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Reproductive diversity of Malawian anurans

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Abstract. Of the 39 described reproductive modes of anurans, few are recognisable among the anuran species of Malawi. The reproductive modes recognised in Malawi anurans are: i) the deposition of aquatic eggs and free feeding tadpoles in lentic water (Mode 1 sensu Kentwood, 2007), e.g. as present in the genera *Amietophrynus*, *Phrynobatrachus*, *Ptychadena*, and *Xenopus* comprising 72% of the species; ii) the deposition of eggs in leaves over water hatching into free feeding tadpoles that drop in lentic water (Mode 24), genera *Afrixalus* and *Hyperolius* representing 13% of the species; iii) direct development of terrestrial eggs (Mode 23) in the genera *Arthroleptis* and *Breviceps*, 8% of the species; iv) terrestrial eggs deposited on ground above water hatching in free feeding tadpoles which move to water (Mode 18) genera *Leptopelis* and *Hemisus*, 4% of the species; v) eggs deposited above water on humid rocks or in rock crevices, hatching into free feeding semiterrestrial tadpoles living on rocks in a water film (Mode 19), two species in two genera *Ptychadena broadleyi* and *Nothophryne broadleyi,* 2% of the species; vi) arboreal foam nest hatching into free feeding tadpoles that drop into ponds or streams (Mode 33), only the species *Chiromantis xerampelina*, 1%. The main characteristic of the Malawian anuran fauna is the low richness of reproductive modes, the predominance of habitat generalist species, and the high similarities of habitats across the country. Among the six occurring reproductive modes, five (Mode 1, 18, 24, 23, and 33) are widespread in Malawi and commonly found in most communities, whereas Mode 19 is restricted to two species occurring at Mulanje and Zomba mountains.

Keywords. amphibians, diversity, Malawi, model animals, reproductive modes.

There have been several attempts to classify the reproductive modes of amphibians (Salthe and Duellman, 1973; Duellmann and Trueb, 1986; Haddad and Prado, 2005; Kentwood, 2007). The definition of different reproduction modes embraces the combination of several reproductive and developmental characters including site of oviposition, shape and size of the egg clutch, kind and duration of development, tadpole type, size at metamorphosis, and parental care (Duellmann and Trueb, 1986; Haddad and Prado, 2005; Kentwood, 2007).

Among vertebrates, amphibians show the highest level of diversification of reproductive strategies, and at the same time they are extremely dependent by the availability of water (Duellmann and Trueb, 1986; McDiarmid, 1994; Vences and Köhler, 2008). Many of these reproductive strategies can be interpreted as an evolutionary trend towards the progressive emancipation from water, allowing reproduction in more terrestrial habitats (Bogart, 1981; Duellman, 1985; Duellman and Trueb, 1986; Lutz, 1947; Salthe and Mecham, 1974). However, the selective pressure (e.g. protection against predators, reduction of larval competition, escape from desiccation, etc) leading to this evolutionary trend is still object of debate (Kentwood, 2007; Martin, 1967; Van Dijk, 1971).

Altogether a total of 39 reproductive modes were described for amphibians with most of them to be found in tropical areas, especially in the New World, and only 12 reproductive modes were listed for sub-Saharan Africa (Duellmann and Trueb, 1986; Haddad and Prado, 2005; Kentwood, 2007). In general, high degrees of diversity of reproductive modes is found in lowland rain forests with high niche heterogeneity, whereas it typically decreases in arid homogeneous regions where generalist pond breeders usually prevail (dos Santos et al. 2008, 2009; Duellmann and Trueb, 1986; Keller et al. 2009; Kentwood, 2007; Perotti, 1997; Prado et al. 2005). Consequently, highly diverse communities are much more sensible to habitat alteration than generalised ones,

