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**INFLUENCE OF STREAM GEOPHONY AND SOCIAL CONTEXTS ON THE
COMMUNICATION OF *HYLODES PERERE* (ANURA: HYLODIDAE)**

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Influence of stream geophony and social contexts on the communication of *Hylodes perere*
(Anura: Hylodidae)

Dissertação apresentada ao Instituto de Ciências Biológicas, Programa de Pós-Graduação Biodiversidade e Conservação da Natureza, da Universidade Federal de Juiz de Fora, como requisito para obtenção do grau de Mestre em Biodiversidade e Conservação da Natureza.

Orientador: Prof. Dr. Renato Christensen Nali

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RESUMO

A comunicação animal envolve a emissão e recepção de sinais entre indivíduos no meio em que vivem. Em anfíbios anuros, os sinais acústicos são os principais utilizados na comunicação, mediando interações sociais em contextos reprodutivos e agressivos. Em espécies territoriais como as rãs-de-corredeira do gênero *Hylodes* (Anura: Hylodidae), são utilizados sinais e estratégias comportamentais distintas em condições de exposição a sons dos riachos (geofonia). No entanto, ainda é incerto como os machos maximizam a comunicação acústica nesta situação, seja ajustando-as ou movendo-se para uma seção de riacho mais silenciosa. *Hylodes perere* é uma rã endêmica do domínio fitogeográfico Mata Atlântica, sudeste do Brasil, e os indivíduos reproduzem-se apenas em riachos com corredeiras. A espécie ainda não foi avaliada pela IUCN, e está classificada como Dados Insuficientes pelo ICMBio, e pouco se sabe sobre o seu repertório de cantos e comportamento reprodutivo. Utilizando esta espécie como modelo, investigamos a influência da geofonia dos riachos sobre seus cantos de anúncio. Marcamos machos e testamos se estes permanecem nos seus territórios, ajustando seus cantos de anúncio para maximizar a sua comunicação em situações de ruído. Também descrevemos os cantos territoriais da espécie, com informações sobre os territórios, períodos do dia, microambientes e contextos sociais de emissão dos cantos. Gravamos indivíduos em áudio e vídeo, medimos parâmetros espectrais e temporais dos cantos, níveis de pressão sonora de cantos e riachos, tamanho corpóreo dos indivíduos e temperaturas ambientais. A relação entre estas variáveis foi analisada por modelos mistos lineares e generalizados. Verificamos que os machos permaneceram no mesmo local ao longo do tempo e aumentaram a intensidade dos cantos de anúncio em situações mais ruidosas, mas não reduziram o esforço de canto nestas situações. Os machos também aumentaram a frequência dominante em resposta ao ruído de riacho. Os cantos territoriais foram formados por dois tipos de notas, que poderiam ser emitidas isoladamente (cantos territoriais simples) ou em conjunto em oito combinações possíveis (cantos territoriais complexos); eles foram emitidos em todos os períodos do dia e microambientes, mas variaram conforme os contextos sociais. Os machos interagiram emitindo cantos de anúncio e territoriais em curtas e longas distâncias, também precedendo um combate físico e durante um evento de corte. Em conjunto, os nossos resultados indicam que a territorialidade é um fator importante para os machos, a ponto de alterarem seus cantos de anúncio para que sobressaíam ao ruído do riacho, mas não se moveram ao longo do riacho. No entanto, o fato de eles não reduzirem o esforço de canto indica que mecanismos de seleção sexual são fundamentais nesta espécie. A defesa do território, para a qual os cantos contribuem largamente, é provavelmente vantajosa para *H. perere* para a sobrevivência e especialmente para a reprodução. Nossos resultados confirmam que a comunicação na espécie é complexa, abrindo possibilidades para estudos comportamentais com espécies do gênero *Hylodes* e ajudando na investigação da evolução da comunicação da família Hylodidae.

Palavras-chave: Anuros. Canto de anúncio. Canto territorial. Comunicação. Eco acústica. Ecologia de riachos. Estudo de marcação e recaptura. Territorialidade.

ABSTRACT

Animal communication involves the emission and reception of signals among individuals in an environment. In anuran amphibians, acoustic signals are the main signal used in communication, which mediate social interactions in reproductive and aggressive contexts. In territorial species such as the torrent frogs of the genus *Hylodes* (Anura: Hylodidae), distinct signals and behavioral strategies are used in conditions in which individuals are exposed to stream background sounds (geophony). However, whether calling males maximize acoustic communication in this situation by adjusting their calls or by moving to quieter section is still uncertain. *Hylodes perere* is a torrent frog endemic from the highly endangered Atlantic Rainforest domain, southeastern Brazil, and individuals breed only in streams with rapids. The species is currently Not Categorized by the IUCN and Data Deficient by the ICMBio, which indicates that little is known about its calling repertoire and reproductive behavior. Using this species as a model, we investigated the influence of stream geophony on its calling behavior. We marked males and tested if they remain in their territories and thus adjust their advertisement calls to maximize their communication. We also described territorial calls with information on the territories, periods of the day, microhabitats and social contexts of emission. We recorded individuals in audio and video, measured spectral and temporal call parameters, sound pressure levels of calls and stream sounds, and body size and environmental temperatures. We ran mixed linear and generalized models to verify the relation between these variables. We found that males remained in the same location across time and increased call intensity in noisier situations, but did not reduce calling effort in these situations. Males also increased the dominant frequency of calls in response to stream noise. Territorial calls were formed by two types of notes that were emitted alone (simple territorial calls) or together in eight possible combinations (complex territorial calls) in all periods of the day and microhabitats, but varied depending on the social contexts. Conspecific males interacted by emitting advertisement and territorial calls in short and long distances, also preceding a physical combat. These calls were also emitted during a courtship. Taken together, our results indicate that territoriality is an important factor for males to the point where they change their advertisement calls to surpass stream noise but not move along the stream. However, the fact that they do not reduce call effort indicates that sexual selection mechanisms are key in this system. Territory defense, to which these calls largely contribute, is likely advantageous for *H. perere* for survival and especially reproduction. Our results confirm that communication in the species is complex, opening possibilities for behavioral studies with species of the genus *Hylodes* and aiding in research of the communication evolution within the family.

Keywords: Anurans. Advertisement call. Communication. Eco acoustic. Recapture study. Stream ecology. Territorial call. Territoriality.

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1 GENERAL INTRODUCTION

Biological evolution is a complex concept but one that can be defined as the transformation of organismal populations in time, mediated by selective mechanisms on individuals who are able to survive and reproduce differentially (natural selection), and by neutral mechanisms such as genetic drift (RIDLEY, 2007). The presence or absence of certain characteristics of living organisms may reflect the success or failure of their ancestors, because the adaptations in a given environment likely reveals the reproductive success of the ancestors for similar environments in which they lived (RIDLEY, 2007).

Among sexually reproducing organisms, sexual selection favors attributes that facilitate reproduction. One aspect that can be applied (although not without exceptions) is that males increase their reproductive success by increasing the number of females with which they reproduce, while females increase their reproductive success by mating with better males (ALCOCK, 2011). The competition that often happens between males (intrasexual sexual) to mate with females (intersexual selection) favors the evolution of sexual attributes that can be naturally selected, which provide variations on primary sexual characteristics (gonads), and secondary sexual characteristics, such as difference in size, color, ornamentation, and behaviors across several generations (CLUTTON-BROCK 2007; RIDLEY, 2007; ALCOCK, 2011).

While all organisms live somewhere, they may differ in how they live in these places. The concept of habitat refers to the place where a particular organism lives, niche refers to its optimal way of life, i.e., how this organism lives, considering the conditions and use of available resources in the environment (BEGON; TOWNSEND; HARPER, 2007). Niche is not a place, but a multidimensional concept and that has multiple dimensions in scope (WHITTAKER, 1972; BEGON; TOWNSEND; HARPER, 2007). For instance, if we try to understand the structure and composition of an aquatic organism assembly, one should look into many abiotic conditions such as pH, temperature, dissolved oxygen in the water, luminosity, salinity, and conductivity, because these environmental variables can be crucial in the maintenance of tolerant and non-tolerant species (BARBOUR et al., 1999; BARRELLA et al., 2000). In addition, the gradient of these factors can explain the presence of a particular species and reveal the functional diversity in a community (WHITTAKER, 1972), which also is influenced by other factors such as individual dispersion, interspecific competition, predation and mutualism (BEGON; TOWNSEND; HARPER, 2007). Thus, biological evolution cannot be detached from

ecological theory because it is directly related to distribution, abundance, and the related environmental characteristics (BEGON; TOWNSEND; HARPER, 2007).

