

## CHAPTER 9

# Diversity of Reproductive Strategies in the Amphibia

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### INTRODUCTION

The reproductive strategies in amphibians are the most diverse among tetrapods, and only rivalled by that of the bony fish among the vertebrates. While amphibians are often considered as an ancient vertebrate lineage that first conquered terrestrial habitats, in fact, extant amphibians (Lissamphibia) are a rather modern clade which reached most of its current diversity after the Cretaceous-Paleogene extinction event (approx. 66 MYA, Jetz and Pyron 2018; Chapter 2). Their contemporary species numbers are comparable to other major tetrapod lineages, like Squamata, Aves or Mammalia. While we might think about amphibians as animals which are bound to aquatic habitats at least during their reproduction and early developmental stages, amphibian life cycles and reproductive strategies are much more diverse, especially in tropical and subtropical areas. This complexity involves variation in fertilisation modes, in sites for egg deposition and larval development, alternative ontogenetic pathways like biphasic versus direct development or paedomorphosis, and tremendous variation in parental care. Although the occupation of terrestrial habitats was first achieved much earlier and independently by the first tetrapods, gaining more independence from water is still one of the major driving forces of the reproductive diversity of modern amphibians.

Most reviews on the diversity of amphibian reproductive strategies were published over a decade (e.g., Salthe 1969, Salthe and Duellman 1973, Crump 1995, 1996, Haddad and Prado 2005, Wells 2007), and since then, several new

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publications arose on different aspects of the reproductive biology. Therefore, it is worth revisiting this field and summarise recent findings and hypotheses. Lissamphibia is monophyletic and all of its three orders, frogs (Anura), salamanders (Urodela or Caudata) and caecilians (Gymnophiona) made remarkable steps towards terrestriality and invented various forms of parental care. However, the three orders have characteristically different body plan, life styles and reproductive biology, and all three have considerably diverse reproduction in their unique way (Table 1). Below we discuss the reproductive strategies of anurans, urodeles and caecilians in separate sections.

## **Diversity of Reproductive Strategies in Anurans**

In the order Anura (tailless amphibians: frogs and toads) the reproductive modes show immense variation (Gomez-Mestre et al. 2012), which can be partially explained by their greatest phylogenetic diversity within the Lissamphibia (Anura: approx. 7000 frog and toad species in 55 families; Lissamphibia in total: approx. 7800 species in 75 families—Amphibiaweb 2021).

### ***Mate Acquisition and Fertilisation***

Despite the predominantly external fertilisation which does not necessarily suppose a physical contact between the male and the female, anuran pairs are formed often long before egg-laying. Males guard the females by embracing them in a firm hug called amplexus (Arak 1983). Amplexus have some distinct forms (Table 1): it is usually inguinal (the male grabs the female in the waist region) in more ancient lineages (e.g., spadefoot toads, fire-bellied toads) and axillary (the male grabs the females just behind the forelimbs) in more derived evolutionary lineages (e.g., treefrogs, true frogs and toads). There are some other specialised forms, as cephalic amplexus in poison arrow frogs (Dendrobatidae). The males of the desert rain frogs (*Breviceps*) that could not grab the stocky gravid females glue themselves onto the females' back using sticky skin secretions. In other frogs the amplexus is altogether missing and eggs are fertilised without a direct contact between the pair (Wells 2007).

The time frame for breeding is mostly governed by climatic conditions, and this is a starting point of reproductive diversity. Species living in more seasonal climates, like many from the temperate region or tropical species which experience a well-defined wet season have an explosive breeding system, where the whole population breeds in a few days (Arak 1983). In the usually male-biased breeding aggregations of frogs, males involve in scramble competition for mating opportunities. The reproductive success is usually body size-dependent: larger, stronger males are more successful finding a mate (Davies and Halliday 1978, Roberts et al. 1999, Vági and Hettyey 2016). Further males may join the breeding pair, and by releasing sperm the resulting egg clutch exhibit multiple paternity (D'Orgeix 1996, Byrne and Roberts 1999, Lodé and Lesbarrères 2004, Sztatecsny et al. 2006, Rausch et al. 2014). In extremely male-biased operational sex ratios (i.e., many more males are sexually active than females) the breeding males form a mating ball with the females inside (Verrell and McCabe 1986), which can have serious consequences, as females may get drowned during the wrestling. The foam nest builder rhacophorids are

**Table 1.** Comparison between the reproductive diversity in frogs and toads (Anura), newts and salamanders (Caudata) and caecilians (Gymnophiona). Based on Wells (2007), San Mauro et al. (2014), Vági et al. (2019, 2022).

