

# Size, Endurance, or Parental Care Performance? Male–Male Competition, Female Choice, and Non-Random Mating Pattern in the Glassfrog *Centrolene savagei*

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**Previous work has shown that *Centrolene savagei* is unique among the more than 150 species in the family Centrolenidae in demonstrating large-male mating advantage. However, it is still unknown whether non-random mating in this species is mediated by intrasexual and/or intersexual selection. To disentangle the effect of these selective pressures on mating pattern in this species, we monitored the breeding behavior of individuals in a population located in the department of Quindío, Central Andes of Colombia. We conducted diurnal and nocturnal surveys each weekend between February and July of 2016 in which we documented morphological (i.e., body size) and behavioral (i.e., chorus tenure, parental-care behavior) characteristics of males to determine their relationship with mating success. We corroborated that in this population of *C. savagei*, larger males obtain a higher number of mates than do smaller males; male body size co-varies positively with chorus tenure and drives this mating pattern. Male body size was not related to higher fertilization efficiency of eggs laid by females, or a higher survival of embryos in clutches cared for by them. In sum, the higher mating success of larger males in the glassfrog *C. savagei* seems most strongly related to a mechanism of endurance rivalry competition (intrasexual selection) than female choice (intersexual selection) based on egg fertilization efficiency or parental care quality.**

**De las aproximadamente 150 especies de ranas de cristal que conforman la familia Centrolenidae, solo en *Centrolene savagei* se ha observado que machos grandes tienen más probabilidad de aparearse que machos pequeños. Sin embargo, se desconoce si esto se debe a selección intrasexual y/o selección intersexual. Con el objetivo de describir el patrón de apareo en esta especie de rana de cristal y sus posibles causas, monitoreamos el comportamiento reproductivo de machos y hembras de *C. savagei* en una población ubicada en el departamento del Quindío, Andes Centrales de Colombia. Se realizó un muestreo diurno y dos nocturnos cada semana durante cinco meses comprendidos entre febrero y julio de 2016, en los cuales documentamos características morfológicas de los machos (e.g., tamaño corporal) y conductuales (e.g., actividad de canto, cuidado parental) para determinar su relación con el éxito de apareo de los individuos. Corroboramos que en esta población de *C. savagei*, los machos de mayor tamaño corporal están activos un mayor número de noches, lo cual se relacionó significativamente con el número de parejas que obtienen. Sin embargo, este patrón de apareo se debe principalmente a que el tamaño corporal de los machos covaría con el número de noches en que están activos cantando. Por otra parte, el tamaño corporal de los machos no se relacionó con una mayor eficiencia en fertilización de huevos dejados por las hembras ni con una mayor sobrevivencia de los embriones en las posturas que cuidan. Todo lo anterior, indica que en *C. savagei* los machos grandes exhiben un mayor éxito de apareo que los machos pequeños, debido principalmente a un mecanismo de competencia intrasexual conocido como rivalidad por resistencia, y no a preferencias de apareo por las hembras basadas en beneficios de eficiencia de fertilización de sus huevos o de la calidad de los machos como padres.**

**S**EXUAL selection is the process that favors individuals with certain phenotypic traits to obtain higher mating success over conspecifics that compete with them for mates (Darwin, 1859). Such competition can happen through two processes. Intrasexual selection consists of competition between individuals of the same sex, usually males, to be conspicuous or monopolize resources that are attractive or necessary to individuals of the opposite sex (Andersson and Iwasa, 1996). In contrast, intersexual selection consists of mate selection by individuals of one sex for individuals of the opposite sex with particular phenotypic traits or monopolized resources (Andersson, 1982, 1994). In most species, females are the choosy sex because their investment in reproductive gametes is far higher than that realized by males (Trivers, 1972; but see Clutton-Brock, 2007). Furthermore, it is assumed females obtain adaptive benefits from mating with males that have particular phenotypes, genotypes, or monopolized resources (Bateson, 1983; Andersson, 1994).

In anurans, male–male competition may include endurance rivalry, warning signal displays, and/or physical com-

