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Complex courtship of *Bokermannohyla capra* (Anura: Hylidae), a treefrog that inhabits lotic environments

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Abstract

Complex courtship of *Bokermannohyla capra* (Anura: Hylidae) a treefrog that inhabits lotic environments. *Bokermannohyla capra* is an endemic species of the Atlantic Forest whose biology and ecology are poorly understood. We studied the reproductive behavior of this species in an ecotonal Atlantic Forest–Caatinga area in south-central Bahia state. We collected data on habitat use, courtship, and calling behavior. Males of *Bokermannohyla capra* were observed calling at night, peaking between 19:00 and 21:00 h. We recorded reproductive activity in *B. capra* non-continuously throughout the period of the study, from February 2020 to September 2021, both in dry and rainy seasons. The number of males calling ranged from one to nine individuals. The vocalization microhabitat is vegetation along stream banks, but the species also uses bromeliads as vocalization sites and shelter. *Bokermannohyla capra* has an elaborate courtship with acoustic, tactile, and visual signals. The male guides the female to the spawning site, where they perform axillary amplexus; oviposition occurs in small puddles along stream banks. Like many species of the Cophomantini tribe, *B. capra* also displays a repertoire of elaborate reproductive behaviors related to the occupation of lotic and noisy permanent environments. The data presented here expand our knowledge about the ecology and reproductive biology of *B. capra*. Our results also contribute to the knowledge of the taxonomic group to which the species belongs.

Keywords: Amphibians, Behavior, Communication, Cophomantini, Ecology, Reproduction.

Resumo

Corte complexa de *Bokermannohyla capra* (Anura: Hylidae), uma perereca de ambientes lóticos. *Bokermannohyla capra* é uma espécie endêmica da Mata Atlântica cuja biologia e ecologia ainda são pouco conhecidas. Para entendermos as características do seu comportamento reprodutivo, estudamos uma população da espécie em uma área ecotonal entre Mata Atlântica e Caatinga no

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centro-sul do estado da Bahia. Nós coletamos dados sobre os aspectos comportamentais de *B. capra*, incluindo informações sobre o uso do habitat, corte e vocalizações. Os machos de *B. capra* foram observados em atividade de vocalização noturna, com pico entre 19:00 e 21:00 h. A atividade reprodutiva foi registrada de forma não contínua durante todo o período de estudo (fevereiro de 2020 a setembro de 2021), tanto em meses considerados secos como em meses considerados chuvosos. O número de machos vocalizando variou de um a nove indivíduos. O micro-habitat de vocalização é a vegetação ao longo das margens dos riachos, mas a espécie também usa bromélias como local de vocalização e abrigo. *Bokermannohyla capra* apresenta uma corte elaborada com sinais acústicos, táteis e visuais. O macho guia a fêmea até o local de desova, onde realizam um amplexo axilar; a oviposição ocorre em pequenas poças ao longo das margens dos riachos. Como muitas espécies da tribo Cophomantini, *B. capra* também apresenta um repertório de elaborados comportamentos reprodutivos relacionados à ocupação de ambientes permanentes lóticos e ruidosos. Os dados aqui apresentados contribuem para a expansão do conhecimento sobre a ecologia e biologia reprodutiva de *B. capra*. Nossos resultados também enriquecem o conhecimento do grupo taxonômico ao qual a espécie pertence.

Palavras-chave: Anfíbios, Comportamento, Comunicação, Cophomantini, Ecologia, Reprodução.

Introduction

Natural history of a species includes data on its environmental use, diet, seasonality, population density, and reproductive cycle (Donnelly and Guyer 1994, Gally and Zina 2013, Almeida *et al*. 2019, Faraulo and Zina 2019, Oliveira *et al.* 2021). Reproduction is a crucial aspect that modulates a number of these descriptors, from the use of the environment to how species are distributed spatiotemporally within their range (Wells 1977, Donnelly and Guyer 1994, Pombal *et al*. 1994), which is particularly perceptible in taxonomic groups showing high reproductive diversity such as frogs (Haddad and Prado 2005).

In anurans reproduction is strongly influenced by both intrinsic factors (e.g., physiology and anatomy) and extrinsic environmental conditions (e.g., climate) (Pombal and Haddad 2005). Abiotic variables such as temperature, humidity, light intensity, and the availability and permanence of water bodies commonly regulate the duration and intensity of reproductive cycles (Rome *et al*. 1992, Stebbins and Cohen 1997, Wells 2007), as well as the selection of calling and oviposition sites (Duellman 1985, Resetarits Jr. 2005, Silva and Giaretta 2008). Given the close relationship between reproductive traits and climatic variability, most frog species exhibit a seasonal reproductive pattern (Wells 1977), with breeding activity typically triggered by the onset of optimal abiotic conditions that enhance the survival and development of eggs and tadpoles (Wells 2007).

Reproductive strategy can be defined as a combination of physiological, morphological, and behavioral attributes that act together to optimize the offspring number under certain environmental conditions (Duellman and Trueb 1994). Such strategies involve the stimulation of the partner (Lantyer-Silva *et al*. 2014, Cayuela *et al*. 2017, Dias *et al.* 2021), which occurs through signals emitted by individuals capable of promoting a change in the behavior of the receptors when courting (Hebets and Papaj 2005, Zina and Haddad 2007, Lima *et al.* 2014, Centeno *et al*. 2015, de Sá *et al.* 2016).

Acoustic signaling is the primary mode of communication mediating intraspecific interactions in most anuran species (Ryan 2001, Alcock 2009), with the advertisement call being the most frequently emitted vocalization (Narins *et al*. 2006). Due to its species-specific nature, the advertisement call serves a dual function: it acts as a key mechanism for prezygotic reproductive isolation and constitutes a valuable taxonomic tool (Martins and Jim 2003, Köhler *et al*. 2017, Forti *et al*. 2019). While certain call traits display phylogenetic conservatism, others are modulated by the environmental context in which populations occur (Gingras *et al*. 2013, Zina and Haddad 2007). Variations in temporal and spectral parameters—such as the number of pulses per note and per call, note and call duration, inter-note intervals, and dominant frequency—may reflect population-specific characteristics (Napoli and Pimenta 2009), thereby contributing to a deeper understanding of the biogeographic and evolutionary history of taxa.

