that unguarded but experimentally protected (from macropredators) embryos of *Desmognathus ochrophaeus* frequently are destroyed by phycomycete fungi. However, tests indicated that water soluble extracts from the skin of females had no antibiotic effect. Similar tests performed by Vial and Preib (1966, 1967) on *Plethodon cinereus* showed that water-soluble skin extracts had no inhibitory influence on a wide variety of bacteria, fungi, and yeasts. Forester's (1979) data indicate that brooding females of *D. ochrophaeus* protect their healthy embryos from mold and bacteria by removing dead and infected embryos.

Smith (1906) noted that the large eggs of the hellbender, *Cryptobranchus alleganiensis*, form adhesions between the embryos and jelly envelopes if allowed to develop motionlessly in the laboratory. Since then, several authors suggested that such developmental anomalies are prevented by regular agitation of the embryos by the attending parent. Forester (1979) provided experimental evidence that mechanical vibrations increase survivorship of unattended eggs of *Desmognathus ochrophaeus*. The significance of agitation of the embryos by attending adults is far from clear. The

differential functions of movement caused by the parent and rotation caused by the epidermal cilia of the embryos need to be investigated.

To date there is no good experimental evidence concerning the proposed antidesiccation function of parental care in salamanders, although Forester (1984) showed that the presence of attending females reduced water loss from embryos of *Desmognathus ochrophaeus*. This function would not apply to species with aquatic nests. For these species, antipredation is likely to be the primary function of parental care, but no experiments have been done on species with aquatic development.

ORIGIN OF PARENTAL CARE IN SALAMANDERS

In salamanders, as well as among many other groups of animals, parental care or egg guarding is closely associated with the production of relatively few large eggs. Some authors have suggested that where parental care exists, selection will favor reduced clutch size and increased egg size. For example, Curtis (1938) believed that species of fish with parental care require fewer eggs "for preservation of the species." Such group-selectionist interpretations for the evolution of reduced clutch size were common during the first half of this century. The views of some recent authors, while not overtly group-selectionist, nevertheless imply that parental care is a precondition for the evolution of reduced fecundity, and that, given reduced fecundity, egg size will naturally increase. Svårdson (1949) believed that parental care in itself is a selective agent against increased fecundity in fishes. In reference to amphibians, Salthe and Duellman (1973) wrote that selection would reduce clutch size "commensurate with paternal care" and that increased ovum size would be an "indirect result" of this process. Cadwallader (1976) thought that where parental care and nest sites were part of the natural history of a species, efficient fertilization would allow the reduction of clutch size and hence egg size would increase. Kuramoto (1978) suggested that species of frogs and salamanders with parental care and protected nest sites will, as a consequence of these characteristics, experience greater selection for egg size than for clutch size; hence the latter will be sacrificed for the former. Parental care as a precondition for the evolution of larger propagules and reduced fecundity is the basis for Shine's (1978) "safe harbor hypothesis."

In my view, these authors have cause and effect reversed. A major thesis of this paper is that in salamanders, and perhaps in many other oviparous poikilotherms, selection for parental care and reduced clutch size is a consequence of selection for increased egg size. I hypothesize that the size-frequency distribution of food available to hatchling salamanders is the selective force that has led to the evolution of large clutches of small eggs and no parental care in pond-breeding salamanders, and to the evolution of small clutches of large eggs with parental care in stream-breeding salamanders.

According to this hypothesis, the evolution of parental care in salamanders proceeded as follows:

1. Selection favors the production of large offspring (first feeding stages) in environments where the greatest abundance of food is available in relatively large sizes, mainly in lotic waters.
2. Large offspring can be produced only from large eggs.
3. Larger eggs require more time to develop.
4. Total embryo-stage mortality (esm) is the product of death rate (dr) and developmental time (dt).
5. Because $esm = (dr)(dt)$, and because larger eggs necessarily have longer dt , relatively low esm can be maintained only by reducing dr .
6. To reduce dr in salamanders with long incubation periods (large eggs), selection has favored the evolution of hidden nest sites and parental care (embryo guarding).
7. Because clutch size must vary inversely with egg size for salamanders of a given female body size, selection to reduce esm will result both from increased dt and reduced clutch size in populations undergoing selection for increased egg size.

I will now examine the assumptions of this hypothesis, present some supportive data, and discuss alternative explanations for the adaptive significance of large eggs in salamanders.

TROPHIC STRUCTURE OF LENTIC AND LOTIC WATERS

A primary assumption of the hypothesis presented above is that to an aquatic carnivore, such as a larval salamander, the trophic environment of lotic waters is fundamentally different from that of lentic waters. This view is opposite that of Salthe (1969), who stated that there "is no reason to believe that larval or egg stage mortality or larval food supplies of salamanders should be different in static and lotic waters."

There is a fundamental difference between streams and ponds in the nature of their productivity. Lentic food chains are based on plankton production whereas lotic food chains are based on aufwuchs production and allochthonous organic matter derived from the terrestrial environment and from connecting lakes and ponds. Lentic environments are characterized by tremendous blooms of zooplankton during the spring months (Birge and Juday, 1922), often peaking in April when many lentic-breeding salamanders are hatching. By contrast, swift streams are virtually devoid of zooplankton (Allen, 1920; Greenberg, 1964; Pennak, 1943; Russell-Hunter, 1970). In reality there is a continuum between lentic and lotic environments if slow streams and rivers are considered. The abundance of plankton across this continuum is best expressed by "Schröder's Law" which states that the amount of plankton varies inversely with the slope of the channel or the rate of flow (Welch, 1935).

Streams and ponds also differ basically in the rate of food production. Streams rarely support animals (prey) with several generations per year, whereas such animals, especially zooplankton, are common in ponds and lakes (Hynes, 1970). In lentic environments, zooplankton represent a tremendously abundant and rapidly renewing prey resource. Stream prey, mainly immature insects, do not replace themselves within a single growing season as they are cropped.

It would be inefficient for a lentic-breeding salamander to increase parental investment to produce larger hatchlings. To do so would not significantly increase the amount of food available to hatchlings, and the cost would be fewer hatchlings and higher embryonic mortality because of longer developmental time. Increased parental investment is also costly for stream-breeders, but in this environment the benefits (increased food for hatchlings) must outweigh the cost (reduced fecundity).

If the hypothesis presented here is correct then lentic- and lotic-adapted larvae should differ in feeding behavior, feeding apparatus, and, of course, realized food. It is readily apparent that such is the case.

FEEDING ECOLOGY OF LARVAL SALAMANDERS

FEEDING BEHAVIOR

Larvae of pond-breeding salamanders feed in both the benthic and limnetic zones. Dineen (1955) found that larval tiger salamanders, *Ambystoma tigrinum*, feed on the bottoms of ponds, "snapping at larger organisms" when light intensity is high, and that they become nektonic plankton-feeders when light intensity is low. Anderson and Graham (1967), Anderson and Williamson (1974), Branch and Altig (1981), Hassinger and Anderson (1970), Hassinger et al., (1970), Lafrentz (1930), and Petranka and Petranka (1980) reported similar observations for other species of pond-breeding salamanders.

Larvae of salamanders adapted for life in streams are essentially benthic-feeders. Larvae of three stream salamanders in the Pacific Northwest, U.S.A. (*Dicamptodon copei*, *D. ensatus*, *Rhyacotriton olympicus*) spend most of their time under stones during the day, emerging mainly at night to feed by crawling slowly along the bottom. Similar observations are reported for larval *Eurycea bistriata* in small streams in Kentucky (Petranka, 1984a). Several lineages of stream-breeding salamanders have independently evolved lunglessness or reduced lungs (Noble, 1927), which seem clearly to be adaptations for negative buoyancy and benthic life in lotic waters.

FEEDING APPARATUS

Associated with planktivory in pond larvae is a more efficient filter-feeding apparatus by comparison to stream larvae. The branchial arches of larval salamanders have series of interlocking gill rakers, much like those of

fishes, which are used for filtering food from water drawn into the mouth and forced out through the gill slits. The filtering efficiency of a gill-raker system should increase with gill-raker density. Observations on numerous species indicate that pond larvae have more gill rakers per row than do stream larvae (Table 2), and that the interdigitation of rakers on opposing arches is much more precise in pond larvae (*cf.* Fig. 1). Rakers are occasionally completely absent from some arches in some specimens of *Dicamptodon copei* and *Rhyacotriton olympicus*, two ambystomatids highly adapted to lotic environments, and there are no rakers on any arches of older larvae of *Eurycea bislineata*, *Gyrinophilus palleucus*, *G. porphyriticus*, *Pseudotriton montanus*, and *P. ruber*, all of which are rheophilic plethodontids.

Gross and Anderson (1984) and Hagen and Gilbertson (1972) similarly found that lentic populations of threespine sticklebacks, *Gasterosteus aculeatus*, had more, longer, and more closely spaced gill rakers than lotic populations of the same species. These authors attributed these differences partly to selection for planktivory in the lentic environments.

FOOD HABITS

Reports of stomach contents of pond adapted larval salamanders indicate the importance of zooplankton as an energy source, especially for the smaller or hatchling-sized larvae. Hatchling *Ambystoma tigrinum* in Colorado ponds fed almost exclusively on zooplankton, but after a few weeks of growth the amount of zooplankton in the diet decreased to less than 10 percent (Dodson, 1970). Large *A. tigrinum* in a Michigan pond consumed 16.4–58.9 percent zooplankton by volume, the lower percentages from late

TABLE 2
NUMBER OF GILL RAKERS OF LARVAL SALAMANDERS

	No. Gill Rakers ¹		
	\bar{x}	range	<i>n</i>
Stream Larvae			
<i>Desmognathus quadramaculatus</i>	4.2	4–5	6
<i>Dicamptodon copei</i>	4.7	4–6	15
<i>Dicamptodon ensatus</i>	5.1	4–6	15
<i>Rhyacotriton olympicus</i>	1.5	0–3	6
Pond Larvae			
<i>Ambystoma macrodactylum</i>	10.3	10–11	6
<i>Ambystoma talpoideum</i>	10.3	9–11	6
<i>Ambystoma tigrinum</i>	13.5	12–15	6
<i>Taricha torosa</i>	7.7	7–8	6

¹Counts were made for the anterior row of rakers on the anterior-most free gill arch.

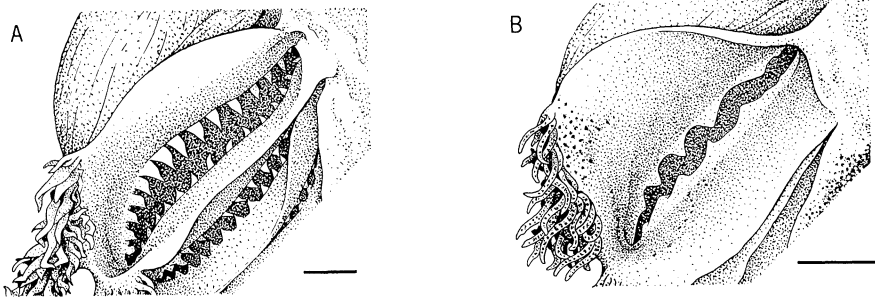


FIG. 1. Gill arches and rakers of *Ambystoma tigrinum* (A) and *Dicamptodon copei* (B). *A. tigrinum* has numerous well-fitted rakers associated with planktivory in lentic environments. *D. copei* has fewer poorly-fitted rakers and feeds on larger prey in plankton-free lotic environments. Scales = 2.0 mm.

afternoon samples and the higher percentages from samples taken at night (Dineen, 1955). In an Illinois pond, planktonic crustaceans formed over 90 percent of the prey numerically, and over 49 percent by weight, of larval *A. tigrinum* (Brophy, 1980). Licht (1975) found that larval *A. gracile* in a sluggish river in British Columbia fed predominantly on zooplankton (crustaceans) and dipertan larvae throughout the year, and that all size classes of larvae fed on zooplankton. In Marion Lake, British Columbia, larval *A. gracile* fed heavily on the planktonic cladoceran, *Sida crystallina*, and other zooplankton (Henderson, 1973). Anderson (1968a) studied the larval food of two subspecies of *A. macrodactylum* and of larval *A. californiense* in ponds and lakes in northern California. Zooplankton were the most frequently eaten prey, and Anderson concluded that (p. 283) "sympatric larvae of *A. t. californiense* [= *A. californiense*] and *A. m. croceum* apparently draw on similar food resources for about the first week of feeding activity, both species being adapted to the bloom of planktonic forms that occur in late winter." Branch and Altig (1981) found that larval *A. maculatum*, *A. opacum*, and *A. talpoideum* consumed mainly microcrustacean zooplankters (87.4–100.0 percent of all items in all cases) in temporary pools in Mississippi. Freda (1983) reported that larval *A. maculatum* in New Jersey ponds ate planktonic cladocerans and copepods predominantly, and that larger larvae began to consume larger benthic prey in addition to zooplankters. Petranka and Petranka (1980) found that hatchling *A. opacum* fed entirely on macrozooplankton and that benthic prey such as isopods, amphipods, and aquatic insects were included in the diet of older larvae. Similar observations were reported by Stewart (1956) for larval *A. opacum*. Larvae of red-spotted newts, *Notophthalmus viridescens*, were opportunistic feeders in a New York pond where zooplankton (*Cyclops*, *Daphnia*, *Diaptomus*, ostracods) were numerically dominant, both in the pond and in the stomachs, and constituted about 20 percent of the diet by volume (Hamilton, 1940). Larval *N.*

viridescens fed mainly on ostracods (79.0 percent numerically, 61.3 percent by weight) in an Illinois pond (Brophy, 1980). The most common food in the stomachs of larval *Triturus cristatus*, *T. helveticus*, and *T. vulgaris* in English ponds was zooplankton (Cladocera, Ostracoda) (Avery, 1968). In a pond at Oxford, England, the food of larval *T. vulgaris* was "almost exclusively planktonic in the youngest larvae," but, "a few other types of mainly non-planktonic prey were found in older larvae" (Bell, 1975).

By contrast, stream-adapted larvae of two species of *Dicamptodon* fed mainly on immature insects in a stream in western Washington state (Antonelli, et al., 1972). Their stomachs contained no plankton. Metter (1963) found no plankton in the stomachs of larval *Dicamptodon ensatus* taken from Idaho streams. Interestingly, larvae of this same species did not feed on plankton in a pond in California (Johnson and Schreck, 1969), although plankton must have been available. This observation suggests that rheophilic larvae are unable to utilize zooplankton even when zooplankton is available because of unusual circumstances.

Larvae ($n=70$) of another stream-adapted salamander, *Rhyacotriton olympicus*, fed primarily on mollusks, insects, and arachnids (96.6 percent by volume) in a small stream in Oregon (Nussbaum, unpublished). There were no zooplankters in their stomachs.

Martof and Scott (1957) reported that larval *Leurognathus marmoratus* in streams in the eastern United States eat aquatic insects almost exclusively (98.5 percent of 840 items). These authors reported no zooplankters in the diet.

FOOD SIZE

Samples of larval *Ambystoma macrodactylum* from a pond in central Oregon and of larval *Dicamptodon ensatus* from mountain streams in western Oregon were collected in order to compare their food habits with particular attention to food size (Nussbaum, unpublished). Each sample consisted of 30 larvae carefully selected to encompass a similar range of body sizes (22.2–34.9 mm snout vent length for *A. macrodactylum*, 23.7–34.4 mm for *D. ensatus*). The stomachs of *A. macrodactylum* contained 1,760 identifiable food items, 1,662 (94.2 percent) of which were planktonic organisms (mainly cladocerans) less than 0.4 mm in diameter. By contrast, the larval *D. ensatus* had consumed only 212 identifiable food items, none of which was planktonic. Only 43 (20.3 percent) food items were less than 0.4 mm in diameter.

FOOD SIZE-BODY SIZE RELATIONSHIP

Unlike mammals and many birds, salamanders are largely incapable of tearing or chewing large prey into smaller pieces for ingestion. Their teeth are small and needle-like and serve only to grasp prey. Therefore, the size of larval salamanders is expected to place a strict upper limit on their prey size.

Dodson and Dodson (1971) showed that food size may be an important limiting factor, even over small ranges of food size, for hatchling *Ambystoma tigrinum*. The smallest larvae (<7 mm) in a kettle pond in Colorado fed on *Daphnia* ranging in size from 0.7 to 0.9 mm, whereas larger larvae fed only on *Daphnia* larger than 1.0 mm.

