

Chapter Seven

Evolution of Parental Care in Frogs

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The implications of increased reproductive effort and parental investment and the manner in which such activities influence the evolution of life history strategies have received considerable attention in recent literature (Williams, 1966; Trivers, 1972; Wilson, 1975; Dawkins and Carlisle, 1976; Stearns, 1976; Maynard Smith, 1977). Most of the supportive data for hypotheses regarding these phenomena come from detailed studies of the reproductive ecology and behavior of social insects, birds, and mammals (reviewed in Wilson, 1976; Thornhill, 1976), although some studies have focused on other groups (e.g., Wilbur, 1977). Salthe and Mecham (1974) summarized the available literature on amphibian reproductive patterns and commented on the complexity of the situation in frogs as compared to that of salamanders and caecilians. While some of the complexity of frog reproductive patterns certainly is attributable to the overall diversity of the group, it reflects in part the inadequacy of available information. With the exception of Crump's work (1974), no detailed studies of the reproductive ecology of complex frog communities (those which are most likely to contain species with some form of parental care, e.g., tropical forest communities) from which general patterns can be drawn exist. Instead, we must deal with a woefully inadequate literature of anecdotal and often conflicting data about a group of organisms that probably exhibits the greatest array of reproductive modes found in any vertebrate class. Detailed studies on about ten species of frogs are available. Unfortunately, all these species exhibit the typical aquatic pattern of repro-

duction in which the eggs, deposited in water, hatch into free-swimming larvae (tadpoles), which, after a period of growth, metamorphose and usually leave the water to grow into adults. In this pattern there is no parental investment in the offspring after the eggs are laid. With the notable exception of work on *Leptodactylus ocellatus* (Vaz-Ferreira and Gehrau, 1975) detailed studies of other species that have a derived reproductive pattern including some form of post-egg-laying parental investment generally are lacking. In fact, Maynard Smith (1977) recently has commented on the need for, and value of, a comparative study of anuran parental care.

In this chapter I review the available information on parental care, one form of parental investment, in frogs. I include pertinent data from a detailed study of the reproductive ecology and behavior of some species of tropical frogs, family Centrolenidae, to illustrate several factors I consider important in the evolution of parental care in frogs. Finally, I pose some questions and make suggestions that I believe will be important for shaping relevant future research in this area of behavioral ecology.

Parental Care in Frogs

Parental care may be defined as any behavior that enables an individual to increase the survivorship of its offspring. For purposes of this review, I restrict my consideration to parental care in post-egg-laying situations, i.e., care for eggs and/or larvae by either parent acting singly or in concert with the other. I assume that this behavior decreases the ability of the investing parent to invest in additional offspring (Trivers, 1972) and thus may be considered as a subset of parental investment. Energy or effort devoted to gamete production, though part of parental investment, is not parental care. Likewise, I consider energy devoted to territorial defense or courtship as a component of parental care only if it is clear that this effort directly benefits the offspring rather than (or in addition to) functioning as a prerequisite for successful mating. For example, if a defended territory provides protection for young rather than or besides providing the appropriate resources needed for egg formation, mating, etc., then I include it in the discussion of parental care.

A review of the literature on frog reproductive behavior and life history strategies indicates that parental care is widely distributed among frog families (Table 1). Some form of such care has been reported from 14 of 20 families from temperate and tropical areas. Even so, parental care is relatively rare among frogs as it is reported from less than 10% of all

TABLE 1. The distribution of parental care among frog families

FAMILY	PARENTAL CARE	PERCENTAGE OF SPECIES WITH PARENTAL CARE
Leiopelmatidae	♂	100%
Pipidae	♀	30%
Rhinophrynidae	—	0%
Discoglossidae	♂	25%
Pelobatidae	—	0%
Pelodytidae	—	0%
Myobatrachidae	♂, ♀, both	5%
Leptodactylidae	♂, ♀, both	5%
Bufo	♂, ♀	1%
Brachycephalidae	—	0%
Rhinodermatidae	♂	100%
Dendrobatidae	♂, ♀, both	100%
Pseudidae	—	0%
Hylidae	♂, ♀	5%
Centrolenidae	♂	50%
Microhylidae	♂, ♀	30%
Sooglossidae	♂	100%
Ranidae	♂ ? , ♀	1%
Hyperoliidae	—	0%
Rhacophoridae	♀ ?	1%

species. As more data on reproductive biology of some groups (e.g., Microhylidae) become available, these figures may change, but I believe that 10% is a reasonable estimate. Parental care apparently is absent from six families. It occurs in fewer than 30% of the species included in nine families, and in six of these, species reported to exhibit parental care account for less than 5% of the family. Usually in these six families (all of which include large numbers of species), one group of species (e.g., species of pouch-brooding or egg-carrying hylid frogs, species of Australian *Pseudophryne*, some species of *Eleutherodactylus*, etc.) exhibits most or all the parental care recorded for that family.

Among five other families in which more than 50% of the included species have some form of parental care, three families are small. The Leiopelmatidae and the Sooglossidae have three species each; the Rhinodermatidae has two species. In the two remaining families parental care has been reported for about half of the nearly sixty species in each. In the Dendrobatidae it probably characterizes the entire family (Silverstone, 1976; also see comments by Wells, 1977). In the Centrolenidae, in

contrast to the Dendrobatidae, an ethocline from species lacking parental care to those with parental care exists.

Salthe and Mecham (1974) presented three general explanations to account for the evolution of parental care in amphibians, arguing that more than a single explanation is necessary because of the parallel development of the behavior as a component of several different reproductive strategies. The three explanations are that parental care evolved in amphibians (1) as a mechanism to increase reproductive success in the absence of high fecundity by reducing predation on early life stages through guarding and active defense or through spatial dispersion of larvae; (2) as a mechanism to decrease developmental abnormalities caused by yolk layering or insufficient oxygen, through constant manipulation or jostling of the eggs; (3) as a mechanism to provide a more suitable microhabitat for the developing offspring in a generally unfavorable environment (i.e., out of water), by covering the eggs to decrease desiccation, or carrying the eggs and/or larvae around in the terrestrial environment or moving them to aquatic environments at different stages in their development.

