The mating system of the reed frog *Heterixalus tricolor* (Anura: Hyperoliidae) from western Madagascar's dry forests

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Abstract. The mating system is an essential part of a species' biology. The reed frog *Heterixalus tricolor* is a prolonged breeder, endemic to the seasonal dry forests of western and northern Madagascar. We examined the mating system of a population from Kirindy Forest by field observations and experimentally. The mating system fulfils many criteria of a lek-system. *Heterixalus tricolor* had a highly male-biased operational sex ratio (0.34 ± 0.17); males were attending the breeding site over a prolonged period of time, while females visited the pond only one or a few days per season; and the distribution of frogs across different microhabitats within the breeding site was unequal, with higher frog densities in the vegetated pond centre as compared to the pond edge. There was no size-assortative mating of males and females, neither in the field nor in experiments. Field and experimental data revealed that males that mated successfully were not larger than non-amplectant males. Whether this mating pattern is more driven by female choice or male-male competition remains unclear.

Key words. Amphibia, breeding ecology, Kirindy forest, lek-system, mating system, reproduction, size assortative mating.

Introduction

Wells (2007) recognized two general temporal patterns in anuran reproduction – explosive breeding and prolonged breeding. Explosive breeders are species that usually use highly temporary waters and breed whenever conditions are suitable, often after the first heavy rainfalls in the season. Females tend to arrive more or less synchronously and remain only for a short time at breeding sites. Males that actively seek females are favoured in this system. As a result, males engage often in scramble competition for females and sometimes fight violently for them (Robertson 1986, Katsikaros & Shine 1997).

Prolonged breeders typically use more reliable breeding sites and breeding extends over a long period, often several months. Females arrive asynchronously and males outnumber females at breeding sites. The irregular arrival of females can favour males that attract females from stationary calling sites. The calling males often space themselves and guard territories, oviposition sites, and/or courtship areas against rivals, although physical contacts between males may be uncommon (reviewed in Wells 2007). The breeding situation superficially resembles the lek-situation in other vertebrates (e.g., Clutton-Brock et al. 1988), where males are displaying in small areas and the females move among them while making their choice. However, only in some anuran species (e.g., in *Lithobates catesbeianus*, *Scinax ruber*, *Pyxicephalus adspersus*; see Emlen 1976, Bourne 1992, Channing et al. 1994) all criteria of a classical lek-system (Bradbury 1977, 1981, Emlen & Oring 1977) have been found to be fulfilled.

The genus *Heterixalus* represents one of the endemic radiations of frogs in Madagascar (Wollenberg et al. 2007) and contains at present eleven species (Glaw & Vences 2007). The first hyperoliid frogs might have reached Madagascar from Africa via overseas dispersal (Vences et al. 2003). *Heterixalus* species differ in coloration pattern but are rather similar in morphology and in call structure (Glaw & Vences 1993, 2007). In contrast to mantellid and microhylid frogs of Madagascar that display an astonishing variety of reproductive modes and breeding behaviours (e.g., Heying 2001, Randrianiaina et al. 2011, Poth et al. 2012), *Heterixalus* species are rather uniform in this respect. All species are most common outside forested areas and breed in stagnant waters such as swamps, ponds and rice paddies (Blommers-Schlösser 1982; Glaw & Ven-

ces 1993, 2007), similar to many species within the African frog genera *Hyperolius*, *Afrixalus* and *Kassina* (Channing & Rödel 2019). As for most Malagasy anurans, knowledge on mating systems is very scarce, i.e. if any mate choice exists in these species and what their critical determinants are. However, the knowledge of a species' ecology and behaviour, with the mating system as an essential part of it, is often a prerequisite for its successful conservation (Araújo et al. 2002). In the tropics, and especially in Madagascar, where anthropogenic landscape modifications rapidly reduce many natural habitats (Harper et al. 2007), the lack of detailed biological knowledge handicaps effective conservation of many species (Stuart et al. 2004, Andreone et al. 2008, Irwin et al. 2010).

