Random size-assortative mating despite size-dependent fecundity in a Neotropical amphibian with explosive reproduction

Running title: Random mating in an explosive breeder

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Abstract
Sexual selection theory predicts that, when body size is correlated with fecundity, there should be fitness advantages for mate choice of the largest females. Moreover, because larger males are expected to monopolize the largest females, this should result in an assortative mating based on body size. Although such patterns could be expected in both explosive and prolonged breeders, non-assortative mating should be more widespread in species under time constraints. However, patterns of sexual selection are largely unexplored in explosive breeding species, and contrasting patterns have been found previously. We expect that the active choice of partners may be particularly risky when the time period during which sexual partners are available is severely limited. Therefore, to avoid missing an entire reproductive act, males and females should pair irrespective of traits, such as body size. We tested this hypothesis by investigating the mating patterns of the Pacific horned toad, *Ceratophrys stolzmanni*, a short-lived fossorial species inhabiting Neotropical dry forests. This species is particularly adequate to test our prediction because it reproduces explosively over the course of a single night per year. Although the number of eggs laid was proportional to the size of females, and individuals of both sexes showed variation in body size, there was no assortative mating based either on size, body condition or age of mates. Egg size was not influenced by either female size or clutch size. The larger body size of females compared to males is likely due to fecundity selection, i.e. the selective pressure that enhances reproductive output. Although we cannot dismiss the possibility that individuals could select their partners based on other criteria than those related to size or age, the results fit well our prediction, showing that the explosive breeding makes improbable an active choice of partners in both sexes and therefore favours a random mating pattern.

1 INTRODUCTION

Mate choice is one of the most important decisions that an individual has to make, potentially having a large impact on individual fitness and offspring survival (Kokko, Brooks, Jennions, & Morley, 2003; Wiley & Poston, 1996). The preferences for a particular phenotype in the potential mate are the result of trade-offs between direct and/or indirect benefits gained by mating selectively, and the costs of expressing such a mating bias (Edward, 2015; Kokko, Jennions, & Brooks, 2006). In many taxa, a larger body size is usually correlated with a greater reproductive output (Cunningham, Courage, & Quinn, 2013; Nali, Zamudio, Haddad, & Prado, 2014; Pincheira-Donoso & Tregenza, 2011) and better fitness in offspring (Ficetola & De Bernardi, 2009; Rollinson & Rowe, 2016), so sexual selection should favour the existence of non-random mating patterns with respect to the size of partners. Even when age is not correlated with size, there are indications that older individuals can represent a better mate choice because they have more experience in mate acquisition and reproductive success (Reading, 2001; Woodward, 1986). Moreover, the fact that an individual was able to survive longer might provide an indirect clue to its high genetic quality (Howard, Whiteman, & Schueller, 1994). As a result, in some species, reproductive success can be attributed to age rather than size (Felton, Alford, Felton, & Schwarzkopf, 2006).

Among ectotherms, anurans are particularly good models to study age and size-selective sexual selection because, in most species, males and females form amplecting pairs (Duellman & Trueb, 1994; Wells, 2010) and age can be assessed by skeletochronology (Sinsch, 2015). Female choosiness of their partners can improve the survival chances of their offspring through genetic effects (Woodward, Travis, & Mitchell, 1988), access to better spawning territory (Howard, 1978; Seidel, 1999), or directly through better paternal care (Böll & Linsenmair, 1998). Because female body size usually correlates with clutch size, males can also improve their fitness by choosing larger females (Liao & Lu, 2009; Marco, Kiesecker, Chivers, & Blaustein, 1998), especially in cases when paternal investment in a given reproductive event is high, e.g. when the male cares for offsprings (Bush, Dyson, & Halliday, 1996). On the other hand, an optimal ratio between the size of partners forming an amplexus can determine an increase in the percentage of fertilized eggs through a favourable juxtaposition of partners as well as resistance to displacement from competing males, so that it is advantageous for smaller individuals to choose smaller partners, resulting in a size selection of mates that are not necessarily the larger ones (Bastos & Haddad, 1996; Pfennig, 2000). As a result of the mentioned selective pressures, assortative mating based on body size is in many cases favoured (Chajma & Vojar, 2016; Hase & Shimada 2014).