Each of these mechanisms is important in and could account for the evolution and development of parental care in amphibians. However, Salthe and Mecham (1974) also indicated that parental care in amphibians almost always is associated with terrestrial reproductive patterns (i.e., reproduction in unfavorable habitats) and pointed to a trend of relatively larger ova and smaller clutches in those species with such care. There are some notable exceptions to this generalization concerning terrestrial reproduction, particularly among more primitive salamanders (e.g., Cryptobranchidae, Sirenidae, Necturidae) which tend to be aquatic. In addition, in aquatic frogs of the genus *Pipa*, the female parent carries the developing eggs in pockets on her back.

Likewise, there are several potential selective situations that act on both adult and egg-larval stages that could account for increased ovum size and decreased clutch size. Ovum volume and clutch size are negatively correlated so that larger eggs are found in smaller clutches. Salthe and Duellman (1973) reported increased ovum size in lotic breeders as well as in species with terrestrial development. They also found a positive correlation between ovum size and female snout-vent length and between ovum size and hatchling size. These findings suggest that lower fecundity (i.e., smaller clutches) can develop without the added investment of parental care. For example, within the hylid genus *Smilisca*, clutch size decreases and ovum diameter increases in a comparison of stream-breeding species to pond-breeding species. None has any form of parental care (Duellman and Trueb, 1966). Heyer (1969) documented a similar trend in the genus *Leptodactylus*. Available data for frogs suggest, however, that

parental care evolves in concert with reduced clutch size. All species of frogs for which parental care has been documented (Tables 1 and 2) have smaller clutches than their closest relatives which lack parental care. Thus, lower fecundity initially may be a preadaptation for parental care. Once the early stages in the evolution of parental care appear, selection should favor a continued gradual reduction in clutch size and a concomitant increase in parental care. It seems, then, that the mechanisms proposed by Salthe and Mecham (1974) must be viewed in a more synthetic framework, which also incorporates the apparent aquatic exceptions discussed previously. Wilson (1975) outlined a theory of parental care that involves a set of environmental conditions which acting singly or in concert will

TABLE 2. Classification of major patterns of parental care in frogs with representative examples

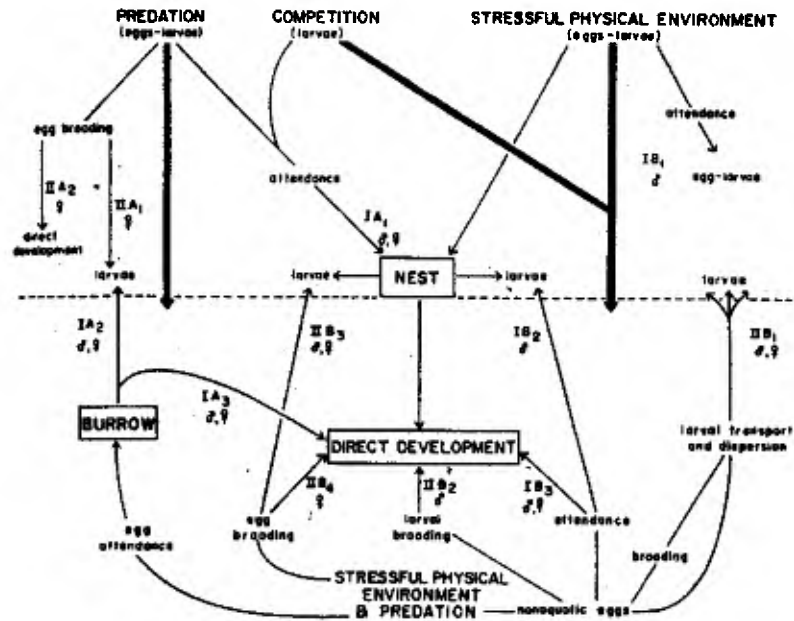
I. Investment at fixed site (philopatry)
A. Nest or burrow
1. eggs and larvae aquatic; male or female attendance (e.g., <i>Hyla rosenbergi</i> , <i>Leptodactylus ocellatus</i>).
2. terrestrial eggs; male and/or female attendance; larvae aquatic (e.g., <i>Pseudophryne</i> spp., <i>Hemisus</i> spp.)
3. terrestrial eggs; direct development; male or female attendance (e.g., <i>Breviceps</i> spp., <i>Phrynomantis</i> spp., <i>Leiopelma</i> spp.)
B. No nest or burrow
1. eggs and larvae aquatic; male attendance (e.g., <i>Nectophryne afra</i>)
2. terrestrial or arboreal eggs; male attendance; larvae aquatic (e.g., <i>Centrolenella</i> spp.)
3. terrestrial or arboreal eggs; direct development; male or female attendance (e.g., <i>Eleutherodactylus</i> spp., <i>Hylactophryne</i> spp.)
II. Investment at mobile site (i.e., parent)
A. Aquatic environment
1. eggs on back of female; larvae aquatic (e.g., <i>Pipa carvalhoi</i>)
2. eggs on back or in stomach of female; direct development (e.g., <i>Pipa pipa</i> , <i>Rheobatrachus silus</i>)
B. Terrestrial environment
1. terrestrial eggs; larval transport in vocal sac of male or on back of male or female; larvae aquatic (e.g., <i>Rhinoderma rufum</i> , <i>Dendrobates</i> spp.)
2. terrestrial eggs; direct development
a. on back of male (e.g., <i>Sooglossus</i> spp.)
b. in vocal sac or inguinal pouches of male (e.g., <i>Rhinoderma darwini</i> , <i>Assa darlingtoni</i>)
3. eggs on legs of male, or back or pouch of female; larvae aquatic (e.g., <i>Alytes obstetricans</i> , <i>Gastrotheca</i> spp.)
4. eggs on back or pouch of female; direct development (e.g., <i>Stefania</i> spp., <i>Gastrotheca</i> spp.)

favor modification of life history parameters and eventually result in parental care. Trivers (1972) and more recently Dawkins and Carlisle (1976) and Maynard Smith (1977) discussed some interesting ideas concerning the relative contribution of each parent to its offspring and made some predictions as to which parent was most likely to provide post-egg-laying investment in the form of parental care. By combining some of these ideas with what is known about frog reproduction and the environmental factors associated with the adaptive responses expected in organisms with parental care, it is possible to generate a classification of anuran parental care (Table 2) and to interpret the evolution of sexual strategies with regard to parental care in frogs. The patterns defined in Table 2 are illustrated in Figure 1 (e.g., *Nectophryne afra* has male parental care at the egg site in the aquatic environment and is listed as item 1B₁ in Table 2 and shown in the upper right corner of Figure 1 using the 1B₁ designation).

