



# Larger is not better: no mate preference by European common frog (*Rana temporaria*) males

Carolyn Dittrich<sup>a,b,\*</sup>, Melanie Tietje<sup>c</sup> and Mark-Oliver Rödel<sup>a,b</sup>

<sup>a</sup> Museum für Naturkunde Berlin, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, 10115 Berlin, Germany

<sup>b</sup> Berlin–Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

<sup>c</sup> Department of Biology, Aarhus University, Ny Munkegade 116, 8000 Aarhus C, Denmark

\*Corresponding author's e-mail address: carolin.dittrich.biol@gmail.com

ORCID iDs: Dittrich: 0000-0002-4447-4481; Tietje: 0000-0003-1157-2963;

Rödel: 0000-0002-1666-195X

Received 30 October 2021; initial decision 24 January 2022; revised 2 April 2022;  
accepted 26 April 2022; published online 17 May 2022

---

## Abstract

In explosive breeding frogs, high intrasexual competition between males leads to a sexual coercion ruled mating system, where males presumably evolved preferences for specific female traits. We tested these preferences in the European Common Frog by excluding intrasexual competition. We hypothesized that all males show preferences towards larger female body size, due to higher fecundity. Our results did not show any preference considering female body size, neither in the attempt to amplex a female nor during the formation of pairs. Additionally, we witnessed a high failure rate of male mating attempts, which hints at high mating costs and offers an explanation for the lack of preferences in males. Nonetheless, we observed a non-random mating pattern in successfully formed pairs, where in the absence of size dimorphism females were on average larger than males. This indicates a different mechanism for selection which is independent from male mating preference or scramble competition.

## Keywords

sexual selection, mating behaviour, mate preference, anura.

## 1. Introduction

Studies addressing the theory of sexual selection revealed that females are the choosy sex in most species (Janetos, 1980; Ryan & Keddy-Hector, 1992;

Paul, 2002; Edward & Chapman, 2011). Here, choosiness is defined as an individual's active effort to invest energy and time to assess potential mates, whereas preference is defined as an intrinsic, passive attractiveness towards specific honest traits that indicate high quality of the opposite sex (Jennions & Petrie, 1997; Cotton et al., 2006). Preferences can enhance the evolution of different mating strategies and tactics to increase reproductive output with behavioural plasticity; depending on sex, age, physiological state or operational sex ratio (Parker, 1982; Gross, 1996). However, female preferences can be overridden by dominant intrasexual competition in males (Qvarnström & Forsgren, 1998; Formica et al., 2016), i.e., male–male competition leading to a higher mating advantage of dominant males, regardless of female preference of traits that are unrelated to dominance.

Nevertheless, males are choosy too, if (1) mate availability is high and simultaneous sampling possible (Barry & Kokko, 2010), (2) there is variation in female quality/fecundity (Krupa, 1995; Johnstone et al., 1996), and (3) the benefits of choosing between females are higher than the costs associated with assessing females (Edward & Chapman, 2011, and references therein). Two prerequisites for males choosiness are the males' ability to detect differences between the females and a preference for particular traits. One of these traits is body size which is an indicator for longevity mediated by good genes and could be heritable (Kokko & Lindström, 1996; Møller & Alatalo, 1999). However, body size is based on a variety of genes and environmental processes which might obscure honesty of the trait, but large body size definitely indicates higher fecundity (Peters, 1986; Shine, 1988; Nali et al., 2014). Mating with a larger female thus should increase a male's individual fitness. A male's choice, however, should be based on an honest signal that indicates high quality of a female, as choice will be impacted by trade-offs concerning the costs for mating chances with a high quality female, and thus individual males indeed may follow very different strategies to access females. Some examples of male alternative tactics are satellite males, usually being smaller than their competitors (Arak, 1983; Halliday & Tejedo, 1995), mate-guarding (Parker, 1974), prudent mate choice (Fawcett & Johnstone, 2003; Härdling & Kokko, 2005), clutch piracy (Vieites et al., 2004) or even functional necrophilia (Izzo et al., 2012).

Mating systems in amphibians are diverse, and apart from environmental parameters, mostly depend on female availability over time (Wells, 2007). In species with a short breeding period (explosive breeders) males are actively

searching for mates and engage in direct male–male competition over the arriving females. Explosive breeding is characterized by an almost equal operational sex ratio, synchronized receptiveness of females and low sexual selection (Emlen & Oring, 1977). In theory all males are able to mate and reproduce, but larger/more dominant males have an advantage to access and dominate receptive females during scramble competition leading to a variation in male mating success (Berven, 1981; Olson et al., 1986; Höglund, 1989; Vagi & Hettyey, 2016). Therefore, some males are considered to sexually dominate the females in explosive breeding systems, leaving little room for male and female mate choice if the cost for mate sampling are too high (Dechaume-Moncharmont et al., 2016). Nevertheless, male mate preferences could have evolved in explosive breeders, because female fecundity highly depends on female body size in most anuran species (Krupa, 1995; Nali et al., 2014). All males should prefer larger high-quality females to increase their own fitness according to adaptation theory, but preferences could be obscured by high intrasexual competition. High intrasexual competition between males to gain access to females, could lead to changes in preferences, e.g. dominant more successful males will influence the preference for potentially high-quality females of smaller males, as described with the concept of ‘prudent choice’ (Härdling & Kokko, 2005). On the other hand, costs associated with mate choice depend on male density and the frequency of different mating tactics within a breeding aggregation (Arak, 1983; Höglund & Robertson, 1988), as well as male’s individual predation risk (Magnhagen, 1991; Bernal et al., 2007), all factors which may vary even during a short breeding season (Olson et al., 1986; Vojar et al., 2015).

