

Chapter 1

Anuran Diversity: Reproductive Modes and Parental Care

Explanations for the diversity of anuran behavior can be found in their history, their current anatomical and physiological characters, and the opportunities afforded by outmaneuvering those constraints. In this chapter, I review what makes amphibians, and anurans in particular, distinct from other vertebrates. I then survey reproductive modes in anurans, giving some examples to demonstrate the diversity of their life histories, without reviewing all that is known. I make particular note of reproductive modes of phytotelm-breeding anurans. This is in order to place my study organism, the phytotelm-breeding *Mantella laevis*, in a broader context of anuran reproduction. I briefly review parental care in anurans, and propose a new functional organization of the types of anuran parental care. I conduct a complete review of the type exhibited by *M. laevis* (see chapter 2), maternal feeding of tadpoles. Again, this serves to give the reader a sense of the diversity of behavior in anurans, and to place *M. laevis* in its broader evolutionary and ecological context.

Amphibians: an ecological summary

Amphibians are so named for the two distinct periods of their lives: the aquatic larval stage, and the terrestrial adult stage. Not all amphibians have these two stages, however, some being fully aquatic, others entirely lacking aquatic stages in their life histories. More precisely, amphibians can be (incompletely) diagnosed as quadrupedal vertebrates with no more than one sacral vertebra (Duellman and Trueb 1986).

Lissamphibia, the taxon that includes extant amphibians, have glandular skin that lacks the epidermal structures that characterize other groups of tetrapods, such as scales, feathers, or hair. Lissamphibia are diagnosed by several morphological characters, two of which are the presence of a *papilla amphibiorum* in the inner ear, which allows them to sense acoustic signals of less than 1,000 Hz; and a reliance on cutaneous respiration through their moist skin. Furthermore, lissamphibians can be distinguished from other classes of vertebrates by karyological characteristics, including a tendency toward genome hypertrophy, and large interspecific variability in genome size, even among closely related species (Duellman and Trueb 1986).

Lissamphibia is comprised of three major groups of extant species: Gymnophiona (caecilians), Caudata (salamanders and newts), and Anura (frogs and toads). The number of recognized lissamphibian species is constantly growing, but the internal make-up of the group remains largely the same: approximately 87% of extant lissamphibian species are anurans, and anuran

species currently number more than 4,000 (Duellman and Trueb 1986, Stebbins and Cohen 1995).

Anurans are the tailless amphibians. They are also diagnosed by having elongated hind limbs that are modified for jumping, as well as postsacral vertebrae that are fused into a single, rodlike element, the coccyx (Duellman and Trueb 1986). Not geographically restricted to the extent that the Gymnophiona and Caudata are, anurans are, nevertheless, more prevalent in the tropics than elsewhere. Most are also nocturnal.

All amphibian eggs lack both shells and the protective membranes of amniote eggs, and so require moist microhabitats in which to develop. Furthermore, almost all anurans have external fertilization, and are oviparous. External fertilization offers individuals a high certainty of paternity, opening the door for the evolution of paternal care. Exceptions to the rule of external fertilization include the phylogenetically basal tailed-frog, *Ascaphus truei*, whose “tail,” actually an extension of the cloaca, acts as an intromittent organ during copulation (Metter 1964). All of the members of the toad genus *Nectophrynoides* have internal fertilization (Noble 1926), two species being viviparous (Xavier 1977, Wake 1980), several ovoviviparous (Grandison 1978), and one oviparous (Wake 1980). *Eleutherodactylus jasperii* is also ovoviviparous (Drewry and Jones 1976), the young emerging as froglets from the cloaca. *Mertensophryne micranotis* (Grandison 1980) and *Eleutherodactylus coqui* (Townsend et al. 1981) both display the unlikely combination of internal fertilization and oviparity, and there is some evidence for the same in *Eleutherodactylus angelicus* (Hayes 1985).

During, and in many cases before, oviposition, the male anuran grasps the female in an embrace known as amplexus. In cases of extended amplexus, which

can last months in some species, this may serve to restrict the female from mating with other males. In all cases, amplexus is understood to insure that the sperm and eggs will actually contact one another.