	<b>Anura</b>	<b>Caudata</b>	<b>Gymnophiona</b>
<b>Amplexus</b>	mostly present in various forms (see text), but can be absent	present, e.g., in <i>Pleurodeles waltl</i> absent, e.g., in <i>Triturus</i> spp.	absent
<b>Fertilisation</b>	external, rarely internal	internal (spermatophore), rarely external	internal (phalloseum)
<b>Developmental mode</b>			
Paedomorphosis	absent	- obligate; e.g., Proteidae - facultative; e.g., <i>Lissotriton vulgaris</i>	absent
Metamorphosis	common	common in most families	present (e.g., <i>Grandisonia</i> )
Direct development	present in many families (e.g., Microhylidae, Craugastoridae)	common in Plethodontidae	present (e.g., <i>Typhlonectes</i> )
<b>Parental care (caring sex)</b>			
No care	common (80–90% of species)	common (30–50% of species)	absent
Male-only care	present	present in families with external fertilisation	absent
Female-only care	present	present in families with internal fertilisation, common in Plethodontidae	common (e.g., <i>Siphonops</i> )
Biparental care	rarely present (e.g., <i>Ranitomeya imitator</i> )	absent	absent
<b>Parental care (forms and functions)</b>			
Nest building	foam, bubble and other types of nests (e.g., <i>Rhacophorus</i> , <i>Engystomops</i> )	absent, but egg concealing occurs (e.g., <i>Triturus</i> , <i>Lissotriton</i> )	absent
Attendance	male and female egg attendance are the most widespread care (10–20% of species); coevolved with terrestriality	male attendance in aquatic environments ( <i>Andrias</i> , <i>Siren</i> ); female attendance in terrestrial environments (Plethodontidae)	female attendance is ubiquitous in oviparous species (e.g., <i>Ichthyophis</i> )
Transportation	Rare. Eggs ( <i>Flectonotus</i> , <i>Alytes</i> ), tadpoles (Dendrobatidae) and juveniles ( <i>Sphenophryne</i> ) can be transported	absent	absent
Internal brooding	rarely occurs (e.g., <i>Assa</i> , <i>Gastrotheca</i> , <i>Pipa</i> , <i>Rheobatrachus</i> )	absent	absent
Viviparity	rarely occurs ( <i>Nectophrynoides</i> , <i>Limnonectes larvaepartus</i> )	rarely occurs ( <i>Salamandra</i> , <i>Lyciasalamandra</i> )	present (e.g., <i>Typhlonectes</i> )
Feeding	Rare. Trophic egg feeding (e.g., <i>Oophaga</i> ), secretions (e.g., <i>Rhinoderma</i> , <i>Ecnomyohyla</i> )	absent	dermatophagy (e.g., <i>Siphonops</i> ) and uterophagy (e.g., <i>Herpele</i> )

characterised by the most male-biased matings among vertebrates (Kusano et al. 1991, Byrne et al. 2002, Byrne and Whiting 2011). It is likely that in these species the males are forced to cooperate with each other and with the female, since any bodily fight would destroy the nest which is under construction. Instead of direct wrestling, the males' competition for the fertilisation of the eggs is decided by sperm competition. For better performance in the latter, these frogs have disproportionately large testes (Kusano et al. 1991, Vági et al. 2020). On the other hand, species with more prolonged breeding may defend territories or other resources, and the role of female choice is more important (e.g., Ryan 1980, Summers et al. 1999). In addition to explosive breeders and resource-based breeding systems there are also frog species which gather in mating leks, defending a small, symbolic mating ground (e.g., Bourne 1992, Friedl and Klump 2005).

The length of the amplexus prior to and during the egg-laying is variable. The time needed for the egg-laying depends much on the form of the created egg-mass. True toads (Bufonidae) which lay long, thin egg-strings only release a small number of eggs at once, and the whole process of egg-laying can last for hours (Davies and Halliday 1978). Obviously, the males need to synchronise their gamete release to that of the females, which can be a time- and energy-consuming process. This can explain why male toads get exhausted after two or three breeding events and refuse further mating opportunities or achieve a decreased success in fertilisation (Hettyey et al. 2009). In contrast, males of, e.g., most of true frogs and related families (Ranoidea) release all or a large portion of their eggs, rapidly forming a more-or-less spherical egg mass. Most anuran eggs are involved in a gelatinous outer layer, which protects the eggs from predation and desiccation. Large amount of this gelatinous envelope can insulate the eggs and help creating more favourable thermal conditions for embryonic development. This can be especially useful in the large mats of aggregated egg clutches of some species which reproduce in the cold early spring in cool temperate regions (e.g., *Rana temporaria*, *Lithobates sylvaticus*).