In this study, we investigate the mating preference of the European Common Frog (*Rana temporaria*) because it is an excellent example of an explosive breeder with high male–male competition. Although former studies suggest a lack of male mate preferences in this species (Elmberg, 1991), we observed non-random mating by body size (size-assortative mating) and found indications of male mate preference for larger females and different mating tactics in former experiments (Dittrich et al., 2018). Larger females were paired more frequently than smaller females, while smaller males showed a different mating approach by being faster in accessing females (Dittrich et al., 2018). Those findings are contrary to the theory that sexual selection is low in explosive breeders and that preferences for high mate quality traits should be negligible. Therefore, we tested if males show a

preference towards high-quality females in the absence of male–male competition. Here, we hypothesized that males will prefer larger females independent of their own body size, when intrasexual male–male competition is absent and males are presented to differently sized females. We predict small males to be faster in attempting to amplex a female to increase their chances to keep an exclusive access to the female during possible scramble competition.

## 2. Methods

### 2.1. Study area and species

The European Common Frog (*Rana temporaria* Linnaeus, 1758) is an explosive breeder that forms dense breeding aggregations in early spring (Gollmann et al., 2014). The males engage in scramble competition over temporally available receptive females (Savage, 1961). Here, larger males have an advantage in direct combat (Arak, 1983), and small males may apply a different mating tactic by being faster in amplexing females (Dittrich et al., 2018). The species exhibits sexual size dimorphism, where females are mostly larger in body size than males (Geisselmann et al., 1971; Elmberg, 1987), however this can vary between populations (Vojar et al., 2015; Dittrich et al., 2018). We did not observe any size dimorphism in our study population (Welsh two-sample *t*-test;  $t = -0.24$ ,  $df = 100.6$ ,  $p = 0.81$ ).

We carried out fieldwork in southern Germany, near the village of Fabrikschleichach in Lower Franconia, Bavaria (49.924°N, 10.555°E, WGS 84). This area comprises roughly 140 ponds, of which *R. temporaria* uses between 35–40 ponds for reproduction annually. In 2019 we fenced the four ponds with the largest known breeding aggregations for the entire reproductive period (14–28 March). The fence consisted of plastic gauze (mesh size 2 mm, approx. height 60 cm) stretched between wooden poles and was monitored twice a day (morning and evening).

We collected individuals that sat at the fence or were on their way to the breeding pond, preferably collecting singles to minimize differences in reproductive status. Amplexed females could potentially be affected by the application of amplexin, which was found in gland tissue under the nuptial pads of male *R. temporaria*. This is a protein similar to the plethodontid modulating factor, a pheromone that influences courtship duration in salamanders (Willaert et al., 2013). So far, it is unknown if male *R. temporaria*

are able to detect differences in the female's reproductive status (Thomas, 2011). To account for potential amplexin interaction effects we recorded if individuals were encountered as singles or in pairs and tested if the former status influences preference behaviour of males.

All individuals were sexed in situ (males show characteristic dark nuptial pads during the reproductive period). We measured snout–vent length (SVL in mm) using a calliper (to the closest 0.5 mm), and mass using a spring scale (1–100 g, 1 g increments). For transport, we placed each individual singly in an opaque, 1 l volume plastic bucket with lid, which contained leaf litter to hide and a thin layer of water to prevent desiccation. The animals were kept in these buckets in the barn of the ecological field station in Fabrikschleichach (temperatures only marginally higher than at the breeding sites) until the start of the behavioural experiments, which started within 12 h after collection. Although this handling could cause stress, studies in Cane Toads, *Rhinella marina*, showed that stress levels will decrease after 8 h and with low temperatures (Narayan et al., 2012a,b). All individuals were released at their respective capture locations after completion of the experiment.

## 2.2. Behavioural experiment

We tested the hypothesis that males prefer the largest female in the absence of intrasexual competition with a mate choice test, by placing two females of different body sizes in the same container with a single male. We categorized body sizes to allocate individuals to respective experimental trials, for the analyses we used the continuous measurements. The size difference between females in each trial exceeded 9 mm, with small females SVL being below 70 mm ( $N = 48$ , range = 48–70 mm, mean  $\pm$  SD =  $63.0 \pm 5.7$  mm), and large females SVL over 71 mm ( $N = 48$ , range = 71–89 mm, mean  $\pm$  SD =  $77.3 \pm 4.4$  mm). In the containers, either a small male ( $N = 23$ , SVL range = 56–70 mm, mean  $\pm$  SD =  $63.8 \pm 4.5$  mm) or a large male ( $N = 25$ , SVL range = 71–89 mm, mean  $\pm$  SD =  $76.6 \pm 5.5$  mm) were introduced. The allocation of individuals in the experimental trials was random, except the premises of a minimum of 9 mm size difference between the females.

The experimental trials were conducted in plastic containers (40 × 60 × 40 cm), filled with 10 litres of rainwater (5 cm water depth). The species can form amplexus terrestrially, during the migration towards the pond in the terrestrial habitat, as well as within the aquatic habitat in the pond. The 5 cm water depth was chosen to match the depth of the edge of the pond, where

we continuously observed couples in amplexus. Although clutches are also laid in deeper water, we kept the water level low to not stress the individuals with the probability of drowning which can be regularly observed in mating balls in the field (*R. temporaria* own observation; other explosive breeders: Davies & Halliday, 1979; Trauth et al., 2000). Before starting the experiment, a non-transparent plastic sheet separated the male from both females. We let the animals acclimatize in the container for 10 min, then removed the plastic sheet and started the experiment. A web camera (Logitech C920) placed at 1.5 m height above the plastic containers recorded each experimental trial for one hour, even if amplexus was formed earlier.