Courtship behavior is an interaction between a female and a male, usually resulting in females evaluating their partner before amplexus and oviposition (Zina *et al*. 2007, Lantyer-Silva *et al.* 2014). Courtship behavior patterns and complexity vary in social organization, reproductive period, and phylogeny (Zina and Haddad 2007, Centeno *et al.* 2015, Nali *et al*. 2022). In anurans, such behaviors generally include chemical, tactile, acoustic, or visual stimuli (see Zina and Haddad 2007, de Sá *et al.* 2016). The combined use of two or more types of these stimuli is called multimodal communication (Preininger *et al.* 2013, de Sá *et al.* 2016) and reinforces a message by exploring more than one sensory channel (Preininger *et al.* 2013, de Sá *et al.* 2016). The use of multimodal communication can facilitate mating by promoting a more accurate location of the partner or the area prepared by a male (see Haddad and Sawaya 2000, Zina and Haddad 2007).

Although we have several records of courtship behavior for some species of Cophomantini (Zina and Haddad 2007, Nali *et al*. 2022), this type of study is rare due to the sporadic nature of observing such behaviors. Observation of courtship behavior requires extensive field observations or favorable conditions that allow similar behaviors to be observed in a laboratory setting as reported for *Bokermannohyla ibitiguara* (Cardoso, 1983) by Nali *et al*. (2022), one of the few documented studies for this genus.

The genus *Bokermannohyla* currently comprises 31 species (Frost 2024), most of which inhabit lotic environments, generally at low population densities (Napoli and Pimenta 2009). Several species within the genus exhibit elaborate courtship behaviors (Nali and Prado 2012, Centeno *et al*. 2015); however, such behaviors remain undescribed for many others. *Bokermannohyla capra* Napoli and Pimenta, 2009 is geographically restricted to small forest fragments at high elevations in the Atlantic Forest of south-central Bahia (Frost 2024), where it occurs at low densities, typically utilizing vegetation along margins of small streams (Napoli and Pimenta 2009). Due to its narrow geographic range and low population density, *B. capra* is highly susceptible to the impacts of anthropogenic activities, particularly those related to land-use change, habitat fragmentation, and habitat loss (Napoli and Pimenta 2009). The lack of ecological and behavioral data, including aspects of its natural history, hampers a reliable assessment of the conservation status of this species.

Herein, we describe the reproductive behavior of *B. capra,* report information on its use of the environment, seasonality, and attributes of the advertisement call. Our data increases our understanding of the biology of this species and others in the genus, thus allowing the formulation of hypotheses about the evolution of some aspects of their natural history.

Materials and Methods

Study Site

The study was carried out in Morro do Mara (MM) (13°53'42.72" S, 39°57'35.64" W), an Atlantic Forest–Caatinga ecotonal and mountainous area in central-southern Bahia, located at the municipality of Jequié, northeastern Brazil (Figure 1). MM is a forest fragment situated at one of the highest elevations in the region, ranging from 560 to 960 m and covering an area of approximately 6.5 km². Unlike the

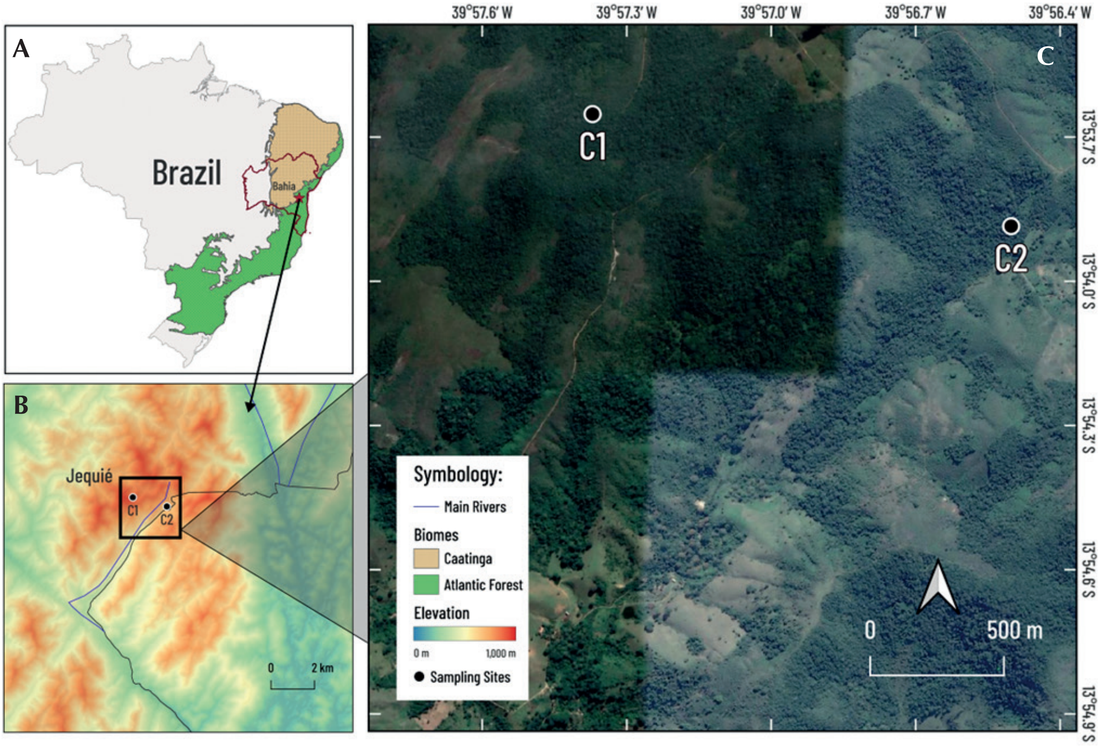

Figure 1. Location of the study area (red star in A). (**A**) General representation of Brazil and the state of Bahia with the presence of the Caatinga (brown) and Atlantic Forest (green) biomes (Source: Google Earth); sampling sites C1 and C2 in Morro do Mara with altimetry (**B**) and satellite view (**C**).