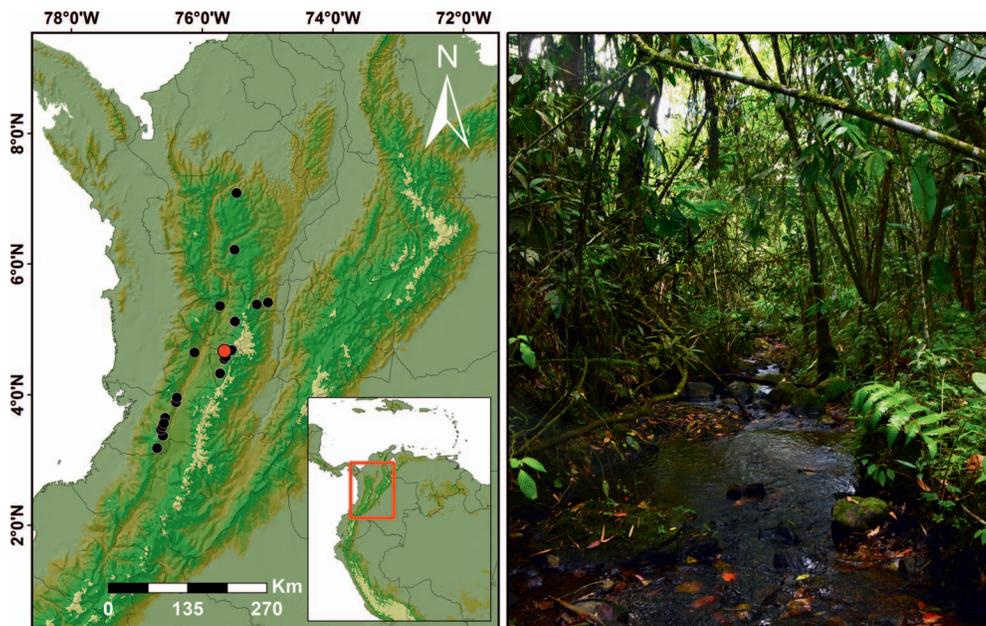
bats (Davies and Halliday, 1977; Arak, 1983; Bosch and Márquez, 1996; Dyson et al., 2013; Bee et al., 2016), while females choose mates based on traits such as efficient egg fertilization (Gibbons and McCarthy, 1986; Sherman et al., 2010), high quality nesting sites (Howard, 1978), reduced predation risk (Grafe, 1997), and quality of parental care (Simon, 1983; Townsend et al., 1984; Cook et al., 2001). It has been also suggested that females choose mates according to genetic quality (Woodward, 1986; Welch et al., 1998; Jaquière et al., 2009). Despite this evidence, the discoveries of novel modalities of communication (e.g., chemical and visual signals on vocal sacs: Starnberger et al., 2013, 2014) and reproductive behaviors (e.g., internal fertilization and live-born tadpoles and a new form of amplexus: Iskandar et al., 2014; Willaert et al., 2016) indicate that much remains unknown about evolutionary aspects of the breeding biology of anurans.

The family Centrolenidae, commonly known as glassfrogs because of their dorsal green translucent color and transparency of their venter, includes more than 150 species of arboreal and nocturnal frogs (Kubicki, 2007; Frost, 2016).

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**Fig. 1.** Left: Geographical distribution of *Centrolene savagei* in Central and Western Andes of Colombia, South America. Historical records (black dots) were obtained from the literature (Ruiz-Carranza and Lynch, 1991, 1997; Cadavid et al., 2005; Palacio-Baena et al., 2006; Rojas-Morales et al., 2011; Vargas-Salinas et al., 2011, 2014; Escobar-Lasso and Rojas-Morales, 2012; Díaz-Gutiérrez et al., 2013); the study area (La Aldea) is represented by the red dot. Right: Image of the creek where individuals and oviposition sites were found.

These frogs breed alongside streams, where males call from rocky and arboreal substrates to attract females; in some species, males are highly territorial (McDiarmid and Adler, 1974; Hutter et al., 2013). Egg clutches are laid on leaves, trunks, or rocks where the embryos develop over several days. When the eggs hatch, individuals fall into the water where they finish development (Kubicki, 2007). Parental care is performed by males in some species, such as *Centrolene lynchi*, *C. savagei*, *Hyalinobatrachium fleischmanni*, *H. orientale*, and *H. valerioi* (Jacobson, 1985; Vargas-Salinas et al., 2007; Vockenhuber et al., 2008, 2009; Dautel et al., 2011; Lehtinen and Georgiadis, 2012), and by females in others (e.g., *Ikakogi tayrona*: Bravo-Valencia and Delia, 2015; *Cochranella granulosa*, *Teratohyla pulverata*: Delia et al., 2017). Parental care in glassfrogs may consist of covering and brooding eggs with the body to hydrate them or protecting offspring from predators (Vockenhuber et al., 2009; Lehtinen et al., 2014; Bravo-Valencia and Delia, 2015; Delia et al., 2017). This behavior can last from a few hours to several weeks and may vary in response to weather conditions (Delia et al., 2013).