In this study we examined the mating system and general breeding biology of a population of *Heterixalus tricolor*, a frog species endemic to western Madagascar (Fig. 1). Our objectives were to examine (1) the population size; (2) the operational sex ratio (OSR); (3) the micro-distribution of the frogs, i.e. their distribution across different micro-habitats within the breeding site. Furthermore, we tested (4) whether the mating system fulfils the criteria of a lek-system sensu Bradbury (1977, 1981) and Emlen & Oring (1977), and (5) finally, we examined if females do select particular males as mating partners and if so, what the decisive factors for their choice are. For the latter point, we tested (a) if females prefer larger males over smaller ones, or (b) if females mate size-assortatively.

Methods
Study species and site

Heterixalus tricolor (Boettger, 1881) has a scattered distribution in northern and western Madagascar's dry forests (Glaw & Vences 2007). This species is a prolonged breeder that uses permanent ponds as breeding sites or ponds that exist for at least one month. It is nocturnal, and calling starts at sunset and ceases around midnight at our study site. Males call consistently throughout the rainy season from within the pond, either from floating leaves or from grass stems. The calling activity is relatively independent of rainfall (Glos 2003). The typical call consists of two unharmonious note types, lasting 80–90 ms (first note type) and 40–60 ms (second note type), arranged in groups, most usually as "1-2" or "1-2-2", rarely "1-2-2-2". Call frequency ranges from 2.2 to 3.8 kHz (Glaw & Vences 1993).

During the day, *H. tricolor* rests on reed grasses or herb leaves either within the pond or at its edge, often fully sun-exposed. The colouration then changes from yellow or brownish at night to bright white during the day (Glos 2003), similar to West-African *Hyperolius nitidulus* where juveniles spend several months of the dry season on grass stems fully exposed to the sun (Spieler 1997, Rödel 2000).

As other hyperoliid frogs, *H. tricolor* has a gland on its subgular vocal sac. This gland is an apomorphic character for the family Hyperoliidae (Drewes 1984) and is known to produce a species-specific cocktail of volatile chemicals in *Hyperolius* and *Heterixalus* species (*H. betsileo*, *H. alboguttatus*). Whether these chemicals are functional in chemical communication, e.g., being important for mate choice, as suggested by Starnberger et al. (2013, 2014a, b), remains to be tested for *Heterixalus,* but appears to be very likely.

The Kirindy Forest (KF) CNFEREF (Centre Nationale de Formation, d'Études et de Recherche en Environnement et Forestière) is a deciduous dry forest at the west coast of Madagascar, 60 km north of Morondava and about 20 km inland (44°39' E, 20°03' S; 18–40 m above sea level (Sorg & Rohner 1996). The area of the KF concession covers about 12,000 ha. It is situated within the Central Menabe forest block which has the dubious reputation of being one of the largest remaining continuous forests in western Madagascar (Nelson & Horning 1993). The forest is intersected by the Kirindy River and is surrounded by a tree-shrub savanna of anthropogenic origin. The climate is characterized by a marked seasonality. Almost all rain falls in the austral summer from November to March associated with temperatures up to 40°C, followed by eight months of virtually no rain (annual mean rainfall: 800 mm; Ganzhorn & Sorg 1996) and very high fluctuations in temperature (between about 10°C at night and 35°C during the day) in the coldest months (June and July).

Figure 1. *Heterixalus tricolor* male (A) and female (B) from Kirindy Forest in life.

The study was conducted at one major breeding pond of *H. tricolor* in KF, locally known as pond A (Glos 2003). This pond is oval shaped and about 50 m long and 28 m wide when completely water filled. At the time of the study (March–April 2003) large parts of the pond were covered with floating water plants (e.g., water lilies *Nymphea lotus*), emergent vegetation (e.g., reed grasses) and twigs from the shrubs on the edge of the pond (Fig. 2).

Field data

We set up 12 line transects (each 5 m long and 1 m wide), three within each of four distinct parts of the study pond. These areas were easily distinguishable by their vegetation and represented different microhabitats within the pond; i.e. (1) edge vegetation (mainly bushes), (2) floating water plants, and (3, 4) reed grasses. In the latter case, we distinguished between (3) edge of the reed grass area and (4) centre of the reed grass area (Fig. 2).