Two populations of *Rhyacotriton olympicus* were studied to determine the food size-body size relationships in a lotic system (Nussbaum, unpublished). The study sites in Oregon were described elsewhere (Nussbaum and Tait, 1977). In both spring samples, there is a significant positive regression of food size on larval size (head width). The regressions are significant for three measures of food size (Table 3). The regressions are weaker (Perdution Trail) or insignificant (Fall Creek) for the autumn samples when fewer and smaller food items were in the stomachs. This latter result may indicate that food is less abundant in the autumn months and that larvae are forced to seek suboptimal (smaller) food during this time of year.

Given that salamanders ingest their prey whole, it is not surprising that prey size and larval body size are correlated to some extent, as is the case in some fishes (Gatz, 1979; Ringler, 1979; Werner, 1974). Although the upper limit of prey size is likely to be limited by the size of the larval mouth opening, the lower limit of prey size is determined by the efficiency of the gill raker filtering system. Observations on hatchling pond larvae (*Ambystoma gracile*, *A. macrodactylum*, *Taricha granulosa*) in aquaria (Nussbaum, unpublished) indicate that plankton-sized prey are stalked and ingested individually. Larger larvae of these species stalk and capture much larger individual prey such as insect nymphs, but they continue to ingest zooplankton by filter-feeding. Because of their small size at hatching, pond larvae are virtually dependent upon plankton during their early postembryonic life. Their dual feeding system allows them to utilize both plankton and larger prey during later life (Dineen, 1955; pers. obs.).

Observations summarized above indicate that (1) the size-frequency distribution of available prey differs between lentic and lotic environments, with more small prey (zooplankton) in lentic environments, (2) pond-dwelling larval salamanders are behaviorally and morphologically adapted to feed on zooplankton, (3) pond larvae actually consume a much higher percentage of smaller prey than do stream larvae, and (4) the body size of larval salamanders partially determines their maximum prey size.

EGG SIZE AND HATCHLING SIZE

Logic dictates that larger ova should produce larger hatchlings, both within and between species, and empirical data for virtually all groups of poikilotherms studied bear out this prediction; e.g., *Daphnia* (Green, 1956); cephalopods (Mangold-Wirz, 1963); Cirripedes (Barnes and Barnes, 1964); land snails (Wolda, 1970); fairy shrimp (Belk, 1977); marine ben-

TABLE 3
 RELATIONSHIP BETWEEN BODY SIZE (HEAD WIDTH) AND FOOD SIZE FOR TWO LARVAL
 POPULATIONS OF STREAM-ADAPTED SALAMANDERS, *Rhyacotriton olympicus*

	d ¹ _{max} vs. Head Width		V ² _{max} vs. Head Width		V ³ _{mean} vs. Head Width		Average Food Volume/ Stomach (mm ³)	Average Food Volume/ Food Item (mm ³)	Number of Stomachs	Total Food Items	
	r	slope	r	slope	r	slope	signif.	signif.			
Perdition Trail											
Spring	0.594	0.399	0.317	4.315	0.497	0.339	=0.0196	16.2	0.49	54	2099
Fall	0.297	0.128	0.228	0.551	0.286	0.058	=0.0614	5.8	0.23	68	1815
Fall Creek											
Spring	0.499	0.391	0.459	4.258	0.446	0.550	=0.0001	15.3	1.12	65	1000
Fall	0.010	0.005	0.127	0.606	0.058	0.064	=0.2960	4.3	0.63	70	552

¹Diameter of largest food item in stomach.

²Volume of largest food item in stomach.

³Mean volume of food items in stomach.

thonic invertebrates (Thorson, 1936, 1950); invertebrates (Strathmann, 1977); fishes (Bagenal, 1967, 1969; Blaxter and Hempel, 1963; Gall, 1974; Marshall, 1953; McDowall, 1970; Rounsefell, 1957; Svårdson, 1949); frogs (Pettus and Angleton, 1967; Salthe and Duellman, 1973); lizards (Derickson, 1976); vertebrates (Ballinger, 1978).

Nussbaum (1968) and Salthe (1969) found that ovum size and hatchling size are positively correlated in salamanders, but neither author presented regression statistics, nor did they explicitly state the criteria for hatchling size. References to egg size and hatchling size of salamanders are often ambiguous. Many authors did not state whether they measured the vitellus or the entire egg including the mucoid capsules. Most authors also did not indicate the developmental stages associated with their measurements of "hatchling size." In an ecological sense, the size at which the embryo escapes from its egg membranes (hatches) may not be as important as the size at which an embryo becomes dependent upon external sources of energy. Embryos of stream-breeding salamanders often hatch with considerable yolk reserves and may not feed for weeks or even months after hatching (Nussbaum, 1969a,b; Orr and Maple, 1978; Tilley, 1970). In one Oregon population of *Dicamptodon ensatus*, embryos hatch at 23.5 mm total length, but do not necessarily feed until about 220 days later at 35.7 mm total length when maintained in the laboratory at 13°–15° C. Hatchlings of small-egged pond-breeding salamanders of the genus *Triturus* do not feed for 1–4 days after hatching (Himstedt, 1967).

Complete data on ovum size and initial feeding size are available for 36 species of pond- and stream-breeding salamanders in 21 genera and six families (Table 4). For this sample, ovum size and initial feeding size are highly correlated (Fig. 2). Ovum size predicts 95.6 percent of the variance in initial feeding size.

Kaplan (1980) studied the relationship between ovum volume and total length at initial feeding (Harrison stage 46) within four populations of three species of salamanders of the genus *Ambystoma*. All correlation coefficients, ranging from 0.517 to 0.925, were positive and most were significant. Therefore, there is good evidence, both within and between species, that ovum size largely determines the initial feeding size of salamanders.

EGG SIZE AND EMBRYONIC PERIOD

The metabolic rate per unit weight of animal tissue is a decreasing function of total tissue weight (Brody, 1945; Kleiber, 1961), and the developmental rate of amphibian embryos is positively correlated with metabolic rate (Connon, 1947). These facts provide a physiological basis for predicting that ovum size and embryonic period will be positively correlated in animals. Most of the available data for a wide variety of poikilotherms do indicate that larger eggs require more time to develop (Ballinger, 1978; Berrill, 1935; Calow, 1978; Clarke, 1982; Mangold-Wirz, 1963;

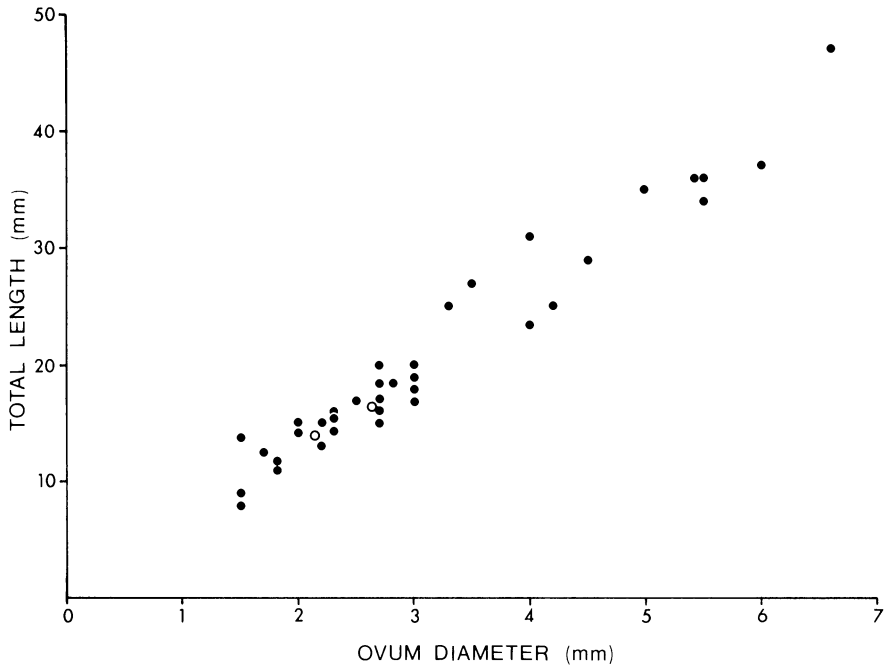


FIG. 2. Scatter plot of egg size and total length of embryos when they begin feeding for 36 species of salamanders (solid dots, data from Table 4) and for two populations of *Ambystoma maculatum* (open dots, from DuShane and Hutchinson, 1944). The least squares regression for the 36 species is described by $Y = -0.168 + 6.638X$, $r = 0.978$, $p < 0.0001$.

McLaren, et al., 1969; Oeldorf, et al., 1978; Perron, 1981; Spight, 1975; Steele, 1977; Steele and Steele, 1973; Thorson, 1935; Wear, 1974).

However, Underwood (1974) in criticism of the models of Vance (1973a,b), argued that there is no correlation between egg size and the length of the embryonic period for invertebrates. Steele (1977) countered this claim with abundant evidence, and Strathmann (1977) showed that a positive correlation often is observed, but that the correlation may be weak or absent for reasons which are taxon specific.

In salamanders and frogs, over small ranges of ovum size, larger ova may develop faster than smaller ova (DuShane and Hutchinson, 1944; Kaplan, 1980; Licht, 1971; Moore, 1939, 1942). However, this relationship is counterintuitive for large changes in egg size, and data for 34 species of salamanders (Table 4, Fig. 3) indicate a positive correlation between ovum size and embryonic period (time to initial feeding). Ovum size accounts for 62.9 percent of the variance in embryonic period, with larger ova requiring more time to develop. Other factors, e.g., temperature, light, oxygen concentration, and concentration of metabolites such as carbon dioxide and ammonia, are known to influence rate of development. If these variables

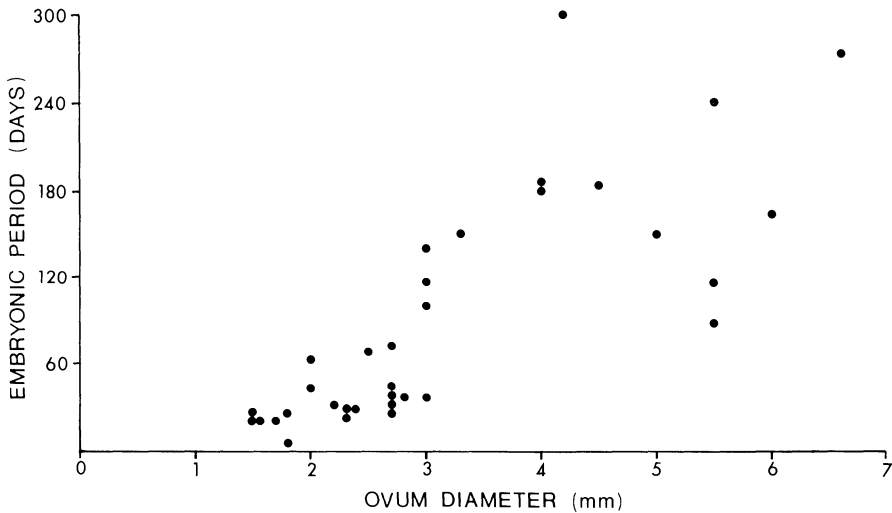


FIG. 3. Scatter plot of egg size and length of embryonic period for 34 species of salamanders (data from Table 4). $r = 0.793$, $p < 0.0001$.

were accounted for, then ovum size would probably determine a far greater percentage of the variance of embryonic period.

It has been argued that interspecific correlations between two variables are meaningless unless the correlations exist at the intrapopulation levels as well, because selection acts on variation only within populations (Tinkle, 1969; Vance, 1974). Kaplan (1980) held this view in regard to ovum size and embryonic period in salamanders. He studied the relationships between egg size and developmental time among five populations of three species of *Ambystoma* and concluded that (p. 59): "The intrapopulation data presented here further contradict the claim that large ova have slower rates of development since, in fact, the offspring of females that produce larger eggs reach the feeding stage more rapidly." Kaplan's (1980) range of ovum diameters across the five populations was < 1.0 mm (estimated from his Fig. 1, p. 54). With such small ranges of egg size, factors other than egg size, both genetic and ecological, may be more important in determining the length of the embryonic period. Small eggs and slow development may be pleiotropic effects of particular genotypes, or may reflect maladaptation maintained by inward gene flow (see Stearns and Sage, 1980). Or, females with small eggs may have suffered poor feeding conditions that affected both the quantity and quality of the yolk, with poor yolk quality causing slow development. Considering this, it is reasonable to predict that the pattern of covariance of egg size and embryonic period will vary both geographically and from year to year within populations as a result of different genotypes interacting with temporally variable ecological factors.

At a more general level, because of the time scale, patterns of covariation observed within populations largely reflect the outcome of stabilizing selec-

TABLE 4
DEVELOPMENTAL DATA FOR SALAMANDERS

	Ovum Diameter (mm)	Initial Feeding Size (mm total length)	Embryonic Period (days)	Authority
<i>Ambystomatidae</i>				
<i>Ambystoma cingulatum</i>	2.3	15.5	29	Anderson & Williamson, 1976
<i>Ambystoma gracile</i>	2.0	15.0	62	Bishop, 1943; Licht, 1975; Brown, 1976
<i>Ambystoma jeffersonianum</i>	2.2	13.0	30	Bishop, 1941
<i>Ambystoma mabeei</i>	2.2	15.0	—	Hardy, 1969
<i>Ambystoma maculatum</i>	2.7	16.0	36	Bishop, 1941
<i>Ambystoma opacum</i>	2.7	18.3	41	Bishop, 1941
<i>Ambystoma tigrinum</i>	3.0	17.0	35	Bishop, 1941
<i>Dicamptodon copei</i>	5.5	34.0	240	Nussbaum, unpublished
<i>Dicamptodon ensatus</i>	6.6	47.0	275	Nussbaum, 1969a, unpublished
<i>Rhyacosciredon rivularis</i>	2.7	20.0	35	Brandon & Altig, 1973
<i>Rhyacotriton olympicus</i>	4.2	25.0	300	Nussbaum, 1969b, unpublished
<i>Cryptobranchidae</i>				
<i>Andrias japonicus</i>	5.5	36.0	115	Kerbert, 1904; Tago, 1920
<i>Cryptobranchus alleganiensis</i>	6.0	37.0	162	Smith, 1907, 1912
<i>Hynobiidae</i>				
<i>Onychodactylus japonicus</i>	5.0	35.0	150	Iwasawa & Kera, 1980

Plethodontidae					
<i>Desmognathus fuscus</i>	3.0	19.0	116		Tilley, 1968; Orr & Maple, 1978
<i>Desmognathus monticola</i>	4.0	23.5	181		Tilley, 1968; Orr & Maple, 1978
<i>Desmognathus ochrophaeus</i>	3.0	18.0	140		Bishop, 1941; Tilley, 1968, 1970; Orr & Maple, 1978
<i>Desmognathus quadramaculatus</i>	4.5	29.0	183		Martof, 1962; Tilley, 1968; Orr & Maple, 1978
<i>Eurycea bislineata</i>	2.7	17.0	70		Bishop, 1941; Duellman & Wood, 1954
<i>Eurycea lucifuga</i>	2.5	17.0	68		Hutchinson, 1956; Green et al., 1967
<i>Cynophihilus porphyriticus</i>	3.5	27.0	—		Bishop, 1941
<i>Hemidactylium scutatum</i>	2.7	15.0	30		Bishop, 1920
<i>Pseudotriton ruber</i>	3.3	25.0	150		Bruce, 1968
Protetidae					
<i>Necturus maculosus</i>	5.5	36.0	86		Bishop, 1926
<i>Proteus anguinus</i>	4.0	31.0	180		Vandel & Bouillon, 1959; Briegleb & Schwartzkopff, 1961; Thorn, 1968
Salamandridae					
<i>Cynops pyrrhogaster</i>	2.0	14.3	42		Anderson, 1943
<i>Euproctus asper</i>	3.0	20.0	100		Casser, 1964
<i>Notophthalmus viridescens</i>	1.5	9.0	25		Pope, 1924; Bishop, 1941
<i>Pleurodeles waltl</i>	1.7	12.6	20		Gallien & Durocher, 1957
<i>Taricha granulosa</i>	1.8	12.0	26		Twitty, 1936; Connon, 1947
<i>Taricha rivularis</i>	2.8	18.5	31		Twitty, 1936; Connon, 1947
<i>Taricha torosa</i>	2.3	14.5	25		Twitty, 1936; Connon, 1947
<i>Triturus alpestris</i>	1.8	11.5	13		Knight, 1938
<i>Triturus helveticus</i>	1.5	10.4	20		Gallien & Bidaud, 1959
<i>Triturus vulgaris</i>	1.5	8.0	20		Thorn, 1968; Bell, 1974; Bell & Lawton, 1975
<i>Tylolotriton verrucosus</i>	2.3	15.3	27		Ferrier, 1974

tion that may involve complex compromises because of pleiotropy, linkage, and related factors. Therefore, covariation within populations cannot be expected to indicate the path of evolution under directional selection, which may involve large changes accumulated over long periods of time. Conversely, for the same reason, patterns of covariation across populations will not necessarily approximate patterns observed within populations. In contrast to Tinkle (1969), Vance (1974), and Kaplan (1980), I argue that in most cases, interspecific comparisons provide stronger evidence for functional relationships between characters or parameters than do intrapopulation comparisons. Correlation across unrelated (at some taxonomic level) species suggests independently evolved combinations of character states as either a common solution to a common problem, or a result of an inescapable cause and effect relationship (see Ridley, 1983 for discussion of this problem).

