

## RESEARCH ARTICLE

# Calling activity determines male mating success in a territorial frog with parental care

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## Abstract

A contentious aspect in dendrobatoid frog behaviour is the recognition of the predominant factor—if any—driving male mating success. This is probably related to an extensive correlation among different male quality predictors. Here, we investigated the diurnal and territorial nurse frog *Allobates subfolionidificans* by means of a field study during one entire breeding season in Brazilian Amazonia. We tested the roles of two intrinsic male properties (body size and calling activity) and five territory-related variables (territory size, vegetation cover, nesting site, perch height and food availability) on male reproductive output. A multiple regression analysis revealed calling activity as the only variable predicting male mating success in *A. subfolionidificans*. Vocalisation probably represents the most energetically expensive activity that a male frog undertakes during his lifetime, thus calling activity may be used by *A. subfolionidificans* females as a cue to mate choice that indicates competitive potential and male quality. Alternatively, non-choosy females also should be more likely to encounter and mate with males that advertise more often throughout the breeding season.

## KEYWORDS

Aromobatidae, Dendrobatoidea, nurse frogs, reproductive behaviour, sexual selection, vocal activity

## 1 | INTRODUCTION

Mating preferences are the sensory and behavioural properties that influence the propensity of individuals to positively select certain phenotypes for mating (Jennions & Petrie, 1997). In most species, females are the choosy sex, and the attractiveness of certain traits determines male mating success and, ultimately, individual evolutionary fitness (Bateman, 1948). Among these traits, a male's territory and the resources contained in it can be regarded as a part of the male's extended phenotype indicating additional reproductive advantages to mates (Dawkins, 1989). As examples of attributes external to the individual, but which are also used as attractive resources for reproduction, we can list bridal gifts in lovebugs (Thornhill, 1980), nest quality in fish (Pärssinen et al., 2019) and territory quality in flycatchers (Alatalo et al., 1986)". Such view broadens the spectrum of characteristics that can be subject of female-mediated sexual selection.

Poison frogs (Dendrobatidae) and nurse frogs (Aromobatidae) comprise the superfamily Dendrobatoidea, in which the possession of territories, a space related to dominance (Kaufmann, 1983), has been recorded in all studied species (Lötters et al., 2007; Pröhl, 2005). Male dendrobatoids typically perch on calling sites and use advertisement calls as behavioural displays to deter male competitors and attract receptive females during prolonged breeding seasons (Wells, 2007). Such a prolonged reproductive period potentially provides numerous mating opportunities for males and females (Juncá & Rodrigues, 2006; Rocha et al., 2018a; Ursprung et al., 2011a). In most species, male dendrobatoid frogs aggressively defend exclusive areas necessary for complex and prolonged courtship and mating interactions, as well as for egg deposition and subsequent protection of the offspring against desiccation, predators and cannibalism (Pröhl, 2005; Rocha et al., 2018b; Stückler et al., 2019). Therefore, these frogs constitute a suitable study system for the

investigation of both intrinsic and extrinsic determinants of male mating success.

Regarding the intrinsic factors that enhance male dendrobatid frog attractiveness, it has been reported that males with larger body sizes and more frequent calling activity are more successful in acquiring mates (Pröhl, 2003; Pröhl & Hödl, 1999; Wells, 2007). Besides this, variation in mating success has been related to territory size (Rocha et al., 2018a). A contentious aspect in dendrobatid frog behaviour is the recognition of the predominant factor—if any—driving male mating success. This is probably related to an extensive correlation among different male quality predictors. From a metabolic point of view, it is expected that larger male frogs are able to vocalise more frequently and to control larger territories, thus monopolising essential resources for reproduction (Prestwich, 1994; Ryan, 1983; Tejedo, 1992; Wells, 1977).

The possession of territories also allows male frogs to dominate a series of resources that can be regarded as extrinsic properties that potentially can affect their reproductive output (Wells, 2007). Even though the function and the type of defended resource remain elusive for most of the species of nurse and poison frogs (Pröhl, 2005), a territory may contain a series of components that are relevant in the course of individuals' life histories. Previous studies have found several such territory-related factors: (a) leaves and bromeliads that are used as nesting sites (e.g. Juncá & Rodrigues, 2006; Kaefer et al., 2012; Poelman & Dicke, 2008); (b) small invertebrates, which represent the entire food source (e.g. Lima & Magnusson, 1998; Lötters et al., 2007); (c) ground vegetation, which functions as shelter (e.g. Montanarin et al., 2011); and (d) perches, used by males to enhance sexual signal propagation within the forest (e.g. Pröhl & Hödl, 1999). The role of these extrinsic (resource-related) variables in mating success is far less studied than individual aspects such as body size and calling activity (Poelman & Dicke, 2008; Wells, 2007), and no study to date has considered all of them in a single approach.