Before starting a new trial, we cleaned the respective container and changed the water completely to minimize the risk of potential effects from residual chemical cues. Each animal was tested only once to reduce any effects of change in motivation or influence of pheromones (Willaert et al., 2013). If successful amplexus did not occur within the one hour experimental time, the trial was terminated. In none of the trials spawning occurred.

We defined several variables that were recorded and analysed: when and towards which female the male attempted to clasp first, the number of successful and failed clasping attempts on each female, and with which female successful amplexus occurred at the end of the experiment. The term attempt is defined by an active, directional, target-oriented movement towards a specific female and trying to clasp her. It does not apply if animals are randomly bumping into each other while exploring the box.

### 2.3. Statistical analyses

The aim of the study was to test if males show a preference for larger females. First we tested with a Chi-square test if former pairing had an effect on the formation of amplexus. We used a logistic regression model to test if body size of individuals and number of total attempts of a male (proxy for effort) influence the formation of amplexus (successful amplexus as binomial response variable). Confounding factors like day of the breeding season, time of the day or temperature did not show effects on amplexus success and therefore were not used in further analyses. We used Pearson correlation to check if number of total attempts correlates with male or female body sizes, as well as the body size difference between females. We run a linear model to test the influence of male and female body sizes on time till first attempt. Additionally, we tested for size-assortment in the pairs with a Pearson correlation and calculated the hypothetical Pearson correlation coefficients if the

males would always choose the large female or the small female, respectively.

We built a null model to assess the average observed correlation between male and female body size if choice was completely random. To do so, we simulated a random choice by the male for one of the females per trial and calculated Pearson correlation for 1000 iterations. This null distribution was used to compare our observed Pearson correlation coefficient of attempted and amplexed pairs with the mean and standard deviation of the bootstrapped null-model. We used the  $z$ -score as a standardized effect size. The same approach was used to investigate the body size difference between the approached female and the respective male and within successfully formed pairs. The body size difference was calculated as SVL of the female minus SVL of the male. For the null-model distribution, we calculated 1000 size differences between the male and a randomly chosen female in the experimental trial. We then calculated the mean size difference for attempted pairs and for pairs in amplexus. The observed data were compared to the mean and standard deviation of the null-model. The deviation from the null-model was significant with a  $p$ -value  $\leq 0.05$  when the  $z$ -score of observed values was above 1.96 or below  $-1.96$ . For all analysis and graphs we used the R statistical environment (R Core Team, 2020, version 3.6.3). We used the packages *car* (Fox & Weisberg, 2019) for model validation (variance inflation factor), *effects* (Fox & Weisberg, 2019) for effect plots of models, *ggplot2* (Wickham, 2016) for drawing graphs, *MuMIn* (Bartoń, 2019) to calculate a coefficient of determination for the logistic regression model based on the likelihood-ratio test, and *plyr* (Wickham, 2011) to count number of occurrences.

#### 2.4. Ethics approval

The government from Lower Franconia issued research permits (55.2 DMS 2532-2-316) and the Bavarian state forestry department provided access to the forest ponds. All animal behavioural experiments followed the guidelines provided by ASAB.

### 3. Results

We found no influence of female and male status (caught as a single or in amplexus) on amplexus during the experimental trials. The proportion of

**Table 1.**  
Detailed results of the logistic regression model ( $\text{glm}(\text{success}(0/1) \sim \text{SVL male} + \text{SVL female 1} + \text{SVL female 2} + \text{total attempts})$ ), with coefficient, estimate, standard error (SE),  $z$ -value and  $p$ -value.

Coefficient	Estimate	SE	$z$	$p$
Intercept	2.33217	5.92414	0.394	0.69
SVL male	−0.01517	0.04754	−0.319	0.75
SVL female 1	−0.08924	0.08924	−0.955	0.34
SVL female 2	−0.06741	0.11717	0.575	0.57
Number of total attempts of a male	−0.07094	0.07730	−0.918	0.36

individuals being in amplexus was not significantly different between single females and paired females ( $\chi^2 = 0.05$ ,  $\text{df} = 1$ ,  $p = 0.83$ ). The same was observed for the males ( $\chi^2 = 0.17$ ,  $\text{df} = 1$ ,  $p = 0.68$ ). Therefore, we pooled the data.

During the 48 trials, a total of 31 males did attempt both females during the one hour experimental run (65%), 15 males did attempt only one of the females (31%), and two males did not attempt any female (4%). In total, 32 trials ended in the formation of pairs; 16 trials were terminated without formation of pairs after one hour. We observed a high failure rate in clasping a female. In total, males approached females 255 times and failed to clasp them in 179 cases (70.2%). We also observed several cases of female avoidance behaviour; in five trials, males failed to clasp a female because she swam or jumped away. In nine cases, males were successful in amplexing a female, but females escaped the male grip. This led to the final  $N$  of 32 pairs that successfully formed. This formation was not influenced by male or female body sizes, nor by the total number of attempts by a male (glm details in Table 1).

The number of total attempts per male, our proxy for the effort invested, was not influenced by being paired before the experiment (Welsh two-sample  $t$ -test,  $t = -0.41$ ,  $p = 0.69$ ), nor did it correlate with male body size (Pearson correlation,  $r = 0.13$ ,  $\text{df} = 46$ ,  $p = 0.37$ ), female body sizes (Pearson correlation; female one,  $r = 0.05$ ,  $\text{df} = 44$ ,  $p = 0.77$ ; female two,  $r = 0.14$ ,  $\text{df} = 44$ ,  $p = 0.34$ ) or the size difference between females (Pearson correlation,  $r = 0.10$ ,  $\text{df} = 44$ ,  $p = 0.53$ ).