Although the fertilisation of the eggs is predominantly external in anurans (Beck 1998), there are some notable exceptions. Both species of North American tailed frogs (Ascaphiidae), one of the most ancient lineages of frogs, have internal fertilisation with the help of a tail-like appendage of the males. Other internal fertilising frogs do not have any copulatory organ, the sperm is transmitted by direct contact of the cloaca. Obviously, all ovoviviparous and viviparous lineages have internal fertilisation, including the small African toadlet *Nimbaphrynoides* and *Nectophrynoides* (Liedtke et al. 2017), and the recently described *Limnoneytes larvaepartus*, which give birth to tadpoles (Iskandar et al. 2014).

### ***Environments for Egg-deposition and Larval Development***

Anurans eggs and larvae can develop in diverse environments. The first categorisation of anuran reproductive modes was proposed by Boulenger (1886) with 10 categories, then Salthe and Duellmann (1973) revisited the topic nearly a century later, which induced numerous research in the field. The most detailed classification was made by Duellman and Trueb (1986), later supplemented by Haddad and Prado (2005) and Schulte et al. (2020). The latest review on amphibian reproductive modes

**Table 2.** Traits used for the classification of amphibian reproductive modes, following the study of Nunes-de-Almeida et al. (2021). Based on the combinations of these traits, they could identify 74 different reproductive modes in amphibians: 71 in anurans, 16 in urodelans and 7 in caecilians. In this classification they concentrated on life history differences and environments for egg deposition, and ignored behavioural diversity, i.e., amplexus, breeding systems or active parental care.

<b>(1) Reproduction type</b>				
Oviparity		Viviparity (incl. ovoviviparity without maternal provisioning)		
<b>(2) Oviposition macrohabitat:</b>				
Environment		Animal (oviduct, pouch, vocal sac, stomach)		
<b>(3) Spawning type</b>				
Froth (foam and bubble nests)		Non-froth		
<b>(4) Oviposition substrate</b>				
Aquatic	Non-aquatic		In/on animal	
<b>(5) Medium surrounding the eggs</b>				
Lentic	Lotic	Terrestrial	Non-oviductal	Oviductal/uterine
<b>(6) Nest construction</b>				
Constructed nest		Adopted nest		No nest
<b>(7) Oviposition microhabitat</b>				
Floating	Ground	Subaquatic ground	Depression	Burrow
Subaquatic chamber	Insect mound	Rock	Wall	Plant leaf
Plant branch	Plant root	Subaquatic plant	Water-filled reservoir	Reservoir without water
<b>(8) Embryonic development</b>				
Indirect		Direct		
<b>(9) Embryonic nutrition</b>				
Lecitotrophic		Matrotrophic		
<b>(10) Larval and newborn nutrition</b>				
Exotrophic (with and without parental feeding)		Endotrophic		
<b>(11) Place of larval development</b>				
Lentic	Lotic	Terrestrial		Internal/on animal

(Nunes-de-Almeida et al. 2021) established a classification based on the combination of 11 individual reproductive traits (Table 2).

Duellman and Trueb’s (1986) original categorisation was mostly based on one biogeographic region, the Brazilian Atlantic rainforests, but developed strategies can arise in other tropical regions as well, like Sub-Saharan Africa (Liedtke et al. 2017, Lion et al. 2019). Some new reproductive mode, e.g., mud-packing on the eggs (Gururaja et al. 2014) or giving birth to larvae, was described from Southeast Asia (Kusrini et al. 2015), increasing the number of reproductive modes over 40. The classification based on multiple aspects of egg and larval development. One of the most important dichotomy is a basic division between aquatic and terrestrial egg-laying (Gomez-Mestre et al. 2012, Lion et al. 2019). Aquatic environments can

be further divided into lentic (standing water) and lotic (flowing water) types, and small, often ephemeral water bodies, e.g., phytotelms, wooden holes, or natural or constructed basins. Therefore, anurans may use arboreal and subterranean sites for egg-laying and during their larval development, vastly expanding the available terrestrial niches.

The development of the larvae can be classified into three basic types. Exotrophic larvae feed on external food sources like algae, detritus or other animals (including their siblings), or sometimes fed by the parents via trophic eggs or secretions. Endotrophic larvae usually stay in protected nest sites and feed exclusively on the yolk content of their egg; while direct-developing species simply skip the larval phase and complete their development inside the egg (or in the body of the mother, Gomez-Mestre et al. 2012). Interestingly, while direct development is a key innovation and thus, ubiquitous in some frog lineage (like the clade of Central and South American rainfrogs of the families Craugastoridae, Eleutherodactylidae and Strabomantidae), in other groups it is a variable trait; we find species both with free-living larvae and with direct development in the genera of *Pipa* (Pipidae) and *Gastrotheca* (Hemiphractidae), both having highly specialised internal brooding strategies.