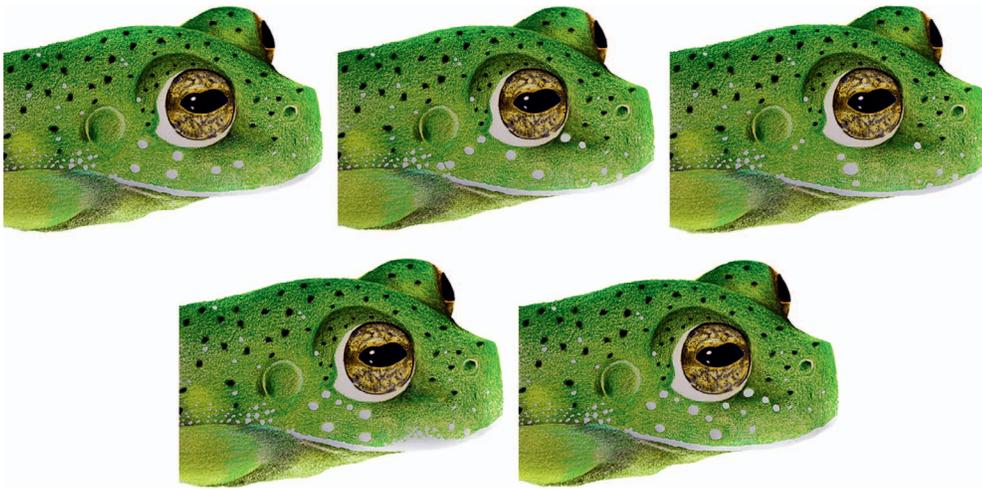
Male mating success in several glassfrog species correlates positively with chorus tenure; that is, the number of nights an individual is active at a breeding aggregation calling to attract a mate or to advise conspecific competitors about calling site occupation (*Hyalinobatrachium fleischmanni*: Greer and Wells, 1980; *Espadarana prosoblepon*: Jacobson, 1985; *Hyalinobatrachium valerioi*: Mangold et al., 2015). Perch position may also influence mating success: males of *H. fleischmanni* calling from higher vegetation perches have greater mating success than males calling from lower ones (Greer and Wells, 1980). Finally, body size is relevant to mating success in at least one species: previously, it was found that there is a positive relationship between male body size and mating success probability in *Centrolene savagei* (Vargas-Salinas et al., 2014). The relative importance of intrasexual and intersexual selection in mediating non-random mating, however, remains untested. Intrasexual selection may play a role, for example, if larger males exhibit longer chorus tenure than smaller males and as a result increase their probability of mating. On the other hand, intersexual selection may have a role if females prefer to mate

with larger males because they offer them adaptive benefits. For instance, larger males could increase the proportion of eggs that are fertilized or may provide better parental care than smaller ones (Davies and Halliday, 1977; Sullivan et al., 1995; Wells, 2007).

In this study, we explored possible mechanisms that influence the mating pattern in *C. savagei*. We monitored the reproductive behavior of individuals in a population in the Central Andes of Colombia over a whole reproductive season. After corroborating a non-random mating pattern in our study population, we analyzed whether larger males had longer chorus tenure than did smaller ones, and how that relationship could be reflected in their mating success. We also evaluated whether fertilization success of eggs laid by a female depends on the amplexant male body size, and whether larger males are better parents than smaller ones. We predicted that if non-random mating is mediated by intrasexual selection, increased chorus tenure and body size would be positively correlated with increased mating success. If intersexual selection mediates this mating pattern, we would expect a positive relationship between male body size and parental care performance and embryo survival in egg clutches. This study offers empirical evidence about the relative role of intrasexual and intersexual selection mechanisms to better understand the evolutionary breeding biology of glassfrogs using *C. savagei* as a model system.

## MATERIALS AND METHODS

**Species and study area.**—*Centrolene savagei* is a species whose individuals are small in body size (snout-vent length, SVL females = 23.3–23.9 mm, SVL males = 19.8–22.6 mm). This species lives in humid montane forest in the Central and Western Andes of Colombia between 1400–2410 masl (Ruiz-Carranza and Lynch, 1991; Fig. 1). The auditory signals, the tadpole, and aspects of breeding behavior of *C. savagei* have been described elsewhere (Díaz-Gutiérrez et al., 2013; Vargas-Salinas et al., 2014; Rios-Soto et al., 2017; Vargas-Salinas et al., 2017). Egg clutches are laid on the upper side of leaves at heights from 0.8 to more than 3 m, and consist of 18 eggs  $\pm$  1.41 SD (standard deviation), on average, with a translucent membrane which permits direct observation of embryo



**Fig. 2.** Example of patterns of white dots on the rostrum of individuals of *Centrolene savagei*, used for individual identification and monitoring.

development around a greenish cream yolk (Ruiz-Carranza and Lynch, 1991). Egg clutches are attended by males (Vargas-Salinas et al., 2007, 2014).

This study was carried out in the creek “El Bosque” located at the country house complex La Aldea (04°38'1.8"N, 75°37'21.8"W), municipality of Circasia, department of Quindío, Central Andes of Colombia (Fig. 1). This creek has a rocky substrate and is 1.5 m wide, on average, and less than 0.4 m deep in most places. At the study area, rural residences, grasslands, and riparian forests dominate the landscape; the ambient temperature ranges from 12 to 18°C, the annual precipitation ranges from 2000–4000 mm, and the mean relative humidity is more than 80% (Vásquez-V. and Serrano-G., 2009).

