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ECOLOGIA REPRODUTIVA DA RÃ CUIDADORA *Allobates sumtuosus*: UM ESTUDO DE CAMPO SOBRE OS DETERMINANTES DA ATIVIDADE TEMPORAL E SUCESSO DO MACHO

Manaus - Amazonas
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Sinopse

Estudou-se o comportamento reprodutivo, sobrevivência da prole e fatores determinantes da atividade e do sucesso reprodutivo da espécie de anfíbio anuro *Allobates sumtuosus*. Apresentou-se informações sobre o uso do espaço, comportamento de corte, vocalização, cuidado parental e estratégias reprodutivas alternativas.

Palavras-Chave: Bioacústica, Dendrobatidae, Comportamento, Sucesso Reprodutivo.

Dedico este trabalho a todos os (as) pesquisadores e naturalistas que se dedicam incansavelmente a investigar a natureza em todas as suas formas, mesmo quando não reconhecidos por isto.

Dedico esta dissertação à minha mãe, Liliane Carvalho Coutinho Sena, a quem devo minha vida, meus princípios e tudo que sou.

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RESUMO

As rãs ponta-de-flecha (Dendrobatidoidea) apresentam comportamentos reprodutivos complexos, elaborados e variados. Abordagens envolvendo testes de hipóteses são importantes para entender como fatores ecológicos afetam a atividade de reprodução e o sucesso reprodutivo sob condições realistas, baseadas em observações de campo. Neste estudo, conduzido em florestas da Amazônia central ao longo de toda uma estação chuvosa, objetivamos: 1) caracterizar a biologia reprodutiva de *Allobates sumtuosus*; 2) testar o efeito de fatores ambientais na atividade de vocalização diária; e, 3) testar se fatores intrínsecos e extrínsecos afetam o sucesso reprodutivo dos machos. A atividade de vocalização dos machos atingiu o pico no início da manhã e no final da tarde sendo influenciada negativamente pela temperatura ambiental. Observamos diferença sexual em comportamento, tamanho e cor: os machos foram territoriais, tiveram tamanhos corporais menores do que as fêmeas, e saco vocal e ventre branco em contraste com fêmeas cuja superfície ventral foi amarela. O crescimento no tamanho do corpo de indivíduos adultos foi insignificante entre duas estações reprodutivas. Casais se envolveram em um elaborado comportamento de corte, onde em 71,4% das observações as fêmeas desertaram. Desovas de mais de uma fêmea foram depositadas em um mesmo ninho de folhas mortas e tinham desenvolvimento assíncrono, os quais foram cuidados pelo macho proprietário do território. Apenas os machos cuidaram dos ovos e larvas, transportando girinos para corpos d'água cerca de 20 dias após a oviposição. Um macho adulto foi encontrado próximo a um par em amplexo dentro de um ninho, constituindo a primeira indicação do comportamento de macho satélite neste gênero. Setenta e seis por cento das oviposições atingiram o estágio de girino e foram transportadas. A primeira descrição do canto de acasalamento de *A. sumtuosus* é apresentada, consistindo em notas contínuas, de baixa amplitude e com arranjos temporais irregulares separados por intervalos silenciosos irregulares. O sucesso reprodutivo do macho foi desigual e não pôde ser previsto pelo tamanho do corpo, permanência no território ou tamanho do território, sugerindo que a escolha da fêmea e o sucesso reprodutivo não dependem desses fatores.

Reproductive ecology of the poison frog *Allobates sumtuosus*: a field study on the determinants of temporal activity and male success

ABSTRACT

Poison frogs (Dendrobatidae) show complex, elaborate, and variate breeding behaviours. Hypothesis-testing approaches are relevant to understand the effect of ecological factors on breeding activity and reproductive success under realistic, field-based conditions. In this study conducted in Central Amazonian forests during an entire rainy season, we aimed to 1) characterize the reproductive biology of *Allobates sumtuosus*; 2) test the effect of environmental cues on diel calling activity; and 3) test the effect of intrinsic and extrinsic predictors of male reproductive success. Male vocalization activity peaks in the early morning and late afternoon, and is negatively influenced by environmental temperature. There are sexual differences in behavior, size and color: males were territorial, had smaller body sizes than females, and white vocal sac and belly in contrast to females whose ventral surface was yellow. Adult individuals did not have a significant increase in body size from one breeding season to the next. Mating pairs showed an elaborate courtship behaviour during which females deserted in 71.4% of the observations. Eggs were deposited in communal nests on dead leaves on the leaf litter, and these nests contained several other spawnings, with asynchronous-developing eggs from the same, territory-owner male. Only males showed egg and larvae attendance, transporting tadpoles to waterbodies ca. 20 days after oviposition. An adult male was found near an amplecting pair inside a nest, constituting the first indication of male satellite behavior in the genus. Approximately 76% of the egg masses reached the tadpole stage and were transported. The mating call of the species is first described and consists of continuous, low-amplitude notes with irregular temporal arrangements separated by irregular silence intervals. Male reproductive success was uneven and not predicted by body size, territory tenure, and territory size, suggesting that female choice and reproductive output do not depend on these traits.

SUMÁRIO

INTRODUÇÃO GERAL

As rãs ponta-de-flecha, rãs venenosas ou rãs cuidadoras (Dendrobatoidea *sensu* Frost, 2020) compreendem um clado de espécies de serapilheira principalmente diurnas e poligâmicas que dependem fortemente de estímulos ambientais e condições que influenciam os principais aspectos reprodutivos, como a atividade reprodutiva temporal (Kaefer *et al*., 2012; Souza *et al*., 2016), taxa reprodutiva e sobrevivência da prole (Juncá, 1996; Kok *et al*., 2013b; Pašukonis *et al*., 2016). A seleção de parceiros, por outro lado, é geralmente realizada pela fêmea que avalia uma série de características potenciais intrínsecas dos machos, como tamanho do corpo (*e.g.*, Hettyey *et al*., 2009; Arak, 1988), padrão de coloração (Montanarin *et al*., 2011), e atividade vocal (*e.g.*, Pröhl, 2003; Roithmair, 1994b), bem como propriedades extrínsecas ao macho como tamanho, ou qualidade do território (Rocha *et al*., 2018b; Meuche *et al*., 2012).

Após a seleção inicial pela fêmea, ocorre uma corte muitas vezes longa e elaborada em que os machos utilizam sinalização multimodal com sinais acústicos, visuais e táteis que, se bem sucedidos, findam na deposição de um colóide hidrofílico espesso que envolve ovos depositados dentro do território do macho, o qual fornece cuidados paternos principalmente por meio da hidratação durante os primeiros estágios de desenvolvimento da prole (Stückler *et al*., 2019; Summers e Tumulty 2013; Montanarin *et al*., 2011; Pröhl, 2005; Lima *et al*., 2002). Portanto, o sucesso de acasalamento dos machos pode ser usado para entender quais fatores são responsáveis por potenciais assimetrias em *fitness*, bem como entender o papel da seleção sexual comumente observada em dendrobatídeos (Rocha *et al*., 2018a). Embora os sistemas reprodutivos poligâmicos e territoriais estejam sujeitos à ocorrência esporádica de táticas alternativas de acasalamento, como a ocorrência de machos satélites, em que os indivíduos adotam um comportamento parasitário ao aproveitar o esforço de outros machos para atrair fêmeas (Wells, 1977), tal estratégia raramente foi observada em rãs cuidadoras (*e.g.*, Juncá, 1996; Meuche e Pröhl, 2011; Rodrigues *et al*., 2017; Rocha *et al.,* 2018a).