The time till first attempt of a male towards one of the females, was not influenced by male body size or female body sizes (linear model details in



**Table 2.**

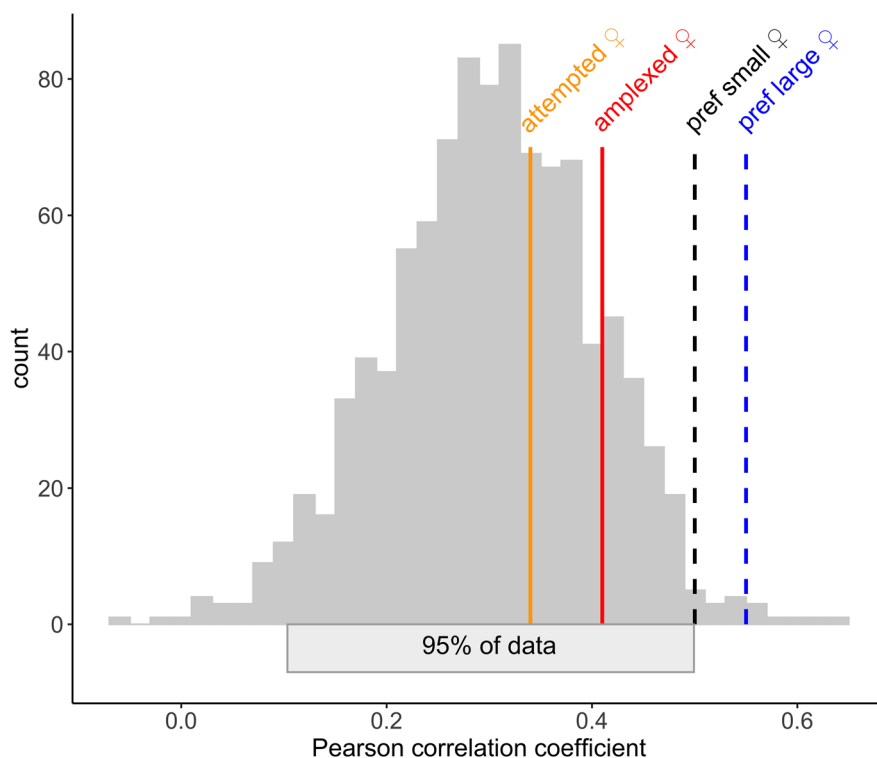
Detailed results of the linear regression model ( $\text{lm}(\text{time till first attempt}) \sim \text{SVL male} + \text{SVL female 1} + \text{SVL female 2}$ ), with coefficient, estimate, standard error (SE),  $z$ -value and  $p$ -value.

Coefficient	Estimate	SE	$z$	$p$
Intercept	-19.5897	30.3000	-0.647	0.52
SVL male	0.3278	0.2527	1.297	0.20
SVL female 1	-0.3558	0.4457	-0.798	0.43
SVL female 2	0.3790	0.5966	0.635	0.53

Table 2). These variables could only explain 7% of the variation observed ( $R^2 = 0.07$ ).

We observed a correlation of body sizes for final pairs in amplexus (Pearson correlation,  $r = 0.41$ ,  $df = 30$ ,  $p = 0.02$ ), and also with the first female that was attempted (Pearson correlation,  $r = 0.34$ ,  $df = 44$ ,  $p = 0.02$ ). Hypothetical preferences would be strongly correlated in body sizes between individuals in a pair (Pearson correlation; large female,  $r = 0.55$ ,  $df = 46$ ,  $p < 0.001$ ; small female,  $r = 0.50$ ,  $df = 46$ ,  $p < 0.001$ ). The null-model showed a mean correlation coefficient of 0.3 and a standard deviation of 0.1 ( $N = 1000$ ). Our observed correlations were not different from this random null-model; attempted female,  $z$ -score = 0.40; amplexed females,  $z$ -score = 1.12, but a preference for one of the females would have been non-random. (Figure 1).

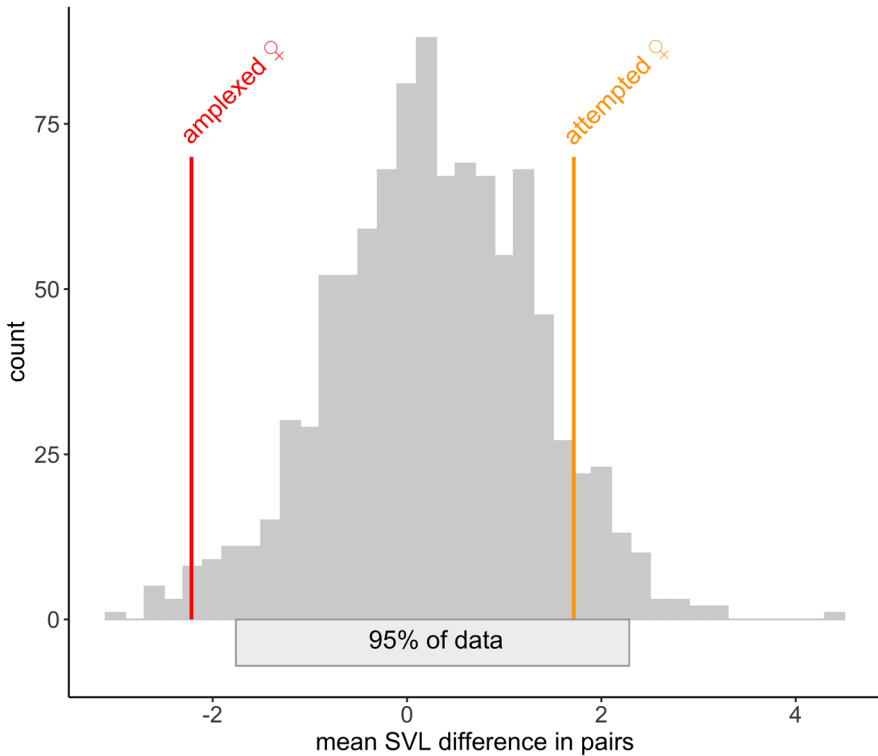
In amplexed pairs the female was on average larger than the male ( $N = 32$ , mean  $\pm$  SD =  $-2.22 \pm 8.42$  mm). Contrary to this observation, the female that was attempted first was on average smaller than the male ( $N = 46$ , mean  $\pm$  SD =  $1.72 \pm 9.99$  mm). The normal distribution of a bootstrapped null-model had a mean of 0.26 mm size difference between pairs and a standard deviation of 1.03 mm ( $N = 1000$ ), if pairs were formed randomly. The size difference of males and attempted females resembled a random value according to the  $z$ -score ( $z$ -score = 1.41; 93% of values smaller than observed), but the size difference of pairs in amplexus indicated a non-random value ( $z$ -score =  $-2.41$ , 99.2% of values larger than observed, Figure 2). The size difference was larger than expected from the null model and females were larger than males, although there was no size dimorphism observed in the sampled population and we did not find any indication for male mate choice or preference.