Classification of Parental Care

There is little doubt that the primitive reproductive mode of frogs is aquatic and involves external fertilization of eggs, free-swimming larvae, metamorphosis, and terrestrial existence of juveniles and adults. The major hazards affecting survivorship of frogs in the aquatic environment act primarily on the eggs and early larval stages. While data are sparse, the studies that have been done report mortality on egg and larval stages in excess of 90%. If this is representative for frogs, which have the primitive aquatic mode of reproduction, then selection favoring mechanisms to reduce aquatic mortality should be strong. I think the major mortality in the aquatic environment is attributable to predation on the eggs and/or early larvae (see also Heyer *et al.*, 1975). Other mortality factors include changes in the physical parameters of water quality (changes in temperature, O₂ availability, etc.) and probability of drying up, especially in temporary ponds and puddles. In these relatively unpredictable situations (e.g., small puddles), competition may play a secondary role. A physical factor of importance in lotic habitats is associated with a sudden rise in water level and the increased velocity of rain-swollen streams. These conditions are common in tropical areas during the rainy season and generally have favored a temporal shift in aquatic stream-breeding species to dry season reproduction (McDiarmid, personal observation). Another possible solution to these unpredictable fluctuations in water level is to get the early stages out of the water. This response will require favorable conditions on land. Such conditions are

AQUATIC ENVIRONMENT



TERRESTRIAL ENVIRONMENT

FIG. 1. A diagrammatic representation of the ecological and evolutionary distribution of parental care in frogs. The dashed line represents the interface between the aquatic and terrestrial environments. The major selective pressures of each environment and the stages upon which they operate are shown at the top and bottom of the diagram. Large arrows indicate a movement out of the aquatic environment as a solution. The narrow arrows represent evolutionary solutions to the selective pressures in each environment. The pattern of parental care is indicated to the side of each arrow and refers to the classification in Table 2. Arrows without associated patterns represent solutions without parental care.

best in tropical environments during the wet season when humidity is highest and problems of egg and larval desiccation at a minimum.

Adaptive responses that represent shifts toward increased parental care in the aquatic environment are not uncommon in aquatic salamanders (Salthe and Mecham 1974) but relatively rare in frogs. In part this is due to the terrestrial habits of most adult frogs. Indeed, the only examples (Table 2) of increased parental care in the aquatic environment are found in the species of aquatic frogs of the genus *Pipa*, in *Rheo-*

batrachus silus, and in the small bufonid *Nectophryne afra*. Females of *Pipa* transport eggs in small pockets on their backs where the eggs either hatch into larvae (IIA₁) which become free-swimming (e.g., *Pipa carvalhoi*) or have a modified form of direct development (IIA₂) with no free-swimming larvae (e.g., *Pipa pipa*) (Dunn, 1948). In the Australian myobatrachid *Rheobatrachus silus* the embryos and developing larvae are brooded in the stomach (Corben *et al.*, 1974). In *Nectophryne afra* (IB₁) the male spends considerable time swimming in place, stirring up water currents directed toward the eggs and tadpoles (Scheel, 1970). This behavior may function to reduce any developmental abnormalities which result from low aeration or poor water circulation.

The major adaptive responses to the hazards of the aquatic environment in frogs are associated with a tendency to get the egg and early larval stages out of the water. This trend includes a wide variety of adaptive modifications of the basic pattern (see recent review by Lamotte and Lescure, 1977) and is indicated by large arrows in Figure 1. Initial stages include species with nonaquatic eggs, aquatic larvae, and no parental care. The evolutionary sequence continues with increased terrestriality, first with the eggs, and then with eggs and larvae, and eventually culminates in some form of direct development, a reproductive mode which has developed independently in many unrelated families of frogs (Salthe and Mecham, 1974; Lamotte and Lescure, 1977). Parental care may have been associated with any of these sequential stages. As the selective advantages of increasing parental care manifested themselves, initially eggs, and then eggs and larvae were tended by one of the parents. In some situations selection favored male attendance; in others it favored that of the female parent. As selection for maintaining or providing the larvae with a suitable "aquatic" habitat out of the water became stronger, parental care became more and more important. As a result, the nature of parental care expanded from an initial one of egg attendance only, to include attendance of later stages, larval transport, and brooding. In this framework, attendance is viewed as an association of either parent with the eggs and/or tadpoles at a fixed site. Attendance is a form of philopatry and probably evolved with the increasing use of nests or burrows. These initial evolutionary efforts to get out of the aquatic environment because of predation and/or physical stress were enhanced by selection favoring philopatric behavior (e.g., construction of a foam nest, burrow, etc.) that provided protection for eggs or eggs and early larval stages. In some species foam nests obviously are structures to prevent egg and/or early larval desiccation. Whether they also protect early developmental stages from predation is unknown but worthy of consideration. Initially, these nests and burrows must have been in close proximity to water and,

thereby, allowed easy return to the aquatic habitat by larger, more mobile larvae that presumably were better able to deal with the rigors of aquatic existence. I view these initial evolutionary experiments as efforts to maintain the aquatic nature of the organisms rather than efforts to become more terrestrial. In so doing, these behavioral modifications led to increased terrestriality. As reproductive modes became more terrestrial, the rigors of the terrestrial environment began to play a greater and greater role in molding reproduction. Probably, the physiological and developmental requirements of the developing egg, particularly with respect to desiccation, favored increasing attendance by one of the parents. It is likely that terrestrial predation also played a leading role in selecting for attendance. In some, this involved transport of the larvae back to the water. As the rigors of transport increased (e.g., increased susceptibility of the transporting parent to predation), selection favored reduction in the free-swimming larval stage, culminating in a form of direct development. If parental care in the form of egg attendance were important in the initial stages of increasing terrestriality, the investment of the attending parent already would be considerable, and the amount needed to get the offspring to near hatching would be less. It follows that the evolution of additional investment would more likely occur than a reduction or abandonment of parental care. The culmination of this evolutionary progression is the actual brooding by one parent, usually the female. As used here, brooding is the form of parental care in which the eggs and/or larvae are maintained and carried on the parent or in specialized parental structures suited for their maintenance. This trend ultimately results in direct development of the young in or on the parent. Direct development in its several forms is wide spread among frogs and reflects the evolutionary experimentation in reproductive modes that so characterizes this vertebrate group (Lutz, 1947; Orton, 1949; Jameson, 1959; Goin and Goin, 1962; Lamotte and Lescure, 1977).