A descrição geral da ecologia reprodutiva de dendrobatídeos raramente se aplica a todas as 328 espécies atualmente conhecidas do clado (Frost, 2020). As diferenças no comportamento e ecologia reprodutiva são frequentemente usadas como caracteres taxonômicos para diferenciar espécies estreitamente relacionadas, já que muitas delas são indicativas de isolamento pré-zigótico (Montanarin *et al.*, 2011; Grant *et al.*, 2017; Souza *et al.*, 2019; Rocha *et al.*, 2018). Esta grande variedade de características reprodutivas também é usada para entender as relações filogenéticas entre as espécies (*e.g.*, Santos *et al.*, 2009; Grant *et al.*, 2016) e para investigações em campos de pesquisa integrativa, como biogeografia (*e.g.*, Amézquita *et al.*, 2009) e cognição animal (*e.g.*, Ringler *et al.*, 2018; Sonnleitner, *et al.*, 2020). Dado que as rãs cuidadoras constituem um grupo modelo recorrente em estudos de biologia integrativa, os dados sobre diferentes espécies e populações são cruciais para a compreensão de questões mais amplas que requerem abordagens que envolvem múltiplos caracteres e disciplinas

Allobates Zimmermann e Zimmermann 1988 é um dos gêneros mais ricos em espécies dentro de Dendrobatidae e apresenta uma alta taxa de descrição de espécies, atualmente compreendendo 55 táxons (Frost, 2020). Essas rãs são conhecidas por não possuírem toxinas cutâneas e por apresentarem coloração opaca em contraste com as "verdadeiras" rãs venenosas, tóxicas e aposemáticas (Lötters *et al.*, 2007; Grant *et al.*, 2016; Hime *et al.*, 2020). A distribuição geográfica de *Allobates sumtuosus* (Morales, 2002) abrange habitats florestais das Amazônias peruana, brasileira, guianense e surinamesa (Simões *et al.*, 2013; Frost, 2020), embora este táxon possa conter linhagens evolutivas independentes dignas de status específico (Motta *et al.*, 2018). Como a maioria das rãs cuidadoras, *Allobates sumtuosus* são pequenos anuros diurnos que habitam áreas ripárias com poças temporárias durante a época de reprodução (Juncá, 1998; Lima *et al.*, 2012; Simões *et al.*, 2013; Jorge *et al.*, 2016). Possuem dimorfismo sexual de cor, em que machos e fêmeas apresentam ventre branco e amarelo, respectivamente (Lima *et al.*, 2012). Os machos apresentam dois tipos de canto de anúncio e a atividade de vocalização e reprodução se intensifica na estação chuvosa, com pico estimado entre março e abril (Juncá, 1998). O amplexo que antecede a oviposição é cefálico e os ovos são depositados em massas gelatinosas nas folhas caídas da serapilheira, permanecendo sob os cuidados do macho em seu território. Do ninho terrestre, as larvas são transportadas pelo pai para um corpo d'água temporário onde completam seu desenvolvimento até uma nova fase terrestre pós-metamórfica na qual esses indivíduos experimentam um crescimento corporal contínuo (Juncá, 1998; Lima *et al.*, 2012).

OBJETIVOS

Geral: Descrever o comportamento reprodutivo de *Allobates sumtuosus*, testando a influência de fatores ambientais no padrão de vocalização diário e o papel de caracteres intrínsecos e extrínsecos do macho sobre o sucesso reprodutivo.

Específico 1: Caracterizar a biologia reprodutiva de *Allobates sumtuosus*, descrevendo o tamanho corporal, comportamento de corte, acasalamento, cuidado parental, territorialidade, comportamento de macho satélite e sobrevivência da prole em condições de campo;

Específico 2: Testar o efeito do ambiente nos padrões de atividade reprodutiva, hipotetizando que a atividade diária de vocalização do macho é influenciada pela temperatura e umidade, e a atividade sazonal por parâmetros pluviométricos;

Específico 3: Testar o efeito de fatores intrínsecos e extrínsecos sobre o sucesso reprodutivo do macho com a hipótese geral de que ambas as classes preditores são determinantes para a escolha da fêmea.

CAPÍTULO 1

Sena, E.M.C.C.; Masseli, G.; Menin, M.; Lima, A.P. & Kaefer, I.L. Reproductive ecology of the poison frog *Allobates sumtuosus*: a field study of the determinants of temporal activity and male success. Manuscrito em preparação para *Ethology, Ecology & Evolution.*

Reproductive ecology of the poison frog *Allobates sumtuosus*: a field study of the determinants of temporal activity and male success

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Reproductive ecology of the poison frog *Allobates sumtuosus*: a field study of the determinants of temporal activity and male success

Abstract

Poison frogs (Dendrobatidae) show complex, elaborate, and variate breeding behaviours. Hypothesis-testing approaches are relevant to understand the effect of ecological factors on breeding activity and reproductive success under realistic, field-based conditions. In this study conducted in Central Amazonian forests during an entire rainy season, we aimed to 1) characterize the reproductive biology of *Allobates sumtuosus*; 2) test the effect of environmental cues on diel calling activity; and 3) test the effect of intrinsic and extrinsic predictors of male reproductive success. Male vocalization activity peaks in the early morning and late afternoon, and is negatively influenced by environmental temperature. There are sexual differences in behavior, size and color: males were territorial, had smaller body sizes than females, and white vocal sac and belly in contrast to females whose ventral surface was yellow. Adult individuals did not have a significant increase in body size from one breeding season to the next. Mating pairs showed an elaborate courtship behaviour during which females deserted in 71.4% of the observations. Eggs were deposited in communal nests on dead leaves on the leaf litter, and these nests contained several other spawnings, with asynchronous-developing eggs from the same, territory-owner male. Only males showed egg and larvae attendance, transporting tadpoles to waterbodies ca. 20 days after oviposition. An adult male was found near an amplecting pair inside a nest, constituting the first indication of male satellite behavior in the genus. Approximately 76% of the egg masses reached the tadpole stage and were transported. The mating call of the species is first described and consists of continuous, low-amplitude notes with irregular temporal

arrangements separated by irregular silence intervals. Male reproductive success was uneven and not predicted by body size, territory tenure, and territory size, suggesting that female choice and reproductive output do not depend on these traits.

INTRODUCTION

Poison frogs (Dendrobatoidea *sensu* Frost 2020) comprise a clade of mostly diurnal and polygamous leaf-litter species, in which environmental cues and conditions influence key reproductive aspects such as timing of breeding activity (Kaefer et al. 2012; Souza et al. 2016), reproductive output, and offspring survival (Juncá 1996; Kok et al. 2013b; Pašukonis et al. 2016). Mate selection, on the other hand, is usually performed by females that appear to rely on a series of intrinsic male traits such as body size (e.g. Arak 1988; Hettyey et al. 2009), vocal activity (e.g. Roithmair 1994b; Pröhl 2003), as well as extrinsic properties such as size or quality of male territory (Meuche et al. 2012; Rocha et al. 2018b).

After initial selection by the female, an often long and elaborate courtship takes place in which males use multimodal signalization that may include acoustic, visual, and tactile signals that, if successful, end up in the deposition of an egg-mass inside the male territory, who provides paternal care mainly through hydration during the early developmental stages of the offspring (Stückler et al. 2019; Summers & Tumulty 2013; Pröhl 2005; Lima et al. 2002). Therefore, male mating success can be used as a proxy by which to understand which factors are responsible for the potential asymmetric fitness and role of sexual selection observed in the breeding ecology of poison frogs (Rocha et al. 2018a). Although polygamous and territorial reproductive systems are subject to the sporadic occurrence of alternative mating tactics such as satellite males, in which individuals adopt a parasitic behavior when taking advantage of the effort of other males in attracting females (Wells et al. 1977), such a strategy has rarely been observed in poison frogs (e.g., Juncá 1996; Meuche & Pröhl 2011).