**Figure 1.** Null-model distribution of the Pearson correlation coefficient if pairing would be random in the 48 *Rana temporaria* pairs (1000 iterations of picking one of the presented females within an experimental trial randomly). The orange line depicts the observed Pearson correlation coefficient of males and the first attempted female ( $z$ -score = 0.4), the red line depicts the observed Pearson correlation coefficient of the pairs in amplexus ( $z$ -score = 1.1). The dashed black line shows the expected Pearson correlation coefficient if males would always pick the smaller female (pref small female) and the dashed blue line the expected Pearson correlation coefficient if males would always pick the large females (pref large female). The grey box underneath shows the 95% data interval. The  $z$ -scores of our observed data are within the boundaries of the 1.96 standard deviations from the mean value and thus random. Histogram bandwidth = 0.02.

#### 4. Discussion

Contrary to our expectations, *Rana temporaria* males did not show a preference for larger, more fecund females and seemed to randomly attempt and amplex females. Our results support findings by Elmberg (1991), who also observes no male mate preference for larger body size in *R. temporaria*.



**Figure 2.** Null-model distribution of mean SVL difference in mm if pairing would be random in the 48 *Rana temporaria* pairs (1000 iterations of picking one of the presented females within an experiment). The orange line depicts the observed mean SVL difference of males and the first attempted female ( $z$ -score = 1.4), the red line depicts the mean SVL difference for the pairs in amplexus ( $z$ -score = -2.4). The grey box underneath shows the 95% data interval. The  $z$ -score of the pairs in amplexus is larger than -1.96 standard deviations from the mean of the null model and thus indicates non-random pairing considering body size differences of pairs. Histogram bandwidth = 0.2 mm.

The evolutionary prerequisites of mate choice may explain the lack of preference for specific traits, in our study female body size. Body size alone is unlikely to be a trait under sexual selection in anurans, because it is age and resource dependent (Halliday & Verrell, 1988; Lodé et al., 2004), hence has a low heritability and cannot be considered a true sexual secondary trait that provides an honest signal concerning mate quality. However, larger body size could be an indirect indicator for good genes (Kokko & Lindström, 1996; Møller & Alatalo, 1999), as larger females could be better survivors and foragers. Additionally, some individuals might have an intrinsic higher

juvenile growth rate which could be passed on to their progeny (Halliday & Verrell, 1988), making them more attractive for mates (high juvenile growth enhances survival probabilities). It also has been shown that female body size is highly correlated with fecundity (Nali et al., 2014; Dittrich et al., 2018) and this alone would be an honest signal for higher reproductive output. Nevertheless, evidence of heritability and reliability of these traits are scarce (Hettley et al., 2010).

The high clasping failure rate and time constraints during the mating season make mate choice by males unlikely. A very surprising result of our study revealed that 70% of all male attempts to clasp a female failed. A high failure rate when attempting to clasp a female should favour non-choosiness in males, due to the evolutionary cost of failing to reproduce in a given season (Krupa, 1995; Fawcett & Johnstone, 2003; Dechaume-Moncharmont et al., 2016). Time constraints can be an important factor in the evolution of mate choice strategies (Sullivan, 1994), and time is a limiting factor in explosive breeding species such as the European Common Frog. The breeding duration highly depends on weather conditions and the time frame varies considerably between populations and locations, from a couple of days to more than two weeks (Dittrich et al., 2018). The assumptions on the evolution of mate choice and the consequences of operational sex ratio between explosive versus prolonged breeding are just ends of a continuum (Wells, 1977), and mating strategies could vary accordingly with the length of the breeding period. Indeed explosive breeders have been reported to exhibit high intraspecific variability of mating patterns between and within population, i.e., with respect to large male advantage, different mating tactics and size-assortment, due to high variability in mate availability, as well as intra-sexual competition and environmental conditions (Olson et al., 1986; Vieites et al., 2004; Vojar et al., 2015; Dittrich et al., 2018). Male mate choice as well as its absence was found in various studies addressing the same species, e.g., male mate choice detected: *Bufo bufo* (Arntzen, 1999), *Rana sylvatica* (Berven, 1991; Swierk & Langkilde, 2019, 2021), no male mate choice detected: *B. bufo* (Höglund & Robertson, 1987; Marco & Lizana, 2002), *R. sylvatica* (Howard & Kluge, 1995). Therefore, the system of explosive, scrambling breeders seems to be context dependent which makes generalization almost impossible.