The evolutionary scheme outlined above finds considerable support among frogs that have various kinds of parental care (Table 2) and is schematically diagrammed in Figure 1. The initial stages of attendance are found in the mud-nest-building species of the *boans* group of hylid frogs and the foam-nest-building frog *Leptodactylus ocellatus* (IA₁). Males of *Hyla rosenbergi*, *H. faber*, and others are territorial and actively defend mud-depression nests constructed at the edge of streams or ponds. The nests are used as sites for egg deposition and early larval development and effectively isolate these stages from aquatic predators (Breder, 1946). Here the male is territorial, larger than the female (Duellman, 1970), and is involved in parental care (guarding) at the nest which contains his eggs and/or larvae. In these species, the male apparently continues to attract

females to the nest, and the added cost of parental care seems to be outweighed by the benefit of increased survivorship of the young resulting in an increase in his reproductive success. This system has considerable potential in elucidating the relationship between male territoriality and parental care and currently is being studied (Kluge, personal communication).

In *Leptodactylus ocellatus* either the female (usually) or the male (occasionally) or both guard the foam nest and the included eggs. On hatching the tadpoles form a school which moves around the pond feeding. The female follows the aggregated tadpoles around the pond and will attack potential predators attempting to feed on the larvae (Vaz-Ferreira and Gehrau, 1975). Unfortunately, data are lacking as to the preamplectic behavior of either parent. In this case it is clear that attendance by the parent usually the female, serves to protect the eggs and larvae from predation particularly by birds. This is the only documented case of protection of free-swimming larvae by a parent. Reports (e.g., Rose, 1962; Poynton, 1964) of the defense of larvae of the African ranid *Pyxicephalus adspersus* by adults generally have been discounted (Wager, 1965) but may deserve additional study considering the findings for *L. ocellatus*.

The next step in this evolutionary progression involves the development of more terrestrial reproduction but with retention of aquatic larvae (IA₂). In the African ranid *Hemisus*, the female sits on the eggs in a burrow she constructs near an aquatic site. After the eggs hatch in the burrow, she tunnels laterally to the water, and the larvae follow (Wager, 1965). Similar patterns involving either parent are found in the Australian myobatrachid *Pseudophryne* (Salthe and Mecham, 1975). In some species of *Pseudophryne*, the males actively defend burrows which also serve as nest sites (Pengilley, 1971). Presumably, desertion of the burrow and contained clutch by the male would decrease his likelihood of attracting another female as quickly as would be possible if he remained. As burrows apparently are contested resources in short supply and are required for successful reproduction, his continued attendance at the egg site, rather than the female's attendance, is not unexpected. This will be true only if he is potentially able to attract other females to the original site. These ideas find some support in a recent study of *Pseudophryne* by Woodruff (1977). With this sequence established, the role of the male or the female at a nest site in those species (*Leiopelma* spp., Stephenson, 1951; *Phrynomantis* spp., Zweifel, 1972; *Breviceps* spp., Wagner, 1965; etc.) which have direct development (IA₃) is more easily interpreted. These same patterns are indicated in species which have terrestrial eggs but no nest site (IB₃); for example, males of *Hylactophryne* spp. are territorial and attend eggs (Jameson, 1950). The males of certain species

of *Centrolenella* are territorial and involved in varying degrees of egg attendance (BI₂). These forms will be discussed in more detail below. Either males or females guard eggs in some species of *Eleutherodactylus* (Myers, 1969; Drewry and Jones, 1976). Little is known about their preamplectic behavior and further comment is unjustified at this time.

The situation in the Malagasy microhylid frogs of the subfamily Cophylinae is somewhat intermediate between modes IA₂ and IA₃. Blommers-Schlösser (1975) reviewed the breeding habits of these frogs and reported direct development with parental care as characteristic of the subfamily. Eggs are deposited in burrows on the ground and attended by the female in the fossorial species *Plethodontohyla tuberosa*. In the arboreal species *Platyhyla grandis*, *Plethodontohyla notosticta*, and *Anodontohyla boulengeri* the eggs are deposited in phytotelmes or other water filled holes in bamboo or tree trunks and attended by the male. In the arboreal species the tadpoles are free-swimming but do not feed. Interestingly the males are larger than females in *P. grandis* pairs. Other microhylid frogs in the subfamilies Asterophryinae and Sphenophryinae (Tyler, 1963; Zweifel, 1972) are more easily assigned to pattern IA₃. Many more data on all three subfamilies are needed before their arrangement in the classification can be made with assurance.