Theoretical studies (Dechaume-Moncharmont, Brom, & Cézilly, 2016; McCauley et al., 2000), supported by empirical observations (Sullivan, 1989; Telford, Dyson, & Passmore, 1989), have shown that both the degree of choosiness and mate acquiring tactics are influenced by the duration of the breeding period, which in turn affects demographic parameters (e.g. density and operational sex-ratio), as well as energetic budgets. In species that breed over long periods of time, males usually tend to defend a territory and show aggressive displays towards other males or display a "lek" mating pattern, and are chosen by females on the basis of individual traits, such as call characteristics (Schwartz, Huth, & Hutchin, 2004; Wells, 2010). On the other hand, in "explosive breeders", reproduction takes place over a short period of time, when all individuals form dense aggregations (Sullivan, Ryan, & Verrell, 1995). It is frequent in these species that the observed mating system is based on scramble competition where males clasp indiscriminately any nearby potential partners (Lu, Ma, Li, & Fan, 2009), allowing few opportunities for females to choose their mates. However, even in explosive breeding species, larger males can in some cases be more competitive both at displacing smaller males from a formed pair, and at resisting dislodging attempts once they reach an amplexus (Bowcock, Brown, & Shine, 2013). Additionally, in both prolonged and explosive breeders, varied selective pressures can operate even before the sexes meet and copulate, causing an apparent absence of size-selectiveness during mating. In some cases, females could also benefit from mating with the first partner they meet, and this regardless of their size, because these males could control territories or call for a longer time (Ursprung et al., 2011; Meuche et al., 2013; Mangold, 2015).

Overall, there is a scarcity of empirical studies that investigate mating systems in species that reproduce explosively. This is particularly the case when breeding occurs during a single night, making multiple opportunities of mating during the same reproductive season improbable for both sexes (Brockmann, 1990). To investigate this topic, we carried out a field study on a tropical fossorial toad, the Pacific horned frog *Ceratophrys stolzmanni* (Anura: Ceratophyidae), that inhabits a xeric environment which imposes a very short breeding season both in terms of mating events' duration and water availability for tadpole development (Székely, Denoël, Székely, & Cogălniceanu, 2017). Moreover, this species is short-lived (Székely et al., in press), having few breeding opportunities during its lifetime. Our main hypothesis is that a direct mate selectivity may be risky for such a species, as this may result in a lack of reproduction over the whole year, and even individual life-time reproductive failure. We therefore expect that *C. stolzmanni* exhibits a random size and age-assortative mating. To this end, we tested the effects of body size, body condition, and age, all having been shown to affect reproductive success of mating pairs (Felton, Alford, Felton, & Schwarzkopf, 2006, Rausch et al., 2014). Moreover, because sexual and fecundity selection should favour a larger number of progenies, especially in unstable and risky environments such as the study area (Pianka, 1970, Colleoni et al., 2014), we expect that females should be larger than males, and that their body size should be correlated with their clutch size.

2 METHODS

2.1 Data collection

The study site is situated in Arenillas Ecological Reserve, El Oro province, southern Ecuador, described in detail in Székely et al. (2016, 2017). Field surveys were carried out during the rainy season – January through May – on two consecutive years: 2015 (38 fieldwork days) and 2016 (65 fieldwork days). The activity of the horned frogs was monitored along transects both during the day and during the night. The observations of mating behaviour were focused on a breeding pond with a surface of approximately 700 m^2 and a maximum water depth of 100 cm (03°33'36S, 80°08'19E, 40 m a.s.l.). Breeding events for the Pacific horned frog occurred on the 18th of March 2015 and the 8th of February 2016. The frogs avoided the densely vegetated areas of the pond and concentrated in a small area with shallow water, resulting in agglomerations of individuals. Animals were collected during the night, by hand, using Petzl Tikka XP-2 headlamps for observations.