Temporal patterns of anuran reproduction vary widely, but can be roughly divided into two broad types: explosive breeding and prolonged breeding (Wells 1977). In many species, the length of the breeding period is limited by climate, or the seasonal availability of breeding sites, such as ephemeral pools. Temperate species are more likely to breed explosively—an entire population breeding over a span of a few days or weeks. By contrast, many tropical anurans breed in every month of the year, although most demonstrate some seasonality as well. Some tropical species restrict their breeding activity to either the wet or the dry season, but this does not tend to limit their breeding season to the same degree that cold limits breeding in the temperate zone (Wells 1977).

Male anurans court females, almost universally, with an advertisement call. Vocalizations are the initial attractor to potential mates in most anuran species, as they can serve to attract females from a broad area. Because of the presence of the *papilla amphibiorum*, anurans can hear and respond to a wider range of vocalizations than humans can detect. Females of most anuran species are mute, or have very weak calls.

The spatial and temporal distribution of females, as determined in part by breeding pattern, determines how males interact with each other. In species with explosive breeding, males tend to form dense aggregations and engage in scramble competition, attempting amplexus with any nearby individual, male or female. In species with prolonged breeding, males often call from stationary positions, attracting females to them, and maintaining intermale spacing (Wells

1977). These male calling sites often represent territories that contain oviposition sites or courtship areas. It is in such prolonged breeders that long-term male territoriality often evolves, and with it, the likelihood that females will choose mates not solely based on male calls, or genetic quality, but also on the resources the male defends.

Reproductive Modes in Anurans

The diversity of life history strategies found in anurans is remarkable. Restricted, in most cases, by external fertilization, and by the need to find moist habitats for their eggs, anurans have nevertheless evolved myriad ways to thrive. Indeed, anuran reproductive modes are so diverse that there is still no single, universally cited source that encompasses all recognized modes. Furthermore, it appears that trends away from the primitive mode of eggs and tadpoles in ponds do not reflect one or two evolutions of increasing specialization, but many independently derived reproductive modes in distinct phylogenetic lineages (Duellman and Trueb 1986:27).

Part of the problem is definitional. Crump (1974) defined reproductive mode simply as the combination of deposition site and type of development. Reproductive mode is defined by Salthe and Duellman (1973), and used by Duellman and Trueb (1986:21) as a “combination of ovipositional and developmental factors, including oviposition site, ovum and clutch characteristics, rate and duration of development, stage and size of hatching, and

type of parental care, if any.” Brown and Alcala (1983) explicitly add larval nourishment to this list. There is room for interpretation in all of these definitions.

The layperson who imagines a frog during its mating season most likely conceives of an explosively breeding species. An entire population convenes about a pond, or perhaps a slowly moving stream or river. During amplexus, large masses or strings of eggs are laid in the water, and afterwards both male and female disperse, never to encounter their offspring again. Those eggs that do not get eaten develop and hatch in the water. Tadpoles survive by eating muck or small aquatic insects, until they finally metamorphose, and only then come on land. This reproductive mode—aquatic eggs deposited in relatively large, permanent bodies of water, with feeding tadpoles developing in the same water—is in fact only one of many reproductive modes now recognized in anurans. It is, however, the most common and phylogenetically widespread (Duellman and Trueb 1986:23).

Jameson (1957) was the first to systematically describe the diversity of anuran reproductive modes, and Salthe and Mecham (1974) formalized his classifications. Jameson’s system includes two broad categories: aquatic and terrestrial development. He assigned aquatic development four subcategories, including 1) aquatic eggs without nests, 2) aquatic eggs in constructed aquatic nests, 3) aquatic eggs in terrestrial nests, from which tadpoles hatch and find their way to water, and 4) eggs or young tadpoles carried by a parent, before being deposited in water to complete development. The layperson’s Platonic ideal of frog reproduction most closely matches the first subcategory, aquatic eggs without nests. But even in the 1950’s, several examples of the more complex

reproductive modes were known. The embryos of some species of *Leptodactylus* were known to develop entirely in aquatic nests (Mulaik 1937). *Phyllomedusa* had been observed ovipositing in nests made of leaves folded by the mating pair; when the eggs hatch, rain is required to move the tadpoles to water (Lutz 1947). And some species of *Alytes* and *Dendrobates* had also been observed mating and ovipositing on land, the males returning after the eggs hatched to carry their tadpoles to water (Jameson 1957).