The transition from fixed to mobile (I to II) sites in my classification (Table 2) is accomplished through species with terrestrial eggs and larval transport (Fig. 1). This pattern is found among the Dendrobatidae (IIB₁) where males (occasionally females) transport the larvae on their backs from the place of egg deposition in forest leaf litter to an aquatic site and in *Rhinoderma rufum* (Formas *et al.*, 1975). Again the territorial nature of most male dendrobatids is well known (Silverstone, 1975, 1976) and probably is responsible for the paternal care in this species. Males of the sooglossid frogs have the same mode, but the tadpoles undergo direct development (IIB_{2a}) on the males' backs rather than becoming free-swimming (Salthe and Mecham, 1974). I interpret male brooding (IIB_{2b}) in the vocal pouch in *Rhinoderma darwini* (Cei, 1962; Busse, 1970) and *R. rufum* (Formas *et al.*, 1975) and in inguinal pouches in *Asa darlingtoni* (Ingram *et al.*, 1975), as the expected evolutionary results of initial efforts at transport of the larvae back to an aquatic site. The fact that *Rhinoderma rufum* has free-swimming larvae and that the larvae of *Rhinoderma darwini* will develop in aquatic situations (Cei, 1962) but at a much slower rate and occasionally in moist terrestrial situations (Busse, 1970), supports this view. With one exception, all other forms of brooding, either with a free-swimming larval stage (IIB₃) or with direct development (IIB₄), involve parental care by the female. I suspect two factors are important here: (1) females often are larger than males and, therefore,

more likely to successfully carry the fertilized eggs which they have produced, and (2) the males in these species probably are capable of multiple fertilizations. Brooding by the male in these species potentially could reduce his ability to successfully mate with another female. On the other hand, the female probably has expended her entire egg complement and, therefore, will not be ready to breed again for some time. Considering this aspect of the female reproductive cycle, her larger initial investment, and the relatively higher costs to her of getting another clutch to the same stage as her current one, selection would favor increased parental care through her brooding rather than the male's. The same pattern can be used to explain the brooding role of the female in the aquatic systems with *Pipa* spp. and *Rheobatrachus silus* (IIA₁, IIA₂).

The single exception to female egg-brooding is found in the discoglossid frog, *Alytes obstetricans*. After an elaborate mating, the male carries the eggs entwined on his hind limbs. When the eggs are near hatching, he moves to a suitable aquatic site. There the eggs hatch, releasing typical free-swimming tadpoles. During drier nights, the male may immerse the eggs in water (Boulenger, 1897). This form of brooding, which allows such activity, apparently has been favored by the relatively harsh terrestrial environment. In view of what is known about other forms of paternal care, I predict that males carrying eggs are not appreciably hindered in the successful completion of additional courtship and have more to gain by brooding a clutch and continuing to attract other females than by abandoning it. Boulenger (1897) remarked that the male is "little impeded in his movements" on land and occasionally successfully fertilizes a second female, adding another clutch of eggs.

In summary, parental care is relatively widespread but uncommon in frogs. The selective pressures (i.e., predation, habitat unpredictability) of the aquatic environment operating on eggs and early larval stages have favored mechanisms which remove these stages of the life cycle from the water. In some instances problems associated with the terrestrial environment, particularly egg desiccation, selected for parental care in the form of attendance at the eggs in these initial efforts at getting away from the hazards of an aquatic existence. As terrestrial pressures (e.g., predation) came into play, selection favored moving egg sites farther away from the water's edge. The greater the distance from an aquatic site, the greater the problems of larval return to the water. Parental care in the form of larval transport became crucial. With the increasing terrestriality, problems of desiccation were added to those of predation and transport and eventually resulted in direct development. Increased parental care coupled with direct development accounts for the incredible diversity of brooding behavior known in frogs.

Parental Care: Case Histories

The scarcity of data on parental care in frogs became obvious to me in reviewing the available literature for this paper. There are very few studies on the reproductive ecology and behavior of any species of frog. None has been published that specifically examines the role of parental care and its effect on species reproductive behavior or individual fitness. The work on *Leptodactylus ocellatus* (Vaz-Ferreira and Gehrau, 1975) is a start, but even in this study many questions remain unanswered. In part the paucity of data is a reflection of the secretive nature of individuals of many of the species that have tending behavior (especially at burrows) and of females of species with brooding behavior. Rarely is there the opportunity to compare the relative selective advantage of different forms of parental care in two similar species. It is appropriate, therefore, to describe the essentials of just such a system in two species of *Centrolenella*. These data are part of a long term study on the reproductive ecology and behavior of centrolenid frogs (McDiarmid and Adler, 1974; McDiarmid, 1975, and unpublished ms).

Species of glass frogs, genus *Centrolenella*, breed on vegetation along small streams in lowland and mid-elevation forests in Central and South America. In many species the males are territorial (McDiarmid and Adler, 1974; Duellman and Savitzky, 1976), and in some they have parental care in the form of attendance at the egg site (pattern IB₂, Fig. 1). I have looked at two species of *Centrolenella*, *C. colymbiophyllum*, and *C. valerioi*, over three field seasons along a small, forest stream near Rincón de Osa, Puntarenas Province, Costa Rica. Selected data from this study are presented here to (1) document the nature of parental care in these frogs, (2) illustrate the relative advantages of differential investment between two closely related species, and (3) examine the evolutionary consequences of parental care with respect to differential survivorship. To my knowledge, this study is the first documenting the relative advantages of differential parental care between two closely related species that are ecologically sympatric and essentially identical in their reproductive behavior. Males of both species are nocturnal and establish territories on appropriate leaves above the stream at least from April through September. Males advertise their reproductive readiness from the undersides of leaves and attract females from the surrounding forest. Eggs are deposited on the underside of the leaves and attended by the male. In both species males continue to advertise and attract females after egg clutches

are deposited. Individuals with up to eight clutches (= females) on one leaf have been recorded for male *colymbiphyllum* and those with up to seven for male *valerioi*. The mean number of clutches per male in 1973 was 2.6 for *C. valerioi* and 1.8 for *C. colymbiphyllum*. The major difference between males of the two species is in the amount of care each devotes to his clutches. Male *colymbiphyllum* spend each night at a leaf site calling and attending any clutches present (Fig. 2). As dawn breaks, *colymbiphyllum* males move off the defended calling and egg site and hide in the vegetation back from the stream. The few males that have been located in the day time are adpressed against the underside of a leaf in a concealed site some distance from the egg clutch. They spend the entire day in this "sleeping" position and return to the calling site each night to resume vocalization and attendance. In contrast, male *C. valerioi* also spend the daylight hours in attendance at the egg site. Instead of assuming the adpressed "sleep" posture, they occupy a position next to their clutch or clutches (Fig. 3) often with their head or a front foot resting on the edge of one of them. In this position they are alert and able to tend the eggs during the day as well as at night. Colored photographs of the sleep posture of male *C. colymbiphyllum* and diurnal guarding behavior of male *C. valerioi* are available elsewhere (McDiarmid, 1975). What we have, then, are two species with very similar ecologies but with different amounts of parental care.