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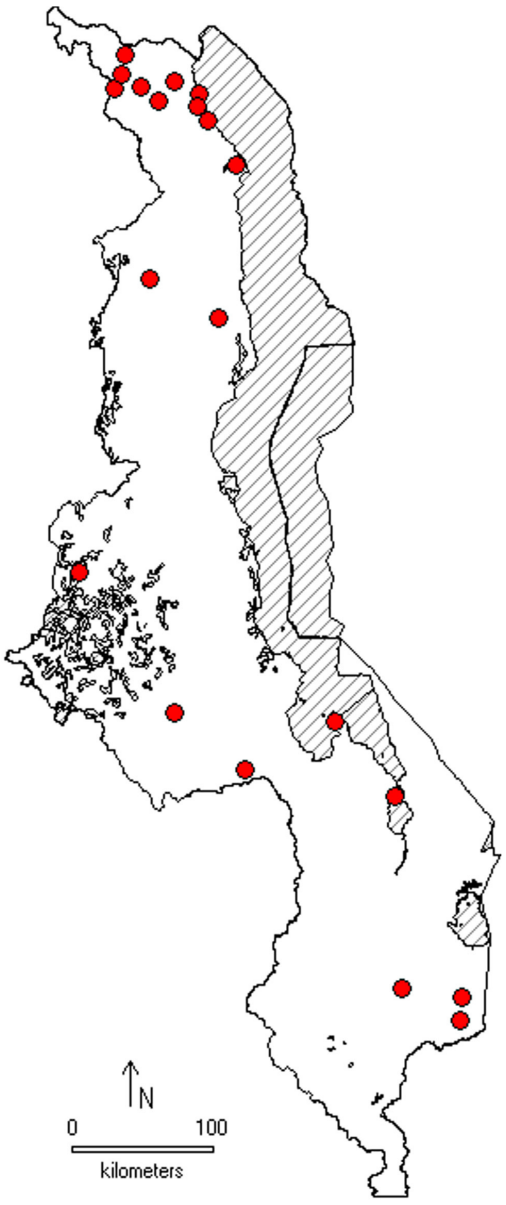

Figure 1. Schematic map of Malawi showing the distribution of the main studied sites.

and the degree of diversification of reproductive modes can be used to roughly predict the possible reactions of communities to habitat modification (Haddad and Prado, 2005; Mercurio, 2009).

Detailed ecological data about African amphibians are scarce (Amiet, 1972; Channing, 2001; Channing and Howell, 2006; Passmore and Carruthers, 1995; Rödel, 1996, 2000; Stewart, 1967; Schiøtz, 1999; Van Dijk, 1972, 1977; Wager, 1965). In many cases available information about species are anecdotal and based on few, or even single, isolated observations. Descriptions about egg deposition sites, clutch size and shape, duration of development, and tadpoles lacks for many African species, as is the case for several Malawian anurans. Any attempt of a comprehensive ecological treatment will be hampered by this absence of data. Therefore, for Malawi, whenever reasonable, baseline ecological information (e.g. eggs deposition site; presence of exotrophic tadpole) have been inferred from closely related species.

Field trips were carried out in four periods: (1) 27th January–9th March 2006; (2) 1st February–30th April 2007; (3) 3rd November–10th December 2007; (4) 19th January–17th March 2008, with a total of 115 days of field activity and 25 visited sites (Fig. 1). Daily search consisted of searching at all hiding places and suitable microhabitats available at the study site (under rocks, inside logs, within leaf litter, under loose bark, and dead tree branches). During the night frogs were located with the aid of flashlights and headlamps, either by opportunistic searches or by the localisation of calling males. Permanence in the study area varied between one and 15 days.