In Jameson's classification, terrestrial development is assigned two subcategories, both of which often involve direct development, wherein eggs hatch directly into froglets, bypassing the larval stage. These two categories are 1) direct development of very large ova deposited in nests on moss or in burrows and 2) eggs or tadpoles carried by a parent before hatching into tadpoles or froglets (Jameson 1957, Salthe and Mecham 1974). Terrestrial oviposition may have evolved in response to pond-drying, competition, or predation in large bodies of water (see Magnusson and Hero 1991 for review).

Direct development in anurans can occur in the oviducts, in the case of some internally fertilized species (e.g. *Eleutherodactylus jasperi*, Townsend et al. 1981), or within eggs laid on land, as in many leptodactylids, including the majority of (neotropical) *Eleutherodactylus* species (Townsend and Stewart 1985) and several Australian species (e.g. *Myobatrachus gouldii*, Roberts 1981). Examples of Jameson's second subcategory of terrestrial development, in which eggs or tadpoles are carried by a parent, are numerous, and I list only a few here. The *Alytes obstetricans* male carries fertilized eggs entwined in his hindlimbs, releasing them into water when they are ready to hatch (Boulenger 1897). *Rhinoderma darwinii* males carry non-feeding tadpoles through metamorphosis in

their vocal sacs, but *Rhinoderma rufum* males only transport tadpoles this way from the nest to water (Salthe and Duellman 1973, Formas et al. 1975). Female marsupial frogs, including those in the hylid genera *Gastrotheca* and *Flectonotus*, have special pouches on their backs in which they brood their young, which emerge either as tadpoles, or as fully formed froglets (Duellman and Maness 1980). And in gastric brooding frogs, *Rheobatrachus silus*, the female swallows fertilized eggs and broods them in her stomach for the duration of their development (Corben et al. 1974). Finally, the young froglets emerge from the passive mother's mouth (Tyler and Carter 1981). Clearly, given the diversity of strategies represented within this single mode, such a broad classification of modes is not particularly informative.

In a review of amphibian reproduction that focused on "live-bearing modes," Wake (1982) proposed a broad definition for ovoviviparity that subsumed many of the species described in the previous paragraph. She defines ovoviviparity as the retention of developing embryos without additional nutrition beyond the yolk supply, and does not specify that embryonic retention need be either maternal or original. With this definition, ovoviviparous species include those in which females retain embryos in their oviducts, stomachs or dorsal skins, or in which males retain embryos on their backs, legs, or vocal sacs (Wake 1982). Carrying of the young is thus interpreted as altering the stage at which offspring are laid or born, and reproductive mode and parental care are more tangled than before.

Most who have reviewed anuran reproductive modes have not been so creative, but this has still not led to consensus. Crump (1974) proposed 10 reproductive modes to describe the anurans of the upper Amazon basin in

eastern Ecuador. Salthe and Duellman (1973) listed nine to represent all of Anura, but they excluded viviparity from consideration. Lamotte and Lescure (1977) broke anuran reproduction into six primary categories, and 18 specific modes. Brown and Alcala (1983), in their review of reproductive modes in Philippine anurans, identified the same two general modes used by Jameson (1957) and Salthe and Mecham (1974), but they recognized 18 specific modes. Duellman and Trueb (1986:26) proposed three general modes (eggs aquatic, eggs terrestrial or arboreal, and eggs retained in oviducts), and divided these into 29 specific modes. Jørgensen (1992) approached the problem qualitatively, and declined to fully separate reproductive mode from reproductive pattern, finding that climatic conditions, latitude, altitude, seasonality, the length of the breeding season and courtship are all inextricably tied to reproductive mode.