However, such a general description of the reproductive ecology of poison frogs rarely applies fully to all the 326 currently known species within the clade (Frost 2020).

Differences in reproductive ecology and behavior are, indeed, often used as characters to differentiate closely-related species because many of them are indicative of prezygotic isolation (Montanarin et al. 2011; Grant et al. 2017). This large array of reproductive traits is also used to understand phylogenetic relationships among species (e.g., Santos et al. 2009; Grant et al. 2016), and for integrative research in such fields as biogeography (e.g., Amézquita et al. 2009) and animal cognition (e.g., Ringler et al. 2018; Sonnleitner et al. 2020). Given that poison frogs constitute a frequent model study system in integrative biology, experimental approaches enable the knowledge about reproductive and behavioral patterns (Pašukonis et al. 2016; Ringler et al 2016a, 2013). However, laboratory conditions may create unrealistic environmental conditions that diverge from field conditions (e.g. Ringler et al. 2015, 2016b, 2017). Field studies allow the description of reproductive patterns and accurate behavioral observations in *Allobates* (e.g. Juncá 1998; Montanarin et al. 2011; Ringler et al. 2013; Pašukonis et al. 2017; Souza et al. 2017; Rocha et al. 2018). Therefore, data on different species and populations is crucial for the base-line understating of broader questions that multi-trait and cross-disciplinary approaches require.

Allobates Zimmermann and Zimmermann 1988 is one of the most species-rich genera within Dendrobatoidea, currently comprising 55 taxa, and new species are frequently described (Frost 2020). These frogs are known to lack skin toxins and to show dull coloration, in contrast to the "true" toxic and aposematic poison frogs (Lötters et al. 2007; Grant et al. 2016; Hime et al. 2020). The geographic range of *Allobates sumtuosus* (Morales 2002) encompasses forest habitats from the Peruvian, Brazilian, Guyanese and Surinamese Amazonia (Simões et al. 2013; Frost 2020), even though this taxon may contain independent evolutionary lineages worthy of specific status (Motta et al. 2018). Like most poison frogs, they are small day-active anurans that inhabit riparian areas with temporary puddles during the breeding season (Juncá 1998; Lima et al. 2012; Simões et al. 2013). They are sexually dimorphic in color, with males and females having a white and yellow belly, respectively (Lima et al. 2012). Males have two types of advertisement calls and the activity of vocalization and reproduction intensifies in the rainy season with a general peak between March and April (Juncá 1998). The amplexus that precedes oviposition is cephalic, and the eggs are deposited in gelatinous masses on fallen leaves in leaf-litter, remaining under the care of the male in whose territory they lie (Lima et al. 2012). From there, tadpoles are transported by the father to a body of water where they complete their development until a new terrestrial, post-metamorphic phase in which these individuals experience continuous body growth (Juncá 1998; Lima et al. 2012).

The knowledge about the reproductive behavior of *Allobates sumtuosus* is superficial when compared to other species of the genus, such as *Allobates femoralis,* for which the knowledge accumulated over the last decades allows for more detailed behavioral investigations (*e.g.* Ursprung et al. 2009; Ringler et al. 2012, Ringler et al. 2018; Sonnleitner et al. 2020; Fischer et al. 2020). Given the relevance of hypothesis-testing approaches to understand the effect of ecological cues on breeding activity and reproductive success under field-based conditions, our objective in this study was three-fold: 1) characterize the reproductive biology of *Allobates sumtuosus,* gaining data on aspects such as adult body growth, satellite behavior, and offspring survival under field conditions; 2) test the effect of the environment on the diel and seasonal activity patterns, hypothesizing that male calling activity is influenced by temperature, humidity, and rainfall parameters; and 3) test the effect of intrinsic and extrinsic predictors of male success with the general hypothesis that both classes of predictors are determinant for the male reproductive output.

METHODS

1. Study area

This field-based study was conducted in the Adolpho Ducke Forest Reserve (RFAD), located north of the city of Manaus, Amazonas, Brazil (59° 55" W, 2° 57" S), between January 15 and May 29, and also between 16 and 23 December 2019. The reserve consists of *terra firme* (upland) rainforest with two drainage basins with distinct physico-chemical characteristics, separated by a central plateau (Baccaro et al. 2011). *Allobates sumtuosus* occurs in greater densities in the western portion (Menin et al. 2011), where the number of isolated puddles used for the final stage of tadpole development is greater and the pH of the water is more acidic (Jorge et al. 2016). The rainy season runs from November to May, with an average annual precipitation between 165.9 and 330.1 mm, and average temperature of 26 °C (Marques Filho et al. 1981). We installed two sampling grids (1,700 m^2 each) in riparian zones with a high density of vocalizing individuals. Each grid was subdivided into 12 quadrants of 10 m^2 to allow georeferencing of individuals and of spawnings (Rocha et al. 2018a).

2. Data Collection

The vocalization cycle was defined based on daily censuses conducted outside the sample grid. Daily, five times a week, for 10 minutes every hour from 0500h to 1800h, a silently-walking researcher counted the number of males engaging in vocalization activity. Each census was carried out alternately between the two grids. We conducted 45 days of censuses between 16 January and 11 April 2019. Average temperature and humidity were measured every hour during the censuses with the aid of a thermo hygrometer. Effects of air temperature and humidity on the number of males calling per hour were tested using linear regression.

All collected individuals had the snout-vent length (SVL) measured in mm with digital calipers and, for recaptured specimens, we used paired t-test to test for body growth between two consecutive reproductive seasons. Individuals were marked uniquely by toe clipping. and returned to the original collection point (e.g., Montanarin et al. 2011; Kaefer et al. 2012; Souza et al. 2017; Rocha et al. 2018). This technique is used frequently and has been shown to not interfere with survival or recapture rate in individuals of a congeneric species, *Allobates femoralis* (Ursprung et al. 2011; Souza et al. 2017; Rocha et al. 2018a). To determine if significant differences in body size between females and males were present, we used a Student's t test.

Male territories were defined based on vocalization perches, monitored from 0500h to 1800h (GMT-04:00), five times a week during a five-month sampling period. When a male was found to be vocalizing, we captured the individual, checked the identification and marked the location with a tag containing the male identification code. Territory size was estimated using the minimum convex polygon method (Roithmair 1992; Souza et al. 2017; Rocha et al. 2018a), derived from a minimum of four distinct observation points. Measurements of distance from the perch to the two lines closest to the grid were collected, obtaining Cartesian coordinates (x, y) for each sampled vocalization point. Whenever observed, females were also marked and georeferenced.

We monitored and recorded movement and courtship behavior of all adults, females and males, and vocalization of males between 05:30 and 18:00 for 90 non-consecutive days using *ad libitum* and focal animal methods (Altmann 1974). The number of observations for each behavior (n) refers to independent observations of different individuals. Some behavioral units were observed in all individuals and, in these cases, the number of samples per unit was omitted (Rocha et al. 2018a). Visual signs were described according to the classification proposed by Hödl & Amézquita (2001), Hartmann et al. (2005) and Montanarin et al. (2011).

Courtship, mating and oviposition behaviors were observed *in situ* and described for the mean and standard deviation of their duration times, as well as visual and acoustic signals from seven couples (n = 7). Territory defense behavior was observed for all males with monitored territories (n = 64), via vocalization activity and defense posture. Aggressive interactions were described only between conspecifics, and were based on four observations (n = 4).

The number of nests, as well as number of spawnings and eggs contained within each territory, was recorded and monitored on daily visits by inspecting leaf surfaces within the leaf-litter. Each nest was marked and numbered, and the offspring development stage classified according to Gosner (1960).