### ***Parental Care***

The diversity of parental care forms in frogs and toads is unparalleled among tetrapods (i.e., terrestrial vertebrates: amphibians, reptiles, birds and mammals). Interestingly, only 10–20% of the species shows any form of parental care, however, caring ranges from relatively simple forms as egg attendance to complex solutions for the internal development and cooperation between the parents (Crump 1996, Furness and Capellini 2019, Vági et al. 2019). The main functions of care provision are protection of the eggs, tadpoles and juveniles; and nourishing the offspring. All of these can be provided by both male and female frogs (Vági et al. 2019, 2020).

The prevalence of male and female parental care is comparable among frogs: around 20% of species cares by the male only and around 10% by the female only, whereas 5% of species exhibit biparental care (incl. cooperative nest building) of the clutch and/or eggs ( $n = 1044$  species, Vági et al. 2019; see also Furness and Capellini 2019). The evolutionary drivers of care, however, have remained an unresolved issue. First, the mode of fertilisation is long considered an important predictor for the care-providing sex, however, this link was failed to be demonstrated in frogs, possibly due to the relatively low number of internally fertilised lineages (Beck 1998). This means that female care is surprisingly widespread in lineages with external fertilisation. Second, territorial males often attend egg clutches (Vági et al. 2020), but there are also many instances of female attendance and this behaviour proved to be plastic both within a species (Ringler et al. 2015) and labile in evolutionary terms (Delia et al. 2017, Furness and Capellini 2019). Last, in biparental nest building the parents cooperate in similar roles, while in other species the parents fulfil complementary roles (Furness and Capellini 2019), where usually feeding is the females' task (Brown et al. 2010).

Nest building is often considered a form of parental care, albeit it precedes fertilisation. Some anurans build nests as a passive protection for their eggs. In

aquatic breeders there are submerged nests and constructed basins which provide a predator-free environment for the developing tadpoles (Martins et al. 1998, Schäfer et al. 2019). In some frog species basin construction is a variable trait, and its presence is depending on the actual environmental conditions (Martins et al. 1998). In species where the males are the main nest builders the constructed structures may represent quality of the builder, and can be the basis for female choice. In other species foam nests are constructed in a cooperative fashion by the male(s) and the female. Nests provide efficient shelter from predators and from adverse climatic conditions. However, we found no trace that nest building is linked to the climatic environment (Vági et al. 2020), suggesting that the nests themselves provide some independence from climate and enabled the colonisation of less suitable habitats. Foam nests were indeed key innovation in the radiation of at least two successful lineages, the South-East Asian and African arboreal rhacophorids (Meegaskumbura et al. 2015) and the leptodactylids of South America (Heyer 1969, Pereira et al. 2017).

Attendance of the eggs and sometimes the larvae and juveniles are widespread, yet these seem to be the most labile forms of anuran parental care (Vági et al. 2019, Furness and Capellini 2019). Due to the lack of detailed behavioural observation attending and actual active protection of the egg clutch can be hardly discerned. However, there is a growing number of evidence which confirms the importance of the parent's presence near the clutch and specify functions of this care form. Amphibian eggs developing in a terrestrial environment are at the risk of desiccation, and attending parents can minimise this risk by hydric brooding: urinating on the eggs or moisture them and reduce evaporation by the physical contact with their own body (Bickford 2004, Poo and Bickford 2013). Many anurans also actively protect the clutch against various predators, like wasps or katydid, which can cause substantial mortality of the eggs and larvae (Chuang et al. 2017, Delia et al. 2017). Fungal or bacterial infections may also contribute to the mortality of unattended eggs (Simon 1983).

Transportation of eggs, tadpoles or juveniles evolved multiple times among anurans (Furness and Capellini 2019, Vági et al. 2020). Eggs may be placed onto the females back and remain exposed throughout their development, like in *Flectonotus* species in the Hemiphractidae family. Other hemiphractids enclose eggs in variously developed dorsal pouches. In the European midwife toads (*Alytes*) the males wrap the egg strings around their hind limb. These long-term forms of transportation last until the hatching of the tadpoles or, in species with direct development, the juveniles, like in some small microhylids from New Guinea (Köhler and Günther 2008). In contrast, poison arrow frogs (Dendrobatidae) deposit their clutch on the ground, and after hatching, they carry tadpoles to streams or small arboreal basins like phytotelmata of the bromeliads. This single, short term transportation mostly carried out by the male, but in one genus, *Oophaga*, it is performed by the females. Some behavioural plasticity also occurs, as the female may take over transportation when the male would not provide it (Ringler et al. 2015). By delivering tadpoles to these small water bodies the parents may reduce competition and predation risk (McKeon and Summers 2013). The parents may also assess the quality of the phytotelms to some degree based on the nutrients available for the tadpoles (Poelman et al. 2013) and the presence of previously deposited larvae (Poelman and Dicke 2007, Rojas 2014).