Male European Common Frogs usually arrive earlier at breeding ponds than the females and stay longer than the females (Savage, 1961; Geisselmann et al., 1971). In this system male mating success is positively correlated

with the amount of time spent at breeding sites (Woodward, 1982). However, if males spend too much time with selecting particular females or amplexing/defending a non-receptive female, males' chances to reproduce in a given year decrease over time. Thus, males should minimize female selection time in order to increase the probability to reproduce in a given year and in the best case, reproduce more than once.

Here, we present other explanations than trait preference for the observed size assortment in our study. Although, we could not detect preference of larger females, yet females in amplexus were on average larger than the males. The null-model indicated that pairs should be of similar size, if pair formation would be random. We therefore conclude that a selective mechanisms other than male competition and male mate preferences is responsible for the observed size assortment pattern.

Sexual size dimorphism can be observed in most anuran species, where females grow larger than males, but males reach maturity earlier so that sexual size dimorphisms depends more on population demography and less on sexual selection (Monnet & Cherry, 2002). We did not observe size dimorphism in our study population, hence ruling out size dimorphism as the mechanism responsible for the observed size assortative mating pattern.

The proximate mechanism behind larger females in amplexus could be mechanical and independent from male preferences. If females are smaller than the amplexing male, males may not be able to hold them tight enough to maintain amplexus. In Cane Toads (*Rhinella marina*) it was shown that males with shorter arms could cling better to females compared to males with longer arms, the latter being replaced more often as they could not hold the females properly (Clarke et al., 2019). However, in the Woodfrog (*Rana sylvatica*), a species morphologically and ecologically very similar to the European Common Frog, longer arm length was beneficial to maintain amplexus during scramble competition (Howard & Kluge, 1985). We found that females showed avoidance behaviour which led to the high failure rate in amplexus. This behaviour included the turning of females' bodies to escape the male clasp and the release of calls by the female (Dittrich & Rödel, 2020). This behaviour will be described and discussed in another publication in more detail. If females start to turn their bodies in order to escape the male, the mechanical force of amplexus would depend on males' arm length. Therefore, a specific size ratio would be beneficial to stay amplexed.

We tested one aspect of mate preferences, however preferences are often based on multiple cues like body size plus coloration, call characteristics, chemical cues and/or genetic incompatibility (Engeler & Reyer, 2001; Taylor et al., 2007; Willaert et al., 2013; Starnberger et al., 2014; Bossuyt et al., 2019), which could not be tested in this study, but which might offer another explanation for the observed size assortment.

In conclusion, we showed that male European Common Frogs do not prefer larger females and seem to mate randomly in regard to female body size. However, there is a non-random mating pattern of males being in amplexus with larger females, which indicates other selective mechanisms independent from male mate preferences or male–male competition. Other selective forces which shape the observed mating pattern could include mechanical force transmission due to the ratio of male to female body size and the capability of the male to hold the female. Future studies might provide a more detailed view onto the alternative explanations of the complex patterns of size assortative mating in amphibians.

## Acknowledgements

We thank the government from Lower Franconia for research permits and the Bavarian state forestry department in Ebrach for access permission to the forest ponds. The staff of the ecological field station, University of Würzburg, provided access to crucial infrastructure, which is highly appreciated. We thank Jurek Ritz for his help analysing the video material and Sami Asad for proof reading concerning English grammar and style. Additionally, we thank two anonymous reviewers for their helpful comments which are highly appreciated and improved the quality of the manuscript. Carolin Ditttrich received a PhD scholarship from the Elsa–Neumann Foundation from the state of Berlin, Germany. The datasets generated and analysed during the current study, including the R script, are available at the Museum für Naturkunde repository, doi: 10.7479/zpnq-pj77.

## References

- Arak, A. (1983). Male–male competition and mate choice in anuran amphibians. — In: Mate choice (Bateson, P., ed.). Cambridge University Press, Cambridge, p. 181–210.
- Arntzen, J.W. (1999). Sexual selection and male mate choice in the common toad, *Bufo bufo*. — Ethol. Ecol. Evol. 11: 407–414.