All individuals found transporting tadpoles to water bodies were identified and tracked by observation, and the number of tadpoles attached to their backs was counted along with the time and distance traveled. We use mean and standard deviation to describe reproductive behaviors. We used multiple linear regression to test the relationship between abiotic factors (temperature and humidity) and male vocalization activity.

All nests were monitored until the end of offspring development (s), and classified in one of nine categories according to the final state. These were: 1. *Accident* - when spawn suffered some physical damage, for example: the nest fell, compromising the entire spawning; 2. *Unknown* - when the tadpoles and/or the nest disappeared with no evidence of transport or predation; 3. *Transport* - when tadpoles were being transported on the male's back or the nest contained evidence of transport; 4. *Predation in egg phase* - when the spawning was preyed while at the egg stage; 5. *Predation in tadpoles phase* - when the spawning was predated at the tadpole stage; 6. *Predation-army ants* - when the spawning was preyed on by army ants; *7. Washed away* - when the eggs were displaced and/or were washed away by rain, *8. Fungi* - when eggs were infested with fungi and did not develop and *9. Abandoned* - when the father disappeared, leaving the nest and spawnings unattended.

Advertisement calls were recorded using a Sony PCM-D50 digital recorder (44.1 kHz sample rate; 16-bit resolution) and a Sennheiser K6/ME66 directional microphone. Acoustic parameters were obtained using Raven Pro 1.4 software (Windows type: Blackman; size: 20.5 ms; Charif et al. 2010). Spectral measurements were taken following a fast Fourier transform with frequency resolution of 21.5 and 2048 points. Spectrogram and oscillogram graphic representations were constructed with the "Seewave" package in the R computer environment (R Core Team 2018). Temporal and spectral characteristics of notes were obtained from the second note of each call. Seven acoustic parameters were used, following Köhler et al. (2017): Call duration (CD, in s); Note duration (ND, in s); Interval between notes (IN, in s); Note modulation, as the difference between call maximum and minimum frequencies (NM, in Hz); Maximum frequency (MF, in Hz); Minimum frequency (LF, in Hz); Peak frequency (PF, in Hz).

As potential predictors of male reproductive success, we evaluated intrinsic variables body size (SVL in mm) and territory occupancy duration (in days) and, as an extrinsic variable, we considered territory area (in m^2). Male size was considered a proxy for both ability to compete for females (Wells 1977), and to produce sexual signals potentially lower-pitched and attractive to females (Kaefer & Lima 2012). Territory occupancy duration was considered a proxy for reproductive effort (Pröhl & Höld 1999; Pröhl, 2003, 2005), and territory area was considered a proxy for the provision of resources (extended phenotype) such as availability of prey and leaves for oviposition (Rocha et al. 2018b). The reproductive success response variable was assessed at four distinct levels: (1) *Number of nests*: total number of nests found in a male's territory; (2) *Number of* spawnings: total number of spawnings found in nests within the male's territory; (3) *Number of initial individuals* (initial offspring): total number of eggs found in spawning(s) of each male; and (4) *Number of final individuals* (final offspring): number of tadpoles that reached the stage where they could be transported by a parent. We used linear regression models to test the reproductive success determinants.

All analyzes were conducted in the R computer environment (R Core Team 2018), using the function "*lm.br*" (Marc Adams 2015).

RESULTS

1. ***Daily Vocalization Cycle***

Males began vocalizing in the early morning, between 05:30h and 05:50h. There were two peaks of vocal activity, at 06:00h and 17:00h. The last vocalizations of the day could be heard between 17:45h and 18:00h (Fig. 1). The number of males vocalizing at each 1-hour-interval was negatively affected by an increase of ambient temperature ($r^2 = 0.11$; $P < 0.001$), while there was no relation with humidity ($P = 0.25$). Rainfall did not affect the total vocalization activity of the day, when considering precipitation on either the day itself ($P = 0.57$), the previous day ($P = 0.92$), or the precipitation acumulated along the three previous days ($P = 0.70$).

2. *Body Size and Individual Spatial Distribution*

A total of 124 individuals were captured and marked, 37 females and 87 males. Body size varied between 13.63 mm and 16.66 mm for males (15.31 ± 0.552) (mean ± standard deviation), and between 14.35 mm and 18.22 mm for females (16.5 ± 0.885). Females were larger than males (t-test: $t = 7.541$; $P < 0.001$). Upon returning to the sampling grid in December 2019, we captured 17 individuals. Of these, six apecimens were recaptured, all males. The average time between last capture and recapture was 282 ± 15 days. Recaptured specimens after the first capture, and these did not show body-length increase between capture events (paired t-test: $t = - 0.71757$; $P = 0.5$). All recaptured males remained in the same quadrant as the previous breeding season. Females did not establish territories based on the low female recapture rate (33.8%; N of captured females = 65), thus not forming polygons inside the study grids. The size of male territories varied between 0.268 m^2 and 4.212 m^2 (1.358 ± 1.0811; N = 20).

3. *Territory Defenses and Aggressive Interactions*

Allobates sumtuosus males were highly territorial to conspecifics, but showed little or no such reactions to *Anomanoglosus stepheni*, a syntopic heterospecific from the same family. We observed a male of each species calling side by side (N = 1), however, no simultaneous nests of the two species were found in overlapping territories.

When an invader or conspecific neighbor approached the perimeter of a male *A. sumtuosus* territory, the territory holder would start emitting advertisement calls. The invading male would remain close and, facing the target territory, and also reply by emitting adversement calls. The challenged male would then issue an advertisement call in response to the invader. Both would then vocalize until the invader gave up (N = 3), or physical aggression ensued (N = 1). In this, the invader would jump to grapple with his opponent, although the territory holder could also initiate. In a single observation, the invading male was grabbed by the territory owner and lost the dispute, leaving the territory. We also observed silent males in vocalization posture, with the vocal sac partially inflated, in the presence of other males nearby.

4. *Courtship, mating and oviposition behaviors*

The courtship behaviors described below were observed for seven different couples. Males emit an advertisement call from a perch within their territory. The female approaches the male and, once at a distance some 20 to 30 cm from the male, the two begin a courtship march, during which the male walks in front of the female, apparently presenting locations for eventual mating and oviposition. Usually the chosen place consists of a dry, folded or curved leaf on the forest floor. However, it can be two or more leaves, open leaves, or green leaves (Table 1). The female decides whether to lay her eggs on the presented leaf, on another leaf, or to abandon the male. During the courtship march, the male emits an advertisement call alternating with a courtship call, a low amplitude vocalization emitted in the presence of females (see Courtship Call, below). The female can withdraw from the procession at any stage prior to amplexus, and/or change direction (N = 5). In this situation, the male stops walking and emits an advertisement call while facing the female. In all withdrawal-related observations, the male was unsuccessful in recovering the female. Upon accepting courtship (N = 2), the female moves to the leaf on which the male is located, whereupon the male emits some notes from the courtship call. The male jumps over the female and begins a cephalic amplexus (Fig. 2). The couple remains in amplexus for 30 to 40 minutes (35 min ± 2.82; N = 2). Following amplexus, eggs are deposited, along with a gelatinous substrate (a thick hydrophilic colloid). It was not possible to observe the exact moment of egg-clutch fertilization. After each recorded mating (mating N = 3), an egg-mass was formed. New spawning can be deposited on new leaves or on those already occupied by other earlier spawnings. Males continued to vocalize and mate after an oviposition event. Eggs were deposited in active nests, leaves occupied by one or more spawning, and on new leaves not previously used. Each nest contained between 1 and 5 spawnings (1.8 ± 0.98; N of nests = 70), with offspring at different stages of development.