In this study, we aimed to test the determinants of frog male mating success in the context of territory ownership and parental care. For this, we investigated the arboreal frog *Allobates subfolioidificans* Lima et al. (2007), a diurnal leaf-litter species characterised by aggressive males that defend territories against other males, while females have larger and non-defended home ranges (Souza et al., 2017). Egg clutches are always deposited on the underside of leaves inside the territory. Egg and larvae attendance, as well as tadpole transport to water environments is performed mostly by males and occasionally by females, probably in cases of absence of the father (Souza et al., 2017). Despite all this information on the natural history of this species, it remains unknown which resources are actually defended through the pronounced territoriality.

We evaluated the role of male characteristics in mating success such as body size and calling activity, as well as size of the owned territory and indicators of potential resources contained in the territory: vegetation cover, nesting site, perch height and food availability. Based on investigations conducted on ecologically similar territorial species such as *A. femoralis* Boulenger 1884 (Roithmair, 1992), *A. paleovarzensis* Lima et al. 2010 (Rocha et al., 2018a, 2018b) and

*Ameerega trivittata* Spix 1824 (Roithmair, 1994) in Amazonia, we hypothesised that calling activity and territory size, but not body size, could equally predict mating success. Because female choice may be based on numerous male frog characteristics (Sullivan & Kwiatkowski, 2007; Wagner & Sullivan, 1995), we conducted a multiple regression approach aiming to recognise the determinants of male mating success in this species.

## 2 | METHODS

Data collection was performed by two observers in an 875 m<sup>2</sup> closed-canopy plot located in the centre of the Zoobotanical Park of the Federal University of Acre, an urban secondary forest fragment of approximately 100 ha located in Rio Branco, Acre State, Brazilian Amazonia (09° 57' S, 67° 52' W). The area was partitioned in 25 m<sup>2</sup> subplots and sampled six days per week from 0,430 to 1,830 between October 2002 and May 2003 and weekly in June 2003. We monitored territories from October to December 2002 to determine which males had stable territories that were followed more closely for the remaining time. Another investigation characterising temporal patterns of reproductive activity and spatial organisation of individuals was conducted concomitantly (Souza et al., 2017).

We captured 181 individuals: 105 males and 76 females. Most of the individuals ( $n = 112$ ) were marked in the first sampling month. Among the marked males, 38.1% ( $n = 40$ ) were monitored in established territories from December 2002 to April 2003 and compose the dataset of the present study. Therefore, there was no observable variation in territory permanence (or tenure) among the males monitored during this study.

Below we describe the acquisition of the data regarding male mating success and seven potential predictors considered in this study: male size, territory size, food availability, vegetation cover, nesting site availability, calling activity and perch height.

### 2.1 | Male mating success

Mating success was determined by the number of clutches found within each male territory (Rocha et al., 2018a). This number was estimated by visual search performed each week. Green and dead leaves located up to 30 cm above the ground were examined, and each clutch was tagged with a numbered plastic flag (Souza et al., 2017). Paternity was inferred from observation of mating events and/or parental care towards the clutch.

### 2.2 | Male size

Resident male individuals were manually captured and body size was measured as snout-vent length (in mm). Males were individually marked via toe clipping according to Hero (1989) given that this species has no body marks or patterns that permit reliable individual

identification. Clipping of up to two toes, as performed in this study, had no detrimental effects on recapture rates of the congener *A. femoralis* (Ursprung et al., 2011b). After this procedure, males were immediately returned to the places of capture.

### 2.3 | Territory size

We placed all capture and recapture points of resident males along x and y Cartesian coordinates in relation to the grid of 25 m<sup>2</sup> subplots with 1-cm resolution. The size of the territories was calculated in m<sup>2</sup> via the minimum convex polygon (MCP) method using the programme ranges V (Kenward & Hodder, 1996). Even though MCP can overestimate territory sizes (Brown et al., 2009), it has the advantage of being independent of parameter estimations and has been employed in the study of the spatial ecology of several dendrobatoids (e.g. Brown et al., 2009; Rocha et al., 2018a), including *A. subfolionidificans* (Souza et al., 2017).