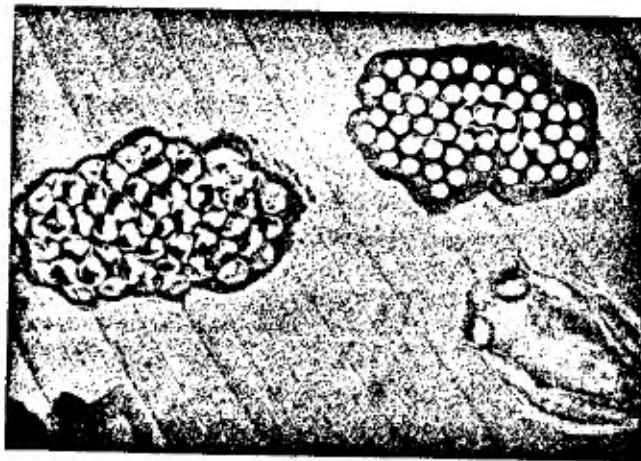


FIG. 2. A male *Centrolenella colymbiphyllum* attending two egg clutches at night. The uniformly green male retreats to the surrounding vegetation to spend each day but returns to the egg site each night to continue calling.

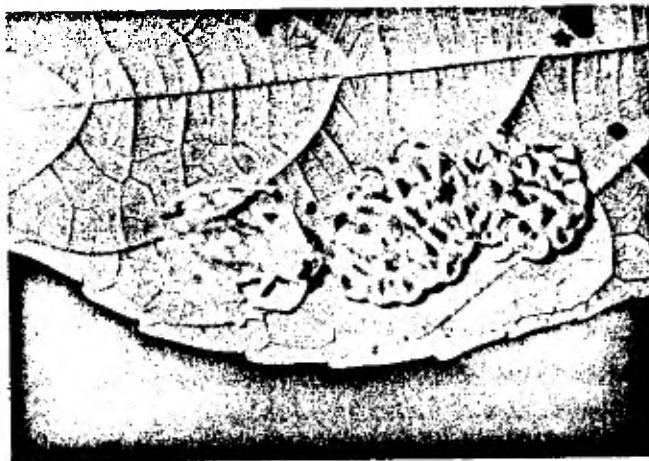


FIG. 3. A male *Centrolenella valerioi* attending two egg clutches during the day. The male is reticulate patterned and alert and resembles his egg clutches especially during the day. He resumes calling at the same site each night.

In Table 3, selected aspects of the reproductive ecology of the two species are compared. Of particular interest are three points. (1) The proportions of male *colymbiphyllum* to *valerioi* for each year, which are remarkably consistent; I interpret this as an indication of the relative stability of numbers of individuals both within and between the species. (2) The higher percentage predation of *colymbiphyllum* eggs as compared to those of *valerioi* in 1971 and 1973: The high mortality of *colymbiphyllum* eggs in 1971 was primarily the result of diurnal predation by a small wasp during drier periods of the study. The wasp searches the under-leaf surfaces for suitable prey. When it finds an egg mass, it lands on the jelly, withdraws a developing egg in its mandibles, and flies off. I suspect the eggs are used to provision a nest. Apparently wasps return to the same site until all eggs in a clutch are gone. The similarly low values in 1969 may have been due to the shorter, wetter sampling period. Similar two-week periods in 1973 had lower predation than is reflected in the 1973 totals over the eight weeks. (3) The larger clutch size of *colymbiphyllum*. In addition, yolk diameters of eggs averaged 1.5 mm in *colymbiphyllum* and 2 mm in *valerioi* within 12 hours of deposition on the leaf.

An analysis of the 1973 data is presented in Table 4. The presence of an egg clutch at a male's call site was used as a measure of individual success. About 73.5% of the 83 male *colymbiphyllum* were successful in

TABLE 3. Selected aspects of the reproductive biology of two sympatric species of *Centrolenella* studied along a forest stream near Rincón de Osa, Puntarenas Province, Costa Rica.

	<i>C. COLYMBIPHYLLUM</i>			<i>C. VALERIOI</i>		
	1969	1971	1973	1969	1971	1973
Time (wk)	2	2	8	2	2	8
Stream length (m)	260	100	260	260	100	260
Number of males	40	27	83	24	14	43
Number of clutches	30	25	152	29	21	112
Success (%)	50	63	73	71	71	67
Predation (%)	3.3	44.0	26.3	3.4	9.5	14.3
Clutch size						
<i>N</i>	21	4	53	20	11	52
range	33-64	50-56	37-70	19-35	27-33	19-45
\bar{x}	49.1	53.7	50.4	29.3	29.2	28.9

TABLE 4. Comparative aspects of the reproductive behavior and ecology of two sympatric species of *Centrolenella* illustrating the role of parental care in their reproductive success

	<i>COLYMBIPHYLLUM</i>	<i>VALERIOI</i>
Number ♂♂ (a)	83	43
Number of clutches (b)	152	112
\bar{x} Clutch size (c)	50.4	28.9
♂♂ with Egg clutch(es)		
<i>N</i> (d)	61	29
% (d/a)	73.5	67.4
♂♂ Producing larvae		
<i>N</i> (e)	47	27
% (e/a)	56.6	62.8
% ♂♂ with Eggs producing larvae (e/d)	77.0	93.1
% Clutches predated (f)	26.3	14.3
\bar{x} Larval production/♂ ($c \times b/a \times 1 - f$)	68.0	64.5

attracting a female that laid eggs. The value was slightly lower (67.4% of 43) for male *valerioi*. In contrast, an average male *valerioi* was slightly more successful in producing larvae (62.8% of the male *valerioi* to 56.6% of the male *colymbiphyllum*). When we examine the percent of males with eggs that produced larvae (i.e., had eggs which were not predated), the values are 93.1 for *valerioi* and 77.0 for *colymbiphyllum*. The increased

success of *valerioi* clearly is the result of the evolution of increased parental care in the form of diurnal attendance at the egg site. Interestingly, the mean numbers of larvae produced by a male of each species do not differ appreciably. The similar values between the two species, 68.0 in *colymbiphyllum* and 64.5 in *valerioi*, in spite of the added investment of *valerioi*, result from the greater mean clutch size of *colymbiphyllum*. The fact that the two species produce nearly equal numbers of larvae per male indicates the trade-off in fitness traits (i.e., clutch size and parental care) between the two species, i.e., that parental care is not the only successful strategy.