surrounding landscape, the study site remains one of the few areas in the municipality that is still minimally impacted by anthropogenic activities such as agriculture and livestock farming. Although the regional climate is classified as semi-arid, the area lies in a transitional zone, resulting in climatic variability across its breadth. The site includes both lentic and lotic water bodies, ranging from streams to seasonally flooded areas such as swamps and temporary puddles.

In the study area, we monitored two streams and their surroundings: stream 1 (C1), located at 882 m altitude, and stream 2 (C2), located in a lower area, at 675 m a.s.l. (Figure 1). In both locations, the species was recorded in a previous study (Bastos and Zina 2022). Locality C1, where we observed courtship behavior, has a large amount of leaf litter, large trees, and dense vegetation (Amaryllidaceae, Asteraceae, Cyperaceae, Poaceae, and Bromeliaceae). The stream, which is next to a 2.5 m wide road, has crystal clear water ranging in depth from 10 to 40 cm with a sandy bottom and slow flow. Throughout the study, we monitored a 10m length of the stream, which was 2 m wide. C2 is also located in a forest environment and has dense, arboreal vegetation along its margin (Fabaceae, Rubiaceae, Asteraceae, and Pteridophytes), with the presence of large trees. Along the stretch where observations were made (20 m), the stream has a depth ranging from 20 to 80 cm, a maximum width of 6 m, a sandy and rocky bed, and slow flow.

During the study period, field-measured temperatures ranged from 17 to 24°C. The coldest months of the year were May to September, during which the average monthly rainfall was lower, ranging from 32 to 50 mm precipitation. This rainfall data is based on a ten-year average obtained from Proclima/CPTEC/INPE (2021).

Data Collection

We visited the sampling sites 10 times from February 2020 to September 2021 (not continuously), with one or two visits per month. The field observations started around 18:00 h, ending when vocalizations decreased (between 22:00 and 23:00 h), totaling about 60 hours of observation. To locate individuals, we used visual and acoustic cues at breeding sites (see Heyer *et al.* 1994). For behavioral observations, we observed focal animals (e.g., Altman 1973, Lehner 1996) using flashlights at low intensity to reduce the amount of light and possible interference in the behavior of the observed individuals.

We collected the following information during sampling: characteristics of vocalization and reproductive sites (height and type of vegetation used as perch), vocalization shift, number of calling males, the distance between calling males, air temperature, and relative humidity. We measured the height of vocalization sites with a tape if it was under 2 m, or we visually estimated heights greater than 2 m. We sacrificed two individuals using 5% lidocaine, which were later fixed in 10% formaldehyde and preserved in 70% alcohol. These specimens were placed in the zoological collection of the Universidade Estadual do Sudoeste da Bahia (UESB)-Campus Jequié (catalog numbers: MHNJCH 00001644; MHNJCH 00001645). A clutch of eggs was collected, fixed, and preserved (cataloged in the zoological collection of UESB-Jequié MHNJCH 00001642), and the eggs were counted using a magnifying glass. We measured the snout–vent length (SVL) of individuals collected in the field using a caliper with an accuracy of 0.1 mm.

Analysis of Calls

Advertisement calls of *B. capra* were obtained using a Marantz® digital recorder (model PMD660) with a coupled Sennheiser® directional microphone (model ME66). Calls were analyzed using software Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics, 2024) with window type = Hann, window size = 12 samples, 5 AVE rate 44.1 kHz, 16-bit precision, and overlap = 75%. Air temperature and relative humidity were measured immediately after all recordings using a thermohygrometer (Incoterm). The recorded calls were categorized according to the social context following Toledo *et al.* (2014). We recorded the time when the vocalization started until it ended or until the point when the interval between calls became sufficiently long, indicating the impending cessation of activity. We analyzed the following temporal and spectral parameters of the calls: pulse number (PN), interval between pulses (IP), note duration (ND), interval between notes (IN), dominant frequency (DF), and frequency amplitude (FA). The units of analysis for vocalizations follow the terminology proposed by Napoli and Pimenta (2009) for *B. capra.* The beginning and end of each note were determined from oscillograms.

Statistical Analysis

To determine whether reproductive activity is seasonal, we analyzed differences in the number of vocalizing males across seasons (dry and rainy). Months were grouped by season, and an Analysis of Variance (ANOVA) was performed. To assess the effect of climatic variables on the number of vocalizing males, we used a generalized linear mixed model (GLMM) with a Bayesian approach, incorporating the Markov Chain Monte Carlo (MCMC) method. This method allows us to incorporate the seasonal effect in the model as a random effect, thereby removing the influence of the collection station from the regression parameters we wish to

Table 1. Regression coefficients from the Generalized Linear Model (GLM) assessing the effect of climatic variables (temperature and relative humidity) on the number of vocalizing males. PM: Posterior Mean; L95%-CI: Lower Credible Interval; U95%-CI: Upper Credible Interval; ES: Effective Sample Size; pMCMC: Bayesian p-value; * Significant at $p < 0.05$; ** Significant at $p < 0.01$.