5. *Egg Clutches and Parental Care*

Egg laying occurred from January to May with 68.6% of the events concentrated in April. In one of the observations, the female laid seven eggs in one nest, followed by 10 in another, totaling 17 eggs released in 2 distinct nests with the same male. Eggs were translucent white, with two distinct poles, the central part being black and circular with a whitish surround (Fig. 2D). The vegetative pole (black part), occupies the most space of the egg (Fig. 2D-E). After 24 hours, the gelatinous area was hydrated and the eggs were spaced further apart (Fig. 2E). Hydration is affected by the male until the embryos reach the encapsulated tadpole stage (Fig. 2F). Within three days of reaching this stage, the tadpoles move to break the capsule and leave (Fig. 2E). By day 15, the tadpoles are fully developed, but remain in the nest until the male transports them to a body of water. Tadpole transport (n= 5) was observed only in March (40%) and April (60%). To carry them, a male will sit on the until the tadpoles climb up and stick to his back. Between 3 and 7 tadpoles were transported at one time (5.8 ± 1.79, N = 5), in trips of up to 5 hours duration (N = 3). Mean distance covered by the males was 72.8 m ± 6.8 (N = 3) to pools of 136.7 ± 25.2 cm wide, 493.3 ± 75, 1 cm long and 1.36 ± 0.11 cm deep (N = 3). The mean transport time from oviposition was 20.6 ± 6.56 days (N = 25), varying between 13 and 37 days.

Males cared for 1 to 3 nests simultaneously, except for one individual who cared for 5 nests (1.4 ± 0.76; N = 45). Males that had nests with spawnings derived from more than one mating (N = 31) took care of up to 7 spawnings at the same time (3.0 ± 1.3).

6. *Indication of Satellite Behavior in* **Allobates** *Males*

During the first of two observed courtship cases, two neighboring males vied for a female. Both were simultaneously broadcasting the advertisement call ⌊07:30⌋. The male identified as MD2PE2 started a courtship walk with the female in his territory ⌊07:40⌋. A few minutes later ⌊07:42⌋, another male begins to follow the couple. During the walk, the MD2PE2 made a few pauses and emitted a few trills of advertisement call. The trio reached a rolled leaf, which MD2PE2 then positioned himself in the innermost part of ⌊07:43⌋. All three individuals then entered the rolled leaf, where they remained silent for a few minutes ⌊07:48⌋. Some low amplitude courtship trills were emitted between 07:53 am and 08:02 within the leaf. At 08:26 the curled leaf was opened by the researcher and the presence of the second male individual confirmed, indicating the occurrence of male satellite behavior or double fertilization (Fig. 3). A spawning of seven eggs had been laid on the leaf. After being interrupted by the observer, the three individuals left the inside of the leaf. Two of the three individuals, a male and a female, were identified by toe-clips as MD2PE2 and ME4PE5F, respectively. The pair went to another leaf approximately 1 m away from the first few minutes latter, where they produced a new nest, containing nine eggs.

7. *Offspring Survival*

A total of 103 spawnings were found in 70 nests of 45 different males. Of these, 76.06% of the spawnings reached the tadpole stage and were transported. Na avareg of eigh eggs were deposited in each spawning (min= 04; max= 16; mean= 8; ± 2; N =

103). The remaing embryos were consumed by predators or died for others factors (Table 1).

8. Courtship Call

The courtship call (sensu Wells 1977) was recorded for a male during the courtship process on January 24, 2019 at 17:00. The call was emitted during the courtship march (sensu Rocha et al. 2018a), and preceded cephalic amplexus. *Allobates sumtuosus* courtship call temporal structure is the same as the second type of advertisement call (sensu Simões et al. 2013), consisting of continuous notes with irregular temporal arrangements, separated by intervals of silence of varying lengths. The duration of the notes was 0.1 ± 0.04 seconds (N = 21) separated by the interval of 0.33 ± 0.17 seconds, with a minimum frequency of 5.1 ± 0.52 kHz, maximum of 7.1 ± 0.64 kHz, peak of 6.3 ± 0.22 kHz and modulation of 2.06 ± 1.02 kHz.

9. Predictors of male reproductive success

The number of spawnings laid in a nest and territory varied considerably among males: the male with the greatest mating success had seven spawnings in five different nests, totaling 65 eggs. In contrast, most males had between one and five spawnings (2.32 ± 1.29; N = 43), distributed between one and three nests (1.36 ± 0.53), with a minimum of five eggs, and a maximum of 52 eggs (13.30 ± 12.06). Body size was not determinant for the number of nests ($P = 0.17$), number of spawnings ($P = 0.20$), initial offspring ($P = 0.90$) and final offspring ($P = 0.16$). Territory size was not determinant for the number of nests ($P = 0.76$), number of spawnings ($P = 0.45$), initial offspring ($P = 0.61$), and final offspring ($P = 0.46$). This was also the case for territory occupancy duration in relation to number of nests ($P = 0.54$), number of spawnings ($P = 0.92$), initial offspring ($P = 0.85$) and final offspring ($P = 0.93$).

DISCUSSION

Allobates sumtuosus had two daily vocalization peaks, at dawn and dusk. This has also been reported for the congeners *Allobates femoralis, A. subfolinidificans* and *A. paleovarzensis* in the Brazilian Amazon (Kaefer et al. 2012; Souza et al. 2017; Rocha et al. 2018a), and for an *A. sumtuosus* population at another central Amazon location (Biological Dynamics of Forest Fragments Project - BDFFP) (Juncá 1998). This pattern is due to a negative correlation between increase of temperature, which is highest at midday, and vocalization activity. Calling is probably the most energetically expensive activity that a male frog undertakes during his lifetime (Pough et al. 1992). Therefore, environmental temperature, which affects evapotranspiration and neuromuscular activity in ectotherms (Prestwich 1994), appears to be the main modulator of daily vocalization patterns in *Allobates*, as well as many other semi-terrestrial breeding frogs (Lima et al. 2012). Given that the reproductive season of the species takes place during the rainy season (Juncá 1998, this study), subtle changes recorded here in rainfall and humidity of the studied rainforest were not factors limiting the calling activity of *A. sumtuosus*.

Even though some species of *Allobates* lack sexual body size dimorphism (e.g. Rocha et al. 2018b, Lima & Keller 2003, Simões 2016), many others have larger females (Lötters et al. 2007), as is the case with *A. sumtuosus.* Larger females are able to produce larger egg spawnings, thus fecundity might be a selective force favoring this morphological pattern (Wells 2007).

As with all known poison frogs, males of *A. sumtuosus* were highly territorial (Pröhl 2007, Souza et al. 2017, Rocha et al. 2018). However, the inter-seasonal territory permanence has rarely been reported (Montanarin et al. 2011, Kaefer et al. 2012). The male site fidelity observed in this study indicates that individuals could survive and persist locally from one rainy season to the next in central Amazonia, despite the occurrence of intermediate drier periods (Marques Filho et al. 1981). The lack of inter-seasonal body growth observed in *A. sumtuosus* suggests that adults reach maximum body sizes by the first reproductive season, as also observed for the poison frog *Ameerega trivittata* (Neu et al. 2016).

Males of *A. sumtuosus* showed high aggressiveness in territorial defense against other conspecific males, including acoustic, visual displays and combat with body contact, as reported by Juncá (1998) for another population of the species. However, the lack of aggressive behavior by *A. sumtuosus* to the poison frog *Anomaloglossus stepheni* is noteworthy. The distribution of this species is sympatric, syntopic and synchronic with *A. sumtuosus* and it makes use of similar habitat (Juncá 1996, Juncá 1998). The difference in diet and call structure may explain this seemingly harmonious co-occurrence (Lima & Magnusson 1998, Juncá 1998). In addition, it is possible that the temporal difference in the peak of reproduction between the two species (January-February for *Anomaloglossus stepheni*, April-May for *A. sumtuosus*) may alleviate any potential competition between these phylogenetically-related species.