Following the classification proposed by Kentwood (2007), who modified the scheme of Haddad and Prado (2005), six reproductive modes are recognisable in the anuran species of Malawi (Fig. 2); listed from the most common to the rarest with the relative percentage of the fauna: i) aquatic eggs and free feeding tadpoles in lentic water (Mode 1), e.g. genera *Amietophrynus*, *Phrynobatrachus*, *Ptychadena*, and *Xenopus,* 72%; ii) eggs in leaves over water hatching into free feeding tadpoles that drop in lentic water (Mode 24), genera *Afrixalus* and *Hyperolius,* 13%; iii) direct development of terrestrial eggs (Mode 23), genera *Arthroleptis* and *Breviceps,* 8%; iv) terrestrial eggs on ground above water hatching in free feeding tadpoles which move to water (Mode 18), genera *Leptopelis* and *Hemisus,* 4%; v) eggs above water on humid rocks or in rock crevices, hatching into free feeding semiterrestrial tadpoles living on rocks in a water film (Mode 19), two species in two genera *Ptychadena broadleyi* and *Nothophryne broadleyi,* 2%; vi) arboreal foam nest hatching into free feeding tadpoles that drop into ponds or streams (Mode 33), only the species *Chiromantis xerampelina*; 1%. The known reproductive data of Malawian anurans and their allocation to a reproductive mode sensu Kentwood (2007) is summarised in Table 1.

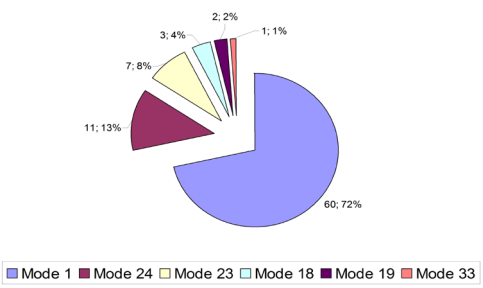

Figure 2. Reproductive modes in Malawian anurans. Occurrence, relative number of species, and percentage of the six reproductive modes. Most of the species reproduce by means of Mode 1.

Mode 1: Pond breeders with free feeding tadpole. This reproductive mode is the most generalised and phylogenetically widespread one, being found worldwide in most of the anuran families (Duellmann and Trueb, 1986; Kentwood, 2007). It is characterised by the deposition of eggs in temporary water bodies which develop into exotrophic aquatic tadpole until metamorphosis (Haddad and Prado, 2005). Of the 12 anuran families which occur in Malawi eight families (66%) and 17 genera (74%) share this reproductive mode. Of the 84 anuran species about two thirds (60; 72%) are generalist pond breeders, and most of them have a benthic tadpole (Table 1). However, despite the majority of Malawian anurans are pond breeders and their reproduction can be adequately described by the Mode 1, the species show some relevant differences in their breeding behaviour including: i) the nature and size of the oviposition sites, ii) clutch size iii) and at lesser extent tadpole type. Nearly all the species within this category normally breed in temporary lentic water bodies of various sizes, and only few species occasionally breed in lotic waters. Examples are the species belonging to the genera *Amietia*, *Amietophrynus*, *Hylarana*, *Ptychadena*, and *Strongylopus* which also breed in stagnant pools within streams with slow moving water. Further differences are evident in the size of the breeding site. Due to the paucity of data and the intrinsic ecological plasticity of Mode 1 it is difficult to categorise these species on the basis of their preferences about breeding site sizes. One exception is represented by the genus *Phrynobatrachus* which often breeds in very small rain puddles, ditches, and road drainages with shallow water. Species with Mode 1 lay their eggs directly in water. In Malawi, one exception is represented by *Hyperolius argus* for which the eggs were reported to be deposited under water, attached to submerged vegetation (Wagner, 1985). However, it is not sure whether this represents a real trait of the reproductive mode or rather the eggs were submerged due to the raising of the water level after heavy rains (Schiøtz, 1999). Relevant differences among Mode 1 species are present in the clutch sizes. Some species like *Ptychadena taenioscelis* and *Strongylopus merumontanus* lay very small clutches with 2–10 and 1–14 eggs respectively, whereas species like *Amietophrynus garmani* and *A. gutturalis* are able to produce clutches containing up to 25000 eggs (Channing, 2001; Stewart, 1967). Unfortunately for 36 species (60%) detail about the egg clutch size are unknown. Channing (2001) reported the clutch size of *Mertensophryne taitana* being composed of 125 eggs with the citation of Stewart (1967). However, no direct information is available for this species in the above mentioned work and 125 eggs were instead reported for *Mertensophryne nyikae*. A total number of 54 species have free feeding benthic tadpoles comprising 90% of this category. Exceptions are two species belonging to the genus *Kassina* (*K. maculata*, and *K. senegalensis*) and the toad *Schismaderma carens*, both with nektonic tadpoles; two *Xenopus* species (*X. laevis* and *X. muelleri*) and *Phrynomantis bifasciatus* both with suspension feeder tadpoles. Within this category one species *Pyxicephalus adspersus* shows some parental care behaviour. Males of this species dig channels for the tadpoles trapped in drying marginal puddles preventing their death through desiccations (Kok, Du Preez and Channing, 1989; Channing, Du Preez and Passmore, 1994). Of the 60 species reproducing by means of Mode 1, 48 species (80%) were found breeding in natural as well as secondary habitats, farm bush landscape and gardens, three species (5%) *Amietophrynus kisoloensis*, *Mertensophryne nyikae*, and *Strongylopus merumontanus* are apparently linked with the presence of a specific habitat, and the remaining nine species (15%) are unclassifiable due to lack of data. In summary, most of the Malawian amphibians are generalised pond breeders showing a considerable ecological plasticity being able to reproduce in significantly different habitat conditions.