CONSEQUENCES OF PROLONGED EMBRYONIC PERIOD

With other factors constant, total embryonic mortality is expected to increase with embryonic period. Spight (1975) found evidence that this occurs with the prosobranch, *Thais lamellosa*, and similar relationships have been suggested for nudibranchs (Gibson, et al., 1970; Todd, 1979). Almost no information is available for salamanders, but Kusano (1980) presented data for *Hynobius nebulosus* that can be interpreted to indicate an inverse relationship between embryonic survival and embryonic period (Fig. 4). Similar conclusions can be extracted from the data of Harris (1980) for *Ambystoma maculatum* and Petranka (1984b) for *A. texanum*. Given this relationship, compensatory mechanisms to reduce the rate of embryonic mortality in large-egged species are expected. At least four such adaptations seem evident.

Firstly, early escape from the egg membranes and dispersal of yolk-laden embryos (discussed above) would increase survivorship in situations where entire nests are subject to predation, and, in cases involving parental care, this mechanism would free the parent(s) to invest earlier in future offspring.

Secondly, developing embryos could be displaced from the nutritive substance in large ova, so that differentiation can proceed unhampered by the need to cleave large yolky cells. This mechanism is apparent in amphibians with large ova (Noble, 1931), and it is observed in extreme form in some prosobranchs where developmental time is minimized by extraembryonic provisioning via nurse eggs (Spight, 1975).

Thirdly, large ova with long developmental times may be provided with protective devices or inaccessible nest sites. According to Nikolsky (1963), sharks and chimaerids have the largest eggs (up to 80 mm diameter) among fishes. These eggs hatch into very large larvae that are capable of devouring young teleost fishes. Nikolsky believed that the tough, horny membrane surrounding shark embryos is an adaptation for increased

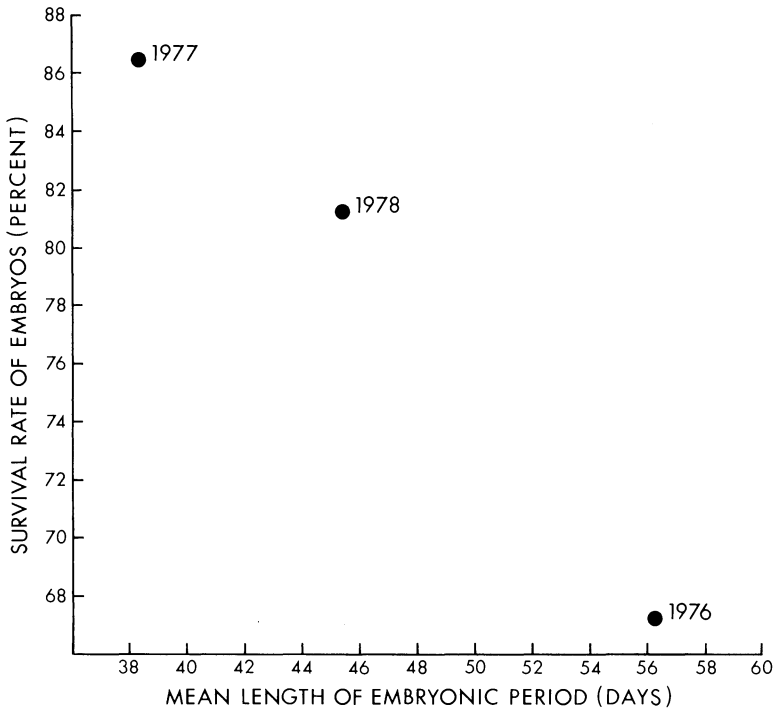


FIG. 4. Survival rate of embryos of *Hynobius nebulosus* as a function of embryonic period. Data extracted from Kusano (1980).

embryonic survival, which evolved to compensate for low fecundity. However, in keeping with their large eggs, sharks have long embryonic periods, often exceeding 250 days (Breder and Rosen, 1966), and this latter factor may be more important than reduced fecundity, per se, in the evolution of protective membranes. Fishes with small eggs and short embryonic periods often scatter their eggs indiscriminately with no attempt to hide them (Marshall, 1953), whereas fishes with larger ova and long developmental times, such as most salmonids, bury theirs in gravel. Among marine gastropods, species with long embryonic periods place their eggs in hidden nest sites and provide them with protective egg capsules, and species with brief embryonic periods attach their eggs in exposed places and provide almost no protective covering (Perron, 1981; Spight, 1975). Calow (1978) found evidence that an extra protective membrane on the eggs of certain freshwater gastropods with large eggs enhanced embryonic survivorship. Benthic marine invertebrates with non-planktonic lecithotrophic embryos have long developmental times and typically have protective egg cases (Vance, 1973a).

Pond-breeding salamanders with small eggs and rapid development, oviposit in relatively exposed sites, whereas large-egged stream-breeding

salamanders with long embryonic periods invariably have well-hidden nest sites. There are a few species with close relatives among pond-breeders that breed in slow-moving streams with physical and biotic characteristics intermediate between those of lentic and lotic environments. Examples are *Ambystoma ordinarium*, *A. rosaceum*, *Hynobius kimurai*, *H. naevis*, and *Taricha rivularis*. Also, populations of *T. torosa* in the Sierra Nevada Mountains have a tendency to breed in slow parts of streams and rivers. And, some populations of *A. texanum* in Indiana and Kentucky breed in streams rather than the usual ponds. These forms all have larger ova, and presumably longer embryonic periods, than most of their congeners among the pond-breeders, but smaller ova than the highly specialized stream-breeders. Their oviposition sites are also intermediate between those of pond-breeders and the more specialized stream-breeders. They attach their eggs to the undersides of superficial objects such as leaves, twigs, logs and flat stones (Anderson and Webb, 1978; Anderson and Worthington, 1971; Petranksa, 1982, 1984c; Tago, 1931; Twitty, 1935, 1942, 1966). In contrast, specialized stream breeders such as *Dicamptodon* spp., *Onychodactylus japonicus*, and *Rhyacotriton olympicus* place their eggs in deep, virtually inaccessible (to collectors) crevices, sometimes more than one meter below the surface (Nussbaum, 1969a,b; Tago, 1931). Hence, among salamanders, there appears to be a direct correlation between egg size or embryonic period and the relative accessibility of the nest site.

The fourth mechanism for reducing embryonic mortality is embryo guarding or parental care. Presumably, providing embryos with protective devices and abandonment of embryos in hidden developmental chambers is less costly than embryo guarding because the latter involves the loss of time and energy that could otherwise be spent on future offspring.

Larger hatchlings can be produced only by increasing egg size, which necessitates reduced clutch size and longer embryonic periods. To compensate for longer embryonic period and reduced clutch size, selection will favor any mechanism to reduce the rate of embryonic mortality. Hidden nests and embryo-guarding seem to be the most important solutions among lotic-breeding salamanders. Therefore, factors that select for large hatchlings among lotic breeders indirectly (ultimately) select for parental care.

LACK OF PARENTAL CARE AMONG LENTIC-BREEDING SALAMANDERS

Reduction of embryonic mortality should be advantageous regardless of breeding site. Lentic-breeding salamanders have evolved a variety of mechanisms to reduce embryonic mortality, including highly toxic eggs (Twitty, 1966), scattering eggs through space and time (Smith, 1964) and hiding single eggs between folds of leaves of aquatic plants (Smith, 1964), but in no case has embryo-guarding evolved among lentic-breeders, *Siren intermedia* excepted (see discussion above). The reasons for this are not clear,

although a few possible explanations exist. Egg-scattering may be a more effective way to insure embryonic survival than guarding if developmental time is short, and embryo guarding is incompatible with egg-scattering. Egg scattering has evolved only among permanently aquatic salamanders (some sirenids) and those that develop secondary aquatic adaptations during the breeding season (many salamandrids). This "second metamorphosis" allows transformed terrestrial adults to return to the aquatic environment, either permanently (some populations of *Notophthalmus viridescens*), or for prolonged periods (*Taricha* spp., *Triturus* spp., *Cynops*, *Paramesotriton*). Adult sirenids obtain all of their food from the aquatic environment, and some adult salamandrids obtain a high percentage of their annual food intake from ponds and lakes: 100 percent in the case of permanently aquatic *N. viridescens* and about 50 percent in *T. vulgaris* in Moravia (Pellantová, 1973). Aquatic feeding may be the reason that females can afford to spend several weeks of the growing season in the aquatic environment while eggs are being scattered. Transformed lentic-breeding ambystomatids and hynobiids do not undergo secondary metamorphosis, do not feed extensively while in the breeding ponds, and females remain in the ponds only a few days. Eggs are usually placed in a single or few clumps among pond-breeding ambystomatids, and in two clumps (one from each oviduct) placed close together among pond-breeding hynobiids. Egg scattering and/or parental care may be too costly in these forms because the adults would lose 2-3 weeks of prime growing season. The cost would be reduced growth, reduced clutch size the following spring, or perhaps even the loss of a breeding season. Instead, these forms seem to be selected for maximal fecundity (small, numerous eggs), maximal adult use of each growing season, and reliance on short embryonic periods for minimal embryonic mortality.

ADAPTIVE SIGNIFICANCE OF EGG SIZE

The major physical factors of the aquatic environment that have been invoked as selective agents for egg size are temperature and oxygen concentration. Often they have been considered together. Among those who suggested that large eggs are adaptations for development in cold water are Brown (1977), Despax (1923), Kuramoto (1975), Licht (1971), Marshall (1953), Moore (1942, 1949a,b), Rass (1941), Salthe (1969), Salthe and Duellman (1973), and Thorson (1936, 1950). Moore (1949b) and Licht (1971) offered no explanation for the adaptive significance for large frog eggs in cold water, and admitted that the evidence is based entirely on correlation of egg size with latitude and habitat. Brown (1977) claimed that the large eggs of the stream-breeding frog, *Ascaphus truei*, provide energy needs for development in cold streams, but he did not explain why "energy needs" are greater in colder than in warmer environments. Kuramoto (1975) thought that frogs deposit smaller eggs in warmer water because of the relatively low oxygen concentration in such habitats. Smaller eggs re-

quire less oxygen per unit time for development. This argument implies that selection always favors large eggs except under conditions of low oxygen concentration. Marshall (1953), following the lead of Rass (1941), argued, unconvincingly, that large eggs in cold-adapted fishes increase the growth rate of embryos and larvae "thus counteracting the retarding influence of low temperature," (p. 340). He also suggested that the reduced surface-to-volume ratio of large embryos reduced metabolic heat loss in cold environments.

Despax (1923) pointed out that salmonid fishes and salamanders of the genus *Euproctus* deposit large eggs in streams, whereas cyprinid fishes and true tritons (salamanders, mainly of the genus *Triturus*) lay smaller eggs in still waters. Despax, along with Salthe (1969), believed that flowing water is generally colder than static water, and, therefore, that colder temperatures select for larger eggs in fishes and aquaticly reproducing salamanders. Neither Despax nor Salthe offered an explanation for the advantage of large eggs in cold water.

There is no evidence to support the assumption that cold temperatures directly select for larger eggs in poikilotherms. Furthermore, the presumed correlation between low temperatures and large eggs is not supported with temperature data taken at nest sites. Rather, it has been assumed that species from high latitudes and high elevations expose their embryos to lower temperatures and that streams are colder than ponds, even during the early spring months. At least for amphibians, these assumptions are oversimplified. Populations at lower latitudes and lower elevations usually breed earlier than those at higher latitudes and higher elevations. Thus, although seasons are delayed and shorter at higher latitudes and elevations, the nest site temperatures there may be nearly the same as those at lower latitudes and elevations because of temporal factors. Furthermore, the assertion that streams are colder than still waters may be questioned, if early springtime, breeding season temperatures of lotic and lentic environments are compared (Table 5). Most pond- and lake-breeding amphibians of temperate-boreal climates breed in the early spring when snow and ice remain near and in the water, and the embryos are subjected to nearly freezing temperatures for the duration of their relatively brief embryonic period. For salamanders, the correlation does not seem to be between egg size and nest site temperature, but rather between egg size and lentic versus lotic environments.

Another physical factor, current, has been envisioned as a selective agent of large egg size in stream-breeding salamanders. Dunn (1923), Noble (1927), and Schmalhausen (1917) noted that stream-adapted larval salamanders hatch in an advanced stage of development compared to hatchlings of pond-breeding salamanders. Both the fore- and hindlimbs of stream-adapted hatchlings are fully developed by the time feeding becomes necessary, and their digits develop nearly simultaneously. Hatchlings of pond-adapted salamanders begin feeding before their limbs are fully developed, and their forelimbs and preaxial digits develop faster than their hindlimbs and postaxial digits. Noble (1927) could see no advantage

TABLE 5
NEST SITE TEMPERATURES FOR LENTIC- AND LOTIC-BREEDING SALAMANDERS

	Temperature (°C) Aquatic Nest Site		Sample Size	Authority
	\bar{x}	Range		
Lentic				
<i>Ambystoma gracile</i>	8.5	4.4–14.3	9	Brown, 1976
<i>Ambystoma macrodactylum</i> <i>croceum</i>	12.2	10.5–18.0	32	Anderson, 1968b
<i>Ambystoma macrodactylum</i> <i>sigillatum</i>	8.7	3.4–13.5	5	Anderson, 1968b
<i>Ambystoma tigrinum</i>	8.8	8.5– 9.0	2	Nussbaum, unpublished
<i>Hynobius dunni</i>	9.2	6.5–13.5	4	Kuramoto, 1966
<i>Hynobius leechii</i>	—	8.0–10.0	—	Tago, 1931
<i>Hynobius nebulosus</i>	8.5	4.8–13.2	7	Kuramoto, 1966
<i>Hynobius nigrescens</i>	—	6.5–13.0	2	Okada, 1933
<i>Hynobius retardatus</i>	—	3.0– 5.0	—	Sasaki, 1924
<i>Hynobius fuscus</i>	—	8.0–12.0	—	Tago, 1931
<i>Taricha granulosa</i>	6.8	5.0– 8.5	6	Nussbaum, unpublished
Lotic				
<i>Andrias japonicus</i>	13.0	—	1	Kerbert, 1904
<i>Cryptobranchus alleganiensis</i>	—	14.0–18.0	—	Smith, 1907
<i>Dicamptodon copei</i>	11.0	9.0–14.0	9	Nussbaum, unpublished
<i>Dicamptodon ensatus</i>	9.5	6.7–12.0	6	Nussbaum, 1969a, unpublished
<i>Hynobius kimurai</i>	—	5.0– 8.0	—	Tago, 1931
<i>Hynobius naevius</i>	—	8.0–10.0	—	Tago, 1931
<i>Hynobius tsuensis</i>	10.1	7.0–11.8	10	Kuramoto, 1966
<i>Rhyacotriton olympicus</i>	8.7	8.3– 9.1	2	Nussbaum, 1969b
<i>Onychodactylus japonicus</i>	—	8.0–15.0	—	Tago, 1931

to pre-feeding development of limbs and digits in stream larvae, but later authors (e.g., Carroll, 1970; Salthe, 1969; Salthe and Duellman, 1973; Salthe and Mecham, 1974) believed that these features allow the hatchlings to orient better and maintain their position in the current. Kishi (1979), McDowall (1970) and Thibault and Schultz (1978) similarly argued that large eggs and large hatchlings were adaptations to resist current in various fishes.