In 2015, we collected a sample of 20 amplexed pairs, while in 2016 we collected 29, which represented all the pairs in amplexus that we encountered at the pond. The individuals in the pairs from both years were used to assess the existence of a size assortative mating pattern. The toads were measured (snout-vent length: SVL) using a Dial-Max calliper with 0.1 mm precision, and weighted (body mass: BM) using a My Weigh Triton T3 portable scale with 0.01 g precision. The males were recognized by the presence of secondary sexual characters, i.e. dark coloration on the throat and nuptial pads on forelimbs (Ron et al., 2016). Additionally, for the 20 amplecting pairs from the 2015 sampling, we clipped the third digit of the right forelimb from each individual, for skeletochronological estimation of age and batch-identification. Each toe was stored individually in microtubes filled with 96% ethanol. Measurements were done *in situ*, and, after toe-clipping, the toads were immediately released at the capture site, and males usually grasped the respective female back in amplexus and continued their reproductive behaviour.

In 2016, we used the 29 encountered pairs to estimate female fecundity relationships. The individuals found in amplexus were briefly separated, weighted, and each pair was individually placed in a 20-l plastic bucket (diameter: 30 cm) filled to a depth of 7 cm with water coming from a well at the study site, and transported to the laboratory (located 300 m from the capture location). A small amount of vegetation from the original pond was placed in the water and the buckets were covered. Even if the frogs in amplexus were separated for measurements, the two partners rapidly returned to amplexus in the bucket with water, and spawned over-night. In the morning, each clutch was photographed (Canon PowerShot SX50 HS) in a Petri dish (diameter: 15 cm) along a millimetric grid plotting paper, and females were re-weighted. Eggs were counted and the diameter of 50 randomly chosen eggs from each egg-clutch was measured using ImageJ 1.46r software (Schneider, Rasband, & Eliceiri, 2012). All individuals, along with the eggs laid, were released in their pond afterwards.

In 2016, to investigate the relationship between male size and male mating success, during the course of the reproduction night, after collecting all pairs as they formed, around 03:00, when we encountered no more females at the pond, we collected all calling males left solitary in and around the pond, up to 10 m from the edges ($n = 52$). We measured these males with the same protocol and compared their size to the ones that had managed to secure an amplexus. To assess the existence of a sexual size dimorphism in the reproductive population at the pond, we used all measured animals from both years (both males and females in pairs, and solitary males).

2.2 Skeletochronology

To estimate the age of the toads, we used the skeletochronological method, which allows to accurately assess how old the individuals are by counting the growth layers in the long bones (in our case the phalanges), without the need to sacrifice the animals (Sinsch, 2015). Each line of arrested growth corresponds to one year (the inactive period during the dry season). The tissue preparation protocol followed the method implemented by Castanet and Smirina (1990) with small modifications. We removed skin and soft tissues, decalcified the bone in 5% nitric acid for 2 to 18 min, depending on size, and afterwards washed in tap water overnight. We included the bones in Tissue-Tek O.C.T. Compound (Sakura, Leiden, The Netherlands), cut 12-16 µm thick cross sections with a Tehsys CR 3000 cryotome, stained with Ehrlich's haematoxylin for 4 hours, and finally washed them in distilled water for 3 min. Sections were mounted on slides using Aquatex (aqueous mounting agent for microscopy, Merck Millipore, Darmstadt, Germany) and those with the smallest medullar cavity and the thickest cortical bone were photographed using an Olympus E-620 microscope-mounted camera (Olympus CX 31 microscope) with Quick Photo Micro 2.3 software.

2.3 Ethical note

The skeletochronological procedure was approved by the Ethics Committee of the Faculty of Natural and Agricultural Sciences, Ovidius University, Constanța. The method is accepted as ethical (Perry et al., 2011) and an appropriate technique to estimate the age in amphibians. During our work, we strictly adhered to the "Guidelines for the treatment of animals in behavioural research and teaching" (*Animal Behavior*, 71, 245–253). The study was approved by the Ministerio del Ambiente de Ecuador (permit number MAE-DNB-CM-2015-0016) and UTPL Ethics Committee (UTPL-CBEA-2016-001).

2.4 Data analysis

Parameters were normally distributed (body mass and number of eggs after log-transformation; Shapiro-Wilk test, all $p > .05$), except for age. We evaluated sexual size dimorphism and size effect on male mating success using Student t-tests. The sexual dimorphism index (SDI) was calculated following Lovich and Gibbons (1992):

$$SDI = \frac{\text{mean size}_{\text{larger sex}}}{\text{mean size}_{\text{smaller sex}}}$$

To obtain the individual body condition indices (BCI) we used the residuals from the regression of ln SVL upon ln BM (Jakob, Marshall, & Uetz, 1996; Băncilă et al., 2010), which is a good proxy of lipid storage in amphibians (Denoël, Hervant, Schabetsberger, & Joly, 2002).