Mode 24: Eggs deposited in leaves over water with free feeding tadpole. In Malawi 11 species (13%) belonging to the genera *Afrixalus* and *Hyperolius* (family Hyperoliidae) are to be found with this reproductive mode (Table 1). These species breed in temporary lentic body waters of various sizes in open habitat, and deposit the eggs in the vegetation above water. However, in absence of vegetation the direct oviposition in water occasionally

Table 1. Reproductive and developmental characters of the anurans of Malawi. Ecological classification of tadpoles follows McDiarmid and Altig (1999). Clutch size and development data are taken from Channing (2001), Channing and Howell (2006), Rödel (2000), Schiøtz (1999), Stevens (1972), Stewart (1967), and Wager, (1965). The terms "generalist" describes a species known to breed in natural, as well as in perturbed, whereas the term "specialist" describes species known to breed in natural and unperturbed areas only. RM = classification of reproductive modes after Haddad and Prado (2005) and Kentwood (2007). See text for further details.

Species	Eggs Deposition	Water	Clutch size	Development	Tadpole	Category	RM
Arthroleptidae							
Arthroleptis francei	leaf litter	—	unknown	direct	—	unknown	23
Arthroleptis reichei	leaf litter	—	unknown	direct	—	unknown	23
Arthroleptis stenodactylus	leaf litter	—	33–80	direct	—	generalist	23
Arthroleptis xenochirus	leaf litter	—	9	direct	—	unknown	23
Arthroleptis xenodactyloides	leaf litter	—	20	direct	—	generalist	23
Leptopelis argenteus	water	lentic	unknown	tadpole	benthic	unknown	1
Leptopelis bocagii	hole underground	lentic	unknown	tadpole	benthic	unknown	18
Leptopelis flavomaculatus	water	lentic	unknown	tadpole	benthic	generalist	1
Leptopelis mossambicus	water	lentic	unknown	tadpole	benthic	generalist	1
Leptopelis parbocagii	water	lentic	unknown	tadpole	benthic	generalist	1
Leptopelis sp.	water	lentic	unknown	tadpole	benthic	unknown	1
Brevicipitidae							
Breviceps mossambicus	subterranean nest	—	20–30	direct	—	generalist	23
Breviceps poweri	subterranean nest	—	unknown	direct	—	unknown	23
Bufonidae							
Amietophrynus garmani	water	lentic	12000–20000	tadpole	benthic	generalist	1
Amietophrynus gutturalis	water	lentic, lotic	15000–25000	tadpole	benthic	generalist	1
Amietophrynus kisoloensis	water	lentic, lotic	unknown	tadpole	benthic	specialist	1
Amietophrynus maculatus	water	lentic, lotic	2000–8000	tadpole	benthic	generalist	1
Mertensophryne lindneri	water	lentic, lotic	unknown	tadpole	benthic	generalist	1
Mertensophryne nyikae	water	lentic	125	tadpole	benthic	specialist	1
Mertensophryne taitana	water	lentic	125	tadpole	benthic	generalist	1
Poyntonophrynus beiranus	water	lentic	unknown	tadpole	benthic	unknown	1
Schismaderma carens	water	lentic	2500	tadpole	nektonic	generalist	1
Hemisotidae							
Hemisus guineensis	hole underground	lentic	unknown	tadpole	nektonic	generalist	18
Hemisus marmoratus	hole underground	lentic	80–250	tadpole	nektonic	generalist	18
Hyperolidae							
Afrixalus brachycnemis	vegetation above water	lentic	50	tadpole	benthic	generalist	24
Afrixalus crotalus	folded leaf above water	lentic	50	tadpole	benthic	generalist	24
Afrixalus delicatus	folded leaf above water	lentic	50	tadpole	benthic	generalist	24