The observed behaviors of an organism reflect the optimization stated by the niche theory (WHITTAKER, 1972). In territorial species, there is active interference among individuals, generally males, while defending the resource space. If territoriality is favored by natural selection, individuals should have more benefits (i.e., increased availability of females, food and breeding sites) than costs (i.e., energy expenditure) (WELLS, 1977; BEGON; TOWNSEND; HARPER, 2007; de SÁ et al., 2015; RICKLEFS; RELYEA, 2016). As life histories of organisms are the result of both long and short-term evolutionary forces, distinct alternatives can increase fitness such as phenotypic plasticity, which can be manifested as behavioral plasticity (PRICE; QVARNSTRÖM; IRWIN, 2003; BRUMM; SLABBEKOORN, 2005; BEGON; TOWNSEND; HARPER, 2007). Phenotypic plasticity indicates the most immediate responses of organisms to the environment and consists of differences in phenotypic expression for the same genotype (LOPEZ et al., 1988; CUNNINGTON; FAHRIG, 2010; WONG; CANDOLIN, 2015). However, phenotypic plasticity is also limited, mainly due to life-history limitations and phylogenetic constraint (BEGON; TOWNSEND; HARPER, 2007; RIDLEY, 2007; MIKULA et al., 2021).

As a behavior, communication occurs across the animal kingdom (BRADBURY; VEHRENCAMP, 2011). The social and ecological contexts are inseparable aspects of this behavior and usually relevant in the reproduction of individuals; consequently the most variable forms of life can thrive (ALCOCK, 2011; BRADBURY; VEHRENCAMP, 2011; VITT; CALDWELL, 2014). In acoustic communication, signaler individuals produce and emit acoustic signals, which propagate generally in the air or water to be received and perceived by other individuals (BRADBURY; VEHRENCAMP, 2011). Acoustic signals from animals are always emitted in mediums with non-desired acoustic components that can interfere with their reception, perception, and interpretation. Geophysical sounds are referred to as geophony, biophony constitutes the background sounds of non-human organisms and human-generated sounds correspond to anthropophony (PIJANOWSKI et al., 2011; FARINA; GAGE, 2017). Noise can shape the spectral and temporal structure of signals (BRENOWITZ, 1989) and influence their effectiveness and evolution (GUILFORD; DAWKINS, 1991). Signalers can increase signal efficacy by adjusting vocal activity (DÍAZ; PARRA; GALLARDO, 2011), by changing the synchrony of the calls (ZELICK; NARINS, 1985), by modifying the call parameters (call plasticity) (SLABBEKOORN; PEET, 2003) or by avoiding areas of high noise (SCHAUB; OSTWALD; SIEMERS, 2008). Anuran amphibians (frogs) have been a useful

model to evidence the use of distinct signals to mediate the interaction between conspecific individuals in the environment (HADDAD; GIARETTA, 1999). In frogs, vocalizations are the most emitted and studied signals, and in the majority of species males use them in reproductive, aggressive and defensive contexts (TOLEDO et al., 2015; KÖHLER et al., 2017). However, communication in frogs is variable, including species that are mute (AUGUSTO-ALVES; DENA; TOLEDO, 2018; FOUQUET et al., 2022) and that use modalities such as tactile signals (de SÁ; ZINA; HADDAD, 2016), visual signals (AMÉZQUITA; HÖDL, 2004; HARTMANN; HARTMANN; HADDAD, 2004), chemical signals (HOUCK, 2009; BRUNETTI et al., 2015) and vibrations (CALDWELL et al., 2010; DUNLOP et al., 2022). Studies involving multimodal communication have elucidated that communication in this group is complex (de SÁ; ZINA; HADDAD, 2016), mainly in naturally noisy environments such as streams with rapids and waterfalls (PARTAN, 2013; PREININGER et al., 2013; CALDART et al., 2016).

Most species of the Neotropical family Hylodidae live and breed on streams with constant background sounds, which warrants the name of torrent frogs (GOUTTE; DUBOIS; LEGENDRE, 2013). This environment creates a strong geophony that varies across time and space (SCARPELLI; RIBEIRO; TEIXEIRA, 2021), but how species combine strategies to maximize the communication in this environment is still poorly known (PARTAN, 2013). Currently, species of this family are divided into four genera: *Megaelosia*, *Hylodes*, *Crossodactylus* and *Phantasmarana* (VITTORAZZI et al., 2021; de SÁ et al., 2022). While species of *Megaelosia* and *Phantasmarana* are predominantly visually oriented, species of the genus *Hylodes* and *Crossodactylus* have vocal sacs and vocal slits and emit audible breeding calls (de SÁ et al., 2022). *Hylodes perere* Silva and Benmaman 2008 is an endemic species from the southeastern part of the Atlantic Rainforest and is included in the *Hylodes lateristrigatus* group, together with *H. ornatus*, *H. papilans*, *H. amnicola*, *H. japi*, *H. sazimai*, *H. ornatus*, *H. phyllodes*, *H. magalhaesi*, *H. vanzolinii*, *H. otavioi*, *H. babax*, *H. uai*, *H. charadranaetes*, *H. regius*, *H. fredii*, *H. meridionalis*, *H. heyeri*, *H. lateristrigatus* and *H. perplicatus* (HEYER 1982; SILVA; BENMAMAN, 2008; de SÁ et al., 2015; de SÁ; LYRA; HADDAD, 2020). Males of *H. perere* breed along streams distributed across a rugged terrain that often forms waterfalls, and only its advertisement call has been described (SILVA; BENMAMAN, 2008). The species is classified as Data Deficient by the Brazilian red list (ICMBIO, 2018), and Not Evaluated by the International Union for Conservation of Nature - IUCN. Thus, it becomes a good model to (1) study the environmental effects and coping mechanisms in frog calling behavior and (2) to improve our knowledge about the behavior of the rich anurofauna of the Atlantic Rainforest (HADDAD et al., 2013).

Here, we expand the knowledge of the social interactions, acoustic repertoire and the role of the environmental sounds on the calling behavior of the stream-dwelling torrent frog *Hylodes perere*. Specifically, this master's dissertation is divided in two chapters. In chapter 1, we investigated whether the background noise of the streams interferes on advertisement calls of this species. Moreover, in a mark-recapture study, we were able to test for the first time in the group if males remain in their territories and thus adjust their advertisement calls to maximize their communication to noisy environments. In chapter 2, we describe the territorial call of *H. perere*, which is formed by two distinct type of notes that can be emitted alone (simple territorial call) or together (complex territorial call) in different combinations. We describe the social context of emission of these calls, which occurred during male-male interactions (physical and non-physical), and male-female interactions (courtship behavior). Taken together, our results contribute to the understanding of the mechanisms in species that inhabit noisy environments and expand the known behaviors associated with reproduction in the family Hylodidae, which includes the extended vocal repertoire of *Hylodes perere*.

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2 CHAPTER 1 - MOVEMENT OR PLASTICITY: ACOUSTIC RESPONSES OF A TORRENT FROG TO STREAM GEOPHONY

2.1 INTRODUCTION

Animal communication is a behavior that involves interactions between signaling and perceived individuals in an environment (WILEY; RICHARDS, 1978; OWREN, RENDALL; RYAN, 2010; BRADBURY; VEHRENCAMP, 2011; STEGMAN, 2013). In many animal taxa, calls are the main mode of communication (ERBE; THOMAS, 2022), and the advertisement call is the most common and emitted by males in the reproductive context with the main function of attracting females and also maintaining spacing between males (GERHARDT; HUBER, 2002; SLABBEKOORN; SMITH, 2002; TOLEDO et al., 2015). Studies have shown that advertisement calls may vary as a result of a myriad of factors and selective forces such as sexual selection, isolation between populations, body size, social context and climatic variables (GERHARDT, 1991; SULLIVAN, 1992; CHARLTON; REBY, 2016; TESSAROLO et al., 2016; TOLEDO et al., 2015; TURIN; NALI; PRADO, 2018). In this sense, studies that incorporate the soundscape elements have helped clarify variation in acoustic signals (FARINA; GAGE, 2017; SCHOEMAN et al., 2022), because environment acoustic conditions can be important to social and reproductive selection context (EY; FISHER, 2009; GOUTTE; DEBOIS; LEGENDRE, 2013; GOUTTE et al., 2016; 2018).

In lotic environments, the natural sounds of streams make up the soundscape and are referred to as geophony (FARINA; GAGE, 2017; SCHOEMAN et al., 2022). This component can vary in sound intensity, both in space – due to variations in the spatial conditions of streams, and in time – according to the season and their associated climatic conditions (TONOLLA et al. 2009; 2010; 2011). The improvement of acoustic communication in these environments could be conditioned on variations in geophony. For instance, the influence of geophony has particular importance in frog species that vocalize and breed along streams with rapids (BOECKLE; PREININGER; HÖDL, 2009; GRAFE et al., 2012). Evolutionary adaptation to these environments may involve proximally causal behaviors, such as vocal adjustments of the same individual by means of acoustic plasticity and/or movements of individuals along streams, which can neutralize noise, increase the signal-to-noise ratio and call efficiency (BEE, 2007; BEE; SWANSON, 2007; PRESTWICH, 2007). However, likely because the eco-acoustics is a growing and still incipient investigation area (ERBE; THOMAS, 2022), no studies have tested simultaneously for these two hypotheses in natural conditions within this diverse group, which

hampers our interpretations of the mechanisms associated with the improvement of call efficiency.