There is incomplete overlap between all of these systems, and none is considered the authority on the subject. What should be clear is that anuran reproductive modes are extremely diverse and numerous, and because they appear to have evolved independently several times, attempts to confine them neatly into a relatively small number of definitional boxes will always fall short.

Reproductive Modes in Phytotelm-Breeding Anurans

For the present study, I am specifically interested in anurans that breed in phytotelmata, the small pools of water found within or upon plants. More than 60 species of anurans, representing at least seven families, breed in phytotelmata (see chapter 4), and the particular ways in which they accomplish this task are,

not surprisingly, quite diverse. The Madagascan ranoid *Mantidactylus pulcher* appears to be an obligate pandanus-breeder, but little else is known of its reproduction (Blommers-Schlösser 1979). The Peruvian microhylid *Syncope antenori* lays its eggs directly in the water of bromeliad axils, and the non-feeding tadpoles develop in the same water (Krügel and Richter 1995). The Philippine bufonid *Pelophryne brevipes* also lays its eggs directly in the water of leaf axils, and has non-feeding tadpoles (Brown and Alcalá 1983). The Thai rhacophorid *Theلودerma stellatum* breeds in treeholes, laying its eggs above the water line, and the tadpoles are able to eat a wide array of food items (Wassersug et al. 1981). The Costa Rican hyliid *Anothea spinosa* breeds in bromeliads, depositing its eggs above the water line, and the tadpoles primarily eat frog eggs, but also ingest insects (Taylor 1954, Jungfer 1996).

Lamotte and Lescure (1977) first distinguished between phytotelm-breeding anurans that deposit their eggs in, as opposed to above, the water. Brown and Alcalá (1983) identified three modes encompassing phytotelm-breeding, defining the first (I(6)) as a “small number of relatively large, nonpigmented eggs attached to wood above water in tree holes. Larvae fall into water where they develop and feed.” The remaining two modes both have small to moderate numbers of eggs deposited in water-filled leaf axil or tree holes (one mode has feeding larvae; in the other, the larvae do not feed). Duellman and Trueb (1986) also distinguished between phytotelm-breeding frogs that deposit their eggs in the water (aquatic), versus above phytotelmata (arboreal). In some cases, these distinctions may be critical, as “arboreal” eggs may drown if deposited in water, “aquatic” ones dry out. In reality, of course, these lines are rarely so clear. In *Mantella laevigata*, for instance, a single egg is usually laid above the water line

(see chapter 2). But eggs that are covered in water after heavy rains can develop and hatch, and mating pairs occasionally oviposit at or below the water line (*pers. obs.*).

It is commonly presumed that the primitive reproductive mode for anurans is by means of large numbers of relatively small aquatic eggs deposited into lentic water, in which the tadpoles also develop (Duellman and Trueb 1986:27, Jørgensen 1992). The move away from this mode to any of those associated with phytotelm-breeding enhances the possibility that one or both parents will exhibit parental care. The first requirement of parental care is met in phytotelm-breeders: the offspring can be found, as they exist in a confined space that does not move over time. Furthermore, the relatively confined space of phytotelmata limits the mass of reproductive investment at any moment in time: either the number of eggs, the size of individual eggs, or both, is restricted by physical limitations. Reduced numbers of offspring are expected to be correlated with an increase in parental investment, as parents have a given amount of energy they can apply to reproductive effort. If less energy is being shunted to the production of gametes, more can be directed to post-zygotic care (Trivers 1972). Finally, in the confined space of the phytotelm, tadpoles are less likely to encounter predators, but they are also less likely to encounter food. Tadpole species dwelling in phytotelmata are therefore predicted to disproportionately display one of two patterns among the many possible: 1) taking in no food until after metamorphosis, or 2) receiving nourishment from a parent, one of the most complex forms of parental care known in anurans.