**Methodology.**—From 13 February to 7 July of 2016 we made 20 fieldtrips, each separated by five days and including two nocturnal (each one between 1830–2300 h) and one diurnal survey (1100–1400 h). Visual encounter surveys (VES; Crump and Scott, 1994) were conducted along 230 m of the creek (Fig. 1) and performed by three persons searching the vegetation from ground to 5 m height. When an individual was observed, we recorded the date, hour, and state of activity (e.g., calling, with upright posture, egg attendance, gravid). The body size of individuals (SVL) was obtained by analyzing a photograph of them taken from a lateral perspective with a scale and using the software Image-J (Abràmoff and Magalhães, 2004). This methodology reduced disturbance, especially when males were performing egg attendance (i.e., covering eggs with a part or the whole body). Because it is necessary to measure body size with the frog held in a specific position so that his posture does not affect the measurement, for those males observed for the first time when attending eggs, we repeated the recording of body size in later captures when they were alone or not touching eggs. In the latter case the males were gently manipulated and returned in a way that they eventually returned to attend eggs (pers. obs.). In addition, photographs allow us to obtain images of the pattern of individually identifiable white dots on the face of each frog, which was used to monitor individuals (Fig. 2). The use of color patterns of individuals is a common technique for unambiguously discriminating among individuals in several species of anurans (Donnelly et al., 1994; Ferner, 2010).

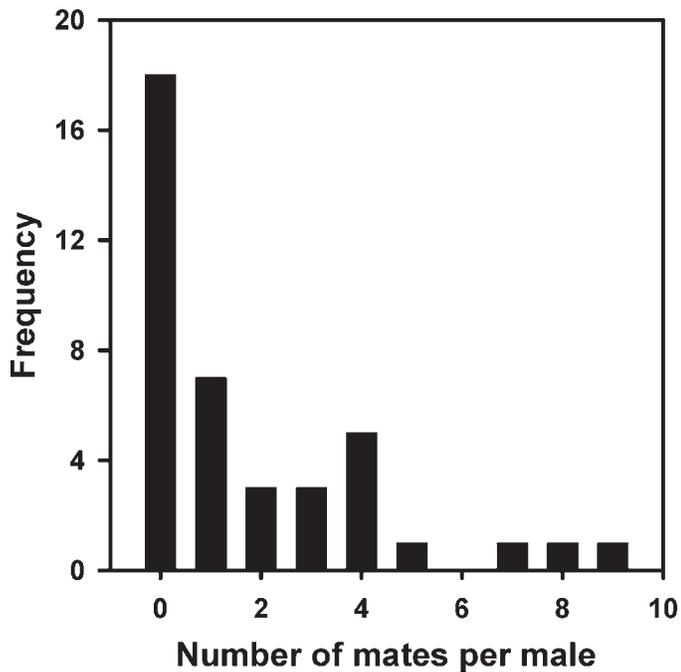
When an egg clutch was observed, we recorded the height from water, substrate, and the presence or absence of a male;

the presence of a male over the egg clutch or adjacent to it was considered as an indicator of paternity. Photographs of egg clutches were taken to determine the embryo development stage according to morphological characteristics (Gosner, 1960; Salazar-Nicholls and Del Pino, 2015). The number of living embryos was determined based on movement of the tail and body, the appearance of the jelly coat surrounding eggs, and a greenish coloration of the yolk.

**Mating pattern and intrasexual selection in males.**—The relationship between male body size and chorus tenure was tested with a Pearson correlation. The relationship between these characteristics and male mating success was subsequently evaluated using linear regressions. A male's chorus tenure, the number of nights a male was observed calling or with an upright posture that suggests calling, was considered an indicator of their effort for attracting a female. A linear regression was also used to analyze whether males of different body size tend to be active at any particular date throughout the reproductive season.

**Fertilization efficiency, parental care performance, and intersexual selection.**—The relationship between male body size and fertilization efficiency of eggs was tested with a Pearson correlation. Fertilization efficiency was measured as the ratio between number of embryos and number of eggs in the clutch. This measure was possible using pictures taken in the field because the jelly of frog eggs is transparent, allowing visualization of embryos. Because over time, eggs hatch or can be depredated, we performed these measures only for clutches whose embryos were observed at development stage  $\leq 11$  (*sensu* Gosner, 1960; Salazar-Nicholls and Del Pino, 2015), allowing a more precise estimate of the initial number of eggs and living embryos in clutches.

We developed a parental care index (PCI) to evaluate whether male body size is associated with his parental care performance and then infer whether females may be receiving a direct benefit that could promote mate selection. This index, expressed as  $PCI = [(\sum P) \cdot D] / M$ , is based on the sum of points assigned (P) according to categories of egg attendance (see next paragraph), multiplied by the number of days between the first and last monitoring of the egg clutch (D), and divided by the number of monitorings made to each egg clutch (M). The PCI permitted us to quantify and compare the parental care performance between males without biases created by differences in the number of



**Fig. 3.** Reproductive skew among 40 males in the glassfrog *Centrolene savagei*.

observations made among egg clutches or by differences in the period over which each egg clutch was monitored.