	PM	L95%-CI	U95%-CI	ES	pMCMC
(Intercept)	1.884.359	520.199	3.167.845	1914	0.0144 *
Temperature (°C)	-35.265	-67.010	-4.202	1250	0.0368 *
Relative air humidity (%)	-14.461	-24.036	-5.599	1250	0.0080 **

estimate (Sun *et al.* 2000). The analysis was performed with 1,500,000 interactions, 250,000 interactions as burn-in and a sampling interval (thinning) at every 1000 interactions. Non-informative priors were assumed for the variance and covariance matrices of fixed (V), random (G), and residuals (R) effects. Descriptive statistics, model summaries, and convergence tests were performed from a sample of 1250 chains obtained using software R (version 4.3). All parameters converged (Geweke, $p > 0.05$), and the chains passed the seasonality test.

Results

Habitat Use and Seasonality

We only recorded *Bokermannohyla capra* in lotic environments at MM; therefore, these environments were selected for monitoring and sampling. We recorded males of *B. capra* calling from the ground and, more commonly, perched on branches in vegetation along the margins of streams. The highest calling perches (6 m) were recorded in the warmest and wettest months of our sampling (Figure 2). During the driest and coldest months of the year, we observed the use of epiphytic bromeliads as vocalization sites at the lowest elevations (3–4 m). Because bromeliads were at a minimum height of 3 m, it was not possible to observe which portion of these plants were used for calling activity.

Individuals called at night, with a peak between 19:00 and 21:00 h. The number of frogs calling at the same time ranged from one to nine individuals (Figure 3), and the distance between males varied from 3 to 7 m. Males of *B. capra* called throughout the study period; however, two peaks occurred in the number of individuals, one in February 2020 (nine individuals), a rainy month, and the other in September 2021 (eight individuals), a dry month. In the GLMM analyses all parameters were significant (Table 1). The negative slope for temperature indicates that the number of observed individuals decreases with the increase in temperature (Figure 4). Population density did not differ between seasons (Table 2), and it appears that there is no relationship between the highest records and the measured factors. Although the model suggests a decrease in the number of individuals observed as temperature and humidity increase, the empirical data suggest the opposite, with the highest number of records in the hot and rainy season.

Table 2. Descriptive statistics of male incidence and climatic variables collected in Morro do Mara, municipality of Jequié, state of Bahia. The values represent the mean ± standard deviation. ^{a}Treatments followed by the same letter do not differ statistically. Numbers of males (GLM, p = 0.303). Temperature (ANOVA, p = 0.08). Humidity (ANOVA, p = 0.353).

	Rainy season	Dry season
Number of males	4 ± 3.082^{a}	2.8 ± 3.033^{a}
Temperature (°C)	21.74 ± 2.173^{a}	18.86 ± 2.408^{a}
Relative Air Humidity (%)	73 ± 10.44^{a}	79.2 ± 9.418^{a}

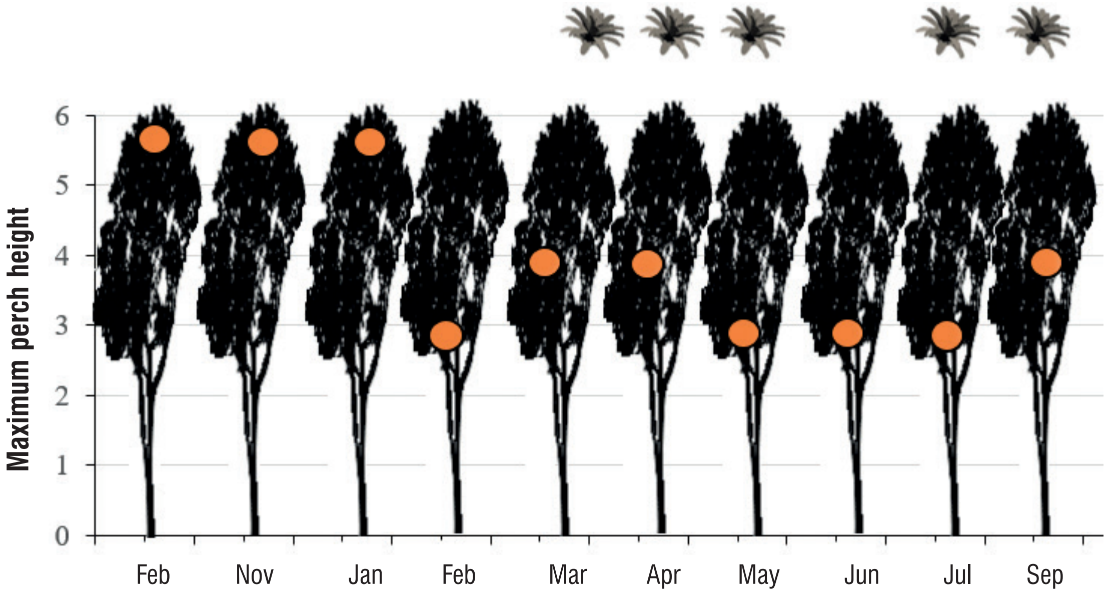

Figure 2. Perch height and use of bromeliads by *Bokermannohyla* from February 2020 to September 2021 in Morro do Mara, Jequié municipality, state of Bahia, Brazil.