### 2.4 | Food availability

We estimated food availability by the invertebrate biomass collected via pitfall traps placed within male territories. The traps consisted of a rectangular (20 × 15 cm) recipient partially burrowed in the forest floor. The trap was ca. 4 cm deep and contained a solution of water and liquid soap. One trap was placed in the centre of each male territory and remained active for a period of 12 hr (6–18 hr). Food availability was accessed once during the study period in order to minimise a possible interference on the diet and overall behaviour of the resident males. Invertebrate biomass was estimated with a precision scale (0.001 g) after removing the excess of humidity. We considered only invertebrates with length equal to or less than the average mouth gap of the males captured during the study.

### 2.5 | Vegetation cover

We estimated herb and shrub cover by an adaptation of the Bullock (1996) method. A line was drawn in the longer axis of each territory, and a plot 1.0 m tall and 0.2 m wide was established over this line. All leaves of living plants were counted within the plot. The sum of leaves was divided by the length of the plot for a normalised index across distances.

### 2.6 | Nesting site availability

The number of leaves potentially available for oviposition in each territory was counted within the same 0.2 m wide plot in which we estimated vegetation cover. However, the leaf availability plot was 0.3 m tall because the maximum height of the observed clutches was 23.0 cm. Potentially available leaves were those lacking trichomes or

dust (Souza et al., 2017). The total number of leaves was divided by the length of the plot resulting in an index of leaf availability.

### 2.7 | Calling activity

Individual calling activity was assessed through censuses conducted once a week, every hour from 4h30 to 18h30 (Souza et al., 2017), from December 2002 to April 2003. Each territory was accessed by a researcher walking along the trails delimiting the subplots 14 times (hours) during each of the 22 sampling days, resulting in 308 hourly assessments of calling activity for each resident male frog. Unlike many other dendrobatoid species, *A. subfolionidificans* males do not seem to alter calling behaviour with the approach of a silently walking observer (Souza et al., 2017). Resident individuals scored one when in vocalisation and zero when silent during each one-hour interval. Individual calling activity was estimated by the sum of the number of records of a male vocalising during the sampling period. It is important to note that our measure of calling activity differs from "calling effort", which normally derives from data on calling rate and call duration (Wells, 2007). Given that all male residents were concomitantly monitored in 308 occasions, we considered calling activity as the number of times each male was observed vocalising during these assessments.

### 2.8 | Perch height

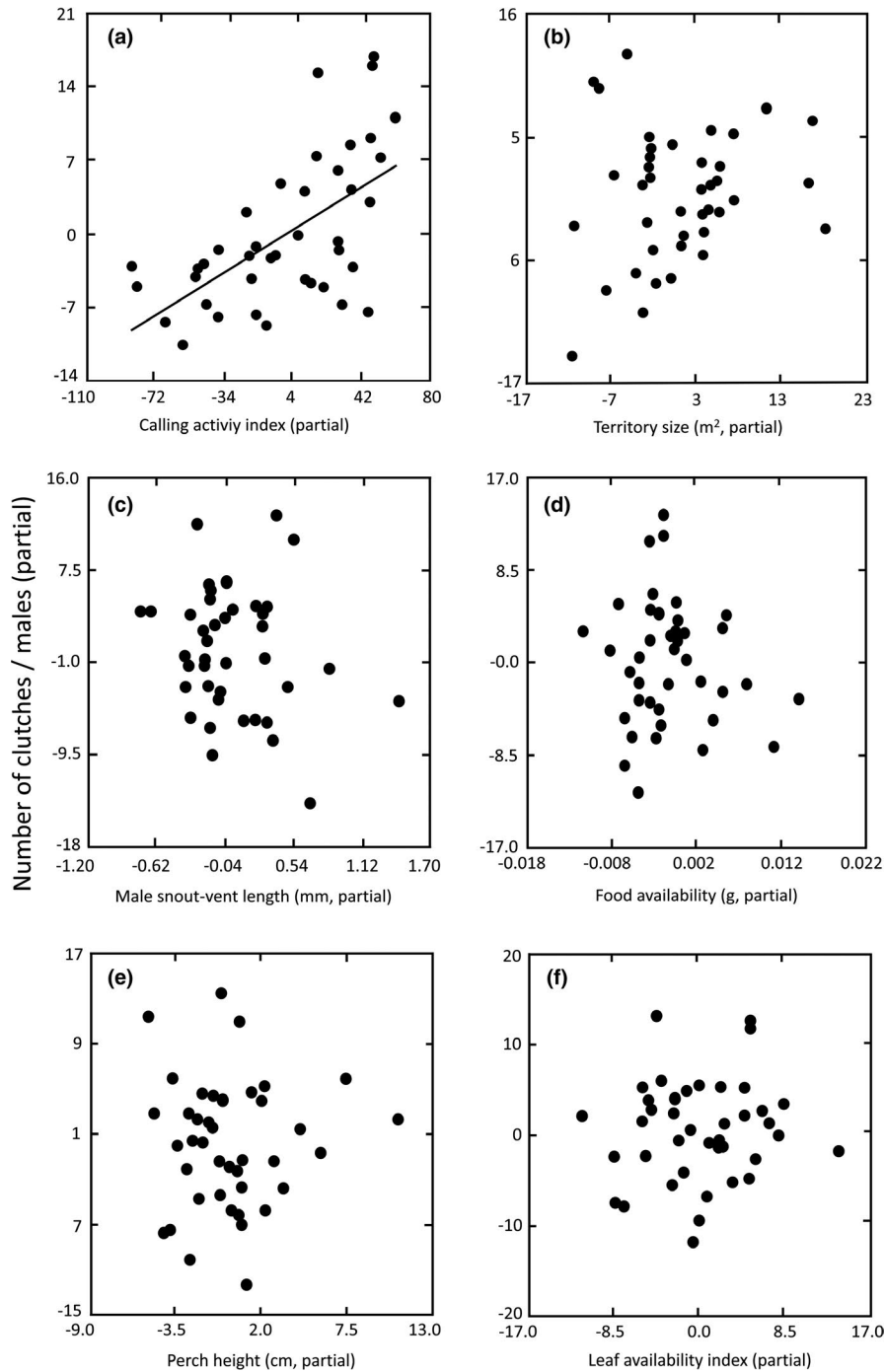
We registered the height from which each male vocalised during the hourly censuses of calling activity. After each census, we calculated daily means, and from these means, we obtained overall means that were considered as individual perch height.