Egg attendance by males during embryonic development was categorized as absence of the male (0 points), presence of the male without making physical contact with his eggs (1 point), extremity or other part of the male covering  $\leq 25\%$  of the eggs (2 points), and body of the male covering  $\sim 50\%$  of the eggs (3 points) or  $\geq 75\%$  of the eggs (4 points). We assigned more points when the male was closer and over the eggs because this behavior has been correlated with higher survivorship of embryos in glassfrogs (Vockenhuber et al., 2009; Delia et al., 2013; Bravo-Valencia and Delia, 2015). The assignment of points was performed during nocturnal and diurnal surveys. Both time periods were chosen because abiotic (e.g., incidence of solar radiation, temperature, relative humidity) and biotic (e.g., predators) environmental attributes can vary between day and night, likely affecting the parental care behavior of males and survivorship of offspring.

Given that the same male can be caring for several egg clutches simultaneously (see Results section), there can be a conflict of interests between mates (Annqvist and Rowe, 2005). This is because it is expected that the reproductive success of males is increased by the number of accumulated female mates (i.e., more egg clutches, even if male attendance decreases per clutch), while the reproductive success of females is increased by male attendance in her egg clutch (i.e., males with fewer simultaneous egg clutches might increase the attendance per clutch; Trivers, 1972; Andersson, 1994). Therefore, we calculated the PCI from both father's and mother's perspectives. The former PCI was calculated by adding up a male parental care performance value in every simultaneous egg clutch and averaging the obtained value with those in separate mating events. The latter PCI consisted of the value obtained for each egg clutch separately, even if there were other simultaneous egg clutches. To assess whether male body size was related to both PCIs and embryo survival, we used linear regression

analyses. In these analyses of parental care, we included only egg clutches for which embryos were in development stages  $\leq 11$ . This criterion was used due to a similar reason to that mentioned above for measures of fertilization efficiency.

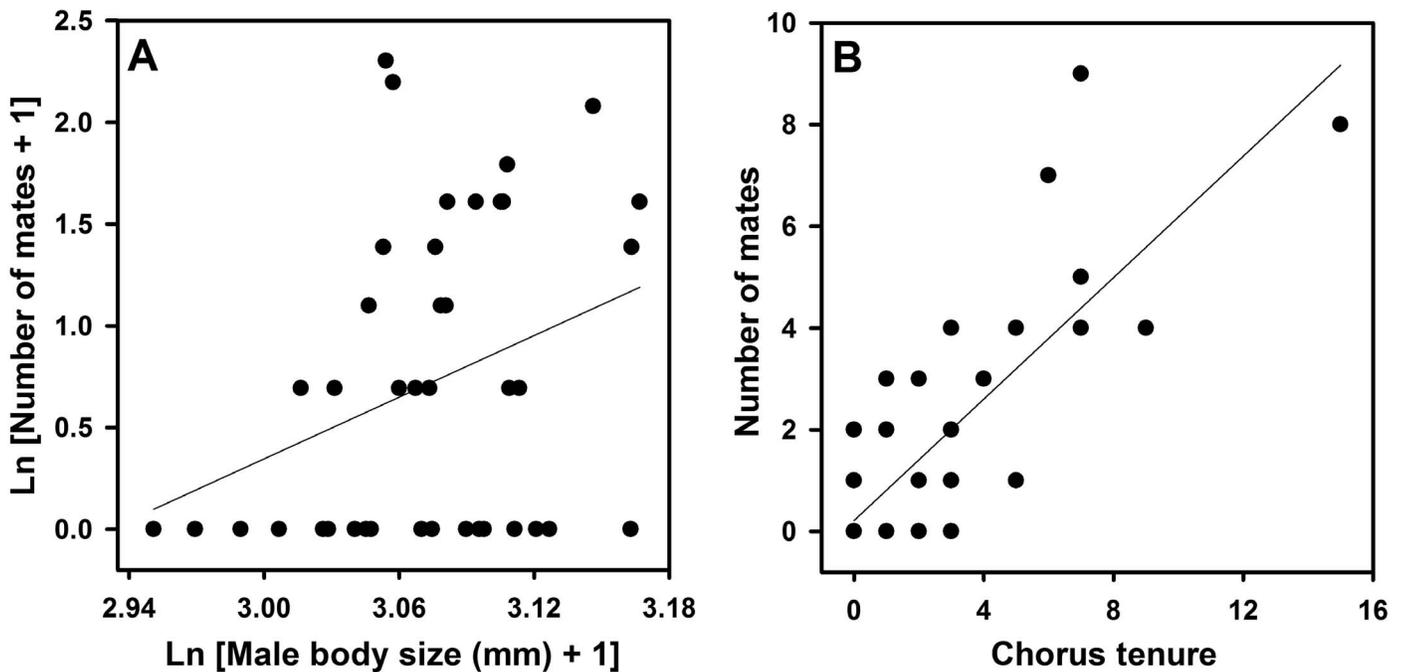
## RESULTS

We observed 40 males (mean SVL = 21.64 mm  $\pm$  1.06 SD, range = 19.12–23.73 mm) and 14 females (mean SVL = 25.26 mm  $\pm$  1.31 SD, range = 23.15–26.98 mm). Males were recaptured an average of 6.33 times  $\pm$  5.40 SD (range = 1–21 recaptures,  $n = 25$  males), and the mean time elapsed between the first observation and the last recapture of a same male was 59.28 days  $\pm$  37.57 SD (range = 1–120 days,  $n = 25$ ). No females were recaptured. We found 74 egg clutches and were able to assign paternity to 69 clutches. Egg clutches were always found on the upper side of leaves at a mean height of 1.55 m  $\pm$  0.84 SD (range = 0.19–4.50 m,  $n = 60$ ) and contained on average 23.09 eggs  $\pm$  3.20 SD (range = 13–29 eggs,  $n = 63$ ).