Table 1. (continued)

Afrixalus fornasini	folded leaf above water	lentic	80	tadpole	benthic	generalist	24
Hyperolius argus	under water	lentic	200	tadpole	benthic	generalist	1
Hyperolius kachalolae	water	lentic	unknown	tadpole	benthic	generalist	1
Hyperolius kivuensis	vegetation above water	lentic	unknown	tadpole	benthic	generalist	24
Hyperolius m. marginatus	water	lentic	390	tadpole	benthic	generalist	1
Hyperolius m. taeniatus	water	lentic	unknown	tadpole	benthic	generalist	1
Hyperolius minutissimus	water	lentic	unknown	tadpole	benthic	unknown	1
Hyperolius mitchelli	vegetation above water	lentic	50–100	tadpole	benthic	generalist	24
Hyperolius nasutus complex	water	lentic	200	tadpole	benthic	generalist	1
Hyperolius pictus	vegetation above water	lentic	60–90	tadpole	benthic	generalist	24
Hyperolius pusillus	water	lentic	20–120	tadpole	benthic	generalist	1
Hyperolius quinquevittatus	water	lentic	unknown	tadpole	benthic	generalist	1
Hyperolius spinigularis	vegetation above water	lentic	150–200	tadpole	benthic	generalist	24
Hyperolius substriatus	water	lentic	unknown	tadpole	benthic	generalist	1
Hyperolius tuberilinguis	vegetation above water	lentic	236–400	tadpole	benthic	generalist	24
Hyperolius v. albofasciatus	vegetation above water	lentic	515	tadpole	benthic	generalist	24
Hyperolius v. nyassae	vegetation above water	lentic	369	tadpole	benthic	generalist	24
Kassina maculata	water	lentic	unknown	tadpole	nektonic	generalist	1
Kassina senegalensis	water	lentic	260–400	tadpole	nektonic	generalist	1
Microhylidae							
Phrynomantis bifasciatus	water	lentic	400–1500	tadpole	suspension feeder	generalist	1
Phrynobatrachidae							
Phrynobatrachus acridoides	water	lentic	unknown	tadpole	benthic	generalist	1
Phrynobatrachus mababiensis	water	lentic	unknown	tadpole	benthic	generalist	1
Phrynobatrachus natalensis	water	lentic	200–400	tadpole	benthic	generalist	1
Phrynobatrachus parvulus	water	lentic	unknown	tadpole	benthic	generalist	1
Phrynobatrachus perpalmatus	water	lentic	unknown	tadpole	benthic	generalist	1
Phrynobatrachus rungwensis	water	lentic	unknown	tadpole	benthic	generalist	1
Phrynobatrachus sp.	water	lentic	unknown	tadpole	benthic	unknown	1
Phrynobatrachus stewartae	water	lentic	unknown	tadpole	benthic	generalist	1
Phrynobatrachus ukingensis	water	lentic	unknown	tadpole	benthic	generalist	1
Pipidae							
Xenopus laevis	water	lentic	1000	tadpole	suspension feeder	generalist	1
Xenopus muelleri	water	lentic	unknown	tadpole	suspension feeder	generalist	1