The current-adaptation argument is not necessarily mutually exclusive with the prey-size argument because well developed limbs would allow greater mobility in searching for and handling scarcer and larger prey in streams. On the other hand, many small lotic organisms, including hatchling salamanders, manage to avoid currents by living under rocks, in the interstices of gravel, and in pools.

Numerous authors recognized the relationship between egg size and hatchling size and suggested that biotic interactions of hatchlings select for

increased hatchling size and therefore increased egg size. Generally, the arguments are cast in terms of competition, both inter- and intraspecific, and predator avoidance. Seldom is the actual mechanism of competition or predator avoidance discussed. There seems to be no reason to assume that competition and predation are more intense in streams than in ponds or lakes. Furthermore, small numerous eggs with brief embryonic periods may be a more effective way to cope with certain types of competition and predation than the reverse set of adaptations.

Bagenal (1971), Blaxter and Hempel (1963), and McDowall (1970) argued that the competitive advantage of large eggs in fishes lies in their larger yolk reserves, which allow the larvae to survive longer when food is scarce. Other ichthyologists (e.g., Hubbs, 1958; Hubbs et al., 1968; Scott, 1962) believed that large hatchling fishes are selected for in competitive environments, but did not state the nature of the competition nor the kind of environment that leads to competition. Svårdson (1949) and Marshall (1953) thought that, among fishes, selection favored numerous small hatchlings when there was no intraspecific competition and few large hatchlings when intraspecific competition was high. Their arguments are somewhat circular and group-selectionist as both authors thought selection would always favor mechanisms that reduce intraspecific competition. The argument presented here, that egg size is adjusted so that hatchlings can consume prey of the most abundant size classes, has been addressed indirectly and directly by various authors. Jagersten (1972) noted that planktotrophy is the rule among the primary larvae of marine invertebrates that hatch from small eggs poor in yolk. Barnes and Barnes (1964) rejected arguments that egg size in cirripedes is directly adapted to temperature and metabolic efficiency. They argued (p. 393) instead that the "survival value of large eggs would seem to lie not in the eggs themselves but in the fact that they produce large nauplii which will be better adapted to taking the large phytoplanktonic organisms, characteristic of cold waters, as food." Similarly, Strathmann (1977) thought that one advantage of increased egg size among marine invertebrates is increased size of pelagic larvae when feeding becomes necessary. Closer to the issue at hand, Nikolsky (1963) stated that fishes that breed in streams, such as many salmonids, have larger eggs because the larger hatchlings must consume larger food items in the absence or scarcity of planktonic organisms in such environments.

In regard to salamanders with terrestrial development, Piersol (1909, p. 475) argued that "The necessity for the large amount of yolk in the egg arises from the purely terrestrial development of the larva. Aquatic larvae have at command the minute and abundant fresh-water plankton as food supply [Note that this does not apply to salamanders with stream-adapted larvae], and are thus at an early age rendered independent of the nourishment provided in the yolk. The insect life that constitutes the early food of the terrestrial *Plethodon* is of larger size than much of the plankton and much less abundant. Consequently the animal on leaving the egg must be

able to wait for food through comparatively long intervals and also to capture food of larger size than an aquatic larva need do." Piersol (op. cit.) also explained that the demand for large amounts of yolk for larger hatchling size is a factor in reducing the number of eggs. Piersol's argument is essentially the same as mine, except that he failed to point out that terrestrial and lotic environments are equally deficient in small prey and that salamanders with terrestrial nests inherited their large eggs and brooding habits from stream breeding ancestors. Also, Piersol (op. cit.) did not attempt to relate this phenomenon to the evolution of parental care.

PARENTAL CARE AND EGG SIZE

It has been argued that parental care is a prerequisite for the evolution of larger and fewer eggs (Breder, 1935; Cadwallader, 1976; Curtis, 1938; Kuramoto, 1978; Salthe and Duellman, 1973; Shine, 1978; Svårdson, 1949). In this view, parental care relaxes selection for increased clutch size, and may even select for reduced clutch size because fewer eggs can be tended more efficiently. With these conditions, *ceteris paribus*, egg size is expected to increase. This scenario is counter to the hypothesis presented here, and, at least for salamanders, there is contradictory evidence.

The marbled salamander, *Ambystoma opacum*, like most of its congeners, has larvae adapted for life in ponds. Unlike most of its close relatives, *A. opacum* deposits eggs in hidden terrestrial nests, and the eggs are attended by the female (Noble and Brady, 1933). Nest sites are situated in the bottoms of empty ponds soon to be filled with water from autumn rains. When the ponds are flooded, parental care ends and the eggs quickly hatch. Although *A. opacum* has evolved parental care, there is no evidence that clutch size is reduced and egg size increased compared to non-attending species of *Ambystoma*. Among 14 non-attending *Ambystoma*, egg sizes range from 2.0 to 3.0 mm compared to 2.7 mm for *A. opacum*. At least in the case of *A. opacum*, parental care has not led to large egg size. Rather, egg and hatchling size conform to the pattern observed among other salamanders with pond-adapted larvae.

There is complementary evidence that increased egg size precedes parental care in salamanders. Species which are transitional between pond- and stream-adapted reproductive modes have eggs of intermediate size and superficially hidden nests, but no parental care. In western North America, newts of the genus *Taricha* are basically lentic breeders, but the most specialized of the three species, *T. rivularis* breeds in streams. Eggs are attached to the underside of surface stones in slow-moving streams and there is no parental care. Eggs of the two pond-breeders average 1.8 and 2.3 mm, whereas eggs of *T. rivularis* average 2.8 mm in diameter (Twitty, 1936). It is tempting to speculate that further increase in egg size and reduction in clutch size in *T. rivularis* would require deeper nest sites and parental care. Similarly transitional conditions occur in Mexican ambysto-

matids of the genus *Rhyacosiredon*, which are closely related to, and probably derived from, lentic-breeding salamanders of the genus *Ambystoma*. *Rhyacosiredon* spp. have relatively large eggs that are hidden under stones or stream banks in slow to fast streams and there is no parental care (Brandon and Altig, 1973; Campbell and Simmons, 1962; Dunn, 1928). Stream-breeding populations of *Ambystoma texanum* have larger eggs and hidden nests compared to pond-breeding populations of this species, but no parental care (Petranka, 1982, 1984c).

Two genera of fully-adapted lotic breeders, *Euproctus* and *Rhyacotriton*, provide further evidence that parental care evolves last in salamanders. Species of *Euproctus* (European salamandrids) hide eggs singly in crevices and spaces between stones in streams. The spaces where the eggs are placed are too small for access by predators or egg cannibals (Despax, 1923). This is accomplished by a unique morphological adaptation among salamanders. The female cloaca is cone-shaped and has "le role d'un veritable organe l'oviposition" (Despax, p. 167). Despax compared the cloaca of female *Euproctus* to the ovipositor of *Rhodeus amarus*, a freshwater cyprinid fish that uses its elongated cloaca to place eggs inside the mantle cavity of bivalve mollusks. *Euproctus* has combined the egg-scattering strategy (incompatible with egg guarding) of its close relatives (*Triturus*, *Cynops*, *Paramesotriton*) among pond-breeders with egg-hiding and perhaps in this manner has avoided the expense of parental care. *Rhyacotriton olympicus*, of northwestern U.S.A., has large eggs and the smallest reported clutch size of any salamander with aquatic nests (Nussbaum and Tait, 1977). The two reported nest sites were remarkably well hidden deep in narrow cracks in rock faces (Nussbaum, 1969b). There were no attending adults. The small size of adult *R. olympicus* allows them to place eggs in sites that are inaccessible to most other aquatic vertebrates in the region. In this instance lack of parental care may be correlated with the absence of egg predators, although egg cannibalism cannot be ruled out.

The observations presented above are consonant with the argument that large eggs, selected to produce large hatchlings, preceded the evolution of parental care in salamanders. There is evidence that larger and fewer eggs may evolve before parental care in frogs as well (McDiarmid, 1978).

PARENTAL CARE AND MATING SYSTEMS IN SALAMANDERS

MODELS OF MATE DESERTION

Factors that select for parental care are not necessarily the same factors that determine which sex gives care, or whether one or both sexes gives care. Theoretical aspects of male versus female desertion were presented by Baylis (1978), Blumer (1979), Dawkins and Carlisle (1976), Grafen and Sibly (1978), Gross and Shine (1981), Loiselle (1978), Perrone and Zaret (1979), Ridley (1978), Maynard Smith (1977, 1978), Trivers (1972), Wells (1977, 1981), Werren, et al. (1980) and Williams (1975).

Dawkins and Carlisle (1976) argued that if parental care is advantageous, then, among fishes with external fertilization, the sex that spawns first will be selected to desert first, leaving the partner to care for the embryos. They further suggested that because sperm quickly diffuses in water, males cannot afford to spawn first. Therefore, males are likely to be the care-giving sex among fishes with external fertilization.

Loiselle (1978) rejected this idea, because males are the most frequent care-giving sex even among fishes in which the males and females spawn simultaneously. Loiselle suggested instead that limited high-quality sites for spawning selects for territorial behavior and that territoriality leads to parental care by the territorial sex. Males are likely to be the territorial sex because the cost differential of male and female gametes makes territoriality a more profitable venture for males than for females. Males have greater potential for multiple matings within a defended territory than do females.

Baylis (1978) presented an argument similar to that of Loiselle, but thought that "rate" rather than "cost" of gamete production determined the territorial and hence the care-giving sex. According to this scheme, males should be selected to be the territorial and attentive sex because males produce gametes faster and can accept more mates within the territory per unit time than could territorial females. Elements of this same idea were presented by Blumer (1979), Perrone and Zaret (1979), and Ridley (1978).

The paternal certainty argument, reviewed and criticized by Maynard Smith (1977) and Werren, et al. (1980), stated that the confidence of paternity (Trivers, 1972) will determine the care-giving sex. A male has more to gain by investment (parental care) beyond fertilization as his paternal confidence increases. Mating systems in which males are territorial and fertilization is external provide high paternal confidence and should be correlated with paternal care. If fertilization is internal, then paternal confidence may be low, and maternal care is expected to evolve if parental care is advantageous.

Gross and Shine (1981) rejected the spawning sequence hypothesis of Dawkins and Carlisle (1976), and suggested that Williams' (1975) "association" hypothesis best predicts patterns of male versus female care of offspring. According to this hypothesis, an association, for any reason, between one parent or the other and its offspring preadapts that parent for parental care.

PHYLOGENY AND PARENTAL CARE IN SALAMANDERS

At present, salamanders are a poor source for support or refutation of theory on mate desertion because so little is known of their social interactions and reproductive behavior. Furthermore, prospects are not good because salamanders are not diverse. There are 8 families, 58 genera, and about 350 species, with one family (Plethodontidae) accounting for

about 61 percent of the species. Therefore, there is little opportunity to observe independent evolution of similar traits in separate lineages.

Terrestrial breeders with maternal care are mostly plethodontids (Appendix I), and maternal care may have evolved only once in this family. For plethodontids, the interesting question is: Under what conditions is parental (maternal) care secondarily lost (see Maiorana, 1976)? It is conceivable that maternal care evolved only twice in salamanders. This would be true if maternal brooding is an ancestral trait independently retained by species of *Dicamptodon*, *Amphiuma*, *Necturus*, *Proteus*, and the plethodontid species, if maternal brooding in *Ambystoma opacum* is derived from non-brooding ancestors, and if sirenid are not salamanders. There is nothing in the proposed phylogenies of salamanders (Milner, 1983, Naylor, 1978; Noble, 1931; Regal, 1966; Wake, 1966) that bars this possibility.

MODES OF FERTILIZATION

Among salamanders, fertilization is external in the two families (Hynobiidae, Cryptobranchidae) thought to be most primitive based on comparative morphology. Fertilization is internal via a spermatophore in five advanced families (Ambystomatidae, Salamandridae, Proteidae, Amphiumidae, Plethodontidae). The method of fertilization is unknown among sirenids. Transfer of sperm by a spermatophore is nearly unique to salamanders among vertebrates (A few atherinomorph fishes have spermatophores that are transferred directly to the female via a copulatory organ; see Grier, 1984.), and, as will be argued below, the spermatophore may be of significance in determining the care-giving sex in salamanders.

MATING SYSTEMS OF SALAMANDERS

The social aspects of reproduction in salamanders have been little studied. Even so, it is necessary to formulate a preliminary classification of their mating systems as a basis for discussion. For present purposes, five general, or modal, mating systems may be distinguished, the salient features of which are summarized in Table 6.

THE HYNوبيUS-MODE.—*Hynobius* is a genus of the Asiatic family Hynobiidae. There are about 18 species of *Hynobius*, 13 of which are confined to Japan. *Hynobius* spp. typically have aquatic larvae and terrestrial adults. They are average-sized salamanders, with mature individuals ranging from about 120 to 180 mm total length. Small-egged species breed in ponds and lakes and large-egged species breed in streams. The mating system described below is based on pond-breeding species of *Hynobius*.

The mating system includes external fertilization without a spermatophore, no male defense of courtship sites, and no parental care (Kunitomo, 1910; Kusano, 1980; Sasaki, 1924; Tago, 1931). The system is further characterized by explosive breeding during the early spring, with high male/female breeding ratios, as individual males remain in ponds longer than individual females. Females choose oviposition sites, begin to oviposit

TABLE 6
MATING MODES OF SALAMANDERS

	Mode				
	I. <i>Hynobius</i> ¹	II. <i>Cryptobranchius</i>	III. <i>Ranodon</i>	IV. Hypothetical	V. Advanced
Fertilization	external	external	external	external	internal
Spermatophore	no	no	yes	yes	yes
Spawns first	female	female	male	male	male
Chooses oviposition site	female	male	male	female	female
Parental care	none	paternal	paternal	maternal	maternal
Nest site	lentic	lotic	lotic	lotic	variable

¹Includes only lentic-breeding species of *Hynobius*.

before the males ejaculate, deposit their entire clutches at single sites, and leave the pond soon after spawning. Several males of *H. retardatus* (Sasaki, 1924), and *H. nebulosus* (Kusano, 1980) may fertilize the eggs of a single female, while the eggs are being extruded from the oviducts. Sasaki (1924) indicated that males of *H. retardatus* focus their attention solely on the eggs and that there is no male-male aggression during bouts of multiple fertilizations. He also reported that males typically grasp the base of the egg sacks with their forelimbs, place their vents on the emerging egg sacks to fertilize the eggs as they appear, and shove the female backwards with their hindfeet to assist in the delivery of the eggs. Sasaki noted that in atypical cases where males did not assist, oviposition lasted several times longer. This "midwifing" behavior can only be interpreted as a result of sexual selection among males to speed the appearance of eggs after they are in a good position to place spermatozoa directly on the eggs. The bending and stretching of the male's body, which accompanies "midwifing" behavior, may allow the male to coordinate ejaculation with the appearance of each new segment of the egg sacks. This contrasts with Sasaki's interpretation, that "midwifing" by males is an unselfish behavior designed to assist females in the delivery of eggs. Hashimoto (1976; *vide* Kusano, 1980) reported that males of *H. keyserlingi* attempt to monopolize egg sacks by aggression toward other males. Kusano (1980) observed that males of *H. nebulosus* sustained more tail injuries during the breeding season than do females. He concluded that this was not attributable to differential predation and suggested that fighting among males for egg sacks was the cause. Thorn's (1962, 1967) observations of male aggression associated with egg sacks in *H. nebulosus*, which he apparently mistook for paternal care, may reflect sexual selection to prevent other males from fertilizing the exposed eggs. Sasaki (1924), like Thorn, reported that males of *H. retardatus* remain near the eggs for several hours after the female departs, in both laboratory and field conditions, but Sasaki explicitly stated that this behavior was not a form of paternal care.

It is clear that among species of pond-breeding *Hynobius*, males may either attempt to monopolize egg sacks by aggression toward other males or ignore each other and simultaneously fertilize the eggs of single egg sacks. These contrasting strategies could depend on male density relative to female density. Aggression may payoff at low male density, but become a losing endeavor at some point along a gradient of increasing male density. At high male densities, individual males probably cannot drive away all sexual competitors, and, under these conditions, males should forego aggression and attempt to fertilize eggs as quickly as possible.

THE *CRYPTOBRANCHUS*-MODE.—The family Cryptobranchidae is composed of two genera and three species. The two genera are at present widely separated geographically, although morphologically they are very similar. The monotypic *Cryptobranchus* occurs in the eastern United States, and *Andrias* has two species, one in Japan and the other in southeastern

China. Cryptobranchids are permanently aquatic, stream-dwelling salamanders of large size; *Cryptobranchus* may grow to 0.8 m and *Andrias* to 1.8 m in total length.

