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SHORT COMMUNICATION

Territory size as a main driver of male-mating success in an Amazonian nurse frog (*Allobates paleovarzensis*, Dendrobatoidea)

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Abstract In polygamous mating systems, it is most often males that compete for the opposite sex, using strategies to provide access to as many females as possible. Females, on the other hand, constitute the sex that exerts the choice and so require a means of accessing the quality of a potential partner in comparison to its competitors. A common challenge in sexual selection studies is to identify the most relevant trait for mating success, since many are correlated with each other. In addition, little is known about how the female accesses the aspects related to male quality. In this context, we tested the role of different male characteristics on mating success in a natural environment using the Amazonian frog *Allobates paleovarzensis* as a model. A multiple linear regression model showed a positive relationship between territory size and number of male matings, while calling persistence was slightly related to the mating success. We did not detect a relation of the number of matings with the distance to the nearest body of water nor with male body size. Additionally, we observed that territory size was not related to calling persistence, but had a positive relation with the duration of the couple's courting process. Thus, we conclude that: (1) territory size is the main determinant of male-mating success, and this is not correlated with the other attributes tested; and (2) females access the size of the males' territory through the courting process that precedes oviposition.

Keywords Anura · Aromobatidae · behavior · courtship · sexual selection

Introduction

Within a species, interindividual variability in mating success determines the intensity of sexual selection: the greater the uncertainty about reproductive success, the more intense competition for the opposite sex tends to be (Trivers 1972). However, in many species, little is known about the determinants of individual reproductive success, since a number of intrinsic and extrinsic factors, acting alone or in combination, may affect the fitness of a given individual (Sirkiä and Laaksonen 2009). Intrinsic factors include the morphological, behavioral, and/or physiological characteristics of the individual that act as a reproductive or attractive resource for reproduction. Such factors include facial features (Batres and Perrett 2016), courtship displays (Haddad and Giaretta 1999; Soma and Garamszegi 2015), and pheromones (Houck and Reagan 1990; Martín et al. 2007). Extrinsic factors refer to attributes external to the individual, but which are also used as a reproductive or attractive resource for reproduction, such as nest quality (Sargent 1982), bridal gifts (Thornhill 1980), and territory quality (Wells 1977). Variability in mating success, and consequently the strength of intrasexual selection, is usually more pronounced in males because females can be seen as a valuable and scarce resource, a pattern explained by anisogamy (Parker et al. 1972), mating investment, differential parental investment between the sexes (Trivers 1972), and the sex ratio in a population (Fisher 1930).

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Thus, in promiscuous mating systems, males are usually the sex that competes for mating opportunities, using strategies that facilitate access to the greatest possible number of females (Emlen and Oring 1977). Females, on the other hand, exert mate choice, and this requires a means of assessing the quality of a potential partner, and a means of comparing him against competing males (Sargent 1982; Bart and Earnst 1999; Sirkiä and Laaksonen 2009). Anuran amphibians are organisms that have evolved diverse reproductive strategies that are evolutionarily influenced by strong intra- and inter-sexual selection (e.g., Prado and Haddad 2003; Izzo et al. 2012). In addition, Anurans make good models for behavioral studies because they are easy to observe and manipulate in the field. Anurans of the Dendrobatoidea superfamily are especially interesting because they frequently show terrestrial reproduction, territorial behavior, and elaborate strategies of partner attraction, courtship, and parental care (Pröhl 2005; Wells 2007). For this superfamily, the small number of existing studies suggests that male reproductive success is related to the defense of a reproductive territory and to the persistence of vocalization, which simultaneously repulses competing males and attracts females (Roithmair 1992, 1994; Pröhl and Hödl 1999; Pröhl 2003; Wells 2007).