Brazil is a megadiverse country (BACON et al., 2019) known to have the highest richness of anuran amphibians in the world (SEGALLA et al., 2021; FROST, 2022). The Atlantic Rainforest, one of the world's 36 biodiversity hotspots (MITTERMEIER et al., 2004; WEINZETTEL; VAČKÁŘ; MEDKOVÁ, 2018) houses more than 600 species (ROSSAFERES et al., 2017). Several studies of descriptions of species and their advertisement calls have been published in recent decades (GUERRA et al., 2018), but there are large gaps regarding their social and environmental contexts of emission (TOLEDO et al., 2015). Thus, studies focusing on behavioral ecology become key tools to better understand communication, sexual selection, and evolution in this group (WELLS, 2007; de SÁ; ZINA; HADDAD, 2016).

The torrent frog *Hylodes perere* is an endemic species recently described from the Atlantic Rainforest in the Neotropical region (SILVA; BENMAMAN, 2008), and is currently classified as "Data Deficient" by the Brazilian Red List (ICMBIO, 2018) and Not Evaluated by the International Union for Conservation of Nature - IUCN (2022). The individuals reproduce only in streams and are active mainly during the day, but also at night (SILVA; BENMAMAN, 2008; ALMEIDA et al., 2021). They are found year-round inside and outside the first and second orders streams, where males call partially submerged in water, or perched on rocks, associated vegetation of the streams and banks (SILVA; BENMAMAN, 2008). Therefore, this is a species with a prolonged-breeding strategy, i.e., males call throughout the year to attract females and reproduce continuously (WELLS, 2007).

Considering the adaptation of this species to reproduction in lotic environments, and that certain behaviors can make acoustic communication more effective by neutralizing environmental noise and increasing the signal-to-noise ratio (NARINS; ZELICK, 1988; RYAN, 1988; ENDLER, 1992; FARINA; GAGE, 2017), we investigated the influence of stream geophony on the advertisement calls of *H. perere*. First, we tested if males of *H. perere* increase the intensity of their vocalizations to maximize acoustic communication in response to the streams. Second, due to the probable territoriality of *H. perere* based in evidence for several species of the genus (e.g. HADDAD; GIARETTA, 1999; HARTMANN; HARTMANN; HADDAD, 2006; LINGNAU et al., 2013; de SÁ; PUPIN; HADDAD, 2018), we conducted a mark-recapture study and showed if this adjustment in vocalization occurs by vocal plasticity instead of moving to quieter regions. Finally, considering the high energy expenditure associated with call emission in frogs (TAIGEN; WELLS, 1985; RYAN, 1988; GRAFE;

THEIN, 2001), we elucidated if males that emitted more intense calls in response to stream geophony reduces the emission of calling signals. Taken together, our study contributes to the complex scenario of the evolution of behavioral differences regarding acoustic communication in noisy environments.

2.2 MATERIALS AND METHODS

2.2.1 Study area

The study was conducted in a private conservation area, the Reserva Particular do Patrimônio Natural Chapadão da Serra Negra (RPPN-CSN; 21.9643 °S; 43.8001 °W; 784-1602 m asl). It is located in the Serra Negra da Mantiqueira, a region of the Mantiqueira Complex in the municipality of Santa Bárbara do Monte Verde, Minas Gerais State, southeastern Brazil (NEVES et al., 2017; LIMA et al., 2021). The RPPN-CSN is a fully pristine and legally protected area of the biodiversity hotspot Atlantic Rainforest (BRASIL, 2000; MYERS et al., 2000), inserted in a considered a high-priority conservation area (CAMPOS; LOURENÇO-DE-MORAES, 2017). This area contains narrow headwater streams from the Paraíba do Sul River basin and Rio Preto sub-basin (CBHAMRPP, 2021), and the vegetation around is classified as High-Montane Ombrophilous Forest and Ombrophilous Alluvial Forest (VALENTE et al., 2011). The climate is classified as mesothermal climate (Cwb in the Köppen-Geiner classification) with more intense rainy season between November and February (CBHAMRPP, 2021).

2.2.2 Data collection

Field trips occurred between July 2021 and July 2022, totaling 60 days distributed in 12 weeks. We sampled three different streams (streams I, II and III); specifically, we sampled along the water channel and divided each stream in 25 sections of 5 m length in each of them, totaling 125 m sampled per stream. We chose 5 m in length because of previous observations of territories and home range within the genus (NARVAES; RODRIGUES, 2005; LINGNAU; BASTOS, 2007). We sampled individuals at four periods of the day, which were classified taking into consideration the geographical position of the study area, the time of day, and the day of the month when sampling occurred: daytime, nighttime, morning twilight and evening

twilight. The streams were sampled at two or three periods of the day in each week of fieldwork. We made that spatial and temporal division to capture the variation of lotic sounds across time and space.

We searched for adult males of *Hylodes perere* by active search at the breeding sites and sampled them by the focal-animal method (ALTMANN, 1974). Advertisement calls were recorded for approximately two minutes using a digital recorder (Marantz Professional PMD-660) and a unidirectional microphone (Sennheiser ME66) at 16-bits resolution and 44 100 Hz sampling rate (KÖHLER et al., 2017). Concomitantly, we measured the sound pressure levels (SPL) of the call and stream sound with a SPL meter (Minipa MSL-1355b; dB range: 30-130 dB; time weighting: Slow; Frequency weighting: A). By analyzing together the call recording and the time log of the SPL meter, we were able to determine the SPL of the calls and SPL of the stream sounds during intervals between calls. We recorded males at an approximate distance of 0.8 m, but we also measured the real distance between the tip of the microphone and each male after each recording to standardize the SPL (see below). Afterwards, we captured and measured the male snout-vent length (SVL) and weight inside a plastic bag using, respectively, a vernier caliper to the nearest 0.02 mm and a dynamometer of 0.1 N. The weight of the plastic bag was removed. Air and water temperature were measured after each recording using a digital thermometer to the nearest 0.1 °C.

Each male was photographed in the ventral region using either a Moto g30 or a Samsung J5 Prime mobiles at the highest possible quality and then released in the same spot. Non-calling males were also measured and released for more accurate descriptions for the species.

2.2.3 Mark-recapture analysis

For each of the three streams sampled, we compiled the captures (first record) and recaptures (record of the same individual in the same and/or different months) across time. Juveniles (individuals with SVL < 25 mm) and females (adults with no vocal sacs) were excluded from this analysis, because our goal was to infer adult male territoriality and calling activity.

To check if males of *Hylodes perere* remain in their calling site across months instead of moving along the stream sections (i.e., territorial males), we selected the photographs of all individuals captured between July 2021 to July 2022. The images were cropped between the

limits of the SVL of the individuals and compared one by one using a visual comparison procedure, in which photographs were screened for natural skin marks. Only brightness and contrast adjustments were necessary to improve the sharpness, including the usage of white background to best visualization (supplementary figure 1). Besides being non-invasive, the photoidentification method allows for capture-mark-recapture across the time. Several studies have shown its viability for adult frogs (BOLGER et al., 2012; PEREIRA; MANEYRO, 2016; BARDIER et al., 2020; GOULD; CLULOW; CLULOW, 2021; LIMA-ARAÚJO et al., 2021; AEVARSSON et al., 2022).

2.2.4 Acoustic analysis

We analyzed 240 advertisement calls emitted by 81 males recorded between July 2021 and July 2022. We used the Raven Pro 1.6.4 software (Cornell Lab of Ornithology, Ithaca, NY) to measure the parameters: Fast Fourier Transformation = 256 resolution points, contrast and brightness = 60, overlap = 50%, hop size = 128, and window type = Hann. We measured the spectral parameters dominant frequency (KHz), frequency 5% (KHz) and frequency 95% (KHz). Considering the harmonic structure of the species' call (SILVA; BENMAMAN, 2008), we standardized selecting the calls from the fundamental frequency up to the sixth harmonic, which were visible across spectrograms (figure 2). We also measured the temporal parameters call duration (s), note duration (s), call rate (notes/min), note rate (notes/s), interval between advertisement calls (s) and inter note interval (s), all according to Köhler et al., (2017). The variable call effort was calculated as the sum of note duration of all notes within a call, divided by the call duration; it represents the ratio of sound to silence, expressed on percentage (KÖHLER et al., 2017).

2.2.5 Statistical analysis of calls

Before the analyses, all SPL raw values were adjusted to account for the effects of sound attenuation. According to the inverse square law, SPL is inversely related to distance of sound source, although other factors may also influence sound propagation efficiency (FARINA, 2014). Thus, to correct the distance effect on SPL we transformed the values obtained in dB to linear scale as $X = 0.00002 * 10^{(dB_{SPL} / 20)}$ Pa and applied the formula $SPL_{adjusted} = 20 * \log_{10}(((X/K) * Y) / P_0)$ dB, in which K = standardized distance of 0.8 m, Y = measured

distance (m), P_0 = reference sound pressure for airborne sound (20 μ Pa). Reconversion was made to obtain sound pressure measures in absolute units (WILCZYNSKI; BRENOWITZ, 1988; MÁRQUEZ; BOSCH; PENNA, 2006; VER; BERANEK, 2006).