Feeding of young is a care type which is usually provided by female frogs, except in very rare cases where the males provide nutrients through external (skin) or internal secretions (Goycoechea et al. 1986, Hansen 2012). In contrast, the females usually provide food for the tadpoles by producing infertile trophic eggs. This behaviour typically occurs as uniparental female care, but in some rare case it is a part of a cooperation between parents, where the male fulfils the role of a guard for the new generation and a guide for the female (Tumulty et al. 2014). An adaptive significance of feeding is that the species may occupy food-scarce environments. Typically, feeding occurs where smaller water bodies are used for breeding, like tree holes or phytotelmata. The species with the most complex, biparental breeding system, *Ranitomeya imitator* can use *Heliconia* phytotelms which contain only a few millilitres of water (Brown et al. 2010). The main advantage of these small water bodies is that they lack predators and competitors. Another potential benefit is that poison arrow frog females may transfer alkaloids to the tadpoles via trophic egg feeding, which can contribute to the chemical defence of the tadpoles (Saporito et al. 2019).

Active feeding of the tadpoles only provides nutrients until metamorphosis, and the presence of endotrophy and direct development should be also considered a special case of offspring nourishment (Vági et al. 2019). In these forms of development all nutrient needed until the completion of the metamorphosis is provided by the egg's yolk content. However, an important difference is that all these nutrients should be provided at once at the time of the egg formation. Moreover, species with endotrophic tadpoles and direct development do not need to evolve complex and intricate behaviours for parental care.

An interesting aspect of anuran parental care is the various modes of viviparity and internal brooding. In one of the only truly viviparous lineages, *Nectophrynoides* and *Nimbaphrynoides* toadlets from Africa both lecithotrophy (or ovoviviparity) and matrotrophy (viviparity in the strict sense) occur. Other species may brood the eggs and/or tadpoles in variously developed dorsal pouches of the females (*Gastrotheca*, *Flectonotus*), embedded within the dorsal skin (*Pipa*) or even in the stomach (in the extinct *Rheobatrachus* species) of the females, or in paired lateral pouches (*Assa*) or in the vocal sac (*Rhinoderma*) of the males.

### ***Evolutionary Associations between Ecology, Life History and Parental Care***

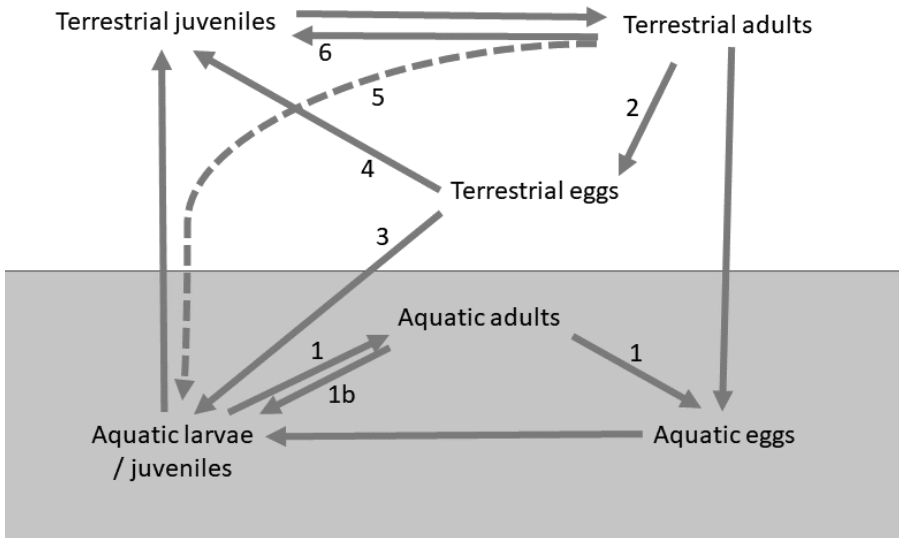
Several ecological, life history and climatic variables have been identified having an association with parenting, although the jury is still out on which of these variables (or suits of variables) may have driven the evolution of caring. For instance, an important predictor of parental care forms is terrestrial reproduction (Gomez-Mestre et al. 2012, Vági et al. 2019). Parental care is associated with basic life history measures, like egg size or clutch volume. A link between parental care and larger eggs is long suggested (Shine 1978), and it was verified by phylogenetic studies in frogs (Summers et al. 2006, Gomez-Mestre et al. 2012, Furness et al. 2022). However, we should also consider that terrestrial egg laying is both a predictor of larger eggs (Rollinson and Rowe 2018) and parental care (Vági et al. 2019), thus, it can mediate the effect of