The dependence between female size and reproductive output was determined using linear regression, while to determine the existence of a relationship between the size of the partners forming an amplexus, individual body mass, SVL, and BCI or egg size and number in an egg-clutch we employed Pearson correlations. To establish whether body size can be predicted by age, in the cases for which we knew the age, we computed a general linear model with sex as fixed factor and age as covariate. We used Spearman correlations to test for age assortative mating. Analysis were carried out with SPSS 21.0 (IBM Corp., Armonk, NY), with a significance level set at 0.05; all used tests were two-tailed.

3 RESULTS

## 3.1 Behavioural observations

Breeding was triggered by heavy rains, and Pacific horned frogs reproduced explosively over the course of a single night in both years. Toads stayed hidden underground during the day, and began activity after sunset (18:30). During the breeding nights, males both actively searched for females in the vicinity of breeding site and called loudly from the edge of the pond, from the land and in shallow water (a few centimetres deep), starting immediately after sunset and continuing throughout the night. Males clasped approaching females both on land and in shallow water in a variation of axillary amplexus, called "neck amplexus" (Figure S1). We did not observe attempts by males to dislodge an amplexed male.

3.2 Body size, age, and sex ratio

We found a significant sexual size dimorphism: females were larger than males (mean SVL ± SD = 65.3 ± 2.9 mm, $n = 49$, and 61.5 ± 3.6 mm, $n = 101$, respectively; $t_{148} = -6.27$, $p < .001$; Figure

1a), the SDI at the breeding pond being 1.06. Females were also heavier than males (mean BM ± SD = 32 ± 5.7 g, $n = 49$; 23.7 ± 4.2 g, $n = 101$; $t_{148} = -10.12$, $p < .001$; Figure 1b). The coefficient of variation for SVL was 6% in males and 4% in females, while for BM it was 18% in both sexes.

FIGURE 1 Sexual size dimorphism in the Pacific horned toad (*Ceratophrys stolzmanni*) in terms of (a) snout-vent length (SVL) and (b) body mass. Box plots show the median (dark midline) and spread of values, with boxes encompassing percentiles 25 - 75 and whiskers denoting minimum-maximum value not higher than 1.5 times the interquartile range.
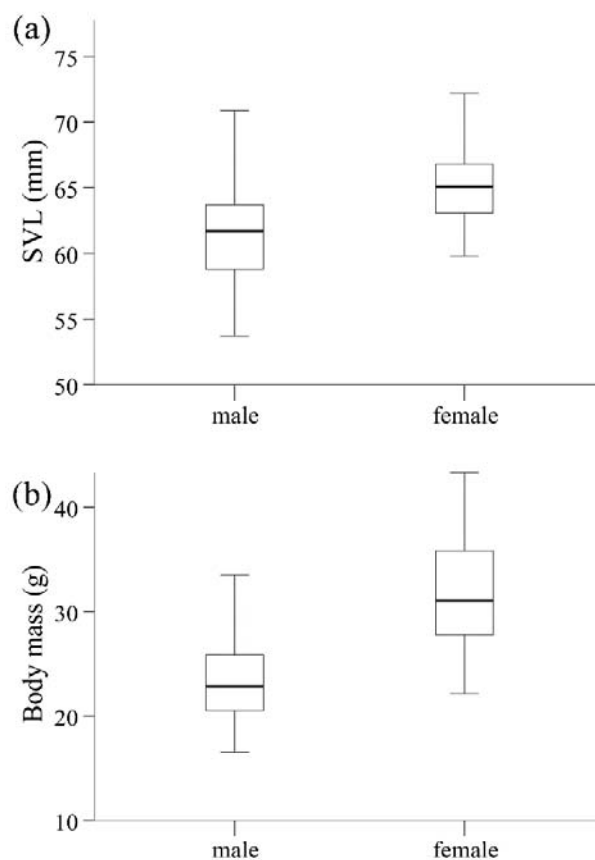
From the 20 pairs in which we investigated the age, in all but one individual (i.e., 97.5%) bone cross-sections showed discernible, intensely stained lines of arrested growth (LAGs) that allowed us to estimate the age of the individuals (Figure 2a). In both males and females, there was a clear pattern with the interval until the first LAG being large, after which LAGs were closer together, indicating a decrease in growth and suggesting the onset of sexual maturity after the first aestivation. Average age of males (± SD) was 1.8 ± 0.5 years ($n = 19$, range 1 − 3) and average