Evolution of Parental Care in Anurans

The origin and evolution of parental care has received much attention in the last 30 years. Trivers (1972) provided the framework for current thinking, and introduced the term “parental investment,” which he defined as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring.” Parental care is usually considered a subset of parental investment, and as such, assumes a cost to the parent as well. Parental care includes all nongametic investments in offspring, and is usually identified as such only after fertilization—that is, only after the care-giver is actually a parent (e.g. Wittenberger 1981).

In anurans, parental care is phylogenetically widespread, but relatively rare. Parental care is known in the great majority of currently recognized families, and those few that have no parental care tend to have very few species (Crump 1995). In 1995, approximately 6% (206/3,348) of anuran species were known to exhibit some form of parental care (Crump 1995). Since then, the number of both recognized species and those with parental care has grown, the latter faster than the former, and it is probable that McDiarmid’s (1978) estimate that 10% of anuran species have parental care will ultimately turn out to be accurate.

Anuran parental care is most common in species living in the wet tropics, with extended breeding seasons, and terrestrial modes of reproduction. More than 90% of anuran species that provide parental care oviposit out of water (Crump 1995). Terrestrial reproduction may reduce the risk of predation, but

increases risks associated with desiccation and starvation, perhaps increasing the need for parental care. It certainly increases the feasibility, as young that are immobile out of water are less likely to get lost on land. Additional correlates of parental care in amphibians are smaller body size, increased egg size and decreased clutch size, relative to closely related species that do not give care (Salthe and Mecham 1974, Nussbaum and Schultz 1989, Crump 1995).

What advantages does the evolution of parental care offer anurans? Salthe and Mecham (1974:399) proposed three general explanations, which include 1) reducing predation on early life stages by guarding or active defense, 2) decreasing the developmental abnormalities that are more likely in large eggs by frequent manipulation, and 3) providing a more suitable microhabitat for terrestrial eggs, either by protecting them from desiccation or by transporting them to water at a later stage of development. In the most comprehensive and detailed review of amphibian parental care to date, Crump (1995) added to this list particular advantages of egg attendance, which include protection from pathogens (such as fungi), aeration of aquatic eggs, and assistance to hatchlings in escaping from the nest.

The evolution of parental care in anurans is far more complex than this brief review can encompass, but two more considerations are worth noting. First, the sex of the care-giving parent is highly variable across anurans, but rarely varies within a species, and even those few exceptions may not be viable. In *Dendrobates pumilio*, both females and males have been observed carrying newly hatched tadpoles to bromeliads on their backs, but tadpoles carried by males do not get fed by their mothers (Weygoldt 1987). Hypotheses explaining the perceived relationship between male parental care and external fertilization

include “certainty of paternity,” which suggests that males are more likely to care for offspring they are “sure” are theirs (Alexander 1974), which is more likely when fertilization is immediate and external (Trivers 1972, Ridley 1978). The relationship has been tested in amphibians, however, and has ambiguous support at best (Gross and Shine 1981, Beck 1998).

Second, parental care exists on a continuum of necessity for the offspring, from obligate to facultative. In one of the first long-term investigations of parental care in any anuran, Kluge (1981) found that male egg attendance in the gladiator frogs *Hyla rosenbergi*, which serves to protect against other intruding males, is facultative, and correlated with population density. In other species, egg attendance may not be parental care at all, but incidental, given where the eggs are laid relative to defended territories (e.g. *Pseudophryne*, Woodruff 1977). In several species of dendrobatids, however, egg attendance is obligate, as it precedes transport of tadpoles to water, without which the offspring die.