**Mating pattern and intrasexual selection in males.**—We observed a reproductive skew in the mating success of males; almost half of them (45%) did not obtain a single mate (Fig. 3). Given that male body size was positively related to chorus tenure ( $r = 0.338$ ,  $P = 0.044$ ,  $n = 36$ ), we examined its influence on mating success separately. Larger males accumulated significantly more female mates than did smaller males ( $R^2 = 0.108$ ,  $\beta = 0.328$ ,  $F = 4.579$ ,  $P = 0.039$ ,  $n = 40$ ; Fig. 4A); however, chorus tenure was an even better predictor of differences in mating success among males than their body size ( $R^2 = 0.63$ ,  $\beta = 0.793$ ,  $F = 57.560$ ,  $P < 0.001$ ,  $n = 36$ ; Fig. 4B). Since there were so many males with zero mates, we have a skewed distribution; however, when we performed the same analyses using non-parametric Spearman rank correlations, results were similar. On the other hand, there was no significant relationship between mean body size of males recorded during each nocturnal survey and date of reproductive season ( $R^2 = 0.055$ ,  $\beta = -0.234$ ,  $F = 1.331$ ,  $P = 0.261$ ,  $n = 25$  nights); that is, both larger and smaller males were active throughout the reproductive season.

**Fertilization efficiency, parental care performance, and intersexual selection.**—There was no relationship between male body size and the fertilization efficiency of eggs ( $R^2 = 0.247$ ,  $\beta = -0.497$ ,  $F = 3.276$ ,  $P = 0.100$ ,  $n = 12$ ). After oviposition, the males covered the egg clutches with their body during day and night (Fig. 5A, B). As time passed and embryos developed, the males began to move off their egg clutches and resumed calling activity (Fig. 5C). When a male obtained additional mates before the previous egg clutch hatched, most of the males (18 of 23) stopped attendance of the older egg clutch to completely attend the younger one (Fig. 5D). Two males continued attending the older one. The remaining three males were observed alternating the egg attendance between clutches; in one survey they were observed attending the younger clutch, but the next day, they were attending the older clutch.

Of 74 egg clutches recorded, only 27 (attributed to 18 males) were observed with embryos at developmental stage  $\leq 11$  and were monitored until embryos either died or eggs hatched. In five of those 27 egg clutches, our monitoring disturbed the males to the degree that they abandoned the clutch, so those five males were excluded from analysis.