### 2.9 | Statistical procedures

The effect of the independent variables listed above on the number of egg clutches per territory (male mating success) was tested through a multiple regression model. Leaf availability and vegetation cover were correlated ( $r^2 = 0.556$ ;  $p < .001$ ). Therefore, the latter variable was excluded from the model given that correlated variables carry the same information and could potentially mask or enhance patterns in additive multiple linear models (Magnusson et al., 2015).

## 3 | RESULTS

The multiple regression model relating male mating success (MMS) to male size (MS), territory size (TS), food availability (FA), nesting site availability (NA), calling activity (CA) and perch height (PH) explained 49% ( $R^2 = 0.49$ ;  $F_{6,33} = 5.25$ ;  $p < .001$ ) of data variation ( $MMS = 42 - 2.65MS + 0.17TS - 108.60FA + 0.12NA + 0.11CA + 0.05PH$ ). Calling activity contributed significantly to the model ( $p < .001$ ; Figure 1a)



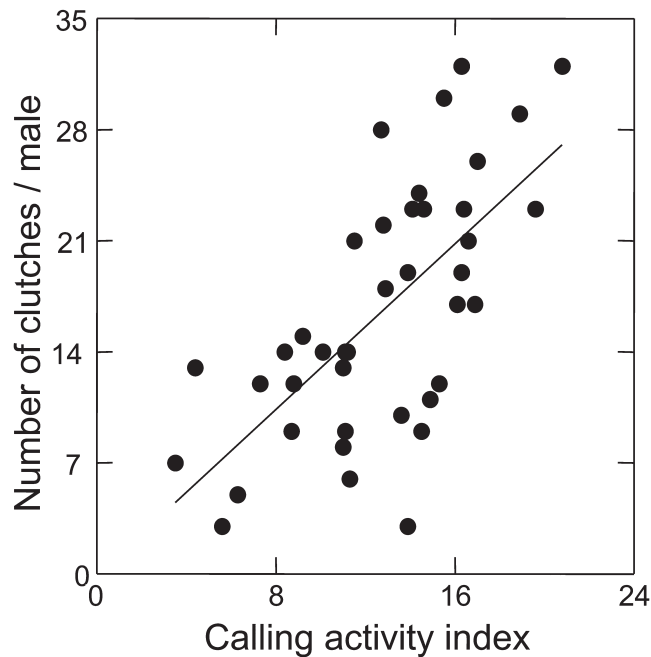
**FIGURE 1** Multiple linear regression model testing the effects of calling activity (a), territory size (b), male size (c), food availability (d), perch height (e) and leaf availability (f) on *Allobates subfolionidificans* male mating success

while the remaining tested variables did not (Figure 1b-1f). A simple linear regression model relating male mating success to calling activity explained 45% of the variation in the number of clutches produced by *A. subfolionidificans* males ( $r^2 = 0.45$ ;  $F_{1,38} = 30.46$ ;  $p < .001$ ; Figure 2).