Types of Anuran Parental Care

Parental care, like reproductive mode, is not easily classified, largely because each “type” is in fact a conglomeration of multiple instances of independently derived behaviors. Those who have reviewed anuran parental care before have identified from five to twelve types (Salthe and Mecham 1974, Lamotte and Lescure 1977, McDiarmid 1978, Wells 1981, Duellman and Trueb 1986, Stebbins and Cohen 1995, Crump 1995). In an attempt to organize what is known, I have divided anuran parental care into six functional types. I have not split into

separate categories similar behavior when it is performed on eggs versus tadpoles, by males versus females, or in aquatic versus terrestrial situations. Nor have I separated the many ways and places that parents brood their young on their bodies (e.g. gastric vs. pouch brooding), except for true viviparity. I have, however, split carrying into two types, discriminating between short-term transport and long-term brooding. These six types are attendance, nest building, transport, brooding, viviparity, and feeding. Many species exhibit more than one type. I will define and discuss each briefly, then provide a more extensive review of type 6: maternal feeding of tadpoles.

Type 1: *Egg and/or larval Attendance*

The most common form of parental care known in anurans (and the only type known in Gymnophiona and Caudata), attendance refers to a parent remaining with the clutch at a fixed location. Parents may protect their young from predators by active defense (e.g. *Anodonthyla boulengeri*, Blommers-Schlösser 1975), from desiccation by emptying their bladders on terrestrial eggs (e.g. *Dendrobates auratus*, Wells 1978), from cannibalism by older conspecifics (e.g. *Eleutherodactylus coquí*, Townsend et al. 1984), or from several other risks, as mentioned above.

Type 2: *Nest Building*

Because nests are usually built before fertilization occurs, technically this is not a form of parental care. But nests are clearly built with the sole intention of protecting offspring, and thus qualify as investment in future offspring. Furthermore, nest maintenance is often performed after the offspring are in it.

Anuran nests function to protect offspring from extreme fluctuations in water level, which bring risks of flooding or desiccation, and to separate offspring from larger bodies of water that may contain predators. Nests may be built by excavating soil (e.g. *Hyla rosenbergi*, Kluge 1981), from foam produced by the parents during amplexus (e.g. *Leptodactylus pentadactylus*, Heyer 1977), or by folding leaves over the eggs during mating, and sealing them shut with oviducal secretions (several species of *Afrivalus*, Wager 1965).

Type 3: Tadpole Transport

Anurans may carry their young for one of two purposes: to transport them to another microhabitat, usually from a terrestrial to an aquatic location (type 3), or to brood them, long-term, on their bodies (type 4). Tadpole transport is particularly widespread among the dendrobatids, although it is found in seven families (Crump 1995). In dendrobatids, it represents an additional phytotelm-related reproductive mode not mentioned above. This mode, Duellman and Trueb's (1986) #14, consists of terrestrial eggs that hatch into feeding tadpoles, at which point they are carried to a phytotelm by a parent. Several of the dendrobatid species then provision their young with trophic eggs (type 6). Tadpoles may be transported singly (e.g. *Dendrobates granuliferus*, Wijngaarden and Bolaños 1992), or en masse (e.g. *Colostethus inguinalis*, Wells 1980), and are usually attached by the mouthparts to the parent's back. The carrying parent may be female or male, territorial or not; for reviews of parental care in dendrobatids, see Weygoldt (1987), Crump (1995), and Summers et al. (1999).

Type 4: *Egg and/or Larval Brooding*

Long-term brooding of young on the body of one of the parents is well-known and diverse in anurans, as discussed extensively above under reproductive modes. This type overlaps perfectly with Wake's (1982) broad definition of ovoviviparity, and includes brooding in the stomach, vocal sacs, or pouch, or on the legs or back.

Type 5: *Viviparity*

In viviparous species, the young develop in the mother's oviducts and receive nutrition from her from outside of the yolk. As noted above, viviparity is extremely rare in anurans, known only in two species of toads. As in therian mammals, viviparity in anurans offers the longest, and closest, parental protection possible.

Type 6: *Tadpole Feeding*

In a few species with tadpoles that live in restricted aquatic habitats, such as phytotelmata, maternal feeding of tadpoles has evolved. The mother returns to her young and oviposits nutritional eggs for her developing tadpoles to eat. The final section of this chapter reviews this type of parental care in depth.