To test if individuals adjust the call intensity (cSPL) in response to the stream SPL (sSPL) and to assess the effects on spectral and temporal advertisement call parameters, we ran linear mixed effects models (LMMs) (ZUUR et al., 2009; HARRISON et al., 2018). The analyses were performed in RStudio platform version 4.1.3 (R Development Core Team, 2022) using the lme4 (BATES et al., 2015) and lmerTest packages (KUZNETSOVA; BROCKHOFF; CHRISTENSEN, 2020). Data exploration was carried out following Zuur et al., (2010). We combined SVL and body mass into body size (BS) by multiplying these values to avoid multicollinearity, because they were moderate correlated ($r = 0.43$) (e.g., GAMBALE; SIGNORELLI; BASTOS, 2014; TURIN; NALI; PRADO, 2018). We constructed mixed effects models with different calls by different individuals for each parameter of interest (response variable). Stream SPL, water temperature and body size were fitted as fixed effects, and identities of individuals as random effects (GRAFE et al., 2012; PREININGER et al., 2013; CALDART et al., 2016; LIMA et al., 2022). Thus, the form of the models followed: parameter of interest \sim stream SPL + water temperature + body size + (1|individual).

The models were visually verified plotting standardized residuals vs. fitted values for entire model and against each explanatory variable of the fixed effect with sjPlot R package (LÜDECKE, 2022). The difference in residuals between random effect levels was compared using default boxplots. We also inspected the random effect distribution with dotplots using lattice package (SARKAR, 2022). The multicollinearity of the predictors variables was verified with variation inflation factor (VIF) of the car package (FOX; WEISBERG, 2022), and only models that had explanatory variables with $VIF < 3$ were used (e.g. ZUUR et al., 2009). To improve the models, we also checked influential points and excluded observations if Cook's distance > 1 . The call and note rates were analyzed fitting a generalized mixed effect models (GLMM) with Poisson family and log link (ZUUR et al., 2009) as follows: first, we rounded the measurements to discrete numbers; afterwards, we log-transformed the fixed effects. For GLMM, SPL was transformed into an absolute scale (in Pa units) and then log transformed (logSP).

To help support our hypothesis of call plasticity, we constructed reaction norm graphs to compare the SPL of calls and streams in individuals that were captured and recaptured in the

same or adjacent section in different days, and to which we had bioacoustics data (i.e., recordings and re-recordings).

2.2.6 Ethical standard

The record and capture of individuals were authorized by the Instituto Chico Mendes de Conservação da Biodiversidade - SISBIO (license 78905-1) and approved by the Ethics Committee on the Use of Animals, Universidade Federal de Juiz de Fora, Juiz de Fora, Brazil (protocol 018/2021).

2.3 RESULTS

2.3.1 Sampling and recapture analysis

We sampled approximately 300 h across sites and captured a total of 145 adult male of *H. perere*. They were found vocalizing in all months with peak during the rainy season (September/21 to March/22) at all periods of the day, but mainly at daytime and during the morning and evening twilight. Most males called inside streams and close to the rapids, directly in the water on different substrates (e.g., partially submerged or on rocks, roots, leaves and branches) or hidden in undercut banks (microhabitat that is formed by the bank that overhangs the stream) and rocky crevices, but eventually perched on associated vegetation of the streams and on stones in the bank (supplementary figure 2). From all of our recordings, 55% percent of individuals called in direct contact with water; the other individuals were less than 1 m from waterflow.

For every five captures of males, we had approximately one recapture. In total, we had 31 recaptures, 27 of which occurred exactly in the same section of the capture. Four other recaptures occurred in adjacent or near adjacent sections, and always upstream (table 1). The seven recaptures that occurred within the same week all occurred within the same section. Four of these recaptured individuals called at different periods of the day. Twenty-four individuals were recaptured across months, two of which recaptured two times for different months and in the same section.

We had call data for six individuals captured and recaptured, i.e., recorded and re-recorded, and one of these was recorded four times and was split in two pairs of events, in two

different months. Thus, we had seven pairs of recorded-rerecorded events to analyze. We found a clear tendency of cSPL to accompany the sSPL (figure 1).

2.3.2 Advertisement call analysis

The 240 advertisement calls of the 81 males consisted of a sequence of average 30 tonal notes with frequency-modulated harmonics and dominant frequency concentrated mainly in the third harmonic. Table 2 summarizes the advertisement call parameters of the studied population. The 81 individuals had a mean SVL of $29.5 \text{ mm} \pm 0.88$ (range = 27.78 - 31.88 mm), and mean body mass of $1.92 \text{ g} \pm 0.18$ (range = 1.53 - 2.35 g). During sampling, the environment had a mean air temperature of $18.07 \text{ }^\circ\text{C} \pm 2.95$ (range = 11.2 - 22.3 $^\circ\text{C}$), mean water temperature of $17.2 \text{ }^\circ\text{C} \pm 1.5$ (range = 14.3 - 19.4 $^\circ\text{C}$), and a mean sSPL of $70.67 \text{ dB} \pm 8.14$ (range = 43.78 - 82.43 dB).

Our statistical models demonstrated the importance of selected fixed effects to explain the calling behavior of individuals of *H. perere*. The cSPL and dominant frequency were positively influenced by sSPL and water temperature. The LMMs analyses also showed that body size correlates positively with ratio of sound to silence within a call (call effort). Regarding temporal parameters, call duration was negatively affected by water temperature. In the same way, note duration was shorter at higher temperatures but also positively affected by sSPL (table 3). Furthermore, GLMMs analysis showed that call rate and note rate are positively related with water temperature (table 4), although the model that included note rate was marginally non-significant ($p = 0.06$).

2.4 DISCUSSION

Our results corroborate the hypothesis that males of *H. perere* increase the intensity of calls (cSPL) in situations of higher stream geophony (sSPL) and that they modify some acoustic parameters of their advertisement call in this situation. Males produced more intense calls in higher frequencies in situations of higher geophony, emitting shorter calls and notes also under the influence of water temperature. According to our second hypothesis, the recaptured males remained in their territories across time (same sections of the stream), showing call plasticity (see figure 1) and territoriality was also observed regarding other associated behaviors. However, contrary to our third hypothesis, males did not decrease their energy expenditure as

males did not reduce the sound-to-silence ratio (call effort). Call effort was positively related only with body size. Taken together, these results can help elucidate the mechanisms of acoustic communication maximization, allowing a better understanding of the fitness of animals under constant background noise interference.

The geophony of streams (geophysical sounds) is a constitutive element of the acoustical environment (SCHOEMAN et al., 2022). Because frogs largely communicate by acoustic signals (WELLS, 2007), characterization and differentiation of patterns of geophony allow the assessment of microhabitat conditions and niches of species (BOECKLE; PREININGER; HÖDL, 2009). Noisy microhabitats are especially limiting for torrent frogs (GOUTTE, DEBOIS, LEGENDRE, 2013), and, in general, geophony influences communication efficiency in frogs to a point in which some parameters of calls tend to be flexible (ZIEGLER; ARIM; NARINS, 2011). Moreover, frog calls are influenced by the effects of biophony (sounds from nonhuman organisms) and anthrophony (human-generated sounds) (VÉLEZ; SCHWARTZ; BEE, 2013; FORTI et al., 2022; LIMA et al., 2022; ZAFFARONI-CAORSI et al., 2022; ZHU et al., 2022). Among the main effects found in animals under the effect of noise in communication is the Lombard effect (BRUMM; SLABBEKOORN, 2005), which states that in noisy environments individuals must emit more intense calls and avoid masking, which includes anurans (CUNNINGTON; FAHRIG, 2010). Indeed, we corroborated the emission of more intense advertisement calls in noisier streams, as seen in other closely-related torrent frogs (CALDART et al., 2016; AUGUSTO-ALVES; DENA; TOLEDO, 2021; FORTI et al., 2022). The physiological state of individuals can also affect cSPL (PRESTWICH, 2007), and we found that cSPL also increases with water temperature. In this sense, Ziegler et al., (2011) argue that the size-dependent energetic reserves, the effect of temperature on metabolic activity and on the potential to allocate energy to reproductive effort may be mechanisms involved in individual call decisions (MCLISTER, 2001; KISS et al., 2009). Frogs can discriminate calls of different intensities (ZELICK; NARINS, 1983; NARINS; ZELICK, 1988; GIL-GUEVARA; AMÉZQUITA, 2020), and females may approach a male calling when spatially separated from the noise source (SCHWARTZ; GERHARDT, 1989; BEE, 2007). However, the intensity of stream noise may also serve as a cue to females to assess calls and microhabitat of males (ZHAO et al., 2017). Thus, sexual selection may be determinant in this process.