Most species in the Dendrobatoidea superfamily reproduce terrestrially, with oviposition occurring on leaves in the litter and part of the development occurring in the aquatic environment (Pröhl 2005). From a certain stage onwards, the offspring require water for development, and there are many different strategies to achieve this while maximizing reproductive success, including the use of water in bromeliad leaf bases (Young 1979), ponds (Eterovick and Fernandes 2002), seed capsules (Moravec et al. 2009), and small streams (Montanarin et al. 2011). Because dendrobatid Anurans are territorial in the reproductive season, the developmental environments of the offspring usually lie within the territorial area of the parents (Pröhl 2005). Females and males may exhibit territorial behavior, depending on which sex is under selective intrasexual pressure and the parental effort of each sex during the development of the young (e.g., Summers 1989). The most commonly found pattern in the superfamily is for males to be territorial and act as caregivers (Pröhl 2005). The most studied aspects of male intrinsic reproductive attributes of the superfamily are the spectral and temporal parameters of adult vocalization, persistence of calling activity, coloration and male size, and residency duration of males on territories (Bourne et al. 2001; Pröhl 2003; Maan and Cummings 2009; Ursprung et al. 2011). The study of extrinsic attributes is usually limited to territory size and those characteristics related to territory quality, and the reproductive resources contained therein, such as sites for tadpole growth (Pröhl and Berke 2001; Pröhl 2002, 2003). Another feature of potential relevance for many species—but never yet investigated—is the distance from the territories to bodies of water, since in most species, the young are transported by their parents to aquatic environments, where they complete their development (e.g., Ringler et al. 2013; Trenkwalder et al. 2016).

A common challenge in sexual selection studies is to separate and identify the feature(s) most closely causally linked to mating success, since many are correlated with each other (e.g., Yasukawa 1981; Bart and Earnst 1999; Candolin and Voigt 2001). Moreover, little is known about the perspectives of the females engaged in such processes, and how they assess attributes related to male quality. Based on previous studies with dendrobatid species (Roithmair 1992, 1994; Pröhl and Hödl 1999; Pröhl 2002, 2003; Juncá and Rodrigues 2006), our hypothesis is that both intrinsic and extrinsic factors of the male are related to male mating success. We used the Anuran *Allobates paleovarzensis* Lima et al. (2010) as a model, a species that inhabits seasonally floodable environments (paleo-várzeas) in central Amazonia. In this context, we aimed to test the role of intrinsic and extrinsic male characteristics on the male-mating success in a natural environment. We also tested a mechanism through which an Anuran female assesses an extrinsic attribute relevant to the male's reproductive success.

Methods

Allobates paleovarzensis is a day-active Anuran inhabiting the forest litter in Amazonian seasonally flooded forests (Lima et al. 2010). The mating system is polygynandrous (Rocha 2017), with defense of reproductive territories by males (Lima et al. 2010, this study). The following description of its reproductive behavior is based on Lima et al. (2010), Kaefer and Lima (2012) and Rocha (2017): courtship begins with the attraction of females by the male advertisement call, which is issued continuously throughout the day. Males call to attract females and repel invading males from their territories. As the female approaches, the male moves across the territory emitting the mating call, and the female follows. Male and female perform a courtship march within the territory, during which the female chooses a leaf for oviposition and decides whether to accept or reject the male. Females may desist before or during the courtship march process and may also visit more than one leaf before choosing on that is a suitable oviposition site. Once the pair is on the selected leaf, cephalic amplexus occurs, which stimulates the female to release her oocytes. In *A. paleovarzensis*, the eggs are deposited in nests of dry leaves in the leaf litter, and they develop there, within the male's territory and under his care, until tadpole phase is reached. The female apparently plays no part in the parental care of the eggs or tadpoles. When tadpoles are close to stage 25 (Gosner 1960), the tadpoles adhere to the male parent's back, in which they are transported to a water body. This is generally as a small permanent or semipermanent lotic water body, connected to other higher order streams. Reproductive activity occurs during the rainy season, which usually begins around mid-November and ends in mid-April.