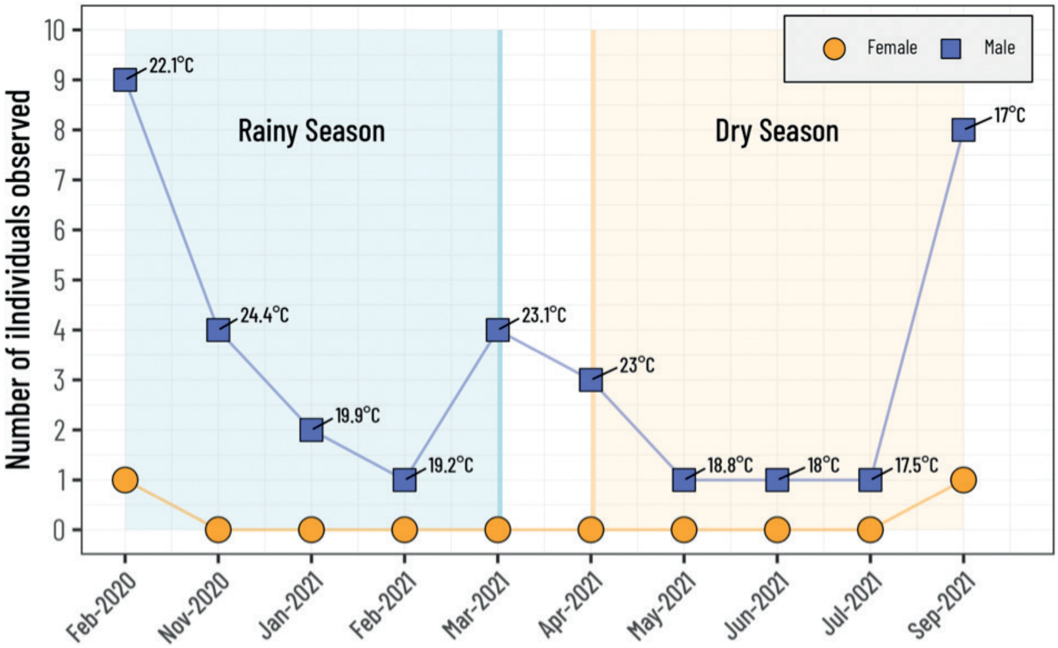

Figure 3. Vocalizing males and females observed in the stream studied from February 2020 to September 2021. Morro do Mara, municipality of Jequié, state of Bahia, Brazil.

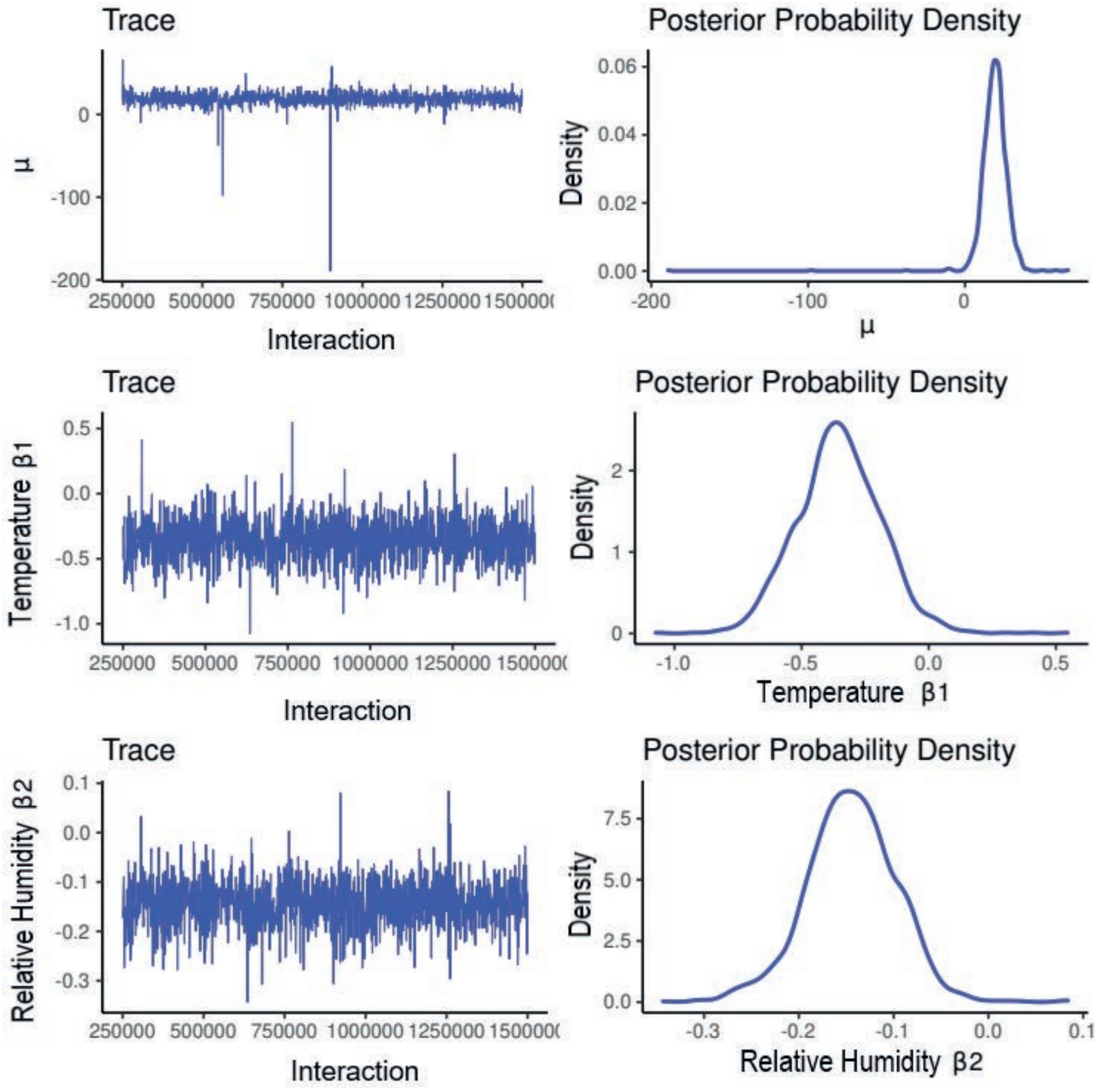

Figure 4. Temperature and humidity parameters indicating that the number of individuals observed decreases with the increase in the magnitude of the two variables. Data collected in Morro do Mara (MM), 20 km from the municipality of Jequié, state of Bahia, Brazil.

Reproductive Behaviors

We observed three courtship interactions (September 2018, February 2020, and September 2021), all of which occurred during nights without rain. The first courtship interaction took place before the sampling period of this study. Only one of the three observed courtship interactions was monitored from the beginning, but this event was unfortunately interrupted by the fall of a tree branch, so it was not carried out until the end.