- Barry, K.L. & Kokko, H. (2010). Male mate choice: why sequential choice can make its evolution difficult. — *Anim. Behav.* 80: 163-169.
- Bartoń, K. (2019). MuMIn: Multi-Model Inference. — R package version 1.43.15. Available online at <https://CRAN.R-project.org/package=MuMIn>.
- Bernal, X.E., Rage, R.A., Rand, A.S. & Ryan, M.J. (2007). Cues for eavesdroppers: do frog calls indicate prey density and quality? — *Am. Nat.* 169: 409-415.
- Berven, K.A. (1981). Mate choice in the wood frog, *Rana sylvatica*. — *Evolution* 35: 707-722.
- Bossuyt, F., Schulte, L.M., Maex, M., Janssenswillen, S., Novikova, P.Y., Biju, S.D., Van de Peer, Y., Matthijs, S., Roelants, K., Martel, A. & Van Bocxlaer, I. (2019). Multiple independent recruitment of sodefrin precursor-like factors in anuran sexually dimorphic glands. — *Mol. Biol. Evol.* 36: 1921-1930.
- Clarke, G.S., Shine, R. & Phillips, B.L. (2019). May the (selective) force be with you: spatial sorting and natural selection exert opposing forces on limb length in an invasive amphibian. — *J. Evol. Biol.* 32: 994-1001.
- Cotton, S., Small, J. & Pomiankowski, A. (2006). Sexual selection and condition-dependent mate preference. — *Curr. Biol.* 16: R755-R765.
- Davies, N.B. & Halliday, T.R. (1979). Competitive mate searching in male common toads, *Bufo bufo*. — *Anim. Behav.* 27: 1253-1267.
- Dechaume-Moncharmont, F.X., Brom, T. & Cézilly, F. (2016). Opportunity costs resulting from scramble competition within the choosy sex severely impair mate choosiness. — *Anim. Behav.* 114: 249-260.
- Dittrich, C., Rodríguez, A., Segev, O., Drakulić, S., Feldhaar, H., Vences, M. & Rödel, M.O. (2018). Temporal migration patterns and mating tactics influence size-assortative mating in *Rana temporaria*. — *Behav. Ecol.* 29: 418-428.
- Dittrich, C. & Rödel, M.O. (2020). Description of female release calls of the European common frog, *Rana temporaria* (Anura: Ranidae). — *Salamandra* 56: 91-94.
- Edward, D.A. & Chapman, T. (2011). The evolution and significance of male mate choice. — *Trends Ecol. Evol.* 26: 647-654.
- Elmberg, J. (1987). Random mating in a boreal population of European common frogs *Rana temporaria*. — *Holarct. Ecol.* 10: 193-195.
- Elmberg, J. (1991). Factors affecting male yearly mating success in the common frog, *Rana temporaria*. — *Behav. Ecol. Sociobiol.* 28: 125-131.
- Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. — *Science* 197: 215-223.
- Engeler, B. & Reyer, H.-U. (2001). Choosy females and indiscriminate males: mate choice in mixed populations of sexual and hybridogenetic water frogs (*Rana lessonae*, *Rana esculenta*). — *Behav. Ecol.* 12: 600-606.
- Fawcett, T.W. & Johnstone, R.A. (2003). Mate choice in the face of costly competition. — *Behav. Ecol.* 14: 771-779.
- Formica, V.A., Donald-Cannon, H. & Perkins-Taylor, I.E. (2016). Consistent patterns of male mate preference in the laboratory and field. — *Behav. Ecol. Sociobiol.* 70: 1805-1812.

- Fox, J. & Weisberg, S. (2019). An (R) companion to applied regression. — Sage, Thousand Oaks, CA.
- Geisselmann, R., Flindt, R. & Hemmer, H. (1971). Studien zur Biologie, Ökologie und Merkmalsvariabilität der beiden Braunfroscharten *Rana temporaria* L. und *Rana dalmatina* Bonaparte. — Zool. Jb. Abt. Syst. 98: 521-568.
- Gollmann, B., Borkin, L., Grossenbacher, K. & Weddeling, K. (2014). *Rana temporaria* Linnaeus 1758 — Grasfrosch. — In: Handbuch der Reptilien und Amphibien Europas, Vol. 5/IIIA: Froschlurche (Anura) IIIA, (Ranidae I) (Grossenbacher, K., ed.). Aula-Verlag, Wiebelsheim, p. 305-437.
- Gross, M.R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. — Trends Ecol. Evol. 11: 92-98.
- Halliday, T.R. & Tejedo, M. (1995). Intrasexual selection and alternative mating behaviour. — In: Amphibian Biology: vol. II: social behaviour (Heatwole, H. & Sullivan, B.K., eds). Surrey Beatty, Chipping Norton, p. 419-468.
- Halliday, T.R. & Verrell, P.A. (1988). Body size and age in amphibians and reptiles. — J. Herpetol. 22: 253-265.
- Härdling, R. & Kokko, H. (2005). The evolution of prudent choice. — Evol. Ecol. 7: 697-715.
- Hettyey, A., Hegyi, G., Puurtinen, M., Hoi, H., Török, J. & Penn, D.J. (2010). Mate choice for genetic benefits: time to put the pieces together. — Ethology 116: 1-9.
- Höglund, J. (1989). Pairing and spawning patterns in the common toad, *Bufo bufo*: the effects of sex ratios and the time available for male-male competition. — Anim. Behav. 38: 423-429.
- Höglund, J. & Robertson, J.G. (1987). Random mating by size in a population of common toads (*Bufo bufo*). — Amphibia-Reptilia 8: 321-330.
- Höglund, J. & Robertson, J.G. (1988). Chorusing behaviour, a density-dependent alternative mating strategy in male common toads (*Bufo bufo*). — Ethology 79: 324-332.
- Howard, R.D. & Kluge, A.G. (1985). Proximate mechanisms of sexual selection in wood frogs. — Evolution 39: 260-277.
- Izzo, T.J., Rodrigues, D.J., Menin, M., Lima, A.P. & Magnusson, W.E. (2012). Functional necrophilia: a profitable anuran reproductive strategy? — J. Nat. Hist. 46: 2961-2967.
- Janetos, A.C. (1980). Strategies of female mate choice: a theoretical analysis. — Behav. Ecol. Sociobiol. 7: 107-112.
- Jennions, M.D. & Petrie, M. (1997). Variation in mate choice and mating preferences: a review of causes and consequences. — Biol. Rev. 72: 283-327.
- Johnstone, R.A., Reynolds, J.D. & Deutsch, J.C. (1996). Mutual mate choice and sex differences in choosiness. — Evolution 50: 1382-1391.
- Kokko, H. & Lindström, J. (1996). Evolution of female preference for old mates. — Proc. Roy. Soc. Lond. B: Biol. Sci. 263: 1533-1538.
- Krupa, J.J. (1995). How likely is male mate choice among anurans? — Behaviour 132: 643-664.
- Lodé, T., Holveck, M.J., Lesbarrères, D. & Pagano, A. (2004). Sex-biased predation by polecats influences the mating systems of frogs. — Proc. R. Soc. Lond. B: Biol. Sci. 271: S399-S401.