The American hellbender, *Cryptobranchus alleganiensis*, has a relatively brief breeding season, lasting for about two weeks in Pennsylvania and New York (Bishop, 1941; Smith, 1907), but it may be longer in other parts of the range (Nickerson and Mays, 1973). Males select and defend hidden courtship-nesting sites (Smith, 1907). A female that chooses to enter a nest spawns just before or simultaneously with the resident male, and fertilization is external. A satellite male was observed to release sperm simultaneously with the dominant male in one instance involving captive animals (Smith, 1907). Resident males may mate with more than one female (Bishop, 1941), and resident males guard the eggs, driving away potential egg predators and egg cannibals (Smith, 1907). The Japanese giant salamander, *Andrias japonicus*, has nearly identical mating habits (Kerbert, 1904; Tago, 1929).

THE *RANODON*-MODE.—This mode is based on scanty but intriguing information on the reproduction of *Ranodon sibiricus*, a stream-breeding hynobiid, found, not in Siberia, but in Kazakhstan, U.S.S.R. This species has a typical amphibian life cycle with aquatic larvae that metamorphose into terrestrial juveniles. Terrestrial adults average about 225 mm total length. The mating season is prolonged, extending from April to August (Paraskiw, 1953). The male attaches a stalkless spermatophore to the substrate, usually under a stone in a stream, one to several females attach their twin egg sacks to the spermatophore, and fertilization is external (Paraskiw, 1953). It is not known whether males defend the courtship-nest sites, nor whether either parent guards the embryos, although males are territorial during the mating season in captivity (Hübener, 1960).

The most significant feature of the *Ranodon*-mode is the fact that the male spawns first and that this is possible because of the antidiffusion quality of the spermatophore. The *Ranodon*-mode, which involves external fertilization with a spermatophore, suggests that the salamander spermatophore initially evolved to allow males to spawn first. The advantage of spawning first for males becomes apparent when the *Ranodon*-mode is compared to the *Hynobius*-mode described above. Males that spawn first are free to drive off sexual competitors during the time the eggs are being deposited and fertilized. Dominant males of *R. sibiricus*, by virtue of their spermatophores, should be better able to cope with satellite males than are males of *Hynobius* spp., especially in cases of relatively high male density.

This argument is counter to the orthodox theory that spermatophores originally evolved among stream-breeding salamanders to prevent spermatozoa from being swept away from the eggs by the current (Salthe, 1967; and earlier authors). Stream-breeding salamanders normally mate under stones or in other protected aquatic chambers where there is almost no current. Therefore, there is little basis for arguing that spermatophores

were originally anti-current devices, although the antidiffusion quality of spermatophores is of significance, both in lotic and lentic environments.

The number of spermatophores produced by male *Ranodon sibiricus* in a single reproductive season is unknown. But, if Paraskiw's (1953) description of the spermatophore is accurate (twin sperm-filled sacks, 40 mm long by 5-6 mm diameter), then it is likely that the entire contents of the Wolfian ducts are placed in one spermatophore, which in turn suggests that males produce only one spermatophore per season. The placement of a single large spermatophore in a defended courtship-nest site may be a viable alternative to the production of numerous small spermatophores, if the large spermatophore has the potential to attract more than one female and to fertilize multiple clutches of eggs, and if the first female does not sequester the spermatophore.

THE HYPOTHETICAL-MODE.—If the *Ranodon*-mode (stalkless spermatophore, external fertilization) is similar to the ancestral mode of advanced salamanders (stalked spermatophore, internal fertilization), then intermediate modes must have existed, or perhaps still exist but are undiscovered. In the *Ranodon*-mode, the female must place her cloaca on the spermatophore to attach the eggs. A simple evolutionary step beyond this mode would be spermatophore sequestering by females. Either by adhesion of the spermatophore to the cloaca or by clasping the spermatophore with the hindfeet, or both, a female could easily swim away with the spermatophore (Females of many species use their hindfeet for various reproductive purposes, e.g., grasping slender twigs while ovipositing, wrapping leaves around single eggs). With this hypothetical mode, fertilization would be external, and yet females would be free to select nest sites away from courtship sites and courting males. With this system, it would be to the male's advantage to produce more and presumably smaller spermatophores, compared to the *Ranodon*-mode.

Although spermatophore sequestering with external fertilization is unknown among salamanders, it may occur in Asian species of *Ranodon*, *Liua* or *Batrachuperus* whose breeding biology is unknown. However, spermatophore carrying and external fertilization would seem to be highly inefficient compared to internal storage of spermatozoa and internal fertilization, and the former mode may have been doomed to rapid replacement by the latter mode.

THE ADVANCED MODE.—This mode includes all species with sperm transfer via a stalked spermatophore and internal fertilization. Normally, there is complete separation of courtship sites and oviposition sites. Males may deposit numerous spermatophores and inseminate more than one female in a single reproductive season. Beyond these general characteristics, the advanced mode encompasses a wide variety of mating systems, including explosive and prolonged breeding, territorial and nonterritorial behavior by males, female sequestering by males and lack thereof, complex courtships with relatively direct transfer of sperm and simple courtships with indirect transfer, and various degrees of promiscuity by both sexes (Arnold, 1976).

MATE DESERTION AND PARENTAL CARE IN SALAMANDERS

Wells (1977) and Ridley (1978) pointed out that among salamanders, paternal care occurs only in species with external fertilization and that maternal care is known only for species with internal fertilization. Both authors noted that these observations are consistent with the current desertion hypotheses that were developed largely for fishes. However, I believe that the correlation is spurious and that closer consideration of the reproductive biology of salamanders leads to another hypothesis: *Among salamanders, the sex that proximally chooses the oviposition site will necessarily be the attentive sex.* In this regard, the spermatophore plays two important roles: (1) it is an antidiffusion device that allows males to spawn first, and (2) it allows females the opportunity to sequester and transfer male gametes to nest sites away from courtship sites.

Good sites for oviposition (those that maximize survival of embryos) may not be good sites for courtship and exchange of gametes (those that maximize the rate of encounter of mates and the efficiency of courtship signalling and gamete exchange). Therefore, if both parents must be present at the time of oviposition, as in most cases of external fertilization, a classical sexual conflict may occur. Because of the greater potential of males for multiple matings, males may gain by sacrificing high quality oviposition sites for high quality courtship sites, but this strategy is not in the best interest of females. The reproductive success of females is measured largely by the survival rate of their embryos, and females should refuse to mate at sites that are of low quality for embryonic development. Therefore, in all mating systems in which females are the limiting sex, the nest site will *ultimately* be determined by female choice. In territorial systems, males may *proximally* choose the courtship-nest sites, but they will be selected to defend high quality oviposition sites to increase their attractiveness to females (Trivers, 1972).

If high quality nest sites are not limiting, and if the breeding season is brief and frenzied, then males gain nothing by establishing nesting territories. Instead, it is to the male's advantage to actively search for females and to spawn at sites chosen by females. This occurs in pond breeding species of *Hynobius* in which the twin egg sacks are abandoned at relatively unprotected sites. Presumably, such open nest sites vary in quality, and females are expected to be selective. But, nest sites of high quality are undoubtedly far more common for open-water spawners than for species that require hidden nest sites. Therefore, it is among species that require increased protection for embryos that nest sites are likely to be most precious.

If females prefer nest sites that by their nature are limited in number, then males should position themselves at these sites and exclude other males by aggressive territorial behavior. Males are not likely to abandon high quality courtship-nest sites after they establish ownership (Loiselle, 1978), and this predisposes males to be the parental sex (Trivers, 1972). In this regard, Smith (1907) suggested that the brooding habits of male *Crypto-*

branchus alleganiensis originated through continued defense of the courtship-nest site "while awaiting the coming of another ripe female."

In species with male territoriality, resident males may increase their chances of future matings by driving away former mates that may interfere with subsequent courtships. Male aggression toward recently spent mates was reported for *Cryptobranchus alleganiensis* (Smith, 1907) and *Andrias japonicus* (Kerbert, 1904). Maternal care is not likely to evolve under these circumstances.

According to the "spawning sequence" hypothesis (Dawkins and Carlisle, 1976), having spawned first, male *Ranodon sibiricus* will be selected to desert first. But, regardless of the different spawning sequence, male *R. sibiricus*, like male *Cryptobranchus alleganiensis*, are not likely to abandon a high quality breeding territory if there is a chance to mate again at that site. Therefore, males are expected to be the caring sex among species with a *Ranodon*-like mode of reproduction.

Spermatophore sequestering must have arisen from an ancestral mode of reproduction like that of *Ranodon*. The advent of this behavior allowed separation of courtship and oviposition sites in space and time, and consequently altered the reproductive strategies of males and females. Males would select and defend courtship sites based on defensibility, female encounter rate, and other courtship-related factors. Females would choose males at courtship sites for genetic advantage and then move to high quality oviposition sites for embryonic survival advantage. With this system, should parental care become advantageous, maternal care would evolve because the female chooses an oviposition site that is not in the male's best interest to guard (Note that this sequence may bear similarity to the evolution of the lek system).

Maternal care is also expected in species with the advanced mode of reproduction, not because fertilization is internal, as is conventionally argued, but because the spermatophore facilitates transport of male gametes by the female and separation of the sexes at the time of oviposition. Whether fertilization is external by virtue of a transportable stalkless spermatophore or internal via a stalked spermatophore, is inconsequential in this regard.

Under what circumstances would females benefit by transporting spermatophores away from courtship sites? To probe this question it is necessary to first consider more carefully the conditions under which the spermatophore may have originated, because those conditions were ancestral to, and perhaps identical to, the conditions associated with the origin of spermatophore sequestering.

The spermatophore is not likely to evolve in a social environment like that described above for pond-breeding species of *Hynobius*, in which breeding is explosive, females choose oviposition sites, and males scramble to fertilize eggs as soon as they appear. This is because, by their essential nature as antidiffusion mechanisms, spermatophores increase the amount of time between ejaculation and fertilization, and time lost during this critical period would be maladaptive for males with promiscuous nonter-

ritorial breeding systems. Furthermore, if females choose oviposition sites, males should not spawn until females have committed themselves to particular sites, otherwise the males may waste their gametes. Females are not committed to a site until they attach the bases of their egg sacks to the substrate and begin to draw the eggs out of their oviducts. Males are expected to spawn immediately after the eggs appear, as was observed by Sasaki (1924) for *Hynobius retardatus*.

Presuming that the spermatophore evolved to allow males to spawn first, then it must have evolved in a social environment that included male selection and defense of oviposition sites, because it is only in these circumstances that spermatophores can function to the male's advantage. As was argued above, male defense of oviposition sites will evolve only if high quality oviposition sites are in short supply, as would occur if hidden, rather than open-water, nests were utilized. Among salamanders with aquatic nests, hidden nests are used only by relatively large-egg species that reproduce in lotic environments, or environments transitional between lentic and lotic. This reasoning suggests that the spermatophore originated among salamanders with a mating system similar to that of *Cryptobranchus* or *Ranodon*.

Females would not transport spermatophores if this behavior led to depressed survival of their embryos. Therefore, transport must have evolved in the absence of paternal care that contributed significantly to embryonic survival. Even with the complete absence of paternal care, transport behavior seems counterintuitive, because males presumably were selected to choose and defend high quality oviposition sites to attract females. Why, then, should females abandon these sites after obtaining a spermatophore? There are at least three possible explanations, which are not mutually exclusive. Firstly, in dense, highly competitive breeding aggregations, females may avoid egg cannibalism, a common phenomenon in salamanders (Kaplan and Sherman, 1980; Nussbaum et al., 1983; Smith, 1907), by ovipositing away from the breeding arenas. Secondly, if high quality males (those with high quality territories) are in short supply, and if males produce a single or few spermatophores, then females can depress the fitness of other females by sequestering spermatophores for their exclusive use. Theoretically, post-spawning females, or females unready to mate, may be selected to induce males to deposit spermatophores and then sequester the spermatophores to interfere with the reproductive success of females that are ready to oviposit. Nussbaum and Tait (1977) noted that females of *Rhyacotriton olympicus* courted and accepted spermatophores even though they were not in reproductive condition. This behavior could reflect either sexual interference or acceptance of spermatazoa for much later use, since females of this species have sperm storage organs and internal fertilization, or both. Thirdly, variance in female readiness to oviposit, combined with female competition for limited spermatophores, would select for sequestering of spermatophores for use at a later time when a high quality male may not be immediately available. Females may not be ready to oviposit at first encounter for either physiological or ecological reasons. In regard to the

latter, Harris (1980), Kusano (1980), and Petranka (1984b) showed that delay of oviposition for a few days to a time when ecological conditions have improved could increase embryonic survival. Regardless of the cause of spermatophore sequestering, the advent of this behavior must have placed selective pressure on males to increase their production of spermatophores.

In conclusion, it appears that spermatophore sequestering evolved among salamanders with hidden courtship-nest sites that were selected and defended by males. Paternal care was poorly or not at all developed. These characteristics are most likely to occur in species with relatively large eggs and long embryonic periods, and with larvae adapted to feed in lotic waters largely devoid of plankton.

SUMMARY

Salamanders that breed in lentic habitats generally have numerous small eggs that are abandoned in open water, brief embryonic periods, and small hatchlings. Those that breed in lotic waters generally have fewer large eggs that are hidden and guarded, long embryonic periods, and large hatchlings. I argue that these two reproductive patterns ultimately are determined by basic differences in the trophic structure of lentic and lotic environments, mainly the abundance of plankton in the former and the virtual absence of plankton in the latter.

Abundant food in lentic waters is present in small (plankton-sized) packets, whereas the most abundant size class of food in lotic waters is necessarily much larger. In both environments, selection will adjust parental investment (per offspring) in such a way that the food supply available to hatchlings is maximized. This will lead to relatively high parental investment in lotic environments because larger hatchlings can ingest larger prey and would, therefore, have significantly more food available to them than would smaller hatchlings. Lentic environments would select for relatively low parental investment because available prey would not be increased significantly (enough to offset cost in fecundity) by increasing the size of hatchlings.

Parental care, restricted to embryo guarding in salamanders, is more likely to evolve in lotic environments than in lentic environments because of the relatively large investment in yolk per offspring in lotic environments. Larger eggs necessarily have longer embryonic periods. To compensate for the increased time component of embryonic mortality in streams, the rate component has been reduced by selection for hidden nests and parental care.

The distribution of parental care among taxa of salamanders indicates a strong phylogenetic component. Parental care possibly evolved as few as two times in salamanders. Maternal care in terrestrial-nesting plethodontids almost certainly was inherited from lotic-nesting ancestors, and the same may be true for terrestrial-nesting amphiumids. Maternal care and terrestrial-nesting evolved independently from lentic-breeding, non-brooding ancestors in *Ambystoma opacum*.

There are no certain cases of biparental care among salamanders. Either the male or the female cares, or there is no care. At least four models of mate desertion have been proposed, none of which seems adequate to explain the distribution of male and female parental care among salamanders.

The "spawning sequence" hypothesis of Dawkins and Carlisle (1976) states that the sex that spawns first will be selected to desert first, and that males normally cannot afford to spawn first because of the diffusibility of sperm. Although the antidiffusion quality of the salamander spermatophore allows the male to spawn first, it will not necessarily be to his advantage to desert first. At least ancestrally, the spermatophore may have served to increase the males' ability to defend against satellite males, in which case the resident male would be unlikely to desert unless there was no chance for future matings.

Contrary to the ideas of Loiselle (1978) and Baylis (1978), the differential cost or rate of production of male and female gametes does not determine the attentive sex, at least in salamanders. Males may be territorial, as predicted by the "cost-rate" hypothesis, but non-attentive because females may sequester spermatophores and choose oviposition sites outside of the males' defended courtship site. By so doing, females are committed to being the attentive sex.

Paternal certainty (Trivers, 1972) seems to play a minor role in determining the care-giving sex in salamanders. Male defense of courtship sites for paternity advantage will lead to paternal care only if the female chooses to deposit eggs in the defended courtship site.