Parental care in phytotelm-breeding anurans: tadpole feeding

Anuran eggs or tadpoles that develop in phytotelmata may receive one of three types of parental care. Adults may attend the developing eggs and/or

tadpoles in the phytotelm, actively defending the clutch (e.g. adult male *Plethodontohyla notostica*, which stay with the clutch through metamorphosis and “bark” at intruders, *pers. obs.*). Adults may transport tadpoles that hatched from terrestrial eggs to phytotelmata (e.g. several *Dendrobates* species, Weygoldt 1987). And females may return to phytotelmata in which their tadpoles are developing, and feed those tadpoles nutritive eggs. It is this maternal feeding that is the focus of this section.

Many species of tadpoles eat conspecific eggs (see Crump 1992 and Alford 1999 for reviews of cannibalism in anurans). In the restricted spaces of phytotelmata, where increasing tadpole density can be detrimental to existing individuals, cannibalistic oophagy is probably relatively common. Several phytotelm-dwelling species are known to eat conspecific eggs (e.g. *Philautus* sp., Wassersug 1981, and several *Hyla* species, Dunn 1926; see Hoff et al. 1999 for a recent review). Some species once thought to be mere egg cannibals are now known to be eating nutritive eggs deposited by their mothers for that purpose (e.g. *Anothea spinosa*, Jungfer 1996). It is likely that, with more research on phytotelm-breeding anurans, additional species will prove to be receiving maternal care.

Obligate maternal provisioning of tadpoles probably evolved each time from populations in which tadpoles were already opportunistically cannibalizing eggs. Behavior intermediate between maternal provisioning and opportunistic cannibalistic oophagy has been described in the hylid *Osteocephalus oophagus*. In this species, mating pairs oviposit in phytotelmata, after which the female returns every 5 to 7 days, usually in amplexus with the same male, and oviposits into the same phytotelm. Existing larvae consume the newly laid eggs, and

larvae starve if not provided with eggs. Those eggs not eaten hatch (Jungfer and Schiesari 1995, Jungfer and Weygoldt 1999). Because the parents are apparently not behaving differently than they would if they had no tadpoles, they are not providing care, even though if they change their behavior, their offspring will die.

Few species are actually known to engage in maternal feeding of tadpoles. Species from only four families have been observed feeding their young: Dendrobatidae, Hylidae, Rhacophoridae, and Ranidae.

Dendrobatidae

The neotropical family Dendrobatidae is known for the aposematic coloration, and associated skin toxins, of members of all its genera except the basal *Colostethus*. Parental care, including male and female egg attendance and larval transport, are common throughout the family, but maternal feeding has only been observed in species of the type genus, *Dendrobates* (Weygoldt 1987). The first observation of maternal feeding in any anuran was of captive *Dendrobates pumilio* (Weygoldt 1980). In 1993, the first field observation of maternal provisioning, in the same species, was made, and confirmed that feeding is obligate in this species (Brust 1993). Since then, several additional species have been observed exhibiting maternal feeding. Phylogenetic relationships within the dendrobatids are not well understood, but two recent analyses (Summers et al. 1999, Clough and Summers 2000) suggest that this behavior exists in two lineages within *Dendrobates*.

Biparental care occurs in members of the clade of Amazonian species, which has sometimes been identified as the *D. ventrimaculatus*, or *D. minutus*, group

(Weygoldt 1987, Clough and Summers 2000). This behavior occurs in at least six species, although several of those were observed solely in captivity (see Weygoldt 1987). The reproductive pattern in this clade involves deposition of 2-4 eggs on bromeliad leaves above the surface of the water. The male attends the eggs, often attracting the female back to the oviposition site. When the eggs hatch, the male attracts the female again, then transports the tadpoles, singly, to different bromeliad axils. After this second deposition, the pair court again, and oviposit eggs into the axil, which the tadpole eats. The male continues to attract the female back to these axils throughout the development of the tadpoles inside, and she deposits nutritive eggs every few days (Weygoldt 1987, but see Clough and Summers 2000, and references therein, for alternative interpretations). In *D. vanzolinii*, the male and female appear to be pair-bonded (Caldwell 1997), but the female does not accompany the male to the tadpole deposition site. After he has deposited the tadpole, and every time thereafter that she deposits unfertilized eggs for her young, the male courts her, guiding her to the tadpole before she oviposits (Caldwell and de Oliveira 1999).