We collected data on these transects by carefully walking along pre-installed lines in ten nights, from 19:30 hours to about 22:30 hours. We captured all individual frogs and couples on these transects and recorded four variables: (1) microhabitat, (2) sex, (3) snout–vent length (SVL; using callipers, accuracy ± 1.0 mm), and (4) weight (laboratory balance, Ohaus CT10®, accuracy ± 0.01 g). All couples in amplexus were transferred into plastic buckets with 10 cm of pond water and gauze spanned over the top until spawning was completed. Submerged vegetation and twigs were provided as spawning substrate. All animals were marked prior to release by toe-clipping (Heyer et al. 1994) to avoid pseudo-replications when capturing the same individuals in subsequent nights. Thereby, all captured animals within one night were marked as cohort, i.e. received the same mark. Toe-clipping was done in a way to assure minimal impact on the animals (compare Grafe et al. 2011).

We analysed the data according to: (1) population size (estimation using mark-recapture methods), (2) operational sex ratio, (3) correlation of frog SVL and weight and clutch size, (4) use of the four microhabitats by the frogs, (5) differences in male size between the four microhabitats, (6) correlation of SVL in amplectant males and females (size-assortative mating), and (7) preference of females for larger males, i.e. if there was a size difference between males that successfully mated (males of amplectant pairs) and single males.

Experimental data

We experimentally analysed female mate choice on animals that were captured as single individuals during our transect walks. Experiments were conducted the same night as the frogs were captured. Females (n = 23) were kept individually in buckets (volume 10 l) filled to 10 cm with pond water and equipped with twigs and *Nymphea* leaves. These structures are naturally used for egg deposition by *H. tricolor* at the study pond (Glos 2003). Subsequently, we added two male *H. tricolor* into each bucket with one male always being considerably larger than the other (SVL: 28.3 ± 0.8 mm versus 24.8 ± 0.5 mm; weight 1.2 ± 0.1 g versus 0.8 ± 0.1 g). These two groups of males were significantly different (T-test for independent sam-

Figure 2. Breeding pond (pond A) of *Heterixalus tricolor*, showing different microhabitats where transects were installed. (A) Edge vegetation, (B) water lilies, (C) edge of reed grass zone, (D) centre of reed grass zone.

ples: SVL: T = 18.5, df = 44, p < 0.0001; weight: T = 12.8, n = 46, p < 0.0001). To minimize the disturbance caused by the observer we checked each trial in intervals of about 10 min by carefully lifting the gauze lid. The experiment was terminated when couples have been formed. Subsequently, we removed the remaining male. After spawning was completed, we measured SVL of both males again to determine which male was the successful one.

We analyzed the data using parametric (ANOVA, T-tests, Pearson correlations) and non-parametric statistics (Signed-rank test) using the software IBM SPSS Statistics 23®. We checked for normal distribution of data. For estimation of population size we used the formula provided by KREBS (1998).

Results
Population size and operational sex ratio

In total (ten nights, 12 transects per night) we captured 155 single males, 36 single females and 27 couples on the transects. Additionally, we recaptured 28 individual males. From these recaptures, seven males were recaptured once, six were captured twice, three were captured in three nights, three in four nights, eight in five nights, and one male in six nights. Additionally, five males out of the 27 amplected males encountered were recaptures. None of the females was recaptured. The male population at the study pond was estimated as 541 individuals (5–95% confidence interval, 405–752; Schnabel population estimation; KREBS 1998). Per night and including recaptures, we found on average 21.0 males ± 6.8 sd (= 0.35 individuals/m²) and 6.3 ± 2.8 females (= 0.11 individuals/m²). The operational sex ratio females/males at the breeding pond per night was 0.34 ± 0.17 (range 0–0.57; n = 10 nights).

Distribution of males and females within the pond

Males and females were not evenly distributed across the different microhabitats of the breeding pond (χ^2-goodness of fit: males χ^2 = 70.7, df = 3, p < 0.0001; females χ^2 = 19.3, df = 3, p < 0.001; Fig. 3). Abundance for single individuals of both sexes and for amplectant couples was lowest in areas at or close to the pond's edge and highest in the centre of the pond (reed grass vegetated areas). There were neither significant differences in SVL (ANOVA: F = 1.6, df = 3, p = 0.20) nor in body mass (F = 1.5, df = 3, p = 0.22) between males captured in different pond areas (Fig. 4).