The forms of courtship, breeding and oviposition behaviors observed in the current study are broadly similar to those reported for another population of the same species in Central Amazonia (Juncá 1998). The high rate of unsuccessful courtships observed by us and other studies with *Allobates* (Rocha et al. 2018) indicates that females assess various males before deciding with whom to copulate. The occurrence of two egg-masses at different stages of development in the same nest was reported only on one occasion by Juncá (1998), while in our study we observed a large number of nests with multiple spawnings in asynchronous development, reaching up to five spawnings in concomitant development within the same nest. This reveals that *A.*

sumtuosus has a very unusual oviposition behavior, previously unreported among poison frogs (Lötters et al. 2007), which was detected in our study probably due to the larger number of sampled nests.

Egg mass deposition by *A. sumtuosus* was temporally localized in a narrow rainy season window (April), and this probably favored the occurrence of nests with multiple spawnings. In the current study, the number of eggs per spawning varied from four to 16, with the exception of one that had only two eggs, probably due to predation before the identification of this spawning. Juncá (1998) reported between six and 14 eggs, though this may be due to the smaller number of samples.

While we observed that parental care was exclusively conducted by males, Juncá (1998) reported transport of tadpoles by females in another *A. sumtuosus* population. This was probably a case of occasional compensatory flexibility in cases of paternal desertion/death, similar to that observed in *Allobates femoralis* in French Guiana (Ringler et al. 2015) and *Allobates subfolionidificans* in Brazil (Souza et al. 2017). The type of care provided by parents before transportation is still poorly-known for most poison frogs (Lötters et al. 2007, Rocha et al. 2018b). However, in the current study we found evidence of post-spawn egg-mass hydration by the father (Fig. 2F), followed by this male remaining for a while with his body positioned directly over the spawning.

The following by a male individual of a couple on courtship march, followed by his entering and remaining at the site where the couple performed amplexus, is strongly indicative of the occurrence of satellite male behavior in *A. sumtuosus*. It is possible that this monitoring is an attempt by the male to intercept the female in the courtship process or even to fertilize the egg mass after it has been laid, thus indicating spawning piracy (Vieites et al. 2004). However, genetic analyses are needed to test these hypotheses.

Even though the occurrence of satellite males is widespread in frogs from a wide variety of phylogenetic groups and mating systems, this alternative tactic has never before been observed in the genus *Allobates* (Wells 1977, Lötters 2007).

About three quarters of the spawnings survived until the phase where they were transported to a body of water. Data on spawning survival in dendrobatids in the natural environment are rarely reported (Rocha et al. 2018) but, as observed in the present study, predation appears to be the major source of mortality in periods of normal rainfall (see also Juncá 1996). However, climatic anomalies, such as increased or reduced rainfall, are likely to affect anuran reproduction negatively and constitute a significant source of mortality for terrestrial and semi-terrestrial breeding frogs (Evans et al. 2020).

Following the pattern widely observed within the family (Lima et al 2002; Toledo et al. 2004), the *A. sumtuosus* courtship call consists a notes of low frequency, that sound like grunts with a rhythm similar to the advertisement call, but with lower spectral characters than advertisement call second type (Juncá 1998; Simões et al. 2013). Normally the courtship call is emitted by the male when close to the female, and when inside the nest, moments before amplexus (Costa & Dias 2019; personal observations). The negative relationship between spectral frequency and body size (Wells 1977) suggests that advertisement calls are a dishonest signal, simulating larger male body size during the courtship process (Kaefer & Lima 2012).

The reproductive success of males of *A. sumtuosus* showed great inter-individual variation, which has also been observed for the poison frog *Oophaga pumilio* (Pröhl & Hödl 1999), and such asymmetry suggests a strong role for sexual selection in the evolution of the studied species mating system, which can be classified as promiscuous, since individuals of both sexes copulate with multiple partners across the reproductive season (Stückler et al 2019). None of the analyzed predictors affected the various mating success and reproductive success metrics considered in the current study. Other anuran species are known to have reproductive success related to intrinsic and extrinsic factors such as: 1) body size, which influences spectral characters of acoustic sexual signals and provides clues to the individual quality, since large size in a male reflects good nutrition up to the current point in life (e.g. Orense & Tejedo-Madueño 1990); 2) territory size, which can be considered as a proxy for the provision of such resources as nesting sites (e.g. Rocha et al. 2018b); and 3) territory tenure, that may be used by females as a cue to mate choice as it indicates competitive potential and male quality (e.g. Pröhl 2003), while for other species male reproductive success is apparently not affected by any of the analyzed factors (Ursprung et al. 2011, Meuche et al. 2013, this study). The sedentary behavior of the *Allobates* females indicates that they do not spend time and energy actively looking for a partner (Ursprung et al. 2011, Fischer et al. 2020), thus probably mating with the nearest male. Our results open-up the possibility that *A. sumtuosus* females are non-choosy, as suggested for *Oophaga pumilio*, where male selection by females is not based on any attribute, and the mating occurs with the male who is nearest (Meuche et al., 2013). This has also been suggested for females of a congeneric, *A. femoralis*, who were considered non-choosy and sedentary, spending most of their time in the centers of their own home ranges (Ursprung et al. 2011, Ringler et al. 2012, Fischer et al. 2020). This suggests that, in some species of poison frogs, male territory location is directly related to reproductive success with males being more likely to mate simply because they are closer to areas of high female density (Meuche et al. 2013).

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FIGURE AND TABLE CAPTIONS

Fig. 1. — Mean number of vocalizating *Allobates sumtuosus* males per hour throughout the day at a forest site in Central Amazonia (n = 359). Vertical bars indicate the standard deviation, while horizontal bars indicate maximum and minimum values for the time.

Fig. 2. — Stages of the reproductive cycle of *Allobates sumtuosus* in Central Amazonia. (A) Male of A. sumtuosus vocalizing on a leaf. (B) Female heading to the male's territory. (C) Amplexus. (D) Egg-mass just after oviposition, in a leaf nest. (E) Egg-mass after hydration, performed by the male. (F) Spawn in the free tadpole stage. (G) Male transporting tadpoles to a body of water. (H) Male releasing tadpoles into a body of water.

Fig 3. — Pair of *Allobates sumtuosus* in amplexus in the presence of a satellite male (at the front).

Fig. 4. — Spectrogram and oscilogram of *Allobates sumtuosus* courtship call, recorded in Reserva Florestal Adolfo Ducke at 17h00 on January 24 2019.

Fig 5. — Histogram of the number of egg-masses per *Allobates sumtuosus* male.

Tabela 1. Survivorship and percentage causes of loss in *Allobates sumtuosus* spawnings (n= 105) in central Amazonia.