The other two courtship interactions were observed during their course, one of them being observed to the end. Due to the small sample size, it was not possible to evaluate or even measure the possible selection criteria used by females. All courtship interactions were observed in stream C1, close to the male's vocalization site. In both sampling sites (C1 and C2), we observed tadpoles of *B. capra* attached to rocks and foraging under them. We did not observe aggregation of these tadpoles; only one or two were observed per visit.

The sequence of reproductive behaviors observed during the monitored events can be summarized as follows: at first, the male emitted the advertisement call, with the female perched on a branch close to the male's vocalization site. The male called for a maximum of 50 minutes and then descended from the calling site (bromeliad or tree) and moved closer to the female, positioning himself on the same branch (Figure 5A). After remaining in this position, the male jumped to a smaller branch closer to the ground. The female remained in the same position for a maximum of 40 min, thereafter jumping onto the branch with the male and facing him with her body extending forward. (Figure 5B). A few minutes later, the male jumped to the ground and walked toward the stream (Figure 5C), while being followed by the female (see Figure 5D). Subsequently, the male moved toward a small artificial puddle created by a cattle footprint (approximately 15 cm in diameter and 10 cm in depth) near the stream. At the puddle, the male emitted what we considered a courtship call (an unrecorded vocalization but sounding similar to the advertisement call). The male was immediately followed by the female. The male grabbed the back of the female, positioned himself in the opposite direction to her, and turned three times on the female (Figure 5E). Finally, the male held the female below the axilla, resting his legs over the female's legs, and engaged in axillary amplexus (Figure 5F). After oviposition, the female made quick movements with her legs to arrange the eggs. Amplexus lasted a maximum of 10 minutes. After oviposition, the female and the male separated, neither remaining at the spawning site. The female exited the spawning site first. We collected the egg mass and counted a total of 290 eggs. The eggs are pigmented at the animal pole, exhibiting a whitish cream color at the vegetative pole, each surrounded by a gelatinous capsule.

Courtship events were observed at the same time as territorial and acoustic interactions between males were also recorded. Both occurred on days with the highest density of vocalizing males ($N = 11$, $N = 9$, and $N = 8$, respectively, September 2018, February 2020, and September 2021).

Vocalizations

Calls of three individuals were recorded, totaling 20 analyzed calls. The majority of the analyzed recordings seemed to be the "type B" advertisement call, with rare emissions of call types A and D (sensu Napoli and Pimenta 2009). The advertisement call (Figure 6) is composed of multi-pulsed notes with 3–4 groups of pulses. The calls were emitted both in the presence and absence of females and were characterized as follows: pulse number of 56━111 pulses; interval between pulses of 0.009–0.08 s; note duration of 0.353–0.513 s; interval between notes of 0.825–5.554 s; dominant frequency 1.38–1.72kHz, and frequency amplitude of 0.89–2.52kHz.

In the field, we observed acoustic interactions between neighboring males that were up to 50 cm apart. Although we did not record these interactions, both males emitted calls similar to the advertisement call of *B. capra,* but shorter in duration. The interaction did not escalate into physical combat, and one of the males ceased calling. Males did not respond acoustically to playback experiments, but one individual did move toward the recorder.

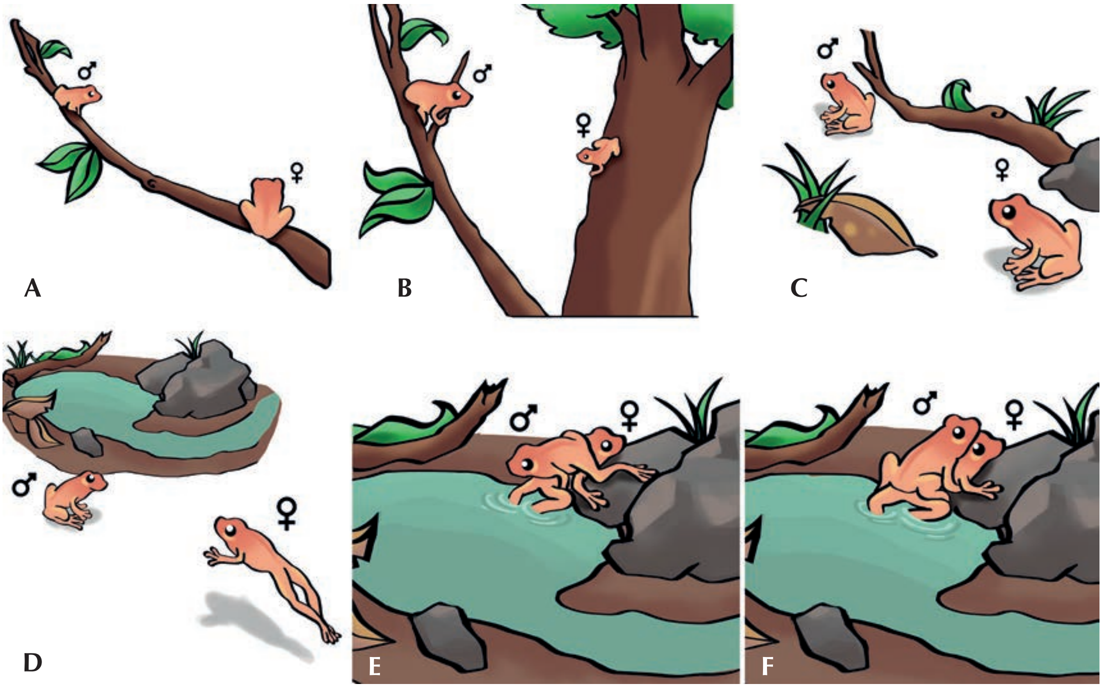

Figure 5. Reproductive behavior of *Bokermannohyla capra* recorded in Morro do Mara (MM), 20 km from the municipality of Jequié, State of Bahia, between 2020 and 2021. (**A**) The male emitted a courtship call directed toward the female; (**B**) the female faced the male, lifting and extending her body forward; (**C**) the male walked toward the water body; (**D**) the male being followed by the female toward the water body; (**E**) the male positioned himself in the opposite direction of the female and rotated three times over the female; (**F**) male entered axillary amplexus with the female.