Do *Heterixalus* females select particular mates?

Field data: We tested whether females mate with males according to their own body size (SVL and weight), i.e. if small females mated with small males and vice versa. This was not the case for 34 couples, including 27 couples found on transects and seven couples found just outside the

transects (Pearson correlation of SVL of amplectant males and the respective females: r = 0.06, p = 0.73, n = 34; Fig. 5).

We tested whether there was a difference in body size or weight between amplectant males, i.e., that mated successfully (all males in amplexus), and single males (all un-mated males). There was no such difference (T-test SVL: T = -1.7, p = 0.10; body mass: T = -1.6, p = 0.10, n_{single} = 155, $n_{amplectant}$ = 27) (Fig. 6).

Experimental data: There was no significant size difference between males that mated with the female and those that did not, i.e., females did not significantly mate more often with the larger male when given the choice be-
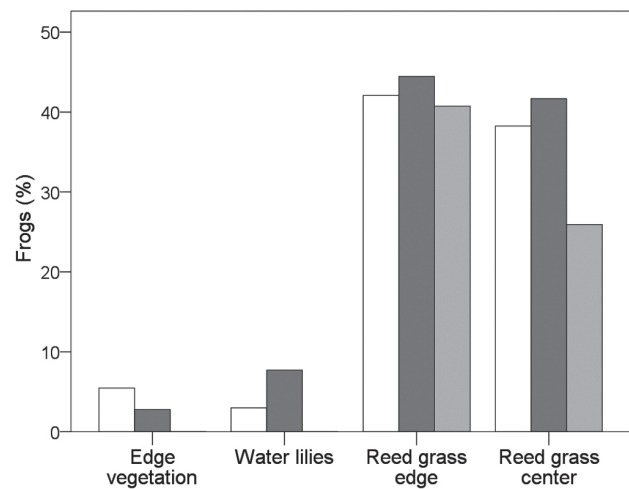

Figure 3. Proportional distribution of *Heterixalus tricolor* over four microhabitats of single males (white bars, n = 183), single females (dark grey bars, n = 36) and amplectant couples (light grey bars, n = 27).
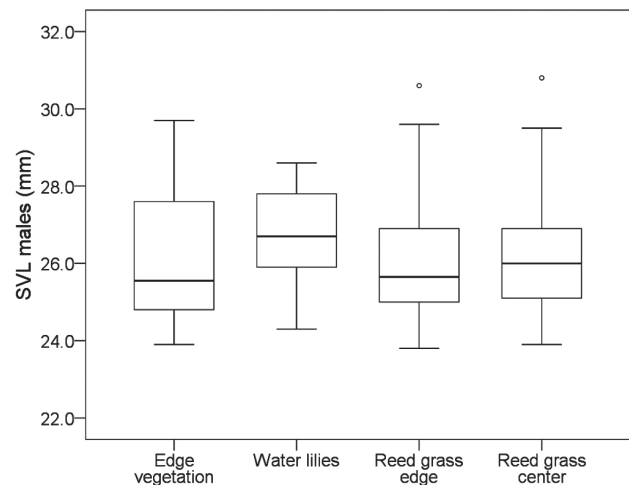

Figure 4. Size distribution for males of *Heterixalus tricolor* (n = 155) over four microhabitats. SVL = snout–vent length. Box plots show median, 25%- and 75%-percentiles, and minimum and maximum, small circles are outliers. Groups were not significantly different (ANOVA: F = 1.6, df = 3, p = 0.20).

tween two different sized males, and/or larger males were not more successful in mating than smaller males (Signed rank-test; SVL and weight: Z = 0.42, p = 0.68, n = 23; Fig. 7).