Table 1. (continued)

Ptychadenidae							
Hildebrandtia ornata	water	lentic	unknown	tadpole	benthic	generalist	1
Ptychadena anchietae	water	lentic	200–300	tadpole	benthic	generalist	1
Ptychadena ansorgii	water	lentic, lotic	unknown	tadpole	benthic	unknown	1
Ptychadena broadleyi	water	lentic	unknown	tadpole	semi-terrestrial	specialist	19
Ptychadena guibei	water	lentic	unknown	tadpole	benthic	unknown	1
Ptychadena mascareniensis	water	lentic	1080	tadpole	benthic	generalist	1
Ptychadena mossambica	water	lentic	unknown	tadpole	benthic	generalist	1
Ptychadena oxyrhynchus	water	lentic	3476	tadpole	benthic	generalist	1
Ptychadena porosissima	water	lentic	unknown	tadpole	benthic	generalist	1
Ptychadena schillukorum	water	lentic	unknown	tadpole	benthic	generalist	1
Ptychadena taenioscelis	water	lentic	2–10	tadpole	benthic	generalist	1
Ptychadena upembae	water	lentic	unknown	tadpole	benthic	unknown	1
Ptychadena uzungwensis	water	lentic	unknown	tadpole	benthic	unknown	1
Pyxicephalidae							
Amietia angolensis	water	lotic	unknown	tadpole	benthic	generalist	1
Amietia cf. *fuscigula*	water	lotic	unknown	tadpole	benthic	generalist	1
Amietia johnstoni	water	lotic, lentic	unknown	tadpole	benthic	generalist	1
Amietia viridireticulata	water	lotic, lentic	unknown	tadpole	benthic	unknown	1
Nothophryne broadleyi	wet moss	lentic	30	tadpole	unknown	specialist	19
Pyxicephalus adspersus	water	lentic	3000–4000	tadpole	benthic	generalist	1
Strongylopus merumontanus	water	lotic	1–14	tadpole	benthic	specialist	1
Tomopterna cryptotis	water	lentic	2000–3000	tadpole	benthic	generalist	1
Tomopterna marmorata	water	lentic	150	tadpole	benthic	generalist	1
Tomopterna tuberculosa	water	lentic	unknown	tadpole	benthic	generalist	1
Rhacophoridae							
Chiromantis xerampelina	water	lentic	500–1250	tadpole	benthic	specialist	33
Ranidae							
Hylarana darlingi	water	lotic, lentic	unknown	tadpole	benthic	generalist	1
Hylarana galamensis	water	lentic	1500–4000	tadpole	benthic	generalist	1

occur (Pickersgill, 2007). *Afrixalus* species are used to lay the eggs above the water level in folded leaves glued together (Channing, 2001, Pickersgill, 1984, Schiøtz, 1999). Apparently, one exception is represented by *A. brachycnemis* were the eggs are not deposited in glued leaves (Channing, 2001). Clutch sizes are different among those genera. *Afrixalus* species lay up to 50–80 eggs, whereas *Hyperolius* species lay up to about 500 eggs (Channing, 2001, Schiøtz, 1999, Stewart, 1967; Pickersgill, 2007). They all share a generalised tadpole of the benthic type (McDiarmid and Altig, 1999). All the above mentioned Mode 24 species were found breeding

in natural as well as secondary habitats, e.g., farm bush landscape and gardens whenever suitable water bodies were available.