parental care on egg size. The larger size of terrestrial eggs can be explained by their longer development in direct-developing species (many terrestrial reproducing species complete their metamorphosis within the egg membrane). Another possible explanation is a smaller surface-to-mass ratio which can prevent desiccation and, in contrast to aquatic environments, does not cause gas exchange difficulties (Rollinson and Rowe 2018). In direct-developing species, the anatomical, physiological and ecological constraints on body size should be also taken into account, which are probably different for tadpoles and metamorphosed froglets (small tadpoles can scrape or filtrate tiny organisms or food particles, while juvenile frogs have to cope with small terrestrial invertebrates—see also this argument in urodelans).

### Diversity of Reproductive Strategies in Urodelans

Urodela (newts and salamanders) is the sister-clade of Anura within the Lissamphibia group, however, their diversity is more limited both in terms of species numbers and reproductive modes. However, they still show considerable variation, and also have a tendency to reproduce independently from water (Table 1, Fig. 1). In addition, they show a number of different lifestyles, for instance, paedomorphic urodelans complete their whole life cycle in water (Fig. 1), whereas others spent substantial part or all of their life in terrestrial habitats (e.g., many salamander).



**Figure 1.** The diversity of amphibian life cycles. The outermost arrows represent the most typical life cycle with aquatic eggs and larvae, and terrestrial juveniles and adults (e.g., *Rana temporaria*, *Triturus cristatus*). (1) Fully aquatic amphibians (e.g., *Pipa*, *Andrias*), incl. paedomorphic urodelans (e.g., *Necturus*) skip the terrestrial phase. (1b) Some fully aquatic caecilians (*Typhlonectes*) give birth to juveniles, also skipping the aquatic egg phase. (2) Many terrestrial anurans, salamanders and caecilians lay terrestrial eggs. These can develop into (3) aquatic larvae (e.g., *Agalychnis*; *Desmognathus*) or (4) to terrestrial juveniles by direct development (e.g., *Speleomantes*; *Eleutherodactylus*). Instead of egg laying terrestrial adults may (5) give birth to aquatic larvae (*Salamandra salamandra*; *Limnonectes larvaepartus*); or (6) to fully metamorphosed terrestrial juveniles (*Lyciasalamandra*; *Nectophrynoides*). Note that by (4) and (6) the life cycle is fully terrestrial.

### ***Pairing and Fertilisation***

Fertilisation shows higher variance among urodeles than in anurans (Table 1), however, this variation can be retracted to a single evolutionary switch from external to internal fertilisation (Vági et al. 2022). In basal clades of urodelans (such as the Asian salamanders Hynobiidae, the giant salamanders Cryptobranchidae and sirens Sirenidae) the fertilisation is external (Reinhard et al. 2013), like in many fish. These families reproduce exclusively in water. In more developed clades a spermatophore evolved which is laid on the ground by the male and sucked in by the female's cloaca. The spermatophore transfer can occur both in aquatic and terrestrial environments. Usually it is preceded by a courtship during which visual, chemical and tactile channels for communication are extensively used (Houck and Arnold 2003). Amplexus can precede mating in some of the species, but it has been lost in many urodelans (Table 1).

### ***Habitats for Egg Laying and for the Offspring***

Salamanders may use either aquatic or terrestrial habitats for reproduction. Aquatic breeding habitats can be classified into lentic and lotic types that refer to standing and flowing water bodies, respectively (Salthe 1969, Nussbaum 1985). Some lotic breeders lay eggs in semiaquatic conditions, above the water, under rocks and logs next to the stream, or in seepage areas. These species have an aquatic larval stage. Species with lentic larvae may also lay eggs in a terrestrial environment. They usually lay eggs before the onset of the rainy season, before the egg-laying sites become filled with water. Other species switched to a completely terrestrial reproduction, and lay direct-developing eggs in terrestrial environment. The latter reproductive mode is typical among lungless salamanders (Plethodontidae), and presumably had an important role in the diversification of this group. Terrestrial reproduction paved the way for occupying completely new environment for urodelans, namely the arboreal habitats, which are exclusively used by the direct-developing plethodontids. However, the high number of species in Plethodontidae, nearly 500 species—two third of total species richness in Caudata—may also be explained by the dispersal abilities of completely terrestrial species are restricted, thus, their complete switch to terrestriality likely favoured genetic isolation and enhanced speciation processes.