- Magnhagen, C. (1991). Predation risk as a cost of reproduction. — Trends Ecol. Evol. 6: 183-186.
- Marco, A. & Lizana, M. (2002). The absence of species and sex recognition during mate search by male common toads, *Bufo bufo*. — Ethol. Ecol. Evol. 14: 1-8.
- Møller, A.P. & Alatalo, R.V. (1999). Good-genes effects in sexual selection. — Proc. Roy. Soc. Lond. B: Biol. Sci. 266: 85-91.
- Monnet, J.M. & Cherry, M.I. (2002). Sexual size dimorphism in anurans. — Proc. Roy. Soc. Lond. B: Biol. Sci. 269: 2301-2307.
- Nali, R.C., Zamudio, K.R., Haddad, C.F.B. & Prado, C.P.A. (2014). Size-dependent selective mechanisms on males and females and the evolution of sexual size dimorphism in frogs. — Am. Nat. 184: 727-740.
- Narayan, E.J., Cockrem, J.F. & Hero, J.M. (2012a). Effects of temperature on urinary corticosterone metabolite responses to short-term capture and handling stress in the cane toad (*Rhinella marina*). — Gen. Comp. Endocrinol. 178: 301-305.
- Narayan, E.J., Molinia, F.C., Cockrem, J.F. & Hero, J.M. (2012b). Individual variation and repeatability in urinary corticosterone metabolite responses to capture in the cane toad (*Rhinella marina*). — Gen. Comp. Endocrinol. 175: 284-289.
- Olson, D.H., Blaustein, A.R. & O'Hara, R.K. (1986). Mating pattern variability among western toad (*Bufo borealis*) populations. — Oecologia 70: 351-356.
- Parker, G.A. (1974). Courtship persistence and female-guarding as male time investment strategies. — Behaviour 48: 15-184.
- Parker, G.A. (1982). Phenotype-limited evolutionarily stable strategies. — In: Current problems in sociobiology (King's College Sociobiology Group, ed.). Cambridge University Press, Cambridge, p. 173-201.
- Paul, A. (2002). Sexual selection and mate choice. — Int. J. Primatol. 23: 877-904.
- Peters, R.H. (1986). The ecological implications of body size, Vol. 2. — Cambridge University Press, Cambridge.
- Qvarnström, A. & Forsgren, E. (1998). Should females prefer dominant males? — Trends Ecol. Evol. 13: 498-501.
- R Core Team (2020). R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, available online at <https://www.R-project.org/>.
- Ryan, M.J. & Keddy-Hector, A. (1992). Directional patterns of female mate choice and the role of sensory biases. — Am. Nat. 139: S4-S35.
- Savage, R.M. (1961). The ecology and life history of the common frog (*Rana temporaria temporaria*). — Sir Isaac Pitman and Sons, London.
- Shine, R. (1988). The evolution of large body size in females: a critique of Darwin's "fecundity advantage" model. — Am. Nat. 131: 124-131.
- Starnberger, I., Preininger, D. & Hödl, W. (2014). From uni- to multimodality: towards an integrative view on anuran communication. — J. Comp. Physiol. A 200: 777-787.
- Sullivan, M.S. (1994). Mate choice as an information gathering process under time constraint: implications for behaviour and signal design. — Anim. Behav. 47: 141-151.
- Swierk, L. & Langkilde, T. (2019). Fitness costs of mating with preferred females in a scramble mating system. — Behav. Ecol. 30: 658-665.

- Swierk, L. & Langkilde, T. (2021). Size-assortative mating in explosive breeders: a case study of adaptive male mate choice in anurans. — Behaviour 158: 849-868.
- Taylor, R.C., Buchanan, B.W. & Doherty, J.L. (2007). Sexual selection in the squirrel treefrog *Hyla squirella*: the role of multimodal cue assessment in female choice. — Anim. Behav. 74: 1753-1763.
- Thomas, M.L. (2011). Detection of female mating status using chemical signals and cues. — Biol. Rev. 86: 1-13.
- Trauth, S.E., McCallum, M.L. & Cartwright, M.E. (2000). Breeding mortality in the wood frog, *Rana sylvatica* (Anura: Ranidae), from northcentral Arkansas. — J. Ark. Acad. Sci. 54: 154-156.
- Vági, B. & Hettyey, A. (2016). Intraspecific and interspecific competition for mates: *Rana temporaria* males are effective satyrs of *Rana dalmatina* females. — Behav. Ecol. Socio-biol. 70: 1477-1484.
- Vieites, D.R., Nieto-Román, S., Barluenga, M., Palanca, A., Vences, M. & Meyer, A. (2004). Post-mating clutch piracy in an amphibian. — Nature 431: 305-308.
- Vojar, J., Chajma, P., Kopecký, O., Puš, V. & Šálek, M. (2015). The effect of sex ratio on size-assortative mating in two explosively breeding anurans. — Amphibia-Reptilia 36: 149-154.
- Wells, K.D. (1977). The social behaviour of anuran amphibians. — Anim. Behav. 25: 666-693.
- Wells, K.D. (2007). The ecology and behaviour of amphibians. — University of Chicago Press, Chicago, IL.
- Wickham, H. (2011). The split — apply — combine strategy for data analysis. — J. Stat. Softw. 40: 1-29.
- Wickham, H. (2016). ggplot2: elegant graphics for data analysis. — Springer, New York, NY.
- Willaert, B., Bossuyt, F., Janssenswillen, S., Adriaens, D., Baggerman, G., Matthijs, S., Pauwels, E., Proost, P., Raepsaet, A., Schoofs, L., Steegen, G., Treer, D., Van Hoorebeke, L., Vandebergh, W. & Van Bocxlaer, I. (2013). Frog nuptial pads secrete mating season-specific proteins related to salamander pheromones. — J. Exp. Biol. 216: 4139-4143.
- Woodward, B. (1982). Male persistence and mating success in Woodhouse's toad (*Bufo woodhousei*). — Ecology 63: 583-585.