Mode 23: Terrestrial nests breeders with direct development. Of the 12 anuran families which occur in Malawi two families (17%) and two genera (8.7%) share this reproductive mode (Table 1). Altogether, seven species (8.2%) belonging to two genera *Arthroleptis* (*A. francei, A. reichei, A. stenodactylus, A. xenochirus,* and *A. xenodactyloides*), and *Breviceps* (*B. mossambicus*, and *B. poweri*) lay their eggs in holes underground or in the leaf litter, from which metamorphosed froglets hatch directly (Barbault and Rodrigues, 1979; Channig, 2001; Guibé and Lamotte, 1958; Lamotte and Perret, 1963; Thibaudeau and Altig, 1999; Wager, 1960, 1965). These species share a small clutch size with clutches containing up to 80 eggs in *A. stenodactylus* and up to 30 eggs in *B. mossambicus* (Channing, 2001; Stewart, 1967). The direct development allows these frogs to breed in a variety of very different habitats provided a certain amount of soil moisture is available. Three of these species (*A. stenodactylus, A. xenodactyloides*, and *Breviceps mossambicus*) can be defined as broad habitat generalists occurring in near all available habitats including cultivated areas and villages. Two of them are geographically restricted to small areas: *Arthroleptis francei* (Mulanje Mountain), and *A. reichei* (Misuku Mountains), but were collected in primary habitats (evergreen mountain forest, grassland, and shrubs) as well as in secondary habitats (e.g., tree plantations). Further studies are essential to assess the ecological plasticity of these species and their ability to survive in altered landscapes. The remaining two species *A. xenochirus* and *B. poweri* are poorly known.

Mode 18: Nest breeders with free feeding tadpole. Of the 12 anuran families occurring in Malawi two families (17%) and two genera (8.7%) share this reproductive mode (Table 1). Three species (3.5%) belonging to *Leptopelis* (*L. bocagii*) and *Hemisus* (*H. guineensis*, *H. marmoratus*) lay their eggs in holes underground close to water bodies were they develop until tadpoles hatch. Subsequently, in the *Leptopelis* species the tadpoles hatch and wriggle into the water, whereas the *Hemisus* tadpoles reach water through a channel dug by the female (Channig, 2001; Channing and Howell, 2006; Lamotte and Perret, 1961; Largen, 1977; Rödel, 1996, 2000; Rödel et al., 1995; Schiøtz, 1999; Wager, 1965). Often they are simply flooded away by rain. Within this category clutch size is known only for *H. marmorartus* comprising 80–250 eggs (Channing, 2001; Rödel, 2000; Wager, 1986). Concerning the tadpoles, *L. bocagii* have a benthic tadpole whereas the two *Hemisus* species have nektonic tadpoles (McDiarmid and Altig, 1999). These three species breed in temporary lentic body waters of various sizes. *H. marmoratus* is known to breed within farm bush landscape and gardens. The remaining two species *L. bocagii* and *H. guineensis* are poorly known.

Mode 19: Humid rocks breeders with semiterrestrial tadpoles. Only two species (2%) *Ptychadena broadleyi* (Ptychadenidae) and *Nothophryne broadleyi* (Pyxicephalidae) are found in Malawi with this peculiar reproductive mode (Table 1). *Ptychadena broadleyi* was reported as a completely rupicolous species with eggs deposited in pools within rocky outcrops from which semiterrestrial tadpoles hatch (Stevens, 1972). Details of oviposition site and clutch size are unknown. Stevens (1972) suggested the presence of aquatic eggs deposited as a floating mass in a single layer. Apparently, the tadpoles of *P. broadleyi* are unique within the genus being able to develop on sun exposed rock faces with only a film of water and the greater part of their bodies out of water (Stevens, 1972; Channing, 2001). They are adapted to move and adhering to the rock surface by means of the mouth and tail, feeding on algae and bacteria growing in the film of water (Channing, 2001; Stevens, 1972). Tadpole morphology differs from that of typical *Ptychadena* of the benthic type in having an elongate body and tail, with low fins resembling those of the genus *Leptopelis* (Stevens, 1972). Very little is known about the breeding behaviour of *Nothophryne broadleyi*. For this species Mazibuko and Poynton (2004) reported that "it is particularly associated with rocky areas in both montane forest and grassland. The eggs are laid in wet moss at the edge of rivulets running over rocks, and the larvae disperse by migration across wet rocks". Both species are restricted to the plateaux of Mulanje and Zomba Mountains at 900–2715 m altitudes and giving their peculiar reproductive mode are here defined as habitat specialist. However, *P. broadleyi* was found in rocky outcrops within forest, clearings, as well as within gardens and tree plantations (Stevens, 1972). Due to the limited distribution both species are considered as endangered (IUCN, 2008). Further studies are essential to assess the status of these species and their ability to survive in altered landscapes.