Discussion

Habitat Use and Seasonality

We observed *B. capra* using vegetation along the margins of lotic environments as a shelter and a vocalization site, following the pattern recognized for most species of *Bokermannohyla* (Haddad and Prado 2005, Haddad *et al.* 2013, Malagoli *et al.* 2021). In addition, *B. capra* used epiphytic bromeliads as vocalization sites. Due to the height of the bromeliads, we were unable to observe *B. capra* using this phytotelm as an oviposition site, thus it can not be classified as a bromeliad-dwelling (sensu Peixoto 1995). However, we do not rule out this possibility, because species that reproduce in bromeliads typically inhabit the arboreal stratum and deposit fewer eggs compared to those that use other aquatic environments (Alves-Silva and Silva 2009), both traits observed for *B. capra* in this study. The use of bromeliads is known for several species within Cophomantini, including other representatives of the genus *Bokermannohyla,* such as *Bokermannohyla astartea* (Bokermann, 1967) (Malagoli *et al.* 2021), which may be considered as an eventual bromeligenous species (sensu Peixoto 1995) (see Malagoli *et al.* 2021). The continuum between using this resource initially as a vocalization site

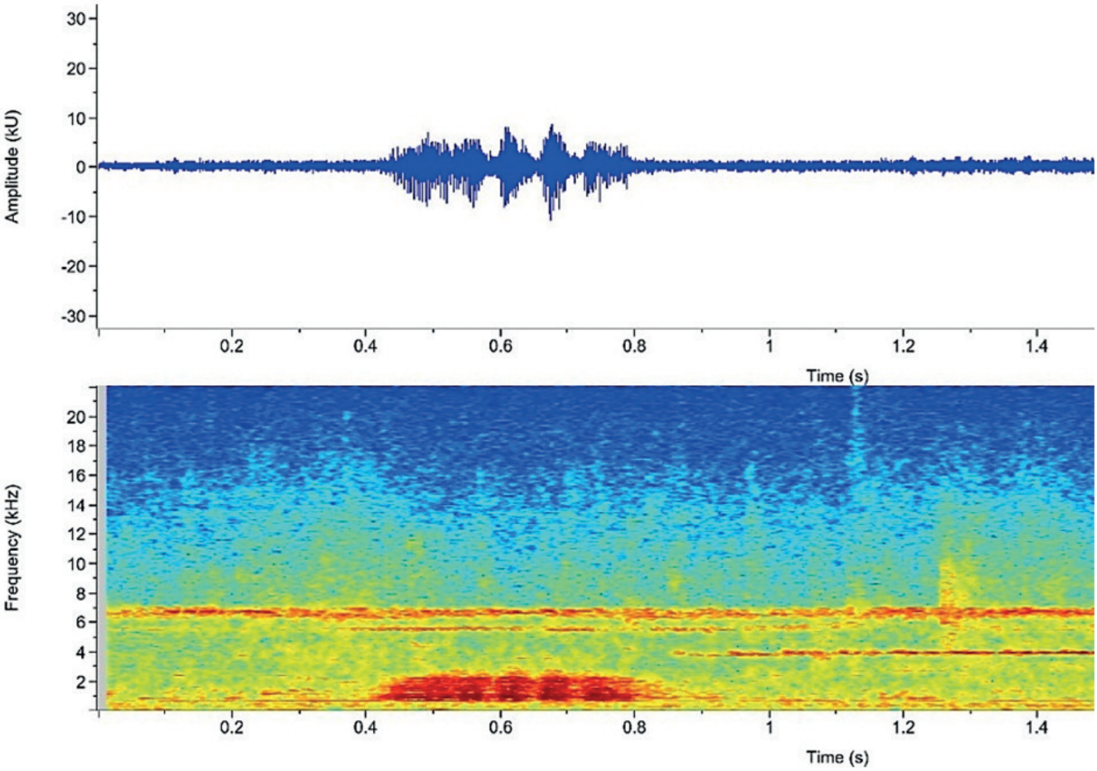

Figure 6. Oscillogram and spectrogram of the advertisement call of *Bokermannohyla capra* recorded in C1, Morro do Mara (MM), municipality of Jequié, state of Bahia, Brazil. Oscillogram—Y Axis: Amplitude (KU); X Axis: Time (s). Spectrogram—Y Axis: Frequency (KHz); X Axis: Time (s). Recorded at a temperature of 22.1°C.

and then as an oviposition site, observed in many anuran species, is a subject to be explored in further studies (Peixoto 1995, Lantyer-Silva *et al.* 2014).

The seasonal use of phytotelms by *B. capra* does not appear to be related to competitor density or rainfall. It may be associated with using the phytotelm as shelter against predators (Ferreira and Faria 2021). We observed greater bromeliad use during the cold season when reproductive activity decreases, making vocalizing males more vulnerable to acoustically oriented predators. Individuals may vocalize inside bromeliads during periods of low activity to reduce predation risk, since only a few males are exposed while vocalizing (Ferreira and Faria 2021).

Because we recorded low male density for *B. capra,* the higher perch heights observed during the warmer and wetter period do not seem to be related to competition for calling sites, which would force some males to choose alternative perches (see Mello *et al.* 2018). Instead, we suggest higher perch heights are associated with increased stream water flow in the wet period, which raises external noise levels. The higher vocalization sites could represent a way to escape from the noisy environment produced by the fast waters that can disturb the emission of the calls, as observed for *Aplastodiscus arildae*

(Cruz and Peixoto, 1987) (see Zina and Haddad 2007). Further studies are needed to confirm the reasons for the change in microhabitat use.