The study was carried out at Careiro da Várzea (03° 22′ 26.3″ S; 59° 52′ 06.4″ W) in the state of Amazonas, Brazil. Average annual precipitation varies from 2000 to 2400 mm (Sombroek 2001). The locality has remnants of paleo-várzea forests, which are located in plains flooded periodically after the rainy season by freshwater systems rich in Andean sediments (Irion et al. 1995; Assis et al. 2014). The study area has periods of total seasonal inundation (Cintra et al. 2013), beginning in mid-March and April with flooding and overflowing of the region's water bodies.

Data were obtained between December 22, 2016 and February 22, 2017 in a forest fragment containing a network of *igarapés* (small streams), and where males of *A. paleovarzensis* occupy territories during the breeding season. Field observations were performed daily for 6 days per week between 06:00 and 18:00 h (GMT-04:00). Individuals resident in territories were identified by means of photographs of their color patterns, which vary individually, and sexed according to the color of the belly, which is dark in males and yellowish in females (Lima et al. 2010).

We considered both intrinsic and extrinsic variables as potential predictors of male-mating success for this species. For intrinsic variables, we assessed body size (snout-vent length, SVL, in mm, $n = 16$ males) and calling persistence, which was defined as the percentage of censuses in which each individual was recorded vocalizing during his territorial residency. The censuses were conducted by a researcher that walked along a sampling grid subdivided in 25 m^2 subplots delimited by walking trails, counting actively vocalizing males. Censuses ($n = 114$) were performed hourly (between 06:00 and 12:00) for 10 min over 26 days (*mean* = 101.31 censuses, SD = 18.44, $n = 16$ males). As an extrinsic factor, the following variables were measured for the territory defended by the male: distance from the territory to the nearest permanent water body (in straight-line meters, $n = 16$ males), and territory size (measurement via sides of the polygon, in m^2, $n = 16$ males). Territory size was measured considering each vocalization platform and spawning sites as vertex of the polygon. The minimum convex polygon (Kenward and Hodder 1995) was used to calculate the area of the territories, since it is a widely used method for dendrobatid territory measurement (e.g., Brown et al. 2009; Kaefer et al. 2012; Valenzuela-Sánchez et al. 2014). The number of spawns in which each male was involved during the sampling period was considered as the measure of mating success.

To test the determinants of mating success (number of spawnings), we used a multiple linear regression model with the following predictor variables: nearest distance to a water body, territory size, male body size, and calling persistence. Statistics and graphs were generated using the R (R Core Team 2016) computer environment.

Results

Males had none to eight successful matings. The model had a high adjustment in relation to the observed data (adjusted $r^2 = 0.82$, $p < 0.01$). Territory size was positively related to the number of spawnings by the resident male (adjusted $r^2 = 0.57$, $p < 0.01$; Fig.1), while calling persistence was marginally related to the number of spawnings by the resident male ($p = 0.05$) and contributed little in the regression model (adjusted $r^2 = 0.05$). No relationship was detected between number of spawnings and water body distance ($r^2 = -0.003$, $p = 0.64$) or male body size ($r^2 = -0.22$, $p = 0.69$). There was no correlation between any of the predictor variables tested in the model.

Since territory size was the only relevant variable and highly correlated with mating success, we tested the relationship of this predictor with calling persistence and duration of the courtship march, hypothesizing that both could be used by a female as indicators of territory size. Courtship march duration was determined by the time elapsed (in seconds) from the beginning of the movement of the male and the female within the territory up until a leaf was selected for oviposition, resulting in a successful mating event. Territory size was not related to calling persistence ($r^2 = 0.008$, $p = 0.74$, $n = 16$ males), but it was positively related to courtship march duration ($r^2 = 0.73$, $p = 0.002$, $n = 9$ males; Fig. 2).

Discussion

The results of this study did not corroborate the hypothesis that both intrinsic and extrinsic factors of the male influence mating success in *Allobates paleovarzensis*, since only one extrinsic factor was responsible for males' success—the size of the territory. Possibly, territory size represents an extended male phenotype and remains under the influence of sexual selection across generations, a pattern also found in other animal species that defend reproductive territories (e.g., Reid and Weatherhead 1990; Dale and Slagsvold 1990; Seddon et al. 2004; Vanpé et al. 2009). All known members of the Dendrobatoidea superfamily show territoriality, and the territory is always a defended resource that is occupied for reproduction (Pröhl 2005). The paramount influence of the territory in dendrobatid courtship, mating, and parental care strategies supports the results of our study, in which the territory was the principle indicator of male quality.