The "association" hypothesis of Williams (1975) accurately predicts the care-giving sex in salamanders, but the generality of this hypothesis masks the significance of the salamander spermatophore. Presence or absence of a spermatophore, may be the crucial dichotomy in determining the attentive sex in salamanders, and not external versus internal fertilization. A spermatophore can affect either external or internal fertilization, but more importantly, the presence or absence of a spermatophore determines whether or not defended courtship sites and oviposition sites can be separated in space and time. The advent of the spermatophore and spermatophore sequestering by females ultimately allowed males to choose and defend courtship sites based on potential multiple mating advantages, and allowed females to choose oviposition sites based on embryonic survival advantages. Where courtship and oviposition sites are separated, the female will necessarily be the care-giving sex; where they are not separated, males are expected to be the care-givers.

ACKNOWLEDGMENTS

I want to thank Peter K. Ducey and David L. Schultz for critical discussions concerning the relationships between egg size, hatchling size, and parental care. Cynthia K. Tait helped in the field and laboratory in regard to analyzing food habits of salamanders. Edmund D. Brodie, Jr., Cynthia Kagarise Sherman, and Kentwood D. Wells reviewed the manuscript and offered invaluable advice. Mark Orsen drew Figure 1, and Jan Hodge typed the manuscript.

LITERATURE CITED

- Allen, W. E. 1920. A quantitative and statistical study of the plankton of the San Joaquin River and its tributaries in and near Stockton, California, in 1913. Univ. California Publ. Zool., 22:1-292.
- Anderson, J. D. 1968a. A comparison of the food habits of *Ambystoma macrodactylum sigillatum*, *Ambystoma macrodactylum croceum* and *Ambystoma tigrinum californiense*. Herpetologica, 24:273-284.
- . 1968b. Thermal histories of two populations of *Ambystoma macrodactylum*. Herpetologica, 24:29-35.
- . and R. E. Graham. 1967. Vertical migration and stratification of larval *Ambystoma*. Copeia, 1967(2):371-374.
- . and R. G. Webb. 1978. Life history aspects of the Mexican salamander *Ambystoma rosaceum* (Amphibia, Urodela, Ambystomatidae). J. Herp., 21:89-93.
- , and G. K. Williamson. 1974. Nocturnal stratification in larvae of the mole salamander, *Ambystoma talpoideum*. Herpetologica, 30:28-29.
- , and G. K. Williamson. 1976. Terrestrial mode of reproduction in *Ambystoma cingulatum*. Herpetologica, 32:214-215.
- , and R. D. Worthington. 1971. The life history of the Mexican salamander *Ambystoma ordinarium* Taylor. Herpetologica, 27:165-176.
- Anderson, P. L. 1943. The normal development of *Triturus pyrrhogaster*. Anat. Rec., 86:59-63.
- Antonelli, A. L., R. A. Nussbaum, and S. D. Smith. 1972. Comparative food habits of four species of stream dwelling vertebrates (*Dicamptodon ensatus*, *D. copei*, *Cottus tenuis*, *Salmo gairdneri*). Northwest Sci., 46:277-289.

- Arnold, S. J. 1976. Sexual behavior, sexual interference, and sexual defense in the salamanders *Ambystoma maculatum*, *Ambystoma tigrinum*, and *Plethodon jordani*. *Z. Tierpsychol.*, 42:247-300.
- Avery, R. A. 1968. Food and feeding relations of three species of *Triturus* (Amphibia Urodela) during the aquatic phases. *Oikos*, 19:408-412.
- Bagenal, T. B. 1967. A short review of fish fecundity. Pp. 89-111, *In* S. D. Gerking, ed. *The biological basis of freshwater fish production*. New York: John Wiley and Sons, Inc.
- . 1969. Relationship between egg size and fry survival in brown trout *Salmo trutta* L. *J. Fish. Biol.*, 1:349-353.
- . 1971. The interrelation of the size of fish eggs, the date of spawning and the production cycle. *J. Fish Biol.*, 3:207-219.
- Baker, C. L. 1945. The natural history and morphology of amphiumae. *Rept. Reelfoot Lake Biol. Sta.*, 9:55-91.
- Baldauf, R. J. 1947. *Desmognathus f. fuscus* eating eggs of its own species. *Copeia*, 1947(1):66.
- Ballinger, R. E. 1978. Variation in and evolution of clutch and litter size. pp. 789-825, *In* R. E. Jones, ed. *The vertebrate ovary, comparative biology and evolution*. New York: Plenum Press.
- Barbour, R. W. 1971. *Amphibians and reptiles of Kentucky*. Lexington: Univ. Kentucky Press, i-ix + 334 pp.
- Barnes, H. and M. Barnes. 1964. Egg size, nauplius size, and their variation with local, geographical and specific factors in some common cirripedes. *J. Anim. Ecol.*, 34:391-402.
- Baylis, J. R. 1978. Paternal behavior in fishes: a question of investment, timing or rate? *Nature*, 276:738.
- . 1981. The evolution of parental care in fishes, with reference to Darwin's rule of male sexual selection. *Env. Biol. Fish.*, 6(2):223-251.
- Behler, J. L. and F. W. King. 1979. *The Audubon Society field guide to North American reptiles and amphibians*. New York: Alfred A. Knopf, 719 pp.
- Belk, D. 1977. Evolution of egg size strategies in fairy shrimps. *Southw. Nat.*, 22:99-105.
- Bell, G. 1974. The reduction of morphological variation in natural populations of smooth newt larvae. *J. Anim. Ecol.*, 43:115-128.
- . 1975. The diet and dentition of smooth newt larvae (*Triturus vulgaris*). *J. Zool.*, (London) 176:411-424.
- , and J. H. Lawton. 1975. The ecology of the eggs and larvae of the smooth newt (*Triturus vulgaris* (Linn.)). *J. Anim. Ecol.*, 44:393-423.
- Berrill, N. J. 1935. Studies in tunicate development. Part III. Differential retardation and acceleration. *Philos. Trans.*, Ser. B, 225:255-326.
- Birge, E. A. and C. Juday. 1922. The inland lakes of Wisconsin. The plankton. I. Its quantity and chemical composition. *Wis. Geol. Nat. Hist. Survey, Bull.*, Sci. Ser., 64:1-222.
- Bishop, S. C. 1920. Notes on the habits and development of the four-toed salamander *Hemidactylum scutatum* (Schlegel). *New York State Mus. Bull.*, 219:251-282.
- . 1924. Notes on salamanders. *New York State Mus. Bull.*, 253:87-102.
- . 1926. Notes on the habits and development of the mudpuppy *Necturus maculosus* (Rafinesque). *New York State Mus. Bull.*, 268:5-61.
- . 1941. The salamanders of New York. *New York State Mus. Bull.*, 324:1-365.
- . 1943. *Handbook of salamanders*. Ithaca: Comstock Press, i-xiv + 555 pp.
- Blanchard, F. N. 1934. The relation of the female four toed salamander to her nest. *Copeia*, 1934(3):137-138.
- Blaxter, J. H. S. and G. Hempel. 1963. The influence of egg size on herring larvae (*Clupea harengus* L.). *J. Cons. Perm. Int. Explor. Mer.*, 28:211-240.
- Blumer, L. S. 1979. Male parental care in the bony fishes. *Quart. Rev. Biol.*, 54:149-161.
- Brame, A. H., Jr. 1967. A list of the world's recent and fossil salamanders. *Herpeton*, 2(1):1-26.
- Branch, L. C. and R. Altig. 1981. Nocturnal stratification of three species of *Ambystoma* larvae. *Copeia*, 1981(4):870-873.
- Brandon, R. A. and R. G. Altig. 1973. Eggs and small larvae of two species of *Rhyacosiredon*. *Herpetologica*, 29:349-351.

- Breder, C. M. 1935. The reproductive habits of the common catfish, *Ameiurus nebulosus* (LeSueur), with a discussion of their significance in ontogeny and phylogeny. *Zoologica*, 19:143-179.
- , and D. E. Rosen. 1966. Modes of reproduction in fishes. Garden City: The Natural History Press, i-xv + 941 pp.
- Briegleb, W. 1962. Zur Biologie und Ökologie des Grottenolms (*Proteus anguinus* Laur. 1768). *Z. Morph. Okol. Tiere*, 51:271-334.
- , and J. Schwartzkopff. 1961. Verhaltensweisen des Grottenolms (*Proteus anguinus* Laur.) und das Problem des Fortpflanzungsraumes. *Naturwissenschaften*, 22:1-3.
- Brimley, C. S. 1939-43. The amphibians and reptiles of North Carolina. *Carolina Tips*, Elon College, North Carolina.
- Brody, S. 1945. Bioenergetics and growth. New York: Hafner, i-xii + 1023 pp.
- Brophy, T. E. 1980. Food habits of sympatric larval *Ambystoma tigrinum* and *Notophthalmus viridescens*. *J. Herpetol.*, 14:1-6.
- Brown, H. A. 1976. The time-temperature relation of embryonic development in the north-western salamander, *Ambystoma gracile*. *Can. J. Zool.*, 54:552-558.
- . 1977. Oxygen consumption of a large, cold adapted frog egg (*Ascaphus truei* (Amphibia: Ascaphidae)). *Can. J. Zool.*, 55:343-348.
- Bruce, R. C. 1968. Life history studies of the salamanders of the genus *Pseudotriton* (Caudata: Plethodontidae). Ph.D. Dissertation, Duke University.
- Cadwallader, P. L. 1976. Breeding biology of a non diadromous galaxiid, *Galaxias vulgaris* Stokell, in a New Zealand river. *J. Fish. Biol.*, 8:157-177.
- Calow, P. 1978. The evolution of life-cycle strategies in fresh-water gastropods. *Malacologia*, 17:351-364.
- Campbell, H. W. and R. S. Simmons. 1962. Notes on the eggs and larvae of *Rhyacosiredon altamirani* (Duges). *Herpetologica*, 18:131-133.
- Carroll, R. L. 1970. Quantitative aspects of the amphibian-reptilian transition. *Forma et Functio*, 3:165-178.
- Clarke, A. 1982. Temperature and embryonic development in polar marine invertebrates. *International J. Invert. Repro.*, 5:71-82.
- Connon, F. E. 1947. A comparative study of the respiration of normal and hybrid *Triturus* embryos and larvae. *J. Exp. Zool.*, 105:1-24.
- Cope, E. D. 1889. The Batrachia of North America. *Bull. U. S. Natl. Mus.*, 34:1-525 pp + 86 plates.
- Curtis, B. 1938. The life story of the fish. New York: D. Appleton-Century Co., i-xiv + 260 pp.
- Dawkins, R. and T. R. Carlisle. 1976. Parental investment, mate desertion and a fallacy. *Nature*, 272:131-133.
- Derickson, W. K. 1976. Ecological and physiological aspects of reproductive strategies in two lizards. *Ecology*, 57:445-458.
- Despax, R. 1923. Contribution a l'etude anatomique et biologique des batraciens urodeles du groupe des euproctes et specialement de l'euprocte des Pyrenes *Triton (Euproctus) asper* Duges. Theses pour Docteur Sci. Nat. Toulouse, Ser. A, No. 929, V plates + 256 pp.
- Dineen, C. F. 1955. Food habits of the larval tiger salamander (*Ambystoma tigrinum*). *Proc. Indiana Acad. Sci.*, 65:231-233.
- Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. *Limnol. and Oceanog.*, 15:131-137.
- , and V. E. Dodson. 1971. The diet of *Ambystoma tigrinum* larvae from western Colorado. *Copeia*, 1971(4):614-624.
- Duellman, W. E. 1959. The eggs and juveniles of the plethodontid salamander *Parvimolge townsendi* Dunn. *Herpetologica*, 15:35-36.
- , and J. T. Wood. 1954. Size and growth of the two-lined salamander, *Eurycea bislineata rivicola*. *Copeia*, 1954(2):92-96.
- Dumas, P. C. 1955. Eggs of the salamander *Plethodon dunni* in nature. *Copeia*, 1955(1):65.
- Dunn, E. R. 1923. The breeding habits of salamanders and their bearing on phylogeny. *Copeia*, (115):25-28.

- . 1926. Salamanders of the family Plethodontidae. Smith College, Fiftieth Anniversary Publ. Ser., Vol. 7, x-viii + 441 pp.
- . 1928. A new genus of salamanders from Mexico. Proc. New England Zool. Club, 10:85–86.
- . 1942. An egg cluster of *Aneides ferreus*. Copeia, 1942(1):52.
- Durand, J. 1967. Sur la reproduction d'*Hydromantes italicus strinatii* Aellen Urodela, Plethodontidae). C. R. Acad. Sci. Paris, Ser. D, 264:854–856.
- , and M. Bouillon. 1964. Observations sur le developpment du Protee, *Proteus anguinus* Laurenti (Batraciens, Urodeles). C. R. Acad. Sci. Paris, 259:4801–4804.
- , and A. Vandel. 1968. *Proteus*: an evolutionary relic. Sci. J., 44–49.
- DuShane, G. P. and C. Hutchinson. 1944. Differences in size and developmental rate between eastern and midwestern embryos of *Ambystoma maculatum*. Ecology, 25:414–423.
- Estes, R. 1981. Handbuch der paläoherpetologie. Tiel 2, Gymnophiona, Caudata. Gustav Fischer, Stuttgart, i-xvi + 115 pp.
- Eycleshymer, A. C. 1906. The habits of *Necturus maculosus*. Amer. Nat., 40:123–136.
- Ferrier, V. 1974. Chronologie du développement de l'amphibien urodèle *Tylotriton verrucosus* Anderson (Salamandridae). Ann. d'Embryol. et de Morphogenèse, 7:407–416.
- Forester, D. C. 1978. Laboratory encounters between attending *Desmognathus ochrophaeus* (Amphibia, Urodela, Plethodontidae) females and potential predators. J. Herpetol., 12:537–541.
- . 1979. The adaptiveness of parental care in *Desmognathus ochrophaeus* (Urodela: Plethodontidae). Copeia, 1979(2):332–341.
- . 1984. Brooding behavior by the mountain dusky salamander: can the female's presence reduce clutch desiccation? Herpetologica, 40:105–109.
- Fowler, J. A. 1952. The eggs of *Plethodon dixi*. Amer. Caver Bull., 14:61.
- Franz, R. 1964. The eggs of the long-tailed salamander from a Maryland cave. Herpetologica, 20:216.
- Freda, J. 1983. Diet of larval *Ambystoma maculatum* in New Jersey. J. Herpetol., 17:177–179.
- Gall, G. A. E. 1974. Influence of size of eggs and age of female on hatchability and growth in rainbow trout. Calif. Fish and Game, 60:26–36.
- Gallien, L. and O. Bidaud. 1959. Table chronologique de developpment chez *Triturus helveticus* Raz. Bull. Soc. Zool. Fr., 84:22–32.
- , and M. Durocher. 1957. Table chronologique du developpment chez *Pleurodeles wallii* Michoh. Bull. Biol. Fr. Belg., 91:97–114.
- Gasser, F. 1964. Observations sur les stades initiaux du developpment de l'urodele Pyraneen *Euproctus asper*. Bull. Soc. Zool. Fr., 89:423–428.
- Gatz, A. J., Jr. 1979. Ecological morphology of freshwater stream fishes in Missouri. Trans. Amer. Fish. Soc., 85:39–57.
- Gibson, R., T. E. Thompson, and G. A. Robilliard. 1970. Structure of the spawn of an Antarctic dorid nudibranch *Austrodoris macmurdensis* Odhner. Proc. Malacol. Soc. Lond., 39:221–225.
- Godley, J. S. 1983. Observations on the courtship, nests, and young of *Siren intermedia* in southern Florida. Amer. Midl. Nat., 110(1):215–219.
- Goin, C. J. 1947. Notes on the eggs and early larvae of three Florida salamanders. Nat. Hist. Miscel. Chicago Acad. Sci., 10:1–4.
- , O. B. Goin and G. R. Zug. 1978. Introduction to herpetology. 3rd ed. San Francisco: W. H. Freeman, i-xiv + 378 pp.
- Gordon, R. E. 1952. A contribution to the life history and ecology of the plethodontid salamander *Aneides aeneus* (Cope and Packard). Amer. Midl. Nat., 47:661–701.
- Gorham, S. W. 1974. Checklist of world amphibians up to January 1, 1970. New Brunswick Museum, Saint John, 173 pp.
- Gorman, J. 1956. Reproduction in plethodontid salamanders of the genus *Hydromantes*. Herpetologica, 12:249–259.
- Grafen, A. and R. Sibly. 1978. A model of mate desertion. Anim. Behav., 26:645–652.
- Green, J. 1956. Growth, size and reproduction in *Daphnia* (Crustacea: Cladocera). Proc. Zool. Soc. Lond., 126:173–204.