Unlike previous studies, not only did we find responses to geophony, but also that (1) males of *H. perere* remained on the same section of the stream for weeks and/or months, and (2) that males effectively change their calls accompanying stream noise, although with a lower

sample size (figure 1). Thus, male responses to call geophony were related with call plasticity (PRICE; QVARNSTRÖM; IRWIN, 2003; BRUMM; SLABBEKOORN, 2005; BEGON; TOWNSEND; HARPER, 2007) 2003). Territorial defense, including call site spacing, seems to be a crucial strategy used to increase male reproductive success in *H. perere*. We recorded males directing calls to rivals in the same section of the stream, performing visual signals and male-male chasing (chapter 2). These territorial behaviors were also observed and described in closely-related species (HADDAD; GIARETTA, 1999; LINGNAU; BASTOS, 2007; de SÁ; PUPIN; HADDAD, 2018; FURTADO et al., 2019), but these studies did not include responses to stream geophony. Moreover, we observed the same males calling at different periods of the day, including nocturnal vocalizations as previously observed to *H. perere* (SILVA; BENMAMAN, 2008; chapter 2), and also reported to other *Hylodes* species (LINGNAU et al., 2013; de SÁ et al., 2015). Because *H. perere* is highly abundant in the study area (NEVES et al., 2017; this study), and advertisement calls also serve as territory spacing (TOLEDO et al., 2015), we suggest that the emission of advertisement calls in individuals of *H. perere* is influenced not only by intersexual selection (female preferences), but also intrasexual selection, to a point where these selective pressures surpass those imposed by noisy environments. Males that are able to remain in their territories are selected and interact with the females and oviposition occurs in subaquatic chambers that are constructed by the males (R.A.F. Turin, unpublished data for *H. perere*; de SÁ et al., 2015). This helps explain the advantages of territoriality in *H. perere* and the pressure to maximize communication efficiency not by moving to a quieter section, but by call plasticity.

Contrary to our expectation, males did not reduce call effort and call rate to compensate for the emission of more intense calls to prevent energy expenditure. Rather, males increased the duration of the notes in noisier streams and emitted more calls and notes in higher water temperatures. Besides, larger animals showed higher call effort. As male secondary sexual characters may reflect its condition and viability (ANDERSSON, 1986), one could expect that animals work in the maximal possible efficiency (PRESTWICH, 2007), especially under high intra and intersexual selection. Because call efficiency depends on acoustic power and net metabolic power ratio (PRESTWICH, 2007), larger males potentially emit more calls more efficiently in situations that demand more energy expenditure, like in noisier sections of the stream. Taken together, the increases of (1) call effort related to body size, (2) the note and call rate (redundancy), and (3) intensity of vocalizations can be an important strategy to increase detectability of males to their rivals and females (BEE; GERHARDT, 2001; BECKERS; SCHUL, 2004; PENNA; POTTSTOCK; VELASQUEZ, 2005; FARINA, 2017). Once again,

our results elucidate that sexual selection pressures are strong, given that body size and these call traits can also be selected by females (GERHARDT, 1991; 1994; BECKERS; SCHUL, 2004).

We also found that call effort can be indirectly explained by the positive correlation between water temperature vs. call and note rates, and by the negative correlation of water temperature vs duration of calls. This becomes especially relevant given that males do not move across sections and have to deal with hampered communication by altering call parameters. As amphibians are ectothermic animals, the environmental temperature can predict the effort attributed to the call emitted (WELLS, 2007), mainly in reproductive sites. Higher temperatures can increase the number of active individuals and number of calls emitted such observed to *H. fredei* (HATANO; ROCHA, VAN SLUYS, 2002), consequently decreasing the intervals between calls and notes. Thus, the complexity of interactions between individuals in choruses can increase along with emissions of advertisement calls for territory spacing, which exemplifies the importance of understanding the social context of calling (GRAFE, 2005; DAPPER; BAUGH; RYAN, 2011; TOLEDO et al., 2015; chapter 2), especially in territorial species such as *H. perere*.

Call dominant frequency in *H. perere* is among the highest for the genus (AUGUSTO-ALVES; DENA; TOLEDO, 2021). This parameter usually correlates negatively with body size in anurans, i.e., larger males tend to emit calls with lower frequencies (GINGRAS et al., 2013; TONINI et al., 2020), which also occurs in closely-related species (AUGUSTO-ALVES; DENA; TOLEDO, 2021). We did not find that significant effect. However, we found that males emitted higher-pitched calls in noisier and warmer sections of the stream. Zhao et al., (2018) found that noise intensity has a positive effect on male call frequency but not on call intensity in another torrent frog, and argues that stream noise drives males to alter call frequency and call as loudly as possible to improve discriminability between individuals. On the other hand, Caldart et al., (2016) found great variation in the spectral structure of advertisement calls of *C. schmidtii*, with sSPL also positively affecting the cSPL. They found dominant frequency modulation for different parts of the call, with differentiation among signal-to-noise ratio of the notes (CALDART et al., 2016). The closely-related *Hylodes perere* may have evolved higher-pitched calls, increasing the signal-to-noise ratio and favoring detection and recognition of conspecifics due to the lack of overlapping of frequencies between calls and streams (HADDAD; GIARETTA, 1999; Wogel; ABRUNHOSA; WEBER, 2004; VARGAS-SALINAS; AMÉZQUITA, 2013; GOUTTE et al., 2016). This creates an interesting scenario regarding environmental pressures vs. sexual selection pressures in this species. The preferred

and selected males might be associated with lower frequency calls (RICHARDSON et al., 2010), especially in territorial species (KELLEHER et al., 2022). However, we show that, even when high sexual selection pressures are in place, responses to noisier habitats can mean (1) emission of higher frequencies, the opposite direction of what can be preferred by females, or (2) involve other forms of communication, such as multimodal communication, as mentioned here for the species (GRAFE et al., 2012; PREININGER et al., 2013; de SÁ; ZINA; HADDAD, 2016; chapter 2). Further studies with *H. perere* will help quantify the roles of sexual and environmental selection in its communication (e.g. MIKULA et al., 2021).

Our research highlights the importance in linking natural history observations and characterization of individual call variation of known individuals across space. We found that the strategy used to maximize acoustic communication in noisy environments is likely mediated by territoriality and intersexual selection, which also involves male size and environmental temperatures. As larger males may call more efficiently, their reproductive success may increase, being able to spend more energy in noisier sections of streams and better spacing their territories. Therefore, our results open interesting avenues of investigation that puts *H. perere* as a good model for the study of the trade-offs between environmental and sexual selective pressures in species that communicate in noisy environments.

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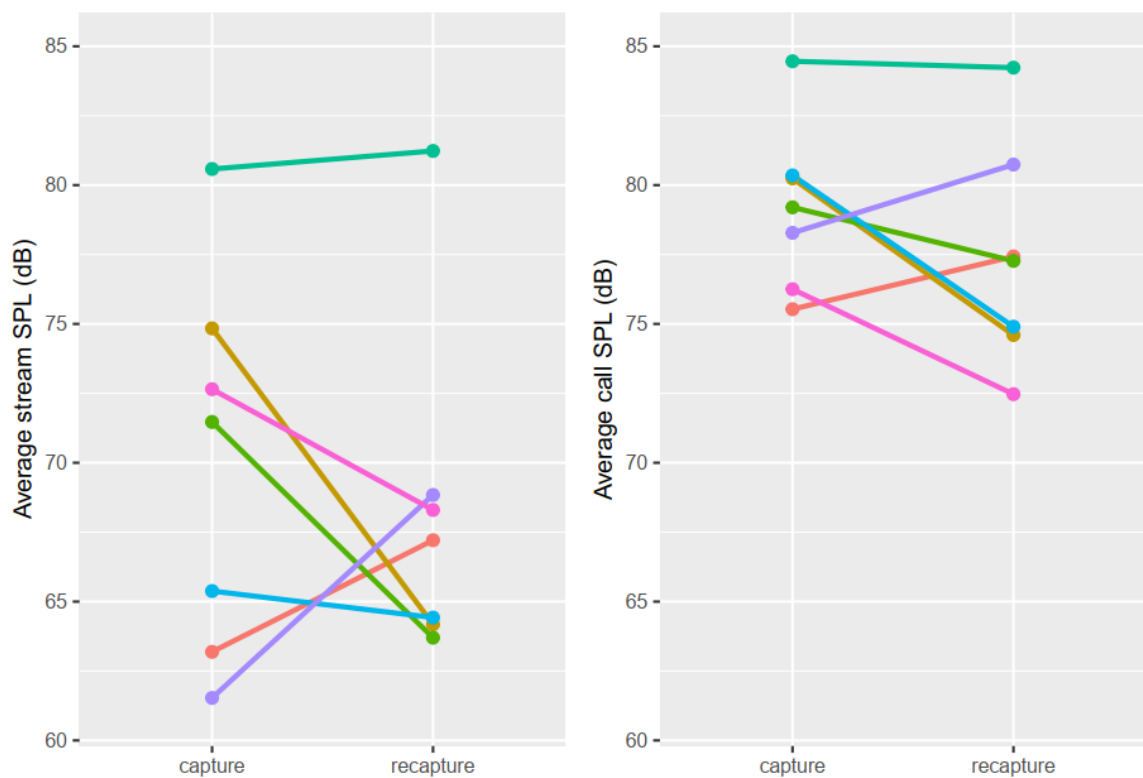
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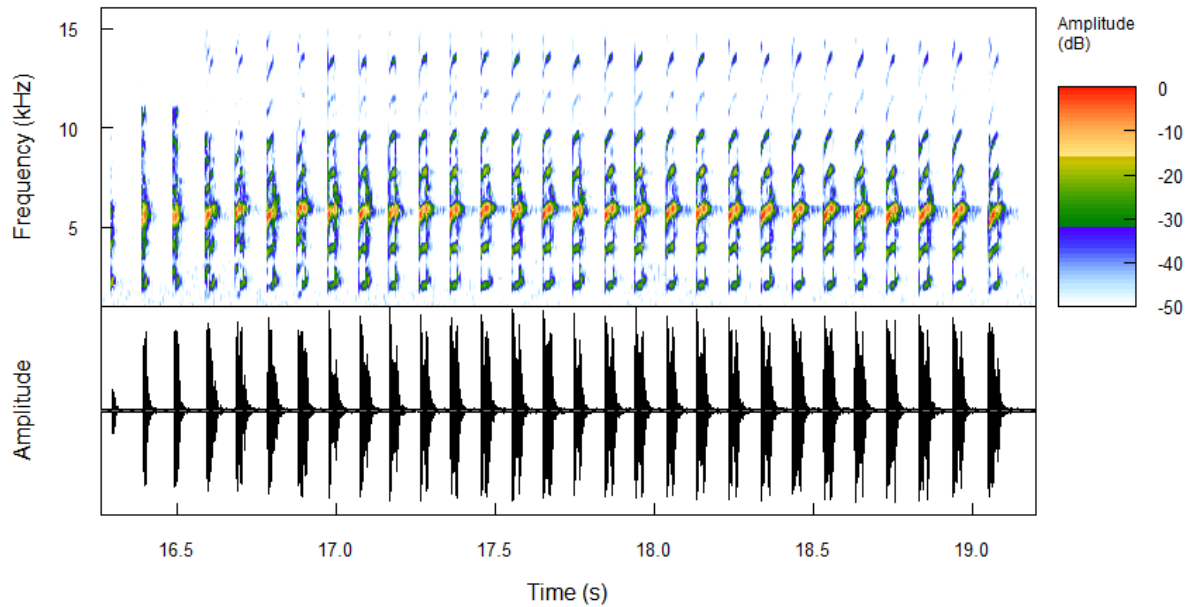
FIGURES