Discussion

Heterixalus tricolor is among the frog species in the seasonal dry forests of western Madagascar with prolonged breeding
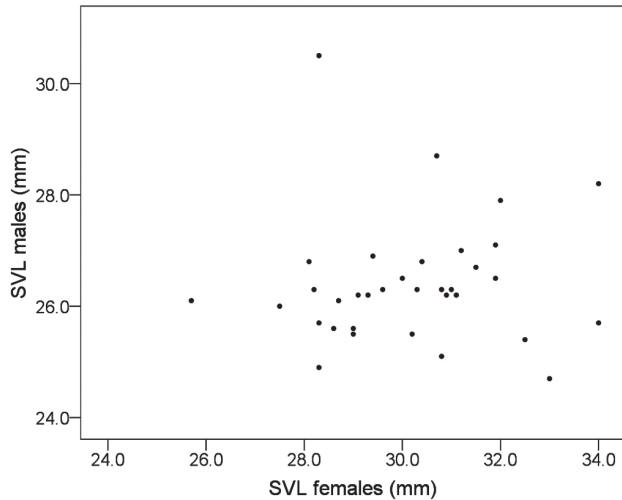

Figure 5. Size relationship of amplectant *Heterixalus tricolor* couples in the field. No size assortative mating could be detected (Pearson correlation: r = 0.06, p = 0.73, n = 34). SVL = snout–vent length.
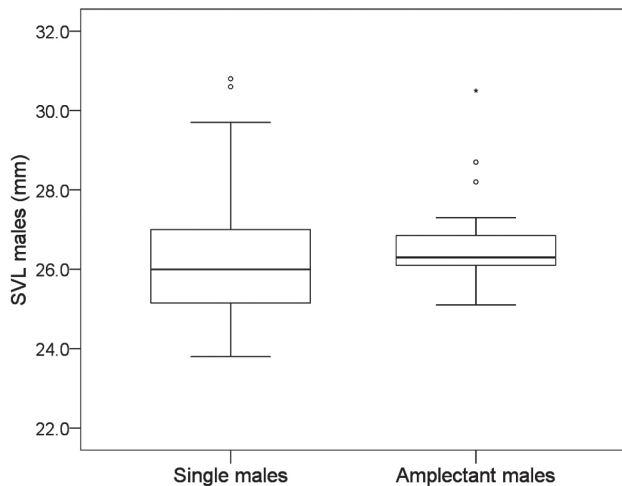

Figure 6. Differences in snout–vent length (SVL) between single males of *Heterixalus tricolor* (all unmated males) and males that mated successfully (all males in amplexus) in the field, independent of microhabitat Box plots show median, 25%- and 75%-percentiles, and minimum and maximum, small circles are outliers. Groups were not significantly different (T-test SVL: T = -1.7, p = 0.10, n_{single} = 155, $n_{amplectant}$ = 27).

(Glos 2003, this study). Although it starts its breeding activities not earlier than one month after the beginning of the first heavy rains, breeding continues throughout the rainy season and then is relatively independent of actual rainfall (Glos 2003). The male-biased sex ratio at the breeding pond is characteristic for this breeding system. Our mark-recapture data showed that individual males were present for at least several nights at the breeding pond, but not continuously throughout the breeding season, while the females visit the pond much less frequent, maybe solely in one night when they actually deposit their eggs. These are some characteristics for a lek-breeding system.

Bradbury (1977, 1981) specified four criteria to distinguish classical lek-breeders from species using alternative mating systems (also see Wiley 1991). These criteria are: (1) there is no male parental care; (2) there is an arena or lek to which females come and on which most of the mating occurs; (3) the display sites of males contain no significant resources (e.g., such as high-quality oviposition sites) required by females except the males themselves; and (4) the female has an opportunity to choose a mate once she visits the arena. If females are relatively asynchronous in reproductive readiness, and males attend continuously the breeding site, then the intensity of male-male competition should affect stable dominance hierarchies or position effects among the advertising males, resulting in aggregations known as leks. Thus, lek-mating systems would be characterized by relatively long breeding seasons, highly skewed operational sex ratios (OSRs), and individual males not being able to control or monopolize resources essential for female acquisition.