- Green, N. B., P. Brant, Jr., and B. Dowler. 1967. *Eurycea lucifuga* in West Virginia: its distribution, ecology, and life history. Proc. W. Virginia Acad. Sci., 39:297-304.
- Greenberg, A. E. 1964. Plankton of the Sacramento River. Ecology, 45:40-49.
- Grier, H. J. 1984. Testis structure and formation of spermatophores in the atherinomorph teleost *Horaichthys setnai*. Copeia, 1984(4):833-839.
- Gross, H. P. and J. M. Anderson. 1984. Geographic variation in the gillrakers and diet of European threespine sticklebacks, *Gasterosteus aculeatus*. Copeia, 1984(1):87-97.
- Gross, M. R. and R. Shine. 1981. Parental care and mode of fertilization in ectothermic vertebrates. Evolution, 35:775-793.
- Hagen, D. W. and L. C. Gilbertson. 1972. Geographic variation and environmental selection in *Gasterosteus aculeatus* L. in the Pacific Northwest, America. Evolution, 26:32-51.
- Hamilton, W. J., Jr. 1940. The feeding habits of larval newts with reference to availability and prediction of food items. Ecology, 21:351-356.
- Hanken, J. 1979. Egg development time and clutch size in two neotropical salamanders. Copeia, 1979(4):741-744.
- Hanlin, H. G., J. J. Beatty, and S. W. Hanlin. 1979. A nest site of the western red-backed salamander *Plethodon vehiculum* (Cooper). J. Herpetol., 13:214-216.
- Hardy, J. D., Jr. 1969. A summary of recent studies on the salamander, *Ambystoma mabeei*. Chesapeake Biol. Lab., Ref. No. 69-20:1-3.
- Harris, R. N. 1980. The consequences of within-year timing of breeding in *Ambystoma maculatum*. Copeia, 1980(4):719-722.
- Harrison, J. R. 1967. Observations on the life history, ecology and distribution of *Desmognathus aeneus aeneus* Brown and Bishop. Amer. Midl. Nat., 77:356-370.
- Hashimoto, M. 1976. Conservation of *Salamandrella keyserlingii*. Animals and Zoos, 28:20-22. (Japanese)
- Hassinger, D. D. and J. D. Anderson. 1970. The effect of lunar eclipse on nocturnal stratification of larval *Ambystoma opacum*. Copeia, 1970(1):178-179.
- , J. D. Anderson, and G. H. Dalrymple. 1970. The early life history of *Ambystoma tigrinum* and *Ambystoma opacum* in New Jersey. Amer. Midl. Nat., 84:474-495.
- Hay, O. P. 1888. Observations on *Amphiuma* and its young. Amer. Nat., 22:315-321.
- Henderson, B. A. 1973. The specialized feeding behavior of *Ambystoma gracile* in Marion Lake, British Columbia. Can. Field Nat., 87:151-154.
- Highton, R. 1956. The life history of the slimy salamander, *Plethodon glutinosus*, in Florida. Copeia, 1956(2):75-93.
- , and T. Savage. 1961. Functions of the brooding behavior in the female red-backed salamander, *Plethodon cinereus*. Copeia, 1961(1):95-98.
- Himstedt, W. 1967. Experimentelle Analyse der optischen Sinnesleistungen in Beutefangverhalten der einheimischen Urodelen. Zool. Jb. Physiol., 73:281-320.
- Houck, L. D. 1977a. Life history patterns and reproductive biology of neotropical salamanders. Pp. 43-72, In D. H. Taylor and S. I. Guttman, eds. The reproductive biology of amphibians. New York: Plenum Press.
- . 1977b. Reproductive biology of a neotropical salamander, *Bolitoglossa rostrata*. Copeia, 1977(1):70-83.
- Howard, W. E. 1950. Eggs of the salamander *Ensatina eschscholtzii platensis*. Copeia, 1950(3):236.
- Hubbs, C. 1958. Geographic variations in egg complement of *Percina caprodes* and *Etheostoma spectabile*. Copeia, 1950(2):102-105.
- . 1962. Effects of a hurricane on the fish fauna of a coastal pool and drainage ditch. Texas J. Sci., 14(3):289-296.
- , M. M. Stevenson, and A. E. Peden. 1968. Fecundity and egg size in two central Texas darter populations. Southw. Nat., 13:301-324.
- Hübener, H. E. 1960. *Ranodon sibiricus* - ein Sibirischer Bachsalamander. Aquarien Terrar. Z., 13:23-25.
- Hutchinson, V. H. 1956. Notes on the plethodontid salamanders, *Eurycea lucifuga* (Rafinesque) and *Eurycea longicauda longicauda* (Green). Occas. Paps. Nat. Speleol. Soc., 3:1-24.

- Hynes, H. B. N. 1970. The ecology of running waters. Toronto: Univ. Toronto Press, i-xxiv + 555 pp.
- Iwasawa, H. and Y. Kera. 1980. Normal stages of development of the Japanese lungless salamander, *Onychodactylus japonicus* (Houttuyn). Jap. J. Herpetol., 8(3):73-89. (Japanese)
- Jagersten, G. 1972. Evolution of the metazoan life cycle, a comprehensive theory. London: Academic Press, i-x + 282 pp.
- Johnson, C. R. and C. B. Schreck. 1969. Food and feeding of larval *Dicamptodon ensatus* from California. Amer. Midl. Nat., 81:280-281.
- Johnston, R. F. and G. A. Schad. 1959. Natural history of the salamander, *Ancides hardii*. Univ. Kansas Publ. Mus. Nat. Hist., 10:573-585.
- Kaplan, R. H. 1980. The implications of ovum size variability for offspring fitness and clutch size within several populations of salamanders (*Ambystoma*). Evolution, 34:51-64.
- , and P. W. Sherman. 1980. Intraspecific oophagy in California newts. J. Herpetol., 14:183-185.
- Kerbert, C. 1904. Zur Fortpflanzung von *Megalobatrachus maximus* Schlegel (*Cryptobranchus japonicus* v. d. Hoeven). Zool. Anz., 27:305-320.
- Kishi, Y. 1979. A graphical model of disruptive selection on offspring size and a possible case of speciation in freshwater gobies characterized by egg-size difference. Researches on Population Ecology, 20:211-215.
- Kleiber, M. 1961. The fire of life, an introduction to animal energetics. New York: John Wiley and Sons, Inc., i-xxii + 454 pp.
- Knight, F. C. E. 1938. Die Entwicklung von *Triton alpestris* bei verschiedenen Temperaturen, mit Normentafel. Wilhelm Roux's Archives, 137:461-473.
- Kunitomo, K. 1910. Über die Entwicklungsgeschichte des *Hynobius nebulosus*. Anat. Hefte, 40:194-283.
- Kuramoto, M. 1966. Embryonic temperature tolerance in three species of Japanese salamanders (genus *Hynobius*). Bull. Fukuoka Univ. Education, 16:125-139.
- . 1975. Adaptive significance in oxygen consumption of frog embryos in relation to the environmental temperatures. Comp. Biochem. Physiol., 52A:59-62.
- . 1978. Correlations of quantitative parameters of fecundity in amphibians. Evolution, 32:287-296.
- Kusano, T. 1980. Breeding and egg survival of a population of a salamander, *Hynobius nebulosus tokyoensis* Tago. Researches on Population Ecology, 21:181-196.
- Lafrentz, K. 1930. Beiträge zur Herpetologie Mexikos. I. Untersuchungen über die Lebensgeschichte mexicanischer *Ambystoma*-Arten. Abh. Berlin Mus. Naturwiss., 6:91-127.
- Licht, L. E. 1971. Breeding habits and embryonic thermal requirements of the frogs, *Rana aurora aurora* and *Rana pretiosa pretiosa*, in the Pacific Northwest. Ecology, 52:116-124.
- . 1975. Growth and food of larval *Ambystoma gracile* from a lowland population in southwestern British Columbia. Can. J. Zool., 53:1716-1722.
- Livezey, R. L. 1959. The egg mass and larvae of *Plethodon elongatus* Van Denburgh. Herpetologica, 15:41-42.
- Loiselle, P. V. 1978. Prevalence of male brood care in teleosts. Nature, 276:98.
- Maiorana, V. C. 1976. Size and environmental predictability for salamanders. Evolution, 30:599-613.
- Mangold-Wirz, K. 1963. Biologie des cephalopodes benthiques et nectoniques de la Mer catalane. Vie et Milieu, Suppl., 13:1-285.
- Marshall, N. B. 1953. Egg size in Arctic, Antarctic and deep-sea fishes. Evolution, 7:328-341.
- Martof, B. S. 1962. Some aspects of the life history and ecology of the salamander *Leurognathus*. Amer. Midl. Nat., 67:1-35.
- , and D. C. Scott. 1957. The food of the salamander *Leurognathus*. Ecology, 38:494-501.
- , W. M. Palmer, J. R. Bailey, and J. R. Harrison, III. 1980. Amphibians and reptiles of the Carolinas and Virginia. Chapel Hill: Univ. North Carolina Press, 264 pp.
- Maslin, T. P., Jr. 1939. Egg-laying of the slender salamander (*Batrachoseps attenuatus*). Copeia, 1939(4):209-212.
- Maynard Smith, J. 1977. Parental investment: a prospective analysis. Anim. Behav., 25:1-9.
- . 1978. The evolution of sex. Cambridge: Cambridge Univ. Press, i-x + 222 pp.

- McDiarmid, R. W. 1978. Evolution of parental care in frogs. Pp. 127–147, *In* G. M. Burghardt and M. Bekoff, eds. The development of behavior: comparative and evolutionary aspects. New York: Garland STPM Press.
- , and R. D. Worthington. 1970. Concerning the reproductive habits of tropical plethodontid salamanders. *Herpetologica*, 26:57–70.
- McDowall, R. M. 1970. The galaxiid fishes of New Zealand. *Bull. Mus. Comp. Zool.*, Harvard, 139:341–432.
- McLaren, I. A., C. J. Corkett, and E. J. Zillioux. 1969. Temperature adaptations of copepod eggs from the Arctic to the tropics. *Biol. Bull.*, 137:486–493.
- Metter, D. E. 1963. Stomach contents of Idaho larval *Dicamptodon*. *Copeia*, 1963(2):435–436.
- Milner, A. R. 1983. The biogeography of salamanders in the Mesozoic and Early Cenozoic: a cladistic-vicariance model. Pp. 431–468, *In* Sims, R. W., Price, J. H., and P. E. S. Whalley, eds. Evolution, time, and space: the emergence of the biosphere. London and New York: Academic Press.
- Moore, J. A. 1939. Temperature tolerance and rates of development in the eggs of Amphibia. *Ecology*, 20:459–478.
- . 1942. The role of temperature in speciation of frogs. *Biological Symposia*, 6:189–213.
- . 1949a. Geographic variation of adaptive characters in *Rana pipiens* Schreber. *Evolution*, 3:1–24.
- . 1949b. Patterns of evolution in the genus *Rana*. Pp. 315–338, *In* G. L. Jepsen, G. G. Simpson, and E. Mayr, eds. Genetics, Paleontology, and Evolution. Princeton: Princeton University Press.
- Naylor, B. G. 1978. The systematics of fossil and recent salamanders (Amphibia: Caudata), with special reference to the vertebral column and trunk musculature. Ph.D. Dissertation, Univ. Alberta.
- . 1980. Radiation of the Amphibia Caudata: Are we looking too far into the past? *Evol. Theor.*, 5(2):119–126.
- Netting, M. G. and C. J. Goin. 1942. Descriptions of two new salamanders from peninsular Florida. *Ann. Carnegie Mus.*, 29:175–196.
- Nickerson, M. A. and C. E. Mays. 1973. The hellbenders: North American "giant salamanders." *Milwaukee Pub. Mus.*, Publ. in Biol. and Geol., No. 1., i–viii + 106 pp.
- Nikolsky, G. V. 1963. The ecology of fishes. London: Academic Press, i–xv + 352 pp.
- Noble, G. K. 1927. The value of life history data in the study of the evolution of the Amphibia. *Ann. New York Acad. Sci.*, 30:31–128.
- . 1930. The eggs of *Pseudobranchius*. *Copeia*, 1930(2):52.
- . 1931. The biology of the Amphibia. New York: McGraw-Hill, i–xiii + 577 pp.
- , and M. K. Brady. 1933. Observations on the life history of the marbled salamander, *Ambystoma opacum* Gravenhorst. *Zoologica*, 11:89–132.
- , and B. C. Marshall. 1932. The validity of *Siren intermedia* LeConte, with observations on its life history. *Amer. Mus. Novit.*, 532:1–17.
- , and L. B. Richards. 1932. Experiments on the egg-laying of salamanders. *Amer. Mus. Novit.*, 513:1–25.
- Nussbaum, R. A. 1968. Geographic variation in *Dicamptodon ensatus* (Eschscholtz) with notes on the life history and zoogeography. M. S. Thesis, Cent. Wash. St. Coll., Ellensburg, 69 pp.
- . 1969a. Nests and eggs of the Pacific giant salamander, *Dicamptodon ensatus* (Eschscholtz). *Herpetologica*, 25:257–262.
- . 1969b. A nest site of the Olympic salamander, *Rhyacotriton olympicus* (Gäige). *Herpetologica*, 25:277–278.
- , and E. D. Brodie, Jr. 1982. Partitioning of the salamandrid genus *Tylostrotitron* Anderson (Amphibia: Caudata) with a description of a new genus. *Herpetologica*, 38:320–322.
- , and C. K. Tait. 1977. Aspects of the life history and ecology of the Olympic salamander, *Rhyacotriton olympicus* (Gäige). *Amer. Midl. Nat.*, 98:176–199.
- , Brodie, E. D., Jr., and R. M. Storm. 1983. Amphibians and reptiles of the Pacific Northwest. Moscow: University Press of Idaho, 332 pp.
- Oeldorf, E., Nishioka, M., and K. Bachmann. 1978. Nuclear DNA amounts and developmental rate in holarctic anura. *Zeit. f. Zool. Syst. Evol.*, 16:216–224.

- Okada, Y. 1933. The herpetological fauna in the vicinity of Nikko, Japan. Sci. Rep. Tokyo Univ. Lit. Sci., Sec. B, 1:159-173.
- Organ, J. A. 1960. Studies on the life history of the salamander, *Plethodon welleri*. Copeia, 1960(4):287-297.
- . 1961. Life history of the pigmy salamander, *Desmognathus wrighti*, in Virginia. Amer. Midl. Nat., 66:384-390.
- Orr, L. P. and W. T. Maple. 1978. Competition avoidance mechanisms in salamander larvae of the genus *Desmognathus*. Copeia, 1978(4):679-685.
- Paraskiw, K. P. 1953. Semiretschskiy triton (Der Siebenstromland-Molch). Akad. Nauk, Kasach. SSR, Biologie, Wypusk, 8:47-56. (Russian)
- Parker, M. V. 1937. Some amphibians and reptiles from Reelfoot Lake. J. Tennessee. Acad. Sci., 12:60-86.
- Pellantová, J. 1973. The food of the newt, *Triturus vulgaris* (Linn.), in southern Moravia. Zoologické Listy, 22:329-340.
- Pennak, R. W. 1943. Limnological variables in a Colorado mountain stream. Amer. Midl. Nat., 29:186-199.
- Perron, F. E. 1981. The partitioning of reproductive energy between ova and protective capsules in marine gastropods of the genus *Conus*. Amer. Nat., 118:110-118.
- Perronc, M., Jr. and T. M. Zaret. 1979. Paternal care patterns of fishes. Amer. Nat., 113:351-361.
- Petranka, J. W. 1982. Geographic variation in the mode of reproduction and larval characteristics of the small-mouthed salamander (*Ambystoma texanum*) in the east-central United States. Herpetologica, 38:475-485.
- . 1984a. Ontogeny of the diet and feeding behavior of *Eurycea bislineata* larvae. J. Herpetol., 18:48-55.
- . 1984b. Incubation, larval growth, and embryonic and larval survivorship of small-mouthed salamanders (*Ambystoma texanum*) in streams. Copeia, 1984(4):862-868.
- . 1984c. Breeding migrations, breeding season, clutch size, and oviposition of stream breeding *Ambystoma texanum*. J. Herpetol., 18:106-112.
- , and J. G. Petranka. 1980. Selected aspects of the larval ecology of the marbled salamander *Ambystoma opacum* in the southern portion of its range. Amer. Midl. Nat., 104:352-363.
- Pettus, D. and G. M. Angleton. 1967. Comparative reproductive biology of montane and piedmont chorus frogs. Evolution, 21:500-507.
- Piersol, W. H. 1909. The habits and larval state of *Plethodon cinereus erythronotus*. Trans. Canad. Inst., 8:469-493.
- Popc, C. H. 1924. Notes on North Carolina salamanders with especial reference to the egg-laying habits of *Leurognathus* and *Desmognathus*. Amer. Mus. Novit., 153:1-15.
- Rass, T. S. 1941. Analogous or parallel variations in structure and development of fishes in northern and arctic seas. Jub. Publ. Mosc. Soc. Natr., 1805 1940:1-60.
- Regal, P. J. 1966. Feeding specializations and the classification of terrestrial salamanders. Evolution, 20:392-407.
- Ridley, M. 1978. Paternal care. Anim. Behav., 26:904-932.
- . 1983. The explanation of organic diversity. Oxford: Clarendon Press, i-x + 272 pp.
- Ringler, N. H. 1979. Prey selection by drift-feeding brown trout (*Salmo trutta*). J. Fish. Res. Board Canada, 36:392-403.
- Ritter, W. E. 1903. Further notes on the habits of *Autodax lugubris*. Amer. Nat., 37:883-886.
- Rose, F. L. 1966. Homing to nests by the salamander *Desmognathus auriculatus*. Copeia, 1966(2):251-253.
- Rounsefell, G. A. 1957. Fecundity of North American Salmonidae. Fish. Bull. U.S. Fish. Wildl. Serv., 57:451-468.
- Russell-Hunter, W. D. 1970. Aquatic productivity: an introduction to some basic aspects of biological oceanography and limnology. London: Macmillan, i-xiii + 306 pp.
- Ryan, M. 1977. Parental care in salamanders. Bull. New York Herp., Soc. 13:23-27.
- Salthe, S. N. 1967. Courtship patterns and the phylogeny of the urodeles. Copeia, 1967(1):100-117.