Pröhl and Hödl (1999) and Roithmair (1992, 1994) demonstrated that male-mating success is positively correlated with territory size in *Oophaga pumilio*, *Allobates femoralis*,

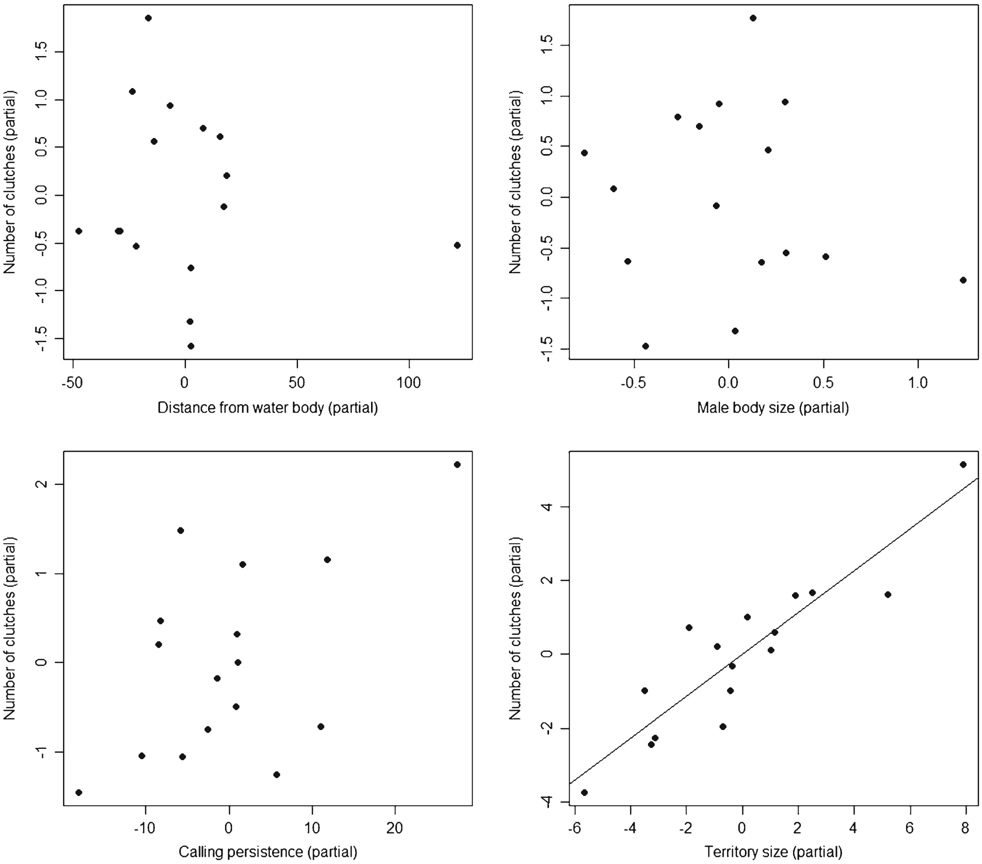

Fig. 1 Relation between the number of spawnings for each male ($n = 16$) and the predicted variable distance from the body of water (meters), size of the territory (square meters), snout-vent length (millimeters), and calling persistence (hours) in *Allobates paleovarzensis* from Central Amazonia