age of females was 2.3 ± 0.4 years (n = 20, range 2 – 3). In a model that included sex as a fixed effect, body size could not be predicted by age (GLM: $F_{1,36}$ = 0.034, p = .855), so that different age classes overlapped in size in both sexes (Figure 2b).

In 2016, when we collected all encountered individuals at the study pond, the sex-ratio was male-biased, with 1 female to 2.79 males.

FIGURE 2 (a) Phalangeal cross section in a 3-year old female *Ceratophrys stolzmanni*. E: endosteum, MC: medullar cavity, small black arrows and numbers: lines of arrested growths (1 line per year); (b) Size distribution according to age and sex (n = 39); full circles: males, empty circles: females.
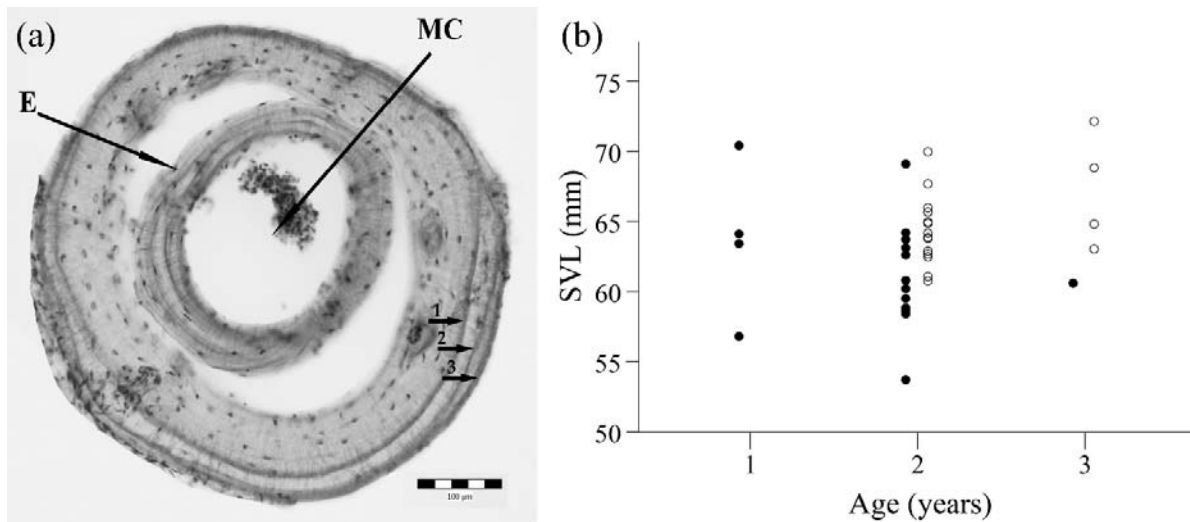
3.3 Female reproductive effort

After egg-laying, females lost an average (± SD) of 10.3 ± 5.2 % of their initial body mass (range: 2.3 – 23.7%). There was a significant effect of the initial body mass on the percentage of body mass loss, with the largest females losing most ($F_{1,27}$ = 5.281, r = 0.4, n = 29, p = .03). Clutches consisted of 513 ± 272 eggs (range: 142 –1374 eggs; Figure S2), with a mean diameter (from 50 eggs measured in each clutch) of 1.95 ± 0.07 mm (range: 1.8 – 2.09). Both initial body mass of the females, and their BCI had a significant effect on clutch size ($F_{1,27}$ = 21.331, r = 0.66, n = 29, p < .001 and $F_{1,27}$ = 13.92, r = 0.58, p = .001, respectively; Figure 3), but not on the average size of the eggs ($F_{1,27}$ =0.18, r = -0.08, p = .675; $F_{1,27}$ = 0.51, r = 0.14, p = .481). There was no significant correlation between the average egg size and the number of eggs (r = 0.16, p = .411).