Figure 1 - Comparisons of stream SPL (sound pressure level) and call SPL in seven capture-recapture events (six individuals, see text for details) of *Hylodes perere*, municipality of Santa Bárbara do Monte Verde, southeastern Brazil. All individuals were recorded and re-recorded in same or adjacent part of the stream. Each color corresponds to an event. It is possible to observe that the changes in call SPL tended to accompany the changes in stream SPL



Fonte: Elaborado pelos autores (2022).

Figure 2 - Advertisement call of *Hylodes perere*, Santa Bárbara do Monte Verde, southeastern Brazil. Male recorded on July 12, 2022, at 9:40 a.m. Water temperature = 14.3°C; Air temperature = 16.6°C; Snout-vent length (SVL) = 29.8 mm; body mass = 1.84g. We used seewave R package (Sueur et al. 2008) with overlap = 90%; Discrete Fourier Transformation (DFT) window = 256 samples.



Fonte: Elaborado pelo autor (2022).

TABLES

Table 1 - Captures and recaptures of males of *Hylodes perere* from Jul/2021 to Jul/2022 in the municipality of Santa Bárbara do Monte Verde, southeastern Brazil. The number streams sections increases upstream

| Strea m | Capture month | Capture section | Recapture month | Recapture section |
|------------|------------------|--------------------|--------------------|----------------------|
| I | Nov/21 | 9 | Nov/21 | same |
| I | Nov/21 | 9 | Dec/21 | same |
| I | Dec/21 | 9 | Dec/21 | same |
| I | Feb/22 | 9 | Apr/22 | adjacent (10) |
| II | Aug/21 | 24 | Aug/21 | same |
| II | Aug/21 | 21 | Nov/21 | adjacent (22) |
| II | Sep/21 | 17 | Dec/21 | same |
| II | Sep/21 | 5 | Oct/21 | same |
| II | Sep/21 | 14 | Sep/21 | same |
| II | Sep/21 | 14 | Oct/21 | same |
| II | Oct/21 | 14 | Nov/21 | same |
| II | Oct/21 | 15 | Dec/21 | same |
| II | Oct/21 | 12 | Nov/21 | same |
| II | Nov/21 | 9 | Jan/22 | same |
| III | Sep/21 | 13 | Nov/21 | same |
| III | Sep/21 | 4 | Oct/21 | same |
| III | Sep/21 | 4 | Nov/21 | same |
| III | Sep/21 | 17 | Nov/21 | same |
| III | Oct/21 | 4 | Nov/21 | same |
| III | Nov/21 | 4 | Dec/21 | same |
| III | Nov/21 | 4 | Dec/21 | same |
| III | Nov/21 | 5 | Dec/21 | same |
| III | Nov/21 | 13 | Jan/22 | same |
| III | Dec/21 | 4 | Dec/22 | same |
| III | Dec/21 | 4 | Jan/22 | same |
| III | Dec/21 | 4 | Dec/21 | same |

| | | | | |
|-----|--------|----|--------|--------------------|
| III | Dec/21 | 11 | Apr/22 | adjacent (12) |
| III | Dec/21 | 4 | Jan/22 | same |
| III | Jan/22 | 13 | Jan/22 | same |
| III | Jan/22 | 12 | Feb/22 | same |
| III | Jan/22 | 14 | Jul/22 | Near adjacent (16) |

Fonte: Elaborado pelo autor (2022)

Table 2 - Descriptive statistics of spectral and temporal traits of the advertisement call of males of *Hylodes perere* (n = 81 males), municipality of Santa Bárbara do Monte Verde, southeastern Brazil.

See text for details on our measurements

| Call parameters | Mean | SD | Range |
|--------------------------------|-------|-------|---------------|
| Call sound pressure level (dB) | 77.19 | 4.15 | 63.27 - 85.32 |
| Dominant frequency (KHz) | 5.533 | 0.333 | 4.306- 6.450 |
| Frequency 5% (KHz) | 3.807 | 1.058 | 1.751- 5.565 |
| Frequency 95% (KHz) | 6.645 | 0.663 | 5.569- 9.234 |
| Call rate (call/min) | 4.45 | 1.82 | 0.83 - 8.86 |
| Note rate (notes/s) | 12.45 | 1.65 | 8.5 - 15.07 |
| Call interval (s) | 19.8 | 15.97 | 5.57 – 119.37 |
| Note interval (s) | 0.056 | 0.01 | 0.04 - 0.086 |
| Call duration (s) | 2.44 | 0.68 | 1.28 - 5.44 |
| Note duration (s) | 0.022 | 0.005 | 0.01 - 0.04 |
| Notes per call | 29.93 | 7.3 | 13 - 49 |
| Call effort (%) | 0.39 | 0.04 | 0.26 - 0.49 |

Fonte: Elaborado pelo autor (2022)

Table 3 - Results of the mixed-effects models (LMMs) to acoustic parameters of a population of *Hylodes perere* in state of Minas Gerais, Brazil. The fixed effects are represented by the sound pressure level of stream (sSPL), water temperature (WT) and body size (BS). Individuals were fitted as random factor. Significant values in bold ($p < 0.05$)

| Call parameters | calls (individuals) | Estimates (standard error), t , and p values | | | |
|-----------------------|------------------------|--|--------------------|---------------------|-----------------|
| | | Estimate | sSPL | WT | BS |
| cSPL | 233 (77) | 47.85 | 0.37 (0.03) | 0.40 (0.17) | -0.07 (0.04) |
| | | (3.71) | $t = 11.8$ | $t = 2.26$ | $t = -1.72$ |
| | | $t = 12.88$ | $p < 0.001$ | $p = 0.02$ | $p = 0.08$ |
| | | $p < 0.001$ | | | |
| Dominant Frequency | 236 (80) | 4.243 | 11.43 (3.7) | 51.11 | -5.83 (4.81) |
| | | (0.406) | $t = 3.1$ | (20.50) | $t = -1.21$ |
| | | $t = 10.43$ | $p = 0.002$ | $t = 2.5$ | $p = 0.22$ |
| | | $p < 0.001$ | | $p = 0.01$ | |
| Call effort | 233 (76) | 0.24 (0.05) | -0.0001 | 0.001 | 0.002 |
| | | $t = 4.3$ | (0.0005) | (0.002) | (0.0006) |
| | | $p < 0.001$ | $t = -0.3$ | $t = 0.59$ | $t = 3.1$ |
| | | | $p = 0.77$ | $p < 0.55$ | $p < 0.01$ |
| Note duration | 239 (81) | 0.045 | 0.0001 | -0.002 | 0.00006 |
| | | (0.006) | (0.00006) | (0.0003) | (0.0005) |
| | | $t = 6.8$ | $t = 2.71$ | $t = -6.59$ | $t = 0.87$ |
| | | $p < 0.001$ | $p < 0.01$ | $p < 0.001$ | $p = 0.38$ |
| Call duration | 234 (80) | 5.94 (0.82) | 0.01 (0.007) | -0.27 (0.04) | 0.004 |
| | | $t = 7.2$ | $t = 1.7$ | $t = -6.78$ | (0.009) |
| | | $p < 0.001$ | $p = 0.07$ | $p < 0.001$ | $t = 0.43$ |
| | | | | | $p = 0.66$ |