The use of vocalizations to attract females is a typical behavior of prolonged breeding species, with long periods of calling activity and territoriality (Wells 1977). *Bokermannohyla capra* has a reproductive period of over three months, a fact corroborated by Bastos and Zina (2022) in a study of an anuran community in MM. Other observations may indicate that *B. capra* has a prolonged reproductive pattern (sensu Wells 1977), such as the use of permanent environments to reproduce. Reproduction in lotic environments enables longer reproductive periods because oviposition sites are available throughout the year and individuals are not dependent on seasonal climatic aspects (e.g., rainfall and humidity) (Zina and Haddad 2006).

Although we did not observe a marked difference in activity due to season, climatic variables still impact the reproductive activity of *B. capra,* since air temperature and humidity affect the number of males. Long-term studies of monitored populations could provide insight into seasonal patterns and identify the metrics (or combinations of metrics) that influence these patterns.

Reproductive Behavior

According to the classification described by Haddad and Prado (2005) and the data collected, we can classify *B. capra* as having reproductive mode 2 because this species deposits aquatic eggs in cavities not constructed by males in lotic waters where exotrophic tadpoles develop. *Bokermannohyla capra* has axillary amplexus, which also occurs in most anuran species (Wells 2007).

The number of eggs (290) in one clutch of *B. capra* we collected was similar to one that was deposited ex situ in January 2025 (389 eggs). *Bokermannohyla capra* has a small clutch when compared with other species of *Bokermannohyla,* such as *B. circumdata* (Cope, 1871) (1176), *B. napolii* Carvalho, Giaretta, and Magrini, 2012 (637) (Mongin *et al.* 2013), and *B. luctuosa* (Pombal and Haddad, 1993) (396 and 613) (Pombal and Haddad 1993). The reasons behind these interspecific differences remain to be studied, but they may result from environmental use or species-specific factors. Clutch size may be a flexible trait influenced by environmental conditions and natural history, allowing a rapid response to random and unpredictable environmental factors (Liao *et al*. 2014). It may also serve as a valuable trait for phylogenetic and natural history studies that highlight differences within a genus (Gomez-Mestre *et al*. 2012). If the deposition of a few eggs at multiple times during the breeding season is possible (especially for species with a long breeding season) (Prado and Haddad 2005), parental fitness may increase (Wells 2007) and may become a fixed population trait and ultimately a species characteristic. Studies analyzing the factors driving clutch size variation are needed.

Complex courtship behaviors can be found in diverse hylid genera (e.g., Haddad and Sawaya 2000, Zina and Haddad 2007). *Bokermannohyla* is not an exception and is similar to other stream-dwellers such as *B. alvaregai* (Bokermann, 1956)*, B. ibitiguara, B. luctuosa,* and *B. nanuzae* (Bokermann and Sazima, 1973)*,* in which elaborate courtship behavior includes vocalizations, tactile contact, and visual signals, as well as males leading females to oviposition site (see Zornosa-Torres and Toledo 2019). The courtship behavior of *B. capra* encompasses visual stimuli (e.g., female body elevation), tactile stimulation (e.g., male positioning at the end of the courtship), and acoustic stimuli (e.g., advertisement and courtship calls).

The complexity of courtship repertoires tends to increase in species breeding in noisy environments such as lotic water bodies, as seen in Hylodidae (de Sá *et al.* 2016). The use of stimuli other than vocalizations may be crucial for species living in noisy environments and ovipositing far from their calling sites (see Zina and Haddad 2007). In such environments, males must guide females to oviposition sites while overcoming environmental acoustic interference, which requires alternative communication strategies to ensure message clarity and effective reproduction.

Vocalizations

Acoustic communication is the primary mode of intraspecific communication among frogs (Wells 2007, Forti *et al.* 2019). By calling, males try to stand out from competitors in order to attract females and fertilize eggs, ensuring gene transmission to the next generation (Duellman and Trueb 1994, Garcia *et al.* 2001, Forti *et al.* 2019). For each social context, frog calls have variable structure (Narins *et al.* 2006). *Bokermannohyla capra* calls are an example of this variable structure because different types of notes seem to be emitted in specific social contexts.

The advertisement call documented in this study differs from that described by Napoli and Pimenta (2009) for populations from Amargosa, Wenceslau Guimarães, Camamu, and Valença, all located in the Brazilian state of Bahia. In our recordings, type B notes were more frequently emitted, whereas the aforementioned authors reported type A notes as predominant. A comparison between our type B notes and those described by Napoli and Pimenta (2009) revealed similarities in the number of pulses and frequency range (0.99–2.84 kHz and 0.89–2.52 kHz, respectively). Nonetheless, subtle differences were observed: the notes in our dataset exhibit longer duration (0.22–0.39 s vs. 0.35–0.51 s), longer inter-note intervals (0.16–3.72 s vs. 0.82–5.55 s), and a lower dominant frequency (1.80–2.32 kHz vs. 1.38–1.72 kHz).

The differences observed in the advertisement call of *Bokermannohyla capra* from MM when compared to the description provided by Napoli and Pimenta (2009) may reflect a population-specific trait. Such variation could result from isolation by distance and distinct historical selective pressures acting on different populations (Rebouças *et al*. 2020), including differences in environmental conditions and habitat characteristics across the range of the species.

The information provided here on the natural history of *B. capra* reinforces how deficient our understanding of the natural history of species of *Bokermannohyla* treefrogs is. Furthermore, it exemplifies the necessity of studies on natural history. The lack of basic information on reproductive biology makes it challenging to formulate conservation strategies for some species, especially for those with restricted geographic distributions and low densities. The study site (Morro do Mara) is home to a great richness and diversity of amphibians (Bastos and Zina 2022), including endangered species. Its protection is crucial, as ongoing research continues to reveal diverse reproductive behaviors driven by its amphibian richness.

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