3.4 Mating patterns

The size of partners forming a pair (i.e., in amplexus) was not significantly correlated (Pearson correlation, $n = 49$, SVL: $r = 0.06$, $p = .68$, Figure 4a; BM: $r = 0.16$, $p = .269$; BCI: $r = 0.26$, $p = .07$). Between partners forming a pair, the SDI was 1.06 ± 0.08 for SVL = (range $0.92 – 1.27$) and 1.36 ± 0.32 for BM (range $0.91 – 2.46$).

There was no significant assortative mating based on the age of the partners (Spearman correlation, $\rho = -0.043$, $n = 19$, $p = .86$). Male age had no significant effect on mating success (i.e., amplexus) with heavier females (Spearman correlation, $\rho = 0.195$, $n = 19$, $p = .42$; Figure 4b).

The males that were found in amplexus in 2016 (SVL = 61.8 ± 3.2 mm, BCI = 0.008 ± 0.02, $n = 29$) did not significantly differ in size from the ones that remained unpaired (SVL = 61.5 ± 3.8 mm, $n = 52$; $t_{79} = 0.331$, $p = .74$) or body condition (BCI = -0.005 ± 0.009, $t_{79} = -.739$, $p = .46$).

FIGURE 3 Egg-clutch size (ln values) in relation to (a) female body mass (ln values, in g) and (b) body condition index before egg laying in *Ceratophrys stolzmanni*.
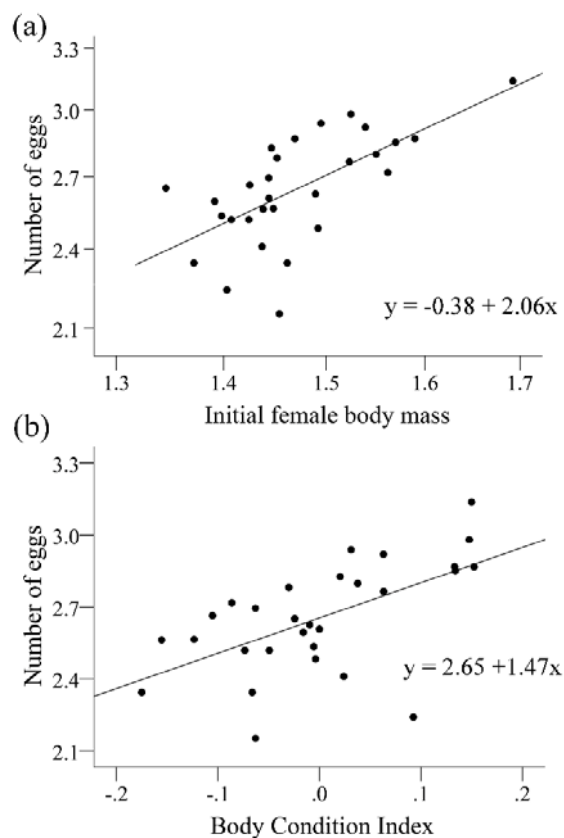
FIGURE 4 (a) Non-assortative mating (snout-vent length of partners found in amplexus, *n* = 49) and (b) female body mass in relation to the age of their partners (*n* = 19) in *Ceratophrys stolzmanni*.
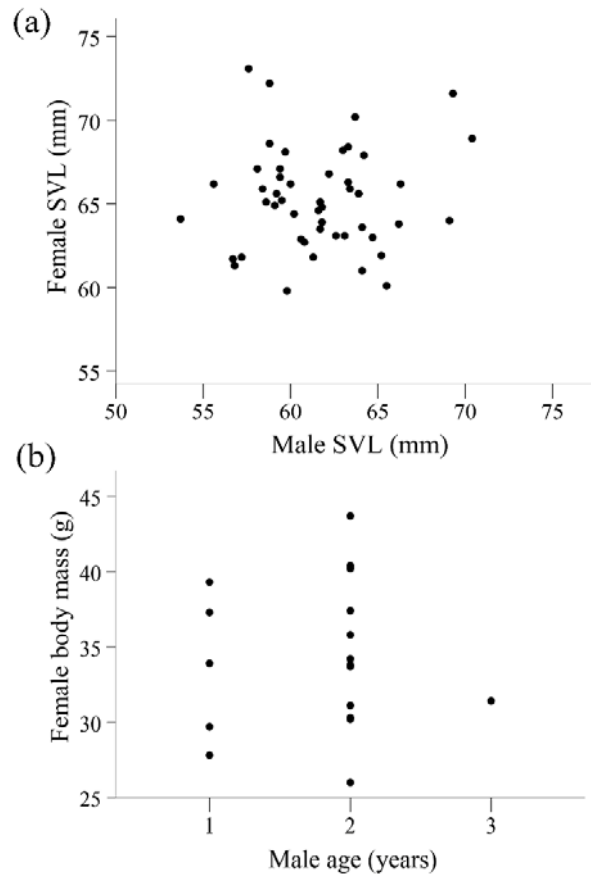
4 Discussion