The mating system of *H. tricolor* fulfils many, but not all, of these criteria. *Heterixalus tricolor* is a prolonged breeder,
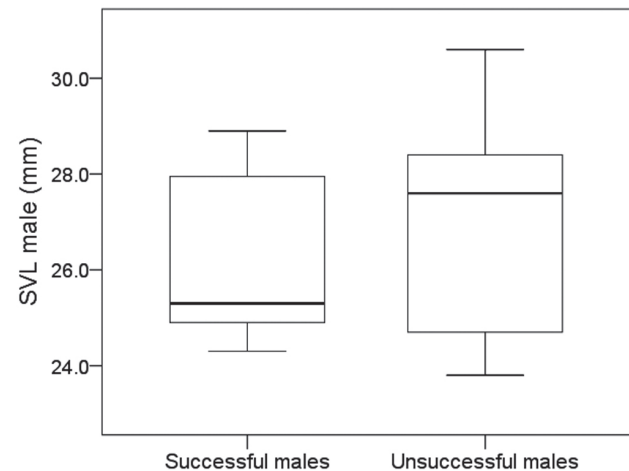

Figure 7. Experimental data of female *Heterixalus tricolor*, given the choice between two different sized males. Females did not prefer larger over smaller males (Signed rank test: p = 0.68, n = 23). SVL = snout–vent length. Box plots show median, 25%- and 75%-percentiles, and minimum and maximum, small circles are outliers.

and the operational sex ratio is highly male skewed. Males display in the pond's centre (in the reed grass area and to a lesser degree in the floating water plants) much more than at the pond's edges, and maintain individual spacing in the chorus (authors pers. obs.). There is no clear-cut definition on the (relative) size of a lek in the literature, i.e. whether an aggregation is dense enough to satisfy Bradbury's criterion. *Heterixalus tricolor* males are aggregated to a certain extent as their density is highest in the reed grass zone. However, their distribution across the breeding pond was by no means as clumped as known from some lek-breeding mammals (e.g., Clutton-Brock et al. 1988), birds (Oring 1982), or frogs (Bourne 1992). Thereby, males were not larger in any one area of the breeding site, in contrast to e.g., some ungulates where males are larger (i.e., of higher quality) in the centre of the lek (Bro-Jørgensen & Durant 2003). We do not have sufficient observations on male – male interactions to unerringly uncover the mechanism that leads to this regular spacing pattern. One possible explanation is that males do physically maintain individual spacing and in the course of this push away individuals resulting in a rather regular spacing. Direct male – male combats are known from many other hyperoliid species (e.g., Rödel 2000, Rödel et al. 2006, Glaw & Vences 2007).

Direct and indirect benefits to females of choosing mates have been suggested to play a role in the evolution of female preferences even in non-resource-based mating systems (e.g., Grafe 1997). Direct benefits may affect the survival or fecundity of females. We did not find any evidence that females obtain direct benefits of mate choice. Calling territories were not known to contain any resources of interest to females, and they were not the place of the actual egg deposition. Eggs were deposited in several small clutches, attached to either vertical structures under water (e.g., dead or living grass stems) or less frequent to horizontal structures on the water surface (mainly leaves of water lilies). Thereby the couples covered, while swimming under water, an area of several m². However, it remains possible that the calling sites are in the ultimate vicinity to highly suitable sites for egg deposition. Therefore, the mere (low) distance of the calling site to the preferred oviposition site would be a decisive factor to choose a respective male.

A second criterion of a female to obtain a direct benefit of mate choice could be to enhance the fertility rates of its eggs. We consider this unlikely for two reasons. First, we found no size-assortative mating, although this is frequently observed in anurans (Halliday 1983, Sullivan et al. 1995, Dittrich et al. 2018). Positive size-assortative mating is commonly suggested to increase fertility rates in anurans as a consequence of an optimal cloaca fit during spawning (Licht 1976, Davies & Halliday 1977, Robertson 1990, Bourne 1993). Second, fertility rates seem to be generally very high in *Heterixalus*, independent of male characteristics. This is supported by an accompanying experiment where different sized males were randomly assigned to females and fertilization rates were analysed (J. Glos unpubl. data).