Figure 1

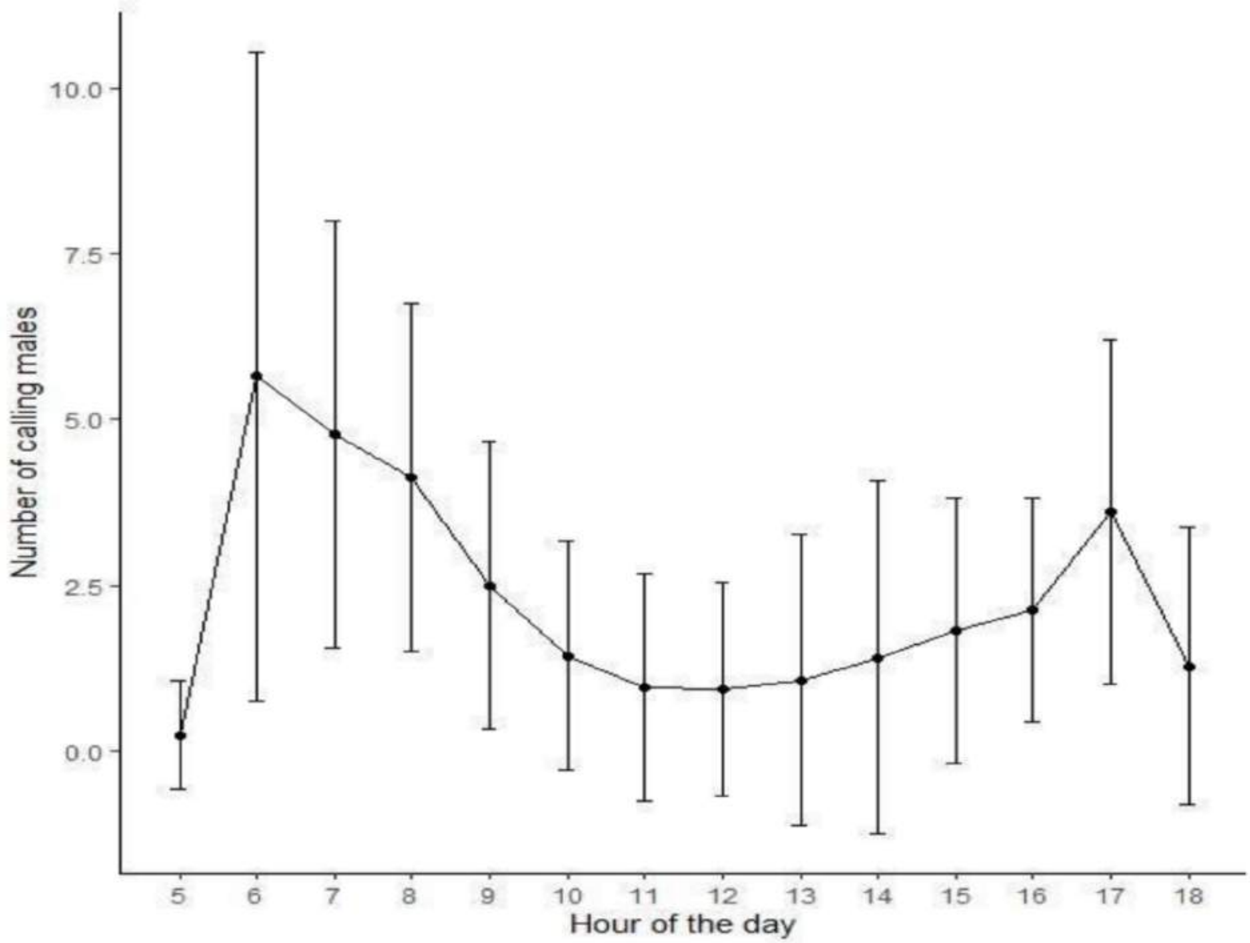
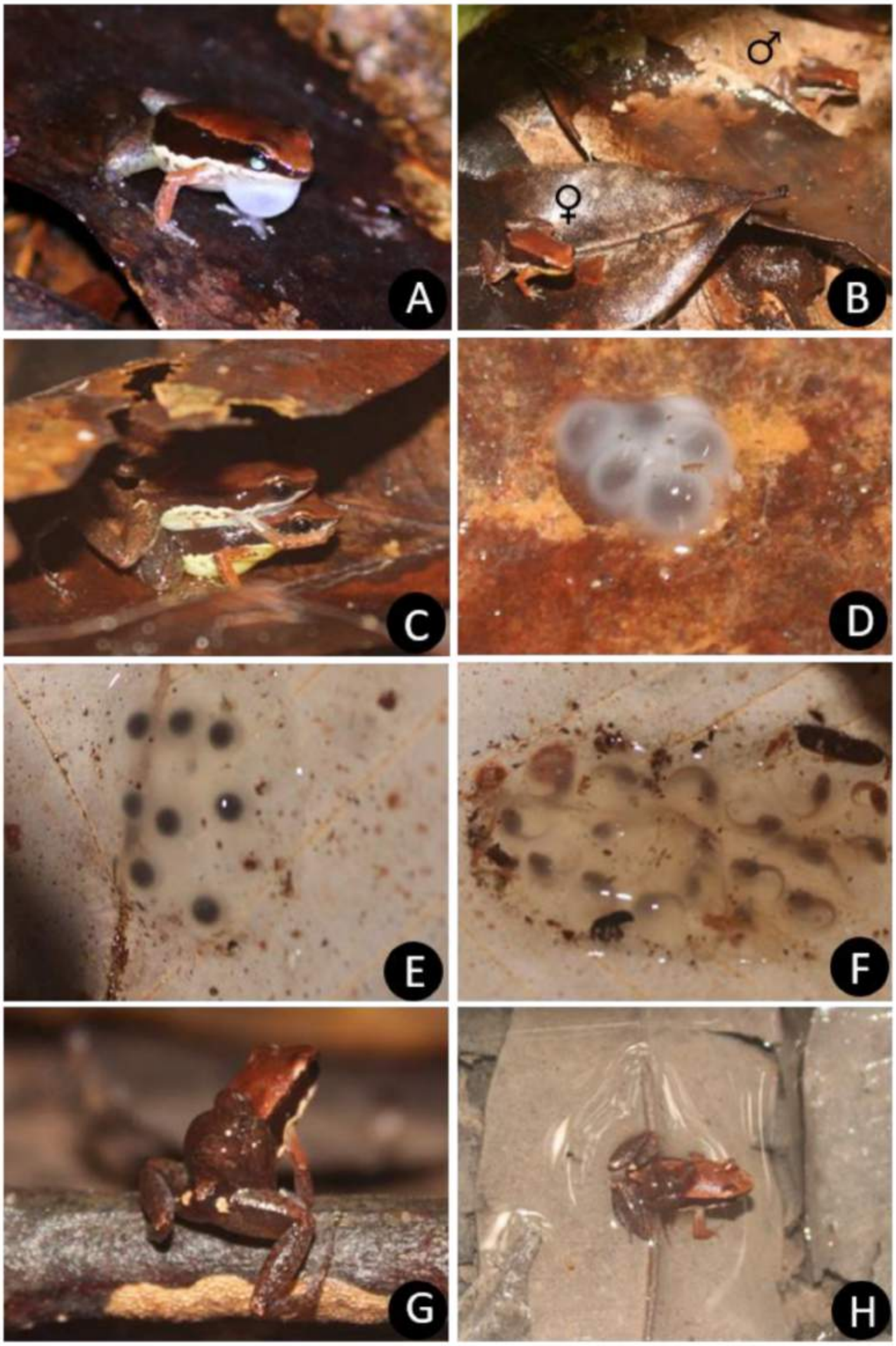