In support of our prediction, our results show that the Pacific horned frog, an explosive breeder, does not exhibit assortative mating by size-related traits despite variations in both body length and mass within and between sexes and despite size-dependent fecundity in females. Individuals at the breeding site have therefore equal opportunities of reproduction, including the younger or smaller ones, since larger males are not able to monopolize the females. This gives support to the hypothesis that time-constraints on reproduction lead to random mating patterns instead of size-assortative mating (Castellano & Cermelli, 2011; Meuche et al., 2013; Dechaume-Moncharmont et al., 2016), as opposed to prolonged breeding, in which mate-choice is often considered adaptive (Castellano, 2009). This pressure is particularly intense in the studied species, as *C. stolzmanni* breeds during just one night annually, making mate choice a risky strategy.

4.1 Sexual dimorphism and size-correlated fitness

The Pacific horned frogs reproducing at the studied pond showed a female-biased sexual size dimorphism, females being on average 6% larger than males. In ectotherms, this is considered to be a result of stronger selective pressure for increased body size in females (because of correlated increase in fertility), compared to selective forces that favour larger males, like sexual selection (Han & Fu, 2013; Shine, 1979). Body size differences between sexes is presumed to be the result of diverse ecological and environmental constraints (Monroe, South, & Alonzo, 2015), although sexual selection alone might generate differences in size between the sexes, at least in some taxa (Colleoni et al., 2014). The pattern is predominant in anurans, with females being larger than males in 89% of the studied species (Nali et al., 2014). In the studied population of *C. stolzmanni*, the difference in size may be attributed to differential growth rates both before and after maturity (Székely et al., in press), but also to a higher average age in females.

As with the majority of anurans (Hartmann, Hartmann, & Haddad, 2010; Wells, 2010), the number of eggs in *C. stolzmanni* increased with the size of females. This relationship has been shown to be more accentuated in explosive breeders, compared to species with prolonged reproductive seasons (Nali et al., 2014). This is justified by the fact that prolonged breeders have more opportunities to reproduce during a given mating season, so selective pressures for increased fertility during individual reproductive events are less strict. The fact that larger *C. stolzmanni* females showed a tendency to invest more in the number of eggs, and not in their quality (i.e., egg size), may be the consequence of the pressure from a harsh and unpredictable environment. This results in a short reproductive lifespan (the r-strategy: Pianka, 1970), making it more advantageous for females to invest in a greater number of offspring at each reproductive opportunity, than to produce a lower number of larger eggs. In some cases, a larger maternal investment in egg size generates tadpoles able to leave the water faster (Berven & Chadra, 1988), which would be beneficial in breeding habitats with unpredictable hydroperiod (Dziminski & Alford, 2005). However, *C. stolzmanni* tadpoles exhibit a high developmental plasticity and high growth rates that favour their survival in drying ponds (Székely et al., 2017).