and *Ameerega trivittata* and suggested that females use the size of a territory as an indicator of male quality. However, it was not known how the female accessed the size of the territory and related this information to owner quality. Some type of land quality assessment is certainly important for any species in which males defend oviposition sites because the quality of these sites may have an immediate effect on a female's reproductive success (Wells 2007). If males defend territories centered on oviposition sites and these locations vary in quality, then females are expected to choose mates based on this attribute. There is an evidence for female choice based on territory size in *Rana clamitans* and *Lithobates catesbeianus* (Wells 1977; Howard 1978). In both species, physical characteristics of the territories were correlated with mating success of the territory owners. Although large males tended to acquire the best territories, small males with good territories were more likely to mate than large males with poor territories. In our study, we obtained evidence that the period when the male leads the female through the territory on the courtship march provides an opportunity for the female to access the information about the size of the territory defended by that male. In this way, the female can know if the male is a good competitor for space and how much space he can maintain and defend for reproduction. We consider that at that moment the female makes the choice between continuing or desisting courtship with the male under evaluation. To date, the function of the courtship march was unknown, generally being interpreted simply as a movement of the female following the male to the nest site within the territory (e.g., Limerick 1980; Lima et al. 2002; Montanarin et al. 2011; Forti et al. 2013). Possibly choice of a nest site by the female is of great importance at this point in the courtship. However, our results suggest that the courtship march also has the additional function of assessing male territory size.

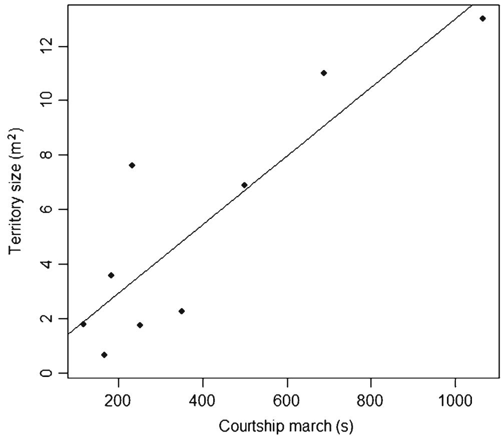

Fig. 2 Relation between courtship march duration and male territory size ($n = 9$) in *Allobates paleovarzensis* from Central Amazonia

Individual male body size is a factor positively related to mating success in various animal groups (e.g., Partridge et al.

1987; Shine et al. 2000; Bourne et al. 2001; McElligott et al. 2001). This factor provides clues to the individual quality, since large size in a male reflects good nutrition throughout life and large females can nurture more young and possibly provide better nutrition for them (Wells 2007). However, in our study, male body size was not a determinant in mating success, and the ability to defend a territory and succeed in attracting and mating with a female was not determined by the size of the male.

In *A. paleovarzensis*, mating success was marginally related to calling persistence. Studies with other Anuran species indicate the importance of this variable in courting and mating success (e.g., Roithmair 1992; Bourne et al. 2001; Pröhl 2003). The persistence of vocalization activity can provide information on energy, endurance, and competitive potential of males, but in the present study, this variable was of little importance as a determinant in male mating success.

Considering the reproductive biology and habitat of the species, we previously suggest the distance to a body of water as a variable determinant of mating success. In *A. paleovarzensis*, transport of the tadpoles by the male from the nest to a body of water where they will continue their development is the main form of parental care. Males that establish territories closer to *igarapés* can reduce costs of tadpole transport (e.g., Townsend 1986; Downie et al. 2005; Ringler et al. 2013; Trenkwalder et al. 2016), but increase the risk of their territories being flooded, and consequently have their fathered clutches drowned or inundated by streams. Thus, based on our results, we conclude that territory location in relation to waterbodies has a negligible importance for male-mating success.

In summary, this study clarifies two important topics for the understanding of mating success in *A. paleovarzensis* and potentially in other species of territorial Anurans: (1) territory size constitutes the main determinant of male-mating success via positive selection by females, and this is not correlated with other extrinsic or intrinsic attributes; and (2) females access the size of the male territory during the courtship march that precedes oviposition. Attempts to integrate male and female perspectives is a growing trend in behavioral studies of Anurans (e.g., Ursprung et al. 2011; Ringler et al. 2012, 2017), and should also allow an understanding of additional factors related to the emergence and maintenance of reproductive strategies in other animal groups.

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Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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