Fonte: Elaborado pelo autor (2022)

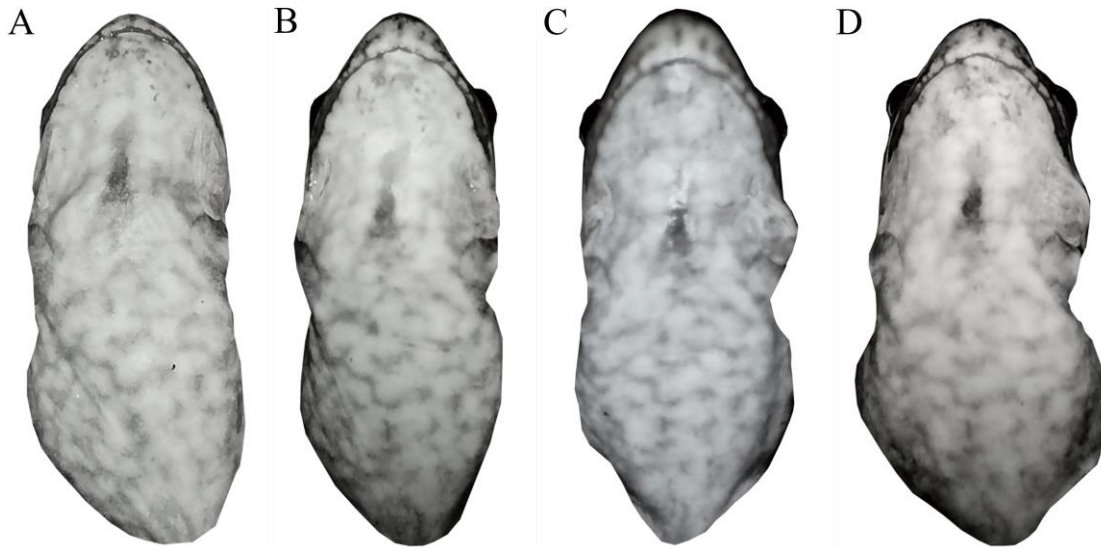
Table 4 - Results of the generalized mixed-effects models (GLMMs) to acoustic parameters of a population of *Hylodes perere* in state of Minas Gerais, Brazil. The fixed effects are represented by the sound pressure of stream log(SP), water temperature log(WT) and body size log(BS), all of which were log-transformed. Individuals were fitted as random factor. Significant values in bold ($p < 0.05$)

| Call parameters | Sample size calls (individuals) | Estimates (standard error), z , and p values | | | |
|-----------------|---------------------------------|--|-------------|---------------|-------------|
| | | Estimate | log(PS) | log(WT) | log(BS) |
| Call rate | 240 (81) | -5.13 | | 2.29 | |
| | | (1.70) | 0.02 (0.04) | (0.46) | 0.04 (0.34) |
| | | $z = -3.01$ | $z = 0.53$ | $z = 4.92$ | $z = 0.125$ |
| | | $p = 0.002$ | $p = 0.58$ | $p < 0.001$ | $p = 0.90$ |
| Note rate | 237 (80) | -1.55 | -0.0005 | 1.43 | 0.006 |
| | | (0.83) | (0.002) | (0.24) | (0.18) |
| | | $z = -1.87$ | $z = -0.21$ | $z = 5.88$ | $z = 0.04$ |
| | | $p = 0.06$ | $p = 0.82$ | $p < 0.001$ | $p = 0.96$ |

Fonte: Elaborado pelo autor (2022)

SUPPLEMENTARY MATERIALS

Supplemental figure 1 - Example of the photographs and visual analyses conducted in our mark-recapture study. Capture (figure A; Nov/21) and recaptures (B = Nov/21; C and D = Dez/21) of the same male of *Hylodes perere*, municipality of Santa Bárbara do Monte Verde, southeastern Brazil. Notice that, even with slight differences in body positions, the ventral pattern clearly evidences the same individual



Fonte: Elaborado pelo autor (2022).

Supplementary figure 2 - Male of *Hylodes perere* partially submerged in the water emitting advertisement call



Fonte: Lucas Nascimento Morgado (imagem concedida).

3 CHAPTER 2 - THE COMPLEX TERRITORIAL CALLS AND THE CONTEXT OF THEIR EMISSION IN THE TORRENT FROG *HYLODES PERERE* (ANURA: HYLODIDAE)

3.1 INTRODUCTION

In anuran amphibians, vocalizations are the most common mode of intraspecific communication, and can be defined as sound signals produced in the passage of air through the vocal cords from the lungs (COLAFRANCESCO; GRIDI-PAPP, 2016; KÖHLER et al., 2017). The calls are units of these signals, and they can be simple or complex, which depends on the quantity and composition in notes (subunits of the calls; TOLEDO et al., 2015; KÖHLER et al., 2017). Each type of vocalization has its bioacoustic peculiarity, because of the social context in which they are emitted; however, all types may indicate the individual locality of the signaler and its size, functioning as honest signals (TOLEDO et al., 2015; KÖHLER et al., 2017; but see NALI; PRADO, 2014).

The repertoire of vocalizations is variable among species, and can include three main types: reproductive, aggressive and defensive calls (TOLEDO et al., 2015; KÖHLER et al., 2017). Reproductive calls encompass the most common and well-studied, the advertisement calls, but also the relatively poorly known courtship and amplexus calls. Aggressive calls include territorial calls, for territorial species only, encounter calls, for all species with some type of male-male vocal interaction, and fighting calls, emitted exclusively during physical combats (TOLEDO et al., 2015). Lastly, defensive vocalizations are known as screams, such as alarm, distress, or warning screams (TOLEDO et al., 2015). There are also feeding vocalizations, but these are still very rare and with unknown functions, occurring in tadpoles and juveniles (KÖHLER et al., 2017).

Studies over the past decades have shown that visual and acoustic communication are frequent in amphibians of diurnal activity and associated with small torrent streams (rheophilic habit), such as the species of the family Hylodidae (HADDAD; GIARETTA, 1999; FURTADO et al., 2019). This Neotropical family of anurans encompass the genera *Crossodactylus*, *Hylodes*, *Megaelosia*, and *Phantasmarana* (VITTORAZZI et al., 2021; de SÁ et al., 2022). Species of the genus *Hylodes* are known as torrent frogs and are distributed in the Atlantic Rainforest domain (de SÁ et al., 2022). Twenty-six species of the genus are known (SEGALLA et al., 2021; FROST, 2022), and the large gaps regarding their social context are slowly being

filled. The use of signals in agonistic contexts has been described for territorial species in the family, which includes aggressive calls like the territorial call, besides bimodal and multimodal communication by the use of combinations of visual and acoustic signals (HADDAD; GIARETTA, 1999; HARTMANN et al., 2005; de SÁ; ZINA; HADDAD, 2016).

Hylodes perere Silva and Benmaman 2008 is an endemic species of the Atlantic Rainforest domain, with occurrence originally described for a restricted region of the Serra Negra da Mantiqueira, Mantiqueira complex, Minas Gerais State, Paraíba do Sul River basin, southeastern Brazil (SILVA; BENMAMAN, 2008). The species is currently classified as Data Deficient by the ICMBio red list (ICMBIO, 2018), but not categorized by the IUCN (International Union for Conservation of Nature) red list. Recent studies have expanded its records in the basin (NEVES et al., 2017; LIMA et al., 2021), as well as the altitude where it is found (ALMEIDA et al., 2021). A recent study reported on its diet, sexual dimorphism and microhabitat use (ALMEIDA et al., 2021). Besides, the tadpoles were described (MONTESINOS et al., 2022).

Adult individuals are small, predominantly active at daytime and found along first-order streams surrounded by riparian vegetation (SILVA; BENMAMAN, 2008; chapter 1). The species presents a prolonged breeding pattern (WELLS, 2007; chapter 1) and the individuals breed in subaquatic chambers within the stream, where the eggs are laid and the exotrophic tadpoles develop (see reproductive modes in NUNES-DE-ALMEIDA; HADDAD; TOLEDO, 2021). However, after its description, the poor publication record has caused large gaps regarding its reproductive behavior and communication. For instance, only the advertisement call has been described, with a harmonic structure and high dominant frequency, but only few observations of calls other than advertisement were noted (SILVA; BENMAMAN, 2008). Thus, the aim of this study was to describe the territorial calls for the species and their context of emissions within the male territories. This is the ninth description of territorial calls for the genus and will contribute to the understanding of the communication evolution within this genus and the family (HADDAD; GIARETTA, 1999; NASCIMENTO; POMBAL; HADDAD, 2001; WOGEL; ABRUNHOSA; WEBER, 2004; HARTMANN; HARTMANN; HADDAD, 2006; CANEDO; POMBAL, 2007; LINGNAU; BASTOS, 2007; LINGNAU et al., 2013; de SÁ; ZINA; HADDAD, 2016; de SÁ; LYRA; HADDAD, 2020), especially in light of the social contexts of emission that we describe.