#### 4 | DISCUSSION

Calling activity stood out as the only variable predicting male mating success in the frog *Allobates subfolionidificans*. Although this predictor has its importance pointed out by previous studies

such as those conducted with the dendrobatoid frogs *A. femoralis*, *Anomaloglossus beebei*, *Ameerega trivittata* and *Oophaga pumilio* (Bourne et al., 2001; Pröhl, 2003; Roithmair, 1992, 1994), this investigation revealed vocalisation activity as the single determinant variable related to reproductive output. In addition to nurse and poison frogs, differences in time spent calling at the reproductive site, but not to body size or relatedness, also determined the variance in male mating success in the glass frog *Hyalinobatrachium valerioi* (Mangold et al., 2015). Anurans expend considerable energy and experience potential predation risk while calling (Sullivan & Kwiatkowski, 2007), and vocalisation probably represents the most energetically expensive activity that a male frog undertakes



**FIGURE 2** Effect of calling activity on male mating success in the Amazonian nurse frog *Allobates subfolionidificans*

during his lifetime (Pough et al., 1992). Therefore, calling activity may be used by *A. subfolionidificans* females as a cue to mate choice that indicates competitive potential and male quality, as observed in different mating systems (reviewed by Wells, 2007). Alternatively, non-choosy females (Ursprung et al., 2011a) also should be more likely to encounter and mate with males that advertise continuously throughout the breeding season. It is also important to note that most of the variation in mating success was not predicted by calling activity alone, and additional variables not considered in this study such as visual and tactile displays and body colour variation (de Luna et al., 2010; Montanarin et al., 2011) may also play important roles in the complex reproductive biology of the species.

Male body size, the other intrinsic factor analysed besides calling activity, was not related to territory size and mating success in *A. subfolionidificans*. Larger male frogs may be energetically and anatomically able to monopolise larger territories (Prestwich, 1994; Wells, 2007) and to emit lower-pitched, longer and more repetitive calls that are usually more attractive to females (Bourne et al., 2001; Meuche et al., 2012; Pröhl, 2003; Ryan, 1980, 1985), thus influencing mate choice decisions (Gerhardt & Huber, 2002 but see Meuche et al., 2013). Studies with the congeners *Allobates paleovarzensis* (Rocha et al., 2018a, 2018b) and *Allobates femoralis* (Ursprung et al., 2011a) also revealed that body size was unrelated to male mating success, suggesting that the subtle body size variation among territory owners in these *Allobates* species does not allow the detection of an effect on reproductive output if it exists.

Territory size and additional territory-related variables (vegetation cover, nesting site, perch height and food availability) did not predict reproductive output in *A. subfolionidificans*. This was unexpected because territories are known to play a central role

in the life history of all known dendrobatoid frogs (Pröhl, 2005) and studies on ecologically similar species have detected such correlation (e.g. Rocha et al., 2018a; but see Ursprung et al., 2011a). Given that the resource defended by male nurse and poison frogs through territory ownership has never been unambiguously identified (Poelman & Dicke, 2008; Pröhl, 2005), the possession of territories might be beneficial by simply allowing space for courtship and offspring attendance with minimal external interference and/or agonistic interactions (Pröhl, 2005; Rocha et al., 2018a). In addition, our operational measures related to extrinsic properties might have failed to reliably indicate the theoretical variables related to the male territories. For example, food availability was estimated during a relatively short sampling interval that, although common in the literature, might not have precisely captured invertebrate biomass availability during the entire study period (Hohbein & Conway, 2018). Another possibility is that territory-related variables are only related to fitness indicators not measured in this study such as hatching success and offspring survival (Howard, 1978).

The comparison of our results with other studies, even within the frog clade Dendrobatoidea, is challenging due to both biological and methodological idiosyncrasies. Every species presents particularities that might be relevant to mating success such as presence of toxins, colouration, mating system and form of parental care, to name a few (Lötters et al., 2007). Besides this, relatively well-studied species such as *Allobates femoralis* and *Oophaga pumilio* comprise several geographically structured evolutionary lineages (Amézquita et al., 2009; Hauswaldt et al., 2011) for which determinants of reproductive success may differ, probably explaining contrasting results among populations of a same taxon. Among methodological idiosyncrasies of the studies we can list the use of different sets of proxies to access male attractiveness, as well as distinct temporal sampling scales that vary from weeks (e.g. Rocha et al., 2018a), to entire reproductive seasons (this study) and multiple reproductive seasons (e.g. Pröhl, 2003). Future research should explicitly address these peculiarities in order to access broader patterns on the determinants of frog male mating success.

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