The dorsal color patterns of the two species also underscore the difference between them with regard to diurnal guarding behavior. *C. colymbiphyllum* are essentially uniform green with small, scattered yellow dots (Fig. 2). *C. valerioi*, on the other hand, have a reticulate green pattern on a yellowish to pale-gold background, and an attending male is strikingly similar in appearance to the egg clutch(es) which he guards, especially during the day (Fig. 3). I suggest that the dorsal coloration of *valerioi* has evolved in response to its daytime presence at the egg site through the activities of visual-hunting diurnal predators. If the predator searching for an egg clutch is small enough to be repulsed by the male (e.g., small wasp), selection should favor a strong resemblance between the guarding male and his clutch. This will increase the probability of successful defense when the predator mistakes the male for the clutch. If the predator is a frog-eating species, it may mistake the frog for another egg clutch, which is not suitable prey, and continue its search. This would not be the case if a *colymbiphyllum* were encountered and would account for the more typical diurnal behavior of this species.

Future Research

The classification proposed earlier in this chapter is based on available data. While the major dichotomies and general trends appear to me to accurately reflect the patterns of parental care in frogs as currently understood, the picture is far from complete. With the exception of my work on frogs of the genus *Centrolenella* and current work on *Hyla rosenbergi* (Kluge, personal communication) there are no detailed studies on the relative importance of parental care in frogs. The relative importance of the various forms of parental care can only be evaluated against a background of detailed ecological information concerning the population dynamics of a particular species. Data relating to specific aspects of the population biology of several species with varying reproductive modes

but occurring in the same habitat are needed. These data must be generated over relatively long periods of time (an entire reproductive season) and from marked individuals in a population. Specifically, studies must consider the reproductive capabilities of individuals in a population with reference to age at first reproduction, number of reproductive efforts per season, number of eggs produced per clutch, number of clutches per lifetime, relationship between age, size, and fecundity, and the sex ratio in the breeding population at the time. In addition workers must address the question of the role of behavior in molding reproductive modes in frogs. An understanding of the preamplectic behavior of males and females in the population is crucial to unraveling the relative trade-off between pre-copulatory and postcopulatory investment. One correlation uncovered in this review is that between marked territorial behavior and male parental care in some species. Does the scarcity of call and/or egg deposition sites result in territorial defense by males and thus favor an additional investment in the form of guarding and attendance by the male rather than female care? If this is true, as suggested by my data for *Centrolenella*, what determines the success of one male compared to another? Is it the site (i.e., a well hidden leaf; a strategically located burrow) that is important or is it the male or some combination of both? Do females evaluate the relative quality of a potential partner by the site that he holds, or do they somehow "count" his previous successes (i.e., egg clutches) and use that information in the selection process? Of particular importance to understanding the role of parental care is a knowledge of the reproductive success of individuals in a population. Crucial questions are: How often does a female breed in a reproductive season? Do quantitative or qualitative differences exist between eggs in her first clutch and eggs in her last clutch? Does she return to the same site or the same mate each time? Does attendance or brooding preclude additional breeding at the same time? What is the probability of an individual breeding successfully a second time if it deserts its first clutch? Are multiple breedings without parental care more likely to produce successful offspring than fewer breedings with parental care? What are the major mortality factors in a population, and how do these relate to the different kinds of parental investment?

Finally, we must have a better understanding of the role of each sex in reproductively related activities to allow for a more meaningful interpretation of the observed patterns. We must know more than the sex of the attending or brooding parent to unravel those factors favoring the evolution of different sexual strategies in terms of parental investment. These are some of the questions which must be considered in selecting a suitable group for study. In addition, the ease with which natural and artificial manipulations can be done should be weighed heavily in selecting

an appropriate system. It is obvious that frogs have a great deal to offer to our understanding of the ecological role and evolutionary impact of parental care. What is needed are more data.

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References

- Blommers-Schlösser, R. M. A. 1975. Observations on the larval development of some Malagasy frogs, with notes on their ecology and biology (Anura: Dicrophinae, Scaphiophryninae and Cophylinae). *Beaufortia* 24(309):7-26.
- Boulenger, G. A. 1897. *The tailless batrachians of Europe*. Part 1. London: Ray Society. 210 pp.
- Breder, C. M., Jr. 1946. Amphibians and reptiles of the Rio Chucunaque Drainage, Darien, Panama, with notes on their life histories and habits. *Bull. Am. Mus. Nat. Hist.* 86(8):375-436.
- Busse, K. 1970. Care of the young by male *Rhinoderma darwini*. *Copeia* 1970:395.
- Cei, J. M. 1962. *Batrachios de Chile*. Santiago: Universidad de Chile. 128 pp.
- Corben, C. J., G. J. Ingram, and M. J. Tyler. 1974. Gastric brooding: unique form of parental care in an Australian frog. *Science* 186:946-947.
- Crump, M. L. 1974. Reproductive strategies in a tropical anuran community. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* 61:1-68.
- Dawkins, R., and T. R. Carlisle. 1976. Parental investment and mate desertion: a fallacy. *Nature* 262:131-133.
- Drewry, G. E., and K. L. Jones. 1976. A new ovoviviparous frog, *Eleutherodactylus jasperi* (Amphibia, Anura, Leptodactylidae), from Puerto Rico. *J. Herpetol.* 10(3):161-165.
- Duellman, W. E. 1970. The hylid frogs of Middle America. *Monogr. Mus. Nat. Hist. Univ. Kansas* 1:1-753.
- Duellman, W. E., and L. Trueb. 1966. Neotropical hylid frogs, genus *Smilisca*. *Univ. Kansas Publ. Mus. Nat. Hist.* 17(7):281-375.
-