It has been suggested that both lotic and terrestrial breeder salamanders produce proportionately larger eggs than lentic breeders. This discrepancy is explained by a multitude of potential factors: (i) according to Shine (1978) parental care increased developmental time by creating a “safe harbour” for the embryos inside the protected eggs; (ii) in contrast, Nussbaum argued that the size of prey available in different habitats was the main driving force as the hatchlings of stream and terrestrial breeders need to cope with larger food items (Nussbaum 1985, 1987); (iii) while Rollinson and Rowe (2018) implied that lower oxygen availability in aquatic environments limited egg size, as in larger eggs the oxygen diffusion is not as efficient. As no study compared the predictions of these three main hypotheses, more research is needed to clarify the evolution of salamander egg size.

### ***Paedomorphosis***

Several salamanders retain their larval external gills while they reach sexual maturity and never leave the water. This phenomenon is called paedomorphosis and its different forms occur in around 10% of urodelans (Denoël et al. 2005). While in some groups (mudpuppies and olms, sirens, amphiumas) paedomorphosis is obligate and all individuals retain larval morphology, in other taxa the occurrence of paedomorphosis shows considerable plasticity. Within the genus *Ambystoma* both paedomorphic and biphasic species (i.e., which undergo metamorphosis) occur, and the metamorphosis of some paedomorphic forms (i.e., the well-known Mexican axolotl, *A. mexicanum*) can be induced by hormonal treatment. In contrast, facultative paedomorphosis may occur among normally biphasic species, like many Eurasian newts (e.g., Ceacero et al. 2010).

In urodelans, the main difference between larvae and adults is the breathing apparatus and related functions (i.e., feeding mechanism), but otherwise they move and live in a similar fashion. This can explain why paedomorphosis is never documented among Anurans: presumably the phenotypic divergence and the discrepancy in lifestyle between larvae and adults is more significant in frogs and toads. Facultative paedomorphosis creates phenotypic plasticity which can be explained by a complex cost-benefit framework (Denoël et al. 2005, Lejeune et al. 2018). However, obligate paedomorphosis can create evolutionary plasticity, as it potentially deliberates the ontogenetic pathways from the constraints that bind together the adult and larval phenotype in the species with biphasic development (Bonett and Blair 2017).

### ***Parental Care***

In salamanders, parental care diversity does not approach the level of frogs (Table 1). Male care occurs only in the more ancient families which use external fertilisation, while female care occurs only in internal fertilisers (Reinhard et al. 2013, Vági et al. 2022). Biparental care has not been reported from urodelans. They do not build elaborate nests, however, the females of some aquatic-breeding newt species may conceal the eggs. Lotic breeders can hide the eggs under stones and other underwater objects (Nussbaum 1985, 1987), while lentic breeding newts in Salamandridae deposit them separately to the leaves of aquatic vegetation and often wrap the leaf around the egg (Tóth et al. 2011). This extended egg-laying period only occurs among internal fertilisers, where fertilisation may be separated from egg-laying in space and time. Therefore, it created an opportunity for the elongation of the egg-laying process with only the participation of the female. The individual placing of the eggs not only reduces predation risk, but also decreases the potential competition between the siblings.

In the Caudata, the only widespread form of parental care is egg attendance, however, its presence can be variable. Males in externally fertilising species may care for egg clutches of multiple females at the same time, so paternal care coevolved with polygyny and nest site defence (Browne et al. 2014). In species with internal fertilisation terrestrial egg laying is associated with maternal care (Vági et al. 2022). In some species mothers attend the clutch after the hatching of the juveniles (Oneto

et al. 2010), however, this should not last long as the hatchling start hunting for live prey on their own soon after hatching. Like in frogs, egg attendance can be an effective way to reduce the risks of predation, pathogens and desiccation (Croshaw and Scott 2005).

Viviparity (including ovoviviparity) likely evolved twice among salamanders, as there is a completely ovoviviparous and viviparous clade within Salamandridae, and a single species within the direct-developing lungless lineage which is presumably ovoviviparous. Ovoviviparous salamandrids give birth to larvae, while viviparous species to fully terrestrial juveniles. Like in some frog genera (e.g., *Pipa*, *Gastrotheca*), the presence of larval and direct development can be plastic within a species (*Salamandra algira*, García-París et al. 2003) and shows interspecific variance within the *Salamandra* genus. Interestingly, direct development appears to be basal in viviparous *Salamandra*. The embryos of the viviparous salamanders initially consume the unfertilised eggs in the uterus of the mother. Later they switch to feed on their developing siblings (adelphophagy or intrauterine cannibalism, in viviparous subspecies of *Salamandra salamandra*; Dopazo and Korenblum 2000) or to feeding on epithelial uterine cells (in *Salamandra atra* and *S. lanzai*; Guex and Chen 1986, Greven 1998).