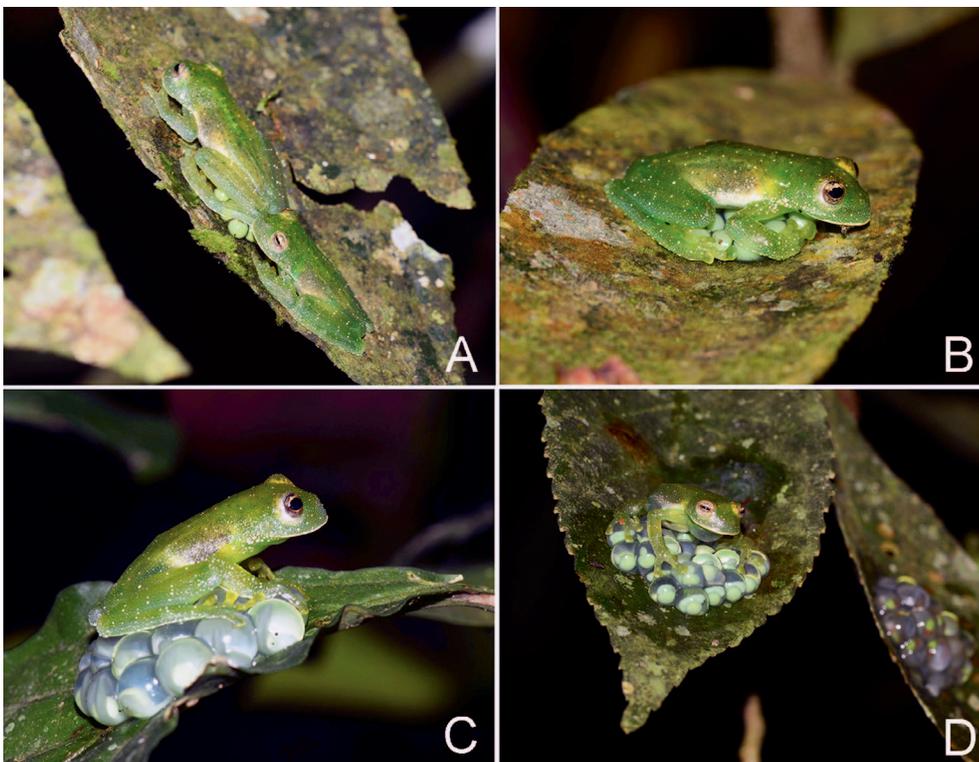


**Fig. 4.** Positive relationship between male body size (A) and chorus tenure (B) with the number of matings obtained. Axes on plot A were transformed using the formula  $\ln(X+1)$  to improve fit of data to a linear model. Chorus tenure = 0 in plot B refers to males that were not recorded calling or in a corporal posture suggesting calling predisposition despite the fact that some of them mated one or twice. In both plots the line represents the best adjustment to the central tendency of data (i.e., minimum squares sum). In plot B there are overlapping dots.

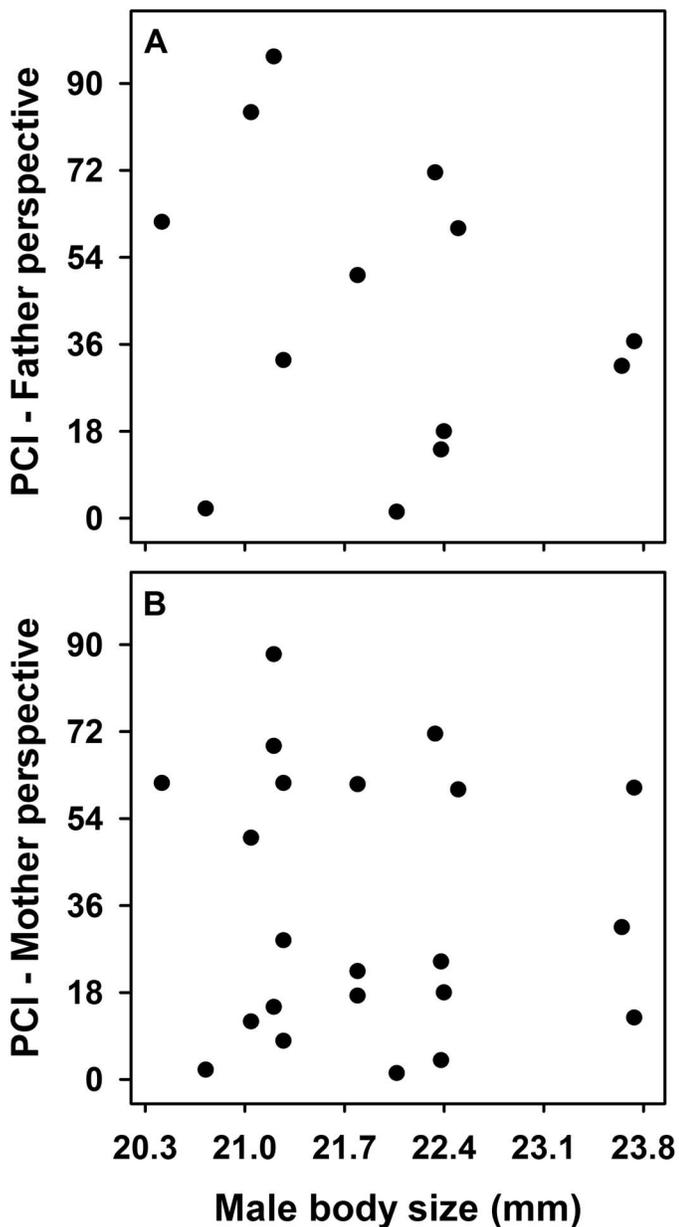
Larger males did not exhibit greater parental care performance than smaller males ( $R^2 = 0.055$ ,  $\beta = -0.234$ ,  $F = 0.636$ ,  $P = 0.442$ ,  $n = 13$ , Fig. 6A); clutches cared for by larger males did not receive more or less attention than did clutches cared for by smaller males ( $R^2 = 0.072$ ,  $\beta = -0.072$ ,  $F = 0.105$ ,  $P = 0.750$ ,  $n = 22$ ; Fig. 6B). Finally, there was no relationship between male body size and embryo survival ( $R^2 = 0.006$ ,  $\beta = 0.080$ ,  $F = 0.059$ ,  $P = 0.814$ ,  $n = 11$ ).

## DISCUSSION

As observed for another population of *C. savagei* (Vargas-Salinas et al., 2014), we found that larger males in this study had greater mating success than smaller males. Although this mating pattern has been reported for species in other anuran families (reviewed by Halliday and Tejedo, 1995, and Wells, 2007), previous studies of glassfrogs did not identify this



**Fig. 5.** Oviposition and parental care in the glassfrog *Centrolene savagei*. After oviposition (A), the male begins to cover the egg clutch with his body (B). After several days, males exhibit an upright posture and calling behavior while caring for eggs (C). A male covering the younger of two egg clutches with his body (D).