- Duellman, W. E., and A. H. Savitzky. 1976. Aggressive behavior in a centrolenid frog, with comments on territoriality in anurans. *Herpetologica* 32:401-404.
- Dunn, E. R. 1948. American frogs of the family Pipidae. *Am. Mus. Novit.* 1384:1-13.
- Formas, R., E. Pugin, and B. Jorquera. 1975. La identidad del batracio Chileno *Heminecetes rufus* Philippi, 1902. *Physis* 34(89):147-157.
- Goin, O. B., and C. J. Goin. 1962. Amphibian eggs and the montane environment. *Evolution* 16:364-371.
- Heyer, W. R. 1969. The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). *Evolution* 23:421-428.
- Heyer, W. R., R. W. McDiarmid, and D. L. Weigmann. 1975. Tadpoles, predation and pond habitats in the Tropics. *Biotropica* 7(2):100-111.
- Ingram, G. J., M. Anstis, and C. J. Corben. 1975. Observations on the Australian leptodactylid frog, *Assa darlingtoni*. *Herpetologica* 31:425-429.
- Jameson, D. L. 1950. Development of *Eleutherodactylus latrans*. *Copeia* 1950:44-46.
- Jameson, D. L. 1957. Life history and phylogeny in the Salientians. *Syst. Zool.* 6(2):75-78.
- Lamotte, M., and J. Lescure. 1977. Tendances adaptatives a l'affranchissement du milieu aquatique chez les amphibiens anoures. *La Terre et la Vie.* 31(2):225-311.
- Lutz, B. 1947. Trends towards non-aquatic and direct development in frogs. *Copeia* 194(7):242-252.
- Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.* 25:1-9.
- McDiarmid, R. W. 1975. Glass frog romance along a tropical stream. *Terra, Los Angeles Co. Mus.* 13(4):14-18.
- McDiarmid, R. W., and K. Adler. 1974. Notes on territorial and vocal behavior of neotropical frogs of the genus *Centrolenella*. *Herpetologica* 30(1):75-78.
- Myers, C. W. 1969. The ecological geography of cloud forest in Panama. *Am. Mus. Novit.* 2396:1-52.
- Orton, G. L. 1949. Larval development of *Nectophrynoides tornieri* (Roux), with comments on direct development in frogs. *Ann. Carnegie Mus.* 31:257-277.
- Pengilley, R. K. 1971. Calling and associated behaviour of some species of *Pseudophryne* (Anura, Leptodactylidae). *J. Zool.* 163:73-92.
- Poynton, J. C. 1964. The Amphibia of Southern Africa: a faunal study. *Ann. Natal Mus.* 17:1-334.
- Rose, W. 1962. *The reptiles and amphibians of Southern Africa*. Cape Town, South Africa: Maskew Miller Ltd. 494 pp.
- Salthe, S. N., and W. E. Duellman. 1973. Quantitative constraints associated with reproductive mode in anurans. In *Evolutionary biology of the anurans*, ed., J. L. Vial, pp. 229-249. Columbia: Univ. Missouri Press.
- Salthe, S. N., and J. S. Mecham. 1974. Reproductive and courtship patterns. In *Physiology of the Amphibia*, ed., B. Lofts, pp. 309-521. New York and London: Academic Press.
- Scheel, J. J. 1970. Notes on the biology of the African Tree-toad, *Nectophryne*

- afra* Buchholz and Peters, 1875, (Bufonidae, Anura) from Fernando Poo. *Rev. Zool. Bot. Afr.* 81(3,4):225-236.
- Silverstone, P. A. 1975. A revision of the poison-arrow frogs of the genus *Dendrobates* Wagler. *Nat. Hist. Mus. Los Angeles Co. Sci. Bull.* 21:1-55.
- Silverstone, P. A. 1976. A revision of the poison-arrow frogs of the genus *Phyllobates* Bibron in Sagra (Family Dendrobatidae). *Nat. Hist. Mus. Los Angeles Co. Sci. Bull.* 27:1-53.
- Stearns, S. C. 1976. Life history tactics: a review of the ideas. *Q. Rev. Biol.* 51:3-47.
- Stephenson, N. G. 1951. Observations on the development of the amphicoelous frogs, *Leiopelma* and *Ascaphus*. *Linn. Soc. J. Zool.* 42:18-28.
- Thornhill, R. 1976. Sexual selection and paternal investment in insects. *Am. Naturalist* 110(971):153-163.
- Trivers, R. L. 1972. Parental investment and sexual selection. In *Sexual selection and the descent of man 1871-1971*, ed., B. Campbell, pp. 136-179. Chicago: Aldine.
- Tyler, M. J. 1963. A taxonomic study of amphibians and reptiles of the Central Highlands of New Guinea, with notes on their ecology and biology. 1. Anura: Microhylidae. *Trans. Roy. Soc. South Aust.* 86:11-29.
- Vaz-Ferreira, R., and A. Gehrau. 1975. Comportamiento epimeletico de la rana comun, *Leptodactylus ocellatus* (L.) (Amphibia, Leptodactylidae). I. Atencion de la cria y actividades alimentarias y agresivas relacionadas. *Physis* 34(88):1-14.
- Wager, V. A. 1965. *The frogs of South Africa*. Cape Town and Johannesburg, Africa: Purnell & Sons Pty. Ltd. 242 pp.
- Wells, K. D. 1977. The social behaviour of anuran amphibians. *Anim. Behav.* 25(3):666-693.
- Wilbur, H. M. 1977. Propagule size, number, and dispersion pattern in *Ambystoma* and *Asclepias*. *Am. Naturalist* 111(977):43-68.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Naturalist* 100(916):687-690.
- Wilson, E. O. 1975. *Sociobiology the new synthesis*. Cambridge, Mass.: Belknap Press. 697 pp.
- Woodruff, D. S. 1977. Male postmating brooding behavior in three Australian *Pseudophryne* (Anura: Leptodactylidae). *Herpetologica* 33:296-303.
- Zweifel, R. G. 1972. Results of the Archbold expeditions. No. 97. A revision of the frogs of the subfamily Asterophryinae family Microhylidae. *Bull. Am. Mus. Nat. Hist.* 148(3):411-546.
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