Mode 33: Foam nest breeders in trees. Of the 12 anuran families occurring in Malawi only one species belonging to the Rhacophoridae built foam nests. *Chiromantis xerampelina* deposit the eggs in foam nest overhanging different kinds of lentic and lotic water

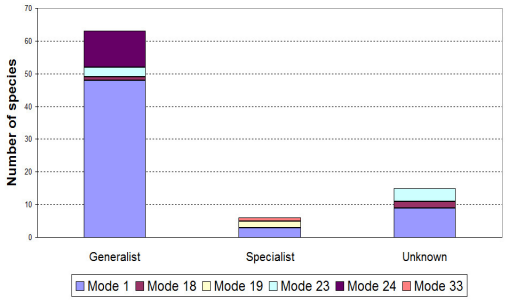

Figure 5. Ecological categorisation of the anuran of Malawi. The graphic shows the number of species in the six different reproductive modes. Habitat generalists are species known to thrive both in primary and altered habitat. Habitat specialists are known to breed only in primary habitat. Unknown, no data available. Most of the anurans of Malawi (75%) can be defined as habitat generalist reproducing in lentic temporary waters and able to survive in altered habitats. See text for further explanations.

bodies (Table 1). Subsequently, tadpoles drop in the water were they feed until metamorphosis is completed (Wager, 1926, 1965; Coe, 1974; Jennions, Backwell and Passmore, 1992; Schiøtz, 1999). Usually *C. xerampelina* lays the eggs in foam nests hanging from branches of trees above water at different heights, but in absence of trees the species lay the eggs in any suitable objects. Therefore, this species shows a remarkable plasticity concerning the choice of oviposition sites. The tadpole is of benthic type (McDiarmid and Altig, 1999). Clutch size comprises 500-1250 eggs (Channing, 2001; Stewart, 1967). *Chiromantis xerampelina* is found in a variety of dry habitats from dry forest, miombo, mopane, savannah, to cultivated areas at low altitudes. However, this species appear to be much common in light wooded savannahs and forested areas. In fact, despite the occasional deposition of eggs directly in water or in grassy vegetation above water, the presence of a vegetation type able to support the large body size of the adults probably plays an important role in determining the occurrence of this species. Therefore, *C. xerampelina* is here preliminarily considered as a habitat specialist.

One main character of the Malawian anuran fauna is the low diversity of reproductive modes, the predominance of habitat generalist species, and the high similarity among used habitats. Among the six observed reproductive modes, five (Mode 1, 18, 24, 23, and 33) are widespread in Malawi and commonly found in most communities, whereas Mode 19 is restricted to two species occurring at Mulanje and Zomba mountains at medium to high altitudes. Furthermore, based on the above mentioned classification and also taking into account the occurrence of many species in different primary and secondary habitats (Mercurio, 2009), 75% of the anuran fauna can be considered as habitat generalist (Fig. 3). As a consequence, these amphibians possess a scarce capacity to act as surrogates of habitat integrity and their use as model animals to detect habitat changes by means of quantitative studies should be valued case by case.

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