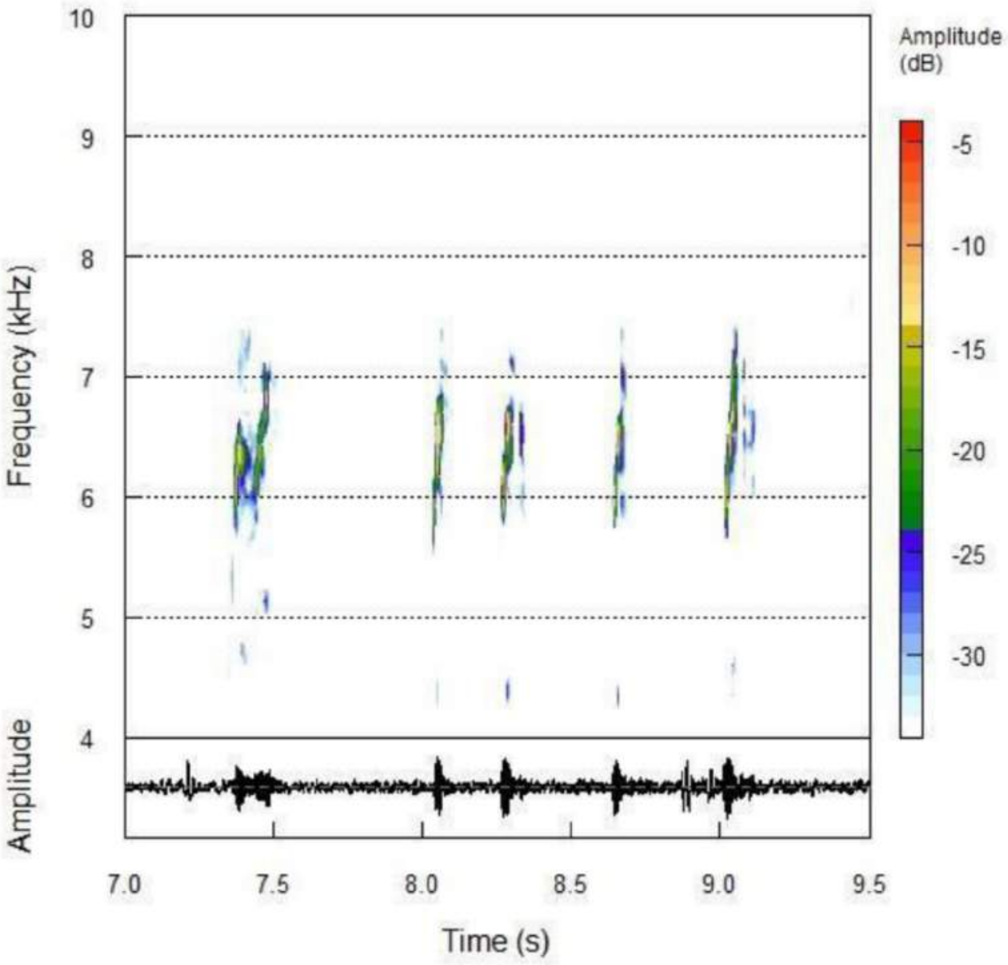
Figure 2



A
♂
♀
B
C
D
E
F
G
H

Figure 3

Figure 4



Amplitude (dB)
-5
-10
-15
-20
-25
-30
Frequency (kHz)
10
9
8
7
6
5
4
Amplitude
7.0
7.5
8.0
8.5
9.0
9.5
Time (s)

Figure 5

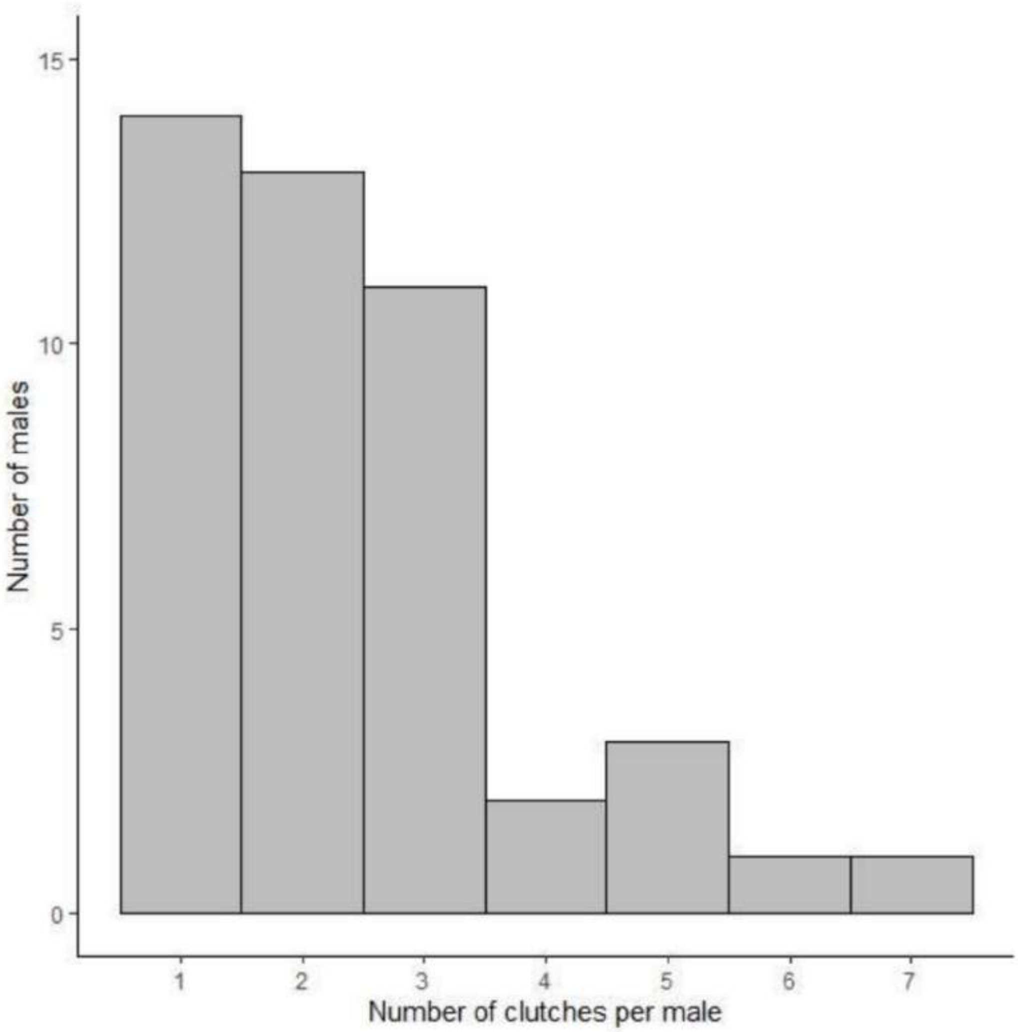


Table 1

Offspring final status	**%**
Accident	1.41
Unknown cause	7.04
Transported	76.06
Predated in the egg phase	1.41
Predated in the tadpole phase	7.04
Predated by amy ants	1.41
Washed away (by rain)	1.41
Fungal attack	2.82
Abandoned	1.41

CONCLUSÕES

- O padrão diário de vocalização de *Allobates sumtuosus* tem relação negativa com a temperatura ambiental;

- Adultos apresentam dimorfismo sexual de tamanho, sendo as fêmeas maiores que os machos e a não detecção de crescimento corporal inter-sazonal sugerindo que adultos atingem o tamanhos corporais máximos ainda na primeira estação reprodutiva;

- Os machos são territorialistas, mantendo seus territórios por mais de um período reprodutivo;

- Há indícios de ocorrência de comportamento de macho satélite em *Allobates;*

- O canto de corte de *A. sumtuosus* consiste em notas com arranjos temporais irregulares com frequência pico de 6.3 kHz;

- A deposição de ovos em *A. sumtuosus* foi concentrada no mês de abril;

- Cerca de três quartos das desovas sobreviveram até a fase de transporte a um corpo d'água;

- O sucesso reprodutivo foi altamente variável entre machos, e nenhum dos preditores intrínsecos ou extrínsecos considerados explicou tal variação.

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