Female parental care is the rule in the *D. histrionicus* (or *D. pumilio*) group, which includes at least six species. Female only parental care probably evolved only once in *Dendrobates*, from biparental care (Summers et al. 1999). A few species in this clade (e.g. *D. pumilio*, Weygoldt 1987) show male egg attendance as well, but this is thought to be plesiomorphic (Weygoldt 1987, Clough and Summers 2000). The reproductive pattern in this clade involves terrestrial egg deposition of a small number of eggs, which the female attends. After hatching, the female transports tadpoles, singly, on her back, to different phytotelmata. She then provisions the tadpoles with unfertilized eggs until metamorphosis

(Silverstone 1973, Weygoldt 1980, H. and E. Zimmermann 1981, Wijngaarden and Bolaños 1992, Jungfer 1985). Tadpoles do a tail-vibrating “dance” that can be seen by visiting frogs, and swim against the cloaca of the female, presumably to stimulate her oviposition of nutritive eggs (Weygoldt 1980). Maternal feeding may be obligate in all members of this group.

Hylidae

Two neotropical hylid species are known to feed their young, one of which represents a unique, facultative variation of the behavior. *Osteopilus brunneus* oviposits relatively large clutches into phytotelmata, after which the mother returns and supplies eggs to her offspring every few days. When her existing offspring are young, she deposits fertilized eggs, some of which do not get eaten, and themselves develop. As the young develop, and are more likely to eat all that is fed to them, the mother begins depositing unfertilized eggs. Tadpoles that are not provisioned die. This behavior may serve to avoid the trade-off of offspring quality vs. quantity that is usually unavoidable in trophic egg production (Thompson 1996).

The only other hylid known to engage in maternal feeding is *Anothea spinosa*. 48-311 eggs are laid per clutch. During amplexus, eggs are laid above the water in a phytotelm. Five to nine days after the first oviposition, the mother returns to the oviposition site and deposits unfertilized eggs on the surface of the water for her tadpoles, and continues this behavior every few days. If a male is present during her return visits, they engage in regular oviposition behavior. Tadpoles immediately eat any eggs to which they have access, and appear to communicate with single females that arrive to feed them (Jungfer 1996).

Rhacophoridae

Chirixalus eiffingeri, a species known from Taiwan and nearby islands, is the only rhacophorid known to engage in maternal feeding of tadpoles. Clutches of approximately 30 eggs are laid above the water line in treeholes or bamboo stumps. Mothers return to these phytotelmata and deposit unfertilized eggs for tadpoles. Tadpoles crowd the female and prod her cloaca during feeding (Ueda 1986). Successful tadpoles consume more than 80 eggs during their development (Kam et al. 1996). Tadpoles not fed eggs do not grow, and eventually die (Kam et al. 1996, 1997). Adverse effects of high density on tadpoles are the result of trophic egg limitation, rather than crowding (Kam et al. 1998).

Ranidae

The only ranid species known to exhibit maternal feeding of tadpoles is the Madagascan endemic *Mantella laevisgata*, the subject of this dissertation. With a mean clutch size of 1.29 (range: 1-3), eggs are precious in this species. During amplexus, eggs are laid above the water line in bamboo stumps or treeholes. Hatching tadpoles drop into the water below, and eat conspecific eggs. Because mating pairs oviposit in the same place that oophagous tadpoles develop, and the fertilized eggs they produce are eaten by opportunistic tadpoles, maternal feeding is facultative. Single females sometimes return to phytotelmata and deposit unfertilized eggs at or below the water line, which tadpoles immediately eat. The placement of fertilized eggs above the water line in this species may not be due to physiological constraints, but an adaptation to avoid cannibalism by preexisting tadpoles (see chapter 2 for further discussion).

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