**Fig. 6.** Male body size and parental care performance are not related in the glassfrog *Centrolene savagei*. Relationship from father's perspective (A) and from mother's perspective (B); see methodology section for details.

result (e.g., *Hyalinobatrachium fleischmanni*: Greer and Wells, 1980; *Espadarana prosoblepon*: Jacobson, 1985; *Centrolene peristictum*: Salgado-Maldonado, 2012). The positive relationship between male body size and the number of accumulated mates is particularly common in anurans with prolonged breeding (e.g., Howard, 1980; Ryan, 1983; see Halliday and Tejedo, 1995) and vertebrates with a lek-like reproductive system or one based on resource monopolization (Höglund and Alatalo, 1995; Shuster and Wade, 2003).

Male-male competition by endurance rivalry has been reported for diverse anuran species (Elmberg, 1990; Ritke and Semlitsch, 1991; Bertram et al., 1996; Pröhl, 2003) and other vertebrates (birds: Alonso et al., 2010; lizards: Keogh et al., 2012; mammals: Higham et al., 2011; Crocker et al., 2012). While we do not observe physical interactions between males of *C. savagei* as those recorded in other glassfrogs (Hutter et al., 2013; Rios-Soto et al., 2017), evidence suggests that

endurance rivalry seems to be the primary mechanism of intrasexual selection determining the mating success of males. Males of *C. savagei* that spend more nights in the chorus are expected to have a higher probability of mating simply because they have a higher probability of being found and selected by a female, regardless of female preference. Given that calling is physiologically costly (Pough et al., 1992; Wells, 2001), it is possible that larger males exhibit longer chorus tenure than smaller males because the former are in better physical condition (Tejedo, 1992). Nevertheless, other independent or complementary characteristics related to body size could also explain the predisposition to spend more nights in the chorus. For example, if larger males forage more efficiently than smaller males, they could recover energy faster and hence return sooner to the chorus and for more nights through the reproductive season (Murphy, 1994).

Chorus tenure of males of other species in the family Centrolenidae is positively related to mating success (*Hyalinobatrachium fleischmanni*: Greer and Wells, 1980; *Espadarana prosoblepon*: Jacobson, 1985; *Hyalinobatrachium valerioi*: Mangold et al., 2015), but male body size is not correlated with chorus tenure for these species. Alternatively, temporal partitioning is a strategy used by some species: smaller males of the tree frog *Scinax boulengeri* tend to be more active at the end of the reproductive season, potentially as a strategy to diminish direct competition with larger males (Bevier, 1997). Our results do not suggest that *C. savagei* follows a similar pattern; body size did not correlate with day of season in this study. Further studies are necessary to know in detail the costs associated with mate searching in glassfrogs and its relation to body size.

The evidence favoring intrasexual selection as a mechanism to explain the mating pattern in *C. savagei* does not exclude intersexual selection. However, if females do prefer larger males, it is probably not because larger males are better at fertilizing eggs or are better fathers. Given that males of any size can be equally efficient at fertilizing eggs laid by females, there is not an adaptive advantage for choosy females based on fertilization efficiency. Such a benefit may be relevant in anurans with aquatic oviposition, or where clutch size is large and highly variable among females with different body sizes (Robertson, 1990; Bourne, 1993); female *C. savagei* exhibit oviposition out of water with the largest clutches containing fewer than 30 eggs. Our results also do not support the hypothesis that larger males provide better parental care than smaller males. First, egg-clutch mortality for species within Centrolenidae is diminished by males or females covering and hydrating them, especially in the first developmental stages (Vockenhuber et al., 2009; Delia et al., 2013, 2017; Bravo-Valencia and Delia, 2015). In *C. savagei*, every male covered their egg clutches after oviposition. This parental performance can be achieved equally by larger or smaller males. Second, if males differed in their performance of parental care, we expect it would be more evident when they care for many simultaneous egg clutches (e.g., >6), but not when they care for only a few (Delia et al., 2013). It is most frequent in *C. savagei* to find males caring for only one egg clutch at a time; when males attended up to three clutches at a time, clutches were at different developmental stages and generally one hatched several days before the others (unpubl. data). Third, if males of different body sizes differ in their performance in hydrating eggs as part of paternal care, it would be expected that those differences are reflected under extremely dry environmental conditions and

not those obtained in our study (>80% average humidity). Finally, an untested possibility is that parental care in *C. savagei* is more related to reducing mortality by predation than by dehydration (Jesse Delia, pers. comm.).

Although our results suggest that the male mating success in *C. savagei* is driven largely by chorus tenure (i.e., endurance rivalry), we do not discard the possibility of female choice. If body size of males and/or their chorus tenure are related to their physical condition, foraging efficiency, and capacity to find a mate, and these aspects are heritable, it is possible that females select mates based on indirect benefits (Woodward, 1986; Welch et al., 1998; Jaquiéry et al., 2009). This possibility and those results recently published with respect to plasticity and sex-role evolution in parental behavior (Delia et al., 2013, 2014, 2017) and geographic variation in calling sites (Delia et al., 2010) indicate we still do not know many aspects about the reproductive biology of glassfrogs and anurans in general.

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