When considering male size as one indicator of good genes, we did not find evidence that females obtain indirect benefits of mate choice by acquiring good genes (in the sense Zahavi 1975 and Hamilton & Zuk 1982 use this term). Neither in the field nor in the experiment female *H. tricolor* preferably mated with larger males. This is in contrast to many other mating systems, including many of other anurans (e.g., Ryan 1980, Passmore et al. 1992, Castellano & Giacoma 1998; but e.g. see Stephenson & Verrell 2003 for a contradicting example). However, the absence of the preference for larger males is not exceptional in hyperoliid frogs. In neither of three African reedfrogs, *Hyperolius igbettensis*, *Hyperolius nitidulus*, and *H. marmoratus*, larger body length or mass predicted the mating success of males (Dyson et al. 1992, Lampert & Linsenmair 2002, Rödel et al. 2006).

There is no indication that females of *H. tricolor* do gain either direct or indirect fitness benefits when mating with large males. Actually mating with large males in a densely vegetated pond could even be disadvantageous if the female's "agility under water during egg deposition is lower when carrying a larger male, and therefore, the dense water vegetation and high density of predators possibly make female agility a limiting factor in mate choice" (Rödel et al. 2006). Accordingly, other (costly) male characteristics might be more decisive for a female's choice, e.g., size-independent call parameters. In African hyperoliids, mainly in *Hyperolius marmoratus*, sound pressure (Bishop et al. 1995), (low) frequency (Dyson & Passmore 1988, Jennions et al. 1995), or call-related environmental factors (Backwell & Passmore 1990) have become known to be important for mate choice. Calling, and some call parameters, in hyperoliid frogs is dependent on the condition of the individual (Docherty et al. 1990). Oxygen consumption in e.g., *H. marmoratus* is up to 15 times higher while calling than resting (Grafe 1996), and energetic constraints are responsible for much of the natural variation in male calling behavior in hyperoliid frogs (Dyson et al. 1992). However, this hypothesis will remain elusive as we do not have data on calling activity and energy demands of male *H. tricolor*. Alternatively, male reproductive success might be solely a function of the time (i.e., number of nights) of individual males spend at the breeding pond, similar to *H. marmoratus* (Dyson et al. 1992). This hypothesis is not exclusive to all other hypotheses but needs further testing. Also, our study provided no data concerning possible satellite behaviour of male frogs, known from some anurans including hyperoliids (*Afrixalus delicatus*, Backwell & Passmore 1991).

The presence of a prominent and often colorful and visual vocal sac gland in hyperoliid frogs (Drewes 1984), including *Heterixalus* spp., indicates that visual and/or chemical signals may play a further role in this breeding system. These glands produce species-specific cocktails of volatile chemicals, and it is suggested that reed frogs use these chemicals as signals in species recognition and mate choice (Starnberger et al. 2013, 2014a, b, Menke et al. 2016). We agree with Starnberger et al. (2014a, b) that hyperoliid

frogs possibly use a combination of acoustic, visual and chemical cues in species recognition and mate choice. This study shows that frog size plays no important role.

We consider it likely that a high predation pressure at the breeding pond influences the mate choice behaviour of females. Our observations suggest that the predation pressure of primarily spiders (Pisauridae) (compare Babangenge et al. 2019), but also of snakes (mainly *Madagascarophis colubrinus*), terrapins (*Pelomedusa subrufa*), and insects (mainly giant water bugs, Belostomatidae) on *Heterixalus* is very high. This might select for a reduction in search time and might explain that we found no evidence of females selecting males for their size which is a character known to be important in other frog species.

It is striking that many behaviours in the context of mating systems are consistent within the family Hyperoliidae but differ from other anuran groups, such as size-independent mating success and a lek-like mating system. These behaviours might be consequences of typical mating characters of hyperoliid frogs. The fact that we found no size-assortative mating, for example, might be explained by the small size of egg clumps that are deposited by *H. tricolor*. Accordingly, we observed that amplectant *H. tricolor* couples divide clutches into separate egg clumps that are distributed and attached to separate structures within the pond (e.g., reed grass stems or water lily leaves). Therefore, males of all sizes might be able to successfully fertilize a high percentage of eggs when only a few eggs are laid at the same time. However, so far it remains unclear what the ecological and evolutionary drivers are that led to the mating system in hyperoliid frogs, emphasizing the need for further in-depth studies on the ecology and natural history of this fascinating group of frogs.

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