In contrast to frogs, the evolutionary drivers of parental care in urodeles are little investigated. While fertilisation mode determines the care-providing sex, it seems likely that male and female parental care had different predictors. In males, territoriality and the fertilisation of multiple clutches may have been the driver of care in aquatic egg-laying sites, while internal fertilisation and female attendance likely opened the avenue for invading terrestrial niches (Vági et al. 2022).

## Diversity of Reproductive Strategies in Caecilians

Caecilians (order: Gymnophiona) are the least-known of the three lissamphibian orders. This is mainly caused by the secretive (underground) life style and the fact that their distribution restricted to tropical and subtropical areas. While their anatomy and phylogenetic relations become better known in recent decades, behavioural observations on their life history are still scarce. Most observations came from captive specimens, and details of the reproduction of most of the species were never observed in the field. Despite these difficulties, several fundamental details of their reproductive biology, behaviour and evolution were published in recent years, and the main phylogenetic transitions in their reproductive biology can be traced back using comparative methods.

In all caecilian the fertilisation is internal and performed by a modified section of the caecum; the so-called phallodeum, an eversible part of the cloaca which is situated at the very end of the body (Wells 2007). The most ancient lineages of caecilians have aquatic larvae, however, the eggs are not placed directly into water, rather concealed in burrows and under logs and rocks next to water bodies, similarly to some salamander and many frog species (Wells 2007). Some caecilians return to aquatic life as adults. More developed lineages switched to direct development skipping the free-living larval phase, but there are also examples for a return to aquatic larvae from direct development (San Mauro et al. 2014). Viviparity evolved

multiple times during caecilian evolution. The maternal attendance by coiling around the clutch is ubiquitous in caecilians (at least in species with known reproductive behaviour), and the mother often remains with the hatchlings or newborn juveniles for some time. In some caecilians the juveniles are precocial and ready for an independent life, in other species they are altricial and need to stay with the mother in the early their life. Caecilian embryos do not feed on trophic eggs, however, in some species they scrape off hypertrophic epithelium of the oviduct (uterus) using their specialised, vernal teeth (San Mauro et al. 2014). Another extraordinary way of feeding offspring is dermatophagy, when the juveniles scrape off hypertrophied layers of the mother's outer epidermis, using the same vernal dentition (Kupfer et al. 2006). According to phylogenetic reconstructions, dermatophagy evolved from uterophagy (Kupfer et al. 2016). By providing alternative pathways for offspring nourishment via uterotrophy and dermatotrophy the females may invest less yolk into the eggs (Kupfer et al. 2016).

## Conclusions

Amphibians provide a unique opportunity to understand the evolution of breeding strategies, because many aspects of their reproductive behaviour show incredible diversity and sometimes plasticity. Moreover, the three extant amphibian orders found different solutions for the challenges of reproduction. General pattern shows that anurans, urodelans and caecilians all invented internal fertilisation, increased protection of the progeny and nutrition for the offspring, and many of these strategies paved their way towards a more terrestrial lifestyle.

As the reproductive behaviour of amphibians is still relatively unexplored compared to other groups, such as birds or mammals, there are still a lot of possible research directions. In a recent review, Schulte et al. (2020) recommended the use of novel techniques from individual tracking to genomic, transcriptomic and hormonal analyses to investigate unexplored connections of amphibian reproductive biology. These can help understanding connections which are largely unexplored to date, like proximate causes of intricate reproductive behaviour or the role of relatedness between individuals. These can substantially influence many aspects of complex reproduction, from communication between individuals to distribution in the habitat. However, along advanced and multidisciplinary studies basic natural history observations are still warranted, especially about salamanders and caecilians (Schulte et al. 2020).

It is also important to understand how these complex adaptations influence the persistence of threatened amphibian species. It is possible that complex reproductive adaptations secure higher survival rates for the eggs and the offspring, which would make these species less vulnerable to anthropogenic threats. On the other hand, it is also plausible that species with intricate reproduction evolved under stable environmental conditions and respond badly to perturbations—at least, the high number of threatened species with advanced reproductive strategies is alarming. A better understanding of the ecological and behavioural drivers of amphibian reproductive diversity is strongly warranted to enhance the conservation of this vertebrate class with exceptional evolutionary and ecological importance.

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