4.2 Explosive breeding and non-assortative mating

Regarding the duration of the reproductive season, the Pacific horned frog shows a highly explosive behaviour, all breeding activity being concentrated in a few hours each year. This strategy appears predominantly in resource-limited environments (McCauley et al., 2000; Olive, 1992) and is characteristic to species that use temporary or ephemeral habitats for egg-laying. As such, these species are under strong pressure to reproduce as early in the season as possible, so that tadpoles have enough time to develop and metamorphose (Wells, 1977). Explosive breeding after the first rains of the wet season is a characteristic of *Ceratophrys* species, especially in seasonal environments, such as *C. cranwelli* in Bolivian Gran Chaco (Schalk & Saenz, 2016), C.

joazeirensis in Brazilian Caatinga (Jorge, Sales, Kokubum, & Freire, 2015), but also in more stable climates such as the Peruvian Amazon basin (Duellman & Lizana, 1994) or French Guyana (Gottsberger & Gruber, 2004) in the case of *C. cornuta.*

Reported mating patterns for explosive breeders show great variability. Studies indicate that mate-choice patterns can vary according to local conditions, amongst populations of the same species (Sullivan, 1989; Yu, Li, & Lu, 2013), or even in the same population at different times (Olson, Blaustein, & O'Hara, 1986; Vargas Salinas, 2006). In prolonged breeding species, active female choice is common (Reynold & Gross, 1990), but this behaviour is predicted to lack in explosive breeding anurans. In these cases, larger males would have a reproductive advantage mainly because of their capacity to displace smaller males from amplexus, especially when the operational sex ratio is highly male biased (Sullivan et al., 1995). Most empirical studies have found a large male advantage (Chajma & Vojar, 2016; Rausch et al., 2014). Alternatively, a size-assortative (Cogălniceanu et al., 2013; Hase & Shimada, 2014; Lu et al., 2009) or random mating pattern with respect to size of mating partners have also been described (Elmberg, 1987; Sullivan, 1989).

Similarly to other tropical anurans (Sinsch & Dehling, 2017), the Pacific horned frog has a low age at maturity and a short reproductive life-span (2 – 3 years). The large difference in the number of eggs laid by large females, compared to small ones, along with the lack of multiple mating opportunities, may indicate that male choice should be selected in *C. stolzmanni*. Instead, we attribute the observed random mating patterns to the explosive breeding warranted by the short permanence of breeding habitats and overall brief activity season (Arak, 1983). The fact that reproduction takes place in the course of a few hours, in addition to the agglomeration of individuals at the breeding site, probably prevents any type of direct mate selection. The high synchrony of female arrival at the breeding site does not allow larger males to monopolize the females, so that even less competitive males (i.e. smaller or younger) have access to reproduction. This, together with the low life expectancy, may explain the observed early maturation (after the first aestivation) at least in males, allowing them to take part in as many reproductive events as possible.

In other species that reproduce explosively, the non-random mating pattern is assumed to be the result of male-male physical competition for the same female, with larger males being able to dislodge from amplexus the smaller ones (Bowcock et al., 2013; Howard & Kluge, 1985), or an optimum ratio between the partners' size offering protection from displacements (Lu, Chen, Zhang, & Ma, 2010). For *C. stolzmanni*, we did not observe such behaviour, which may suggest that because of the very short time-frame for reproduction, it is not advantageous for males to waste time and energy in confrontations. We propose that this behaviour might be especially counter-selected because of the special type of amplexus that *C. stolzmanni* employs. In this species, the male attaches itself just above the shoulders of the female (Ortiz, Almeida-Reinoso, & Coloma, 2013), a behaviour that may be more efficient than the regular axillary amplexus used by most neobatrachians, making the removal of an already clasped male difficult for its rivals.

We cannot rule out the possibility that mating patterns may vary according to environmental or demographic conditions at the breeding site (Ah-King & Gowaty, 2016; Olson et al., 1986; Sullivan, 1989) or with size-independent individual traits (Greene & Funk, 2009). However, ephemeral ponds are the typical breeding place of the studied species and explosive pattern is the common mating strategy. Alternatively, due to the very short breeding period, selection could also act on individuals able to converge on time to the breeding patches. This means consequently that despite an absence of choosiness during mating, females would indirectly choose for the mates that actually showed up. Future research investigating how sexual selection acts in these species, for example by generating alternative mating tactics that encourage multiple paternity (Knopp & Merilä, 2009; Vieites et al., 2004), as well as capture-mark-recapture studies, possibly associated with paternity analyses (see also Ursprung et al., 2011; Mangold et al., 2015), might further our understanding of the selective pressures that control the existence of mate choice in explosive breeders.

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