- . 1969. Reproductive modes and the number and size of ova in the urodeles. *Amer. Midl. Nat.*, 81:467–490.
- , and W. E. Duellman. 1973. Quantitative constraints associated with reproductive mode in anurans. Pp. 229–249, *In* J. L. Vial, ed. *Evolutionary biology of the anurans*. Columbia: Univ. Missouri Press.
- , and J. S. Mecham. 1974. Reproductive and courtship patterns. Pp. 309–521, *In* B. Lofts, ed. *Physiology of the Amphibia*, Vol. 2. New York: Academic Press.
- Sasaki, M. 1924. On a Japanese salamander, in Lake Kuttarush, which propagates like the axolotl. *J. Coll. Agric. Hokkaido Imp. Univ.*, 40:1–36 (3 plates).
- Schmalhausen, I. 1917. On the extremities of *Ranidens sibiricus* Kessl. *Rev. Zool. Russe*, 2:129–135.
- Schmidt, K. P. 1936. Guatemalan salamanders of the genus *Oedipus*. *Zool. Ser. Field Mus. Nat. Hist.*, 20:135–166.
- Scott, D. P. 1962. Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri*. *J. Fish. Res. Board Canada*, 19:715–731.
- Shine, R. 1978. Propagule size and parental care: the “safe harbor” hypothesis. *J. Theor. Biol.*, 75:417–424.
- Smith, B. G. 1906. Preliminary report of the embryology of *Cryptobranchus allegheniensis*. *Biol. Bull.*, 11:146–164.
- . 1907. The life history and habits of *Cryptobranchus allegheniensis*. *Biol. Bull.*, 13:5–39.
- . 1912. The embryology of *Cryptobranchus allegheniensis*, including comparisons with some other vertebrates. *J. Morphol.*, 23:61–157.
- Smith, M. 1964. *The British amphibians and reptiles*. London: Collins, i–xiv + 322 pp.
- Spight, T. M. 1975. Factors extending gastropod embryonic development and their selective cost. *Oecologia*, 21:1–16.
- Stearns, S. C. and R. D. Sage. 1980. Maladaptation in a marginal population of the mosquito fish, *Gambusia affinis*. *Evolution*, 34:65–75.
- Stebbins, R. C. 1954. Natural history of the salamanders of the plethodontid genus *Ensatina*. *Univ. California Publ. Zool.*, 54:47–124.
- Steele, D. H. 1977. Correlation between egg size and developmental period. *Amer. Nat.*, 111:371–372.
- , and V. J. Steele. 1973. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. VII. The duration of embryonic development in five species at various temperatures. *Canadian J. Zool.*, 51:995–999.
- Stewart, M. M. 1956. The separate effects of food and temperature differences on development of marbled salamander larvae. *J. Elisha Mitchell Soc.*, 72:47–56.
- Storer, T. I. 1925. A synopsis of the Amphibia of California. *Univ. Calif. Publ. Zool.*, 27:1–342.
- Storm, R. M. 1947. Eggs and young of *Aneides ferreus*. *Herpetologica*, 41:60–62.
- Strathmann, R. R. 1977. Egg size, larval development, and juvenile size in benthic marine invertebrates. *Amer. Nat.*, 111:373–376.
- Strecker, J. K., Jr. 1908. Notes on the habits of two Arkansas salamanders and a list of batrachians and reptiles collected at hot springs. *Proc. Biol. Soc. Washington*, 21:85–90.
- Svärdson, G. 1949. Natural selection and egg number in fish. *Inst. Freshwater Res., Fishery Board of Sweden, Rept. No.*, 29:115–922.
- Tago, K. 1929. Notes on the habits and life history of *Megalobatrachus japonicus*. X^e Congress International. *Zool. Budapest*, 1:828–838.
- . 1931. *Newts and salamanders*. Maruzen Co., Tokyo, 210 pp. (Japanese)
- Tanner, W. W. 1953. Notes on the life history of *Plethopsis wrighti* Bishop. *Herpetologica*, 9:139–140.
- Thibault, R. E. and R. J. Schultz. 1978. Reproductive adaptations among viviparous fishes (Cyprinodontiformes: Poeciliidae). *Evolution*, 32:320–333.
- Thorn, R. 1962. Protection of the brood by the male of the salamander *Hynobius nebulosus*. *Copeia*, 1962(3):638–640.
- . 1967. Nouvelles observations sur l'ethologie sexuelle de *Hynobius nebulosus* (Temminck

- et Schlegel) (Caudata, Hynobiidae). Archives Grand Ducal de Luxembourg, Sect. Science Naturelles, Physiques, et Mathematiques, Nouvelle Ser., 32:267-271.
- . 1968. Les salamanders d'Europe, d'Asie, et d'Afrique du nord. Paris: Paul Lechevalier, i-iv + 376 pp.
- Thorson, G. 1935. Studies on the egg capsules and development of arctic marine proso-branchs. Meddelelser Gronland, 100:1-71.
- . 1936. The larval development, growth, and metabolism of Arctic marine bottom invertebrates. Meddelelser Gronland, 100:1-155.
- . 1950. Reproduction and larval ecology of marine bottom invertebrates. Biol. Rev., 25:1-45.
- Tilley, S. G. 1968. Size-fecundity relationships and their evolutionary implications in five desmognathine salamanders. Evolution, 22:806-816.
- . 1970. Aspects of the reproductive ecology of *Desmognathus ochrophaeus* in the southern Appalachian Mountains. Univ. Michigan, Ph.D. Thesis.
- . 1972. Aspects of parental care and embryonic development in *Desmognathus ochrophaeus*. Copeia, 1972(3):532-540.
- . 1981. A new species of *Desmognathus* (Amphibia: Caudata: Plethodontidae) from the southern Appalachian Mountains. Occ. Paps. Mus. Zool. Univ. Michigan, 695:1-23.
- Tinkle, D. W. 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. Amer. Nat., 103:501-516.
- Todd, C. D. 1979. Reproductive energetics of two species of dorid nudibranchs with planktotrophic and lecithotrophic larval strategies. Mar. Biol., 53:57-68.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pp. 136-179, In B. Campbell, ed. Sexual selection and the descent of man, 1871-1971. Chicago: Aldine.
- Twitty, V. C. 1935. Two new species of *Triturus* from California. Copeia, 1935(2):73-80.
- . 1936. Correlated genetic and embryological experiments on *Triturus*. I and II. J. Exp. Zool., 74:239-302.
- . 1942. The species of Californian *Triturus*. Copeia, 1942(2):65-76.
- . 1966. Of scientists and salamanders. San Francisco: W. H. Freeman, i-x + 178 pp.
- Underwood, A. J. 1974. On models for reproductive strategy in marine benthic invertebrates. Amer. Nat., 108:874-878.
- Utsunomiya, Y. and T. Utsunomiya. 1977. On the development of *Tylototriton andersoni*. J. Fac. Fish. Anim. Husb., Hiroshima Univ., 16:65-76. (Japanese)
- , ———, and S. Kawachi. 1978. Some ecological observation of *Tylototriton andersoni*, a terrestrial salamander occurring in the Tokunoshima Island. Proc. Jap. Acad., Ser. B, 54:341-346.
- Valdivieso, D. and J. R. Tamsitt. 1965. Reproduction in a neotropical salamander, *Bolitoglossa adspersa* (Peters). Herpetologica, 21:228-236.
- Vance, R. R. 1973a. On reproductive strategies in marine benthic invertebrates. Amer. Nat., 107:339-352.
- . 1973b. More on reproductive strategies in marine benthic invertebrates. Amer. Nat., 107:353-361.
- . 1974. Reply to Underwood. Amer. Nat., 108:879-880.
- Vandel, A. and M. Bouillon. 1959. La reproduction du Protee (*Preteus anguinus* Laurenti). C. R. Acad. Sci. Paris, 248:1267-1272.
- Vial, J. L. 1968. The ecology of the tropical salamander, *Bolitoglossa subpalmata*, in Costa Rica. Rev. Biol. Trop., 15:113-115.
- , and F. B. Preib. 1966. Antibiotic assay of dermal secretions from the salamander, *Plethodon cinereus* (Green). Herpetologica, 22:284-287.
- , and ———. 1967. An investigation of antibiosis as a function of brooding behavior in the salamander, *Plethodon cinereus*. Trans. Missouri Acad. Sci., 1:37-40.
- Wake, D. B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Mem. So. Calif. Acad. Sci., 4:1-111.
- Wallace, J. T. and R. W. Barbour. 1957. Observations on the eggs and young of *Plethodon richmondi*. Copeia, 1957(1):48.

- Wear, R. G. 1974. Incubation in British decapod Crustacea, and the effects of temperature on the rate and success of embryonic development. *J. Mar. Biol. Ass.*, 54:745-762.
- Weber, J. A. 1944. Observations on the life history of *Amphiuma means*. *Copeia*, 1944(1):61-62.
- Welch, P. S. 1935. *Limnology*. New York: McGraw-Hill Book Co., Inc., i-xiv + 471 pp.
- Wells, K. D. 1977. The social behavior of anuran amphibians. *Anim. Behav.*, 25:666-693.
- . 1981. Parental behavior of male and female frogs. Pp. 184-197. *In*: R. D. Alexander, and D. W. Tinkle (eds.). *Natural selection and social behavior*. New York: Chiron Press.
- Werner, E. F. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. *J. Fish. Res. Board Canada*, 31:1531-1536.
- Werren, J. H., M. R. Gross, and R. Shine. 1980. Paternity and the evolution of male parental care. *J. Theor. Biol.*, 82:619-632.
- Wilder, I. W. 1917. On the breeding habits of *Desmognathus fusca*. *Biol. Bull.*, 32:13-20.
- Williams, G. C. 1966. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton: Princeton Univ. Press, 307 pp.
- . 1975. *Sex and evolution*. Princeton: Princeton Univ. Press, i-xii + 200 pp.
- Wolda, H. 1970. Variation in growth rate in the landsnail *Cepaea nemoralis*. *Res. Pop. Ecol.*, 12:185-204.
- Wood, J. T. 1951. Protective behavior and photic orientation in aquatic adult and larval two-lined salamanders, *Eurycea b. bislineata* × *cirrigera*. *Virginia J. Sci., New Ser.*, 2:113-121.
- . 1953a. The nesting of the two-lined salamander, *Eurycea bislineata*, on the Virginia coastal plain. *Nat. Hist. Miscel., Chicago Acad. Sci.*, 122:1-7.
- . 1953b. Observations on the complements of ova and nesting of the four-toed salamander in Virginia. *Amer. Nat.*, 87:77-86.
- , and R. H. Rageot. 1963. The nesting of the many-lined salamander in the dismal swamp. *Virginia J. Sci., New Ser.*, 14:121-125.
- , and F. E. Wood. 1955. Notes on the nests and nesting of the Carolina mountain dusky salamander in Tennessee and Virginia. *J. Tenn. Acad. Sci.*, 30:36-39.

APPENDIX I

SALAMANDERS WITH PARENTAL CARE (EMBRYO GUARDING)
AMONG SPECIES WITH TERRESTRIAL NEST SITES¹

AMBYSTOMATIDAE

Ambystoma opacum (Noble and Brady, 1933)

AMPHIUMIDAE

Amphiuma means (Weber, 1944), *A. tridactylum*² (Hay, 1888; Parker, 1937; Baker, 1945)

PLETHODONTIDAE

Aneides aeneus (Gordon, 1952), *A. ferreus*³ (Dunn, 1942; Storm, 1947), *A. flavipunctatus* (Storer, 1925), *A. hardyi*⁴ (Johnston and Schad, 1959), *A. lugubris*⁵ (Ritter, 1903; Storer, 1925), *Batrachoseps attenuatus*⁶ (Maslin, 1939; Maiorana, 1976), *B. wrighti* (Tanner, 1953), *Bolitoglossa adspersa* (Valdivieso and Tamsitt, 1965), *B. cerroensis* (Nussbaum and Brodie, unpubl.), *B. englehardti* (Houck, 1977a), *B. franklini* (Houck, 1977a), *B. resplendens* (Houck, 1977a), *B. rostrata* (Schmidt, 1936; Houck, 1977b), *B. subpalmata*⁷ (Vial, 1968), *Chiropterotriton magnipes* (Hanken, 1979), *Desmognathus aeneus* (Harrison, 1967), *D. auriculatus* (Rose, 1966), *D. brimleyorum* (Strecker, 1908), *D. fuscus* (Baldauf, 1947; Wilder, 1917), *D. imitator*⁸ (Wood and Wood, 1955), *D. ochrophaeus* (Tilley, 1972), *D. santeetlah* (Tilley, 1981), *D. wrighti* (Organ, 1961), *Ensatina eschscholtzi*⁹ (Howard, 1950; Stebbins, 1954), *Hemidactylium scutatum* (Blanchard, 1934; Wood, 1953b), *Hydromantes genei* (Durand, 1967), *H. italicus* (Durand, 1967), *H. shastae* (Gorman, 1956), *Parvimolge townsendi* (Duellman, 1959), *Plethodon cinereus* (Highton and Savage, 1961), *P. dunni* (Dumas, 1955), *P. elongatus* (Livezey, 1959), *P. glutinosus* (Highton, 1956), *P. hoffmani* (Martof, et al., 1980), *P. nettingi* (Behler and King, 1979), *P. richmondi* (Wallace and Barbour, 1957), *P. vehiculum* (Hanlin, et al., 1979), *P. wehrlei* (Fowler, 1952), *P. welleri* (Organ, 1960), *Pseudoeurycea brunnata* (Houck, 1977a), *P. goebeli* (Houck, 1977a), *P. nigromaculata* (McDiarmid and Worthington, 1970), *P. juarezi* (McDiarmid and Worthington, 1970), *Stereochilus marginatus*¹⁰ (Wood and Rageot, 1963).

¹The female is the attentive sex in all known cases of terrestrial brooding, but see footnotes.

²Baker argued that nests of *A. tridactylum* are normally aquatic and that reports of terrestrial nests are based on situations in which ponds have dried up creating abnormal terrestrial nests.

³Males have been found near the brooding females of this species.

⁴Some nests were unguarded, perhaps because of disturbance by the collectors.

⁵On occasion both males and females were present.

⁶Nests often communal, often unguarded.

⁷A few nests had only males present.

⁸Observations ascribed to *Desmognathus ochrophaeus carolinensis* = *D. imitator* in part.

⁹Clutches sometimes unattended.

¹⁰Often communal, usually fewer females than clutches, sometimes unattended.