3.2 MATERIALS AND METHODS

3.2.1 Study area

Fieldwork was conducted at the Reserva Particular do Patrimônio Natural Chapadão da Serra Negra (RPPN-CSN; 21.9643 °S; 43.8001 °W; 784-1602 m asl) which is located in a region of the Mantiqueira Complex in the municipality of Santa Bárbara do Monte Verde, Minas Gerais State, southeastern Brazil (NEVES et al., 2017). The Serra Negra da Mantiqueira (RPPN) is a legally protected area in biodiversity hotspot Atlantic Rainforest and inserted in a considered a high-priority conservation area (CAMPOS; LOURENÇO-DE-MORAES, 2017). It contains torrent streams from the Paraíba do Sul River basin and Rio Preto sub-basin (CBHAMRPP, 2021); the vegetation is classified as High-Montane Ombrophilous Forest and Ombrophilous Alluvial Forest (VALENTE et al., 2011). The climate is classified as mesothermal (Cwb in the Köppen-Geiner classification) with more intense rains between November and February (CBHAMRPP, 2021).

3.2.2 Data collection: male recordings and acoustic analysis

We observed males emitting territorial calls during fieldwork and recorded them at ca. 0.8 meters using Marantz Professional PMD-660 digital recorder and a unidirectional microphone (Sennheiser ME66) at 16-bits resolution and 44100 Hz sampling rate. We also used a sound pressure level meter to record sound intensity of calls and of the stream noise (Minipa MSL-1355b; dB range: 30-130 dB; time weighting: slow; frequency weighting: A). The records occurred between August 2021 and July 2022. After each recording, we captured and measured the males in the snout-vent length (SVL) and body mass with an analog caliper (to the nearest 0.02 mm) and dynamometer (to the nearest 0.1 N). The air and water temperatures were measured with an analog thermometer (to the nearest 0.1 °C). We also noted the time of the recording to categorize in periods of the day and luminosity categories (daytime, nighttime and in between), the calling site, and the presence of nearby individuals. The captured individuals were released in the same spot and were marked by photoidentification (see chapter 1), so they were not repeated in our analyses.

We used the Raven Pro 1.6.4 software with Fast Fourier Transformation = 256 resolution points, contrast and brightness = 60, overlap = 50%, hop size = 128, and window

type = Hann. We measured the spectral parameters dominant frequency (KHz), frequency 5% (KHz) and frequency 95% (KHz) and we selected every note and the harmonics present in calls. We measured the temporal parameters call duration (s), note duration (s), call rate (number of calls within a series of 10 territorial calls per min), interval between territorial calls within a series (s), and sound pressure level of the call (dB), all according to Köhler et al., (2017). Besides, we described other events of the emission of the territorial calls, using the behavioral sampling methods of focal animal, sequence, and all occurrences (ALTMANN, 1974).

Our recordings occurred in a range of water temperatures from 14.9 to 18.9 °C (mean = 17.11°C; standard deviation = 1.17), air temperatures from 15.3 to 22.1 °C (mean = 18.3 °C; standard deviation = 1.82), and the sound pressure level of the stream ranged from 49 to 73 dB (mean = 61.85; standard deviation = 8.21 dB). Mean SVL of 15 males was 28.46 mm (standard deviation = 0.97; range = 26.74 – 30.12 mm) and mean body mass was 2.18 g (standard deviation = 0.46; range = 1.64 – 3.27 g).

3.3 RESULTS

3.3.1 Time, spacing and description of territorial calls

Males emitted territorial calls in different periods of the day: morning ($n = 1$), afternoon ($n = 6$), afternoon twilight ($n = 4$), night ($n = 3$) and morning twilight ($n = 1$). As a consequence, they emitted these calls in different luminosity categories: daytime ($n = 7$), nighttime ($n = 3$), and in between ($n = 5$; table 1). They emitted territorial calls in the following microhabitats: partially submerged in the water ($n = 4$), perched on the fallen vegetation or on rocks above waterflow ($n = 5$), positioned in less than one meter in banks on rocks, sand, roots, leaves, branches, trunks or soil ($n = 5$) and on undercut banks ($n = 1$). The territorial calls were emitted mostly with the presence of other observed individuals ($n = 14$ out of 15). When present, nearby individuals were within a 5 m radius of the male ($n = 9$) or from 5 to 10 m distant ($n = 5$), most of which were males emitting both territorial and advertisement calls ($n = 13$).

We measured 177 territorial calls emitted by 15 males. The territorial call of *Hylodes perere* was composed of two distinct types of notes, herein called note A and note B, and may be simple or complex (figure 1). Simple territorial calls were composed by a single note type, either alone or repeated, while the complex territorial calls contain notes A and B within the same call, with different types of combinations (figure 5; table 2). The males emitted either

isolated calls, or in series of 4 to 35 calls in succession (mean = 17.2 calls; standard deviation = 9.53). The sum of the duration of the territorial calls and the intervals between them (series of the call) lasted, on average, 44 seconds (standard deviation = 20.9; range = 9.3 – 80 s). Simple territorial calls were the most emitted (86.8% of our measurements; table 2), especially those formed by note A. This note type sounds like a peep and is structurally similar to the notes of the advertisement calls (chapter 1). They were repeated up to 4 times and present in 80.8% of the total territorial calls. Notes type B sound like a squeak and were present in 32.4% of the total territorial calls. Calls containing both note types, i.e., complex territorial calls, occurred in 13.18% of our measurements. All 15 individuals included notes A within their territorial calls at some point, but two of them did not emit note B. Regarding the individuals that emitted complex territorial calls ($n = 13$), when considering the total number of notes, we found an average proportion of one note B to seven notes A. Notes A were always emitted first. Table 3 contains the spectral and temporal acoustic parameters of territorial calls of *H. perere*. Note A is shorter, emitted in higher quantity, shows slightly higher dominant frequency but narrower frequency bandwidth than note B.

3.3.2 Description of the social context of emission

Three males (male 1: SVL = 30.12 mm and body mass = 2.04 g; male 2 and 3: SVL = 29.72 mm and body mass to both = 1.84 g) that emitted territorial calls were captured and recaptured on different months (Sept/21 to Dez/21 and Nov/21 to Dez/21) within 5 m of the first capture. Two of them were recorded in interaction by means of advertisement call and series of territorial calls with males nearby. These occurred on December 17 and 18, 2021, around 5 pm and with air temperature of ca. 18-20°C and water temperature of ca. 17.6 °C. Both emitted simple and complex territorial calls in a series plus advertisement calls emitted in between, with an average of 22 territorial calls and 5.5 advertisement calls in between. The territorial calls and intervals also lasted longer than those for advertisement calls. They synchronized their territorial calls with those of the neighbors, but it was overlapped when nearby neighbors emitted advertisement calls.

On October 29, 2021, we observed and registered the interaction of two males that emitted territorial calls from 3:40 a.m. until 3:55 a.m. (water and air temperature = 16.9 °C). The males were initially above a rock inside stream and positioned ca. 15 cm distant from each other. Male 1 was a few centimeters higher on the rock and behind the individual 2, which was

partially submerged in the water. Within 30 s, both males emitted synchronized simple and complex territorial calls inflating both vocal sacs. Afterwards, male 2 raised and lowered the arm; only male 1 continued to emit territorial calls, until he changed his body posture and jumped on the bank and became visible for male 2. Male 1 emitted simple and complex territorial calls, and so again jumped and remained partially submerged in the water and under leaves, facing male 2 at ca. of 60 cm. Immediately he emitted territorial calls towards male 2, also changing his body postures and inflating both vocal sacs while emitting territorial calls. While male 1 emitted visual and acoustic signals, male 2 remained stationary.

In other event that occurred from 5 to 10 m distant, three individuals (male 1: SVL = 28.42 mm, body mass = 2.04g male 2: SVL = 27.36 mm, body mass = 2.04g; Non-sexed individual = not captured and undefined sex) were recorded from 4:26 a.m. until 4:35 a.m. Two of them interacted emitting advertisement and territorial calls. One male and the non-sexed individual were at approximately 70 cm of each other, while the other male was ca. 1.5 meter distant and less than 50 cm from the waterflow. One of the two closest males dove and moved toward the non-sexed individual, which noticed the male coming up beside him and soon jumped forward and took cover partially submerged in the water ca. of 60 cm from him and close of the bank. Then, male 1 emitted 12 simple and complex territorial calls, raised and lowered his right front arm in the water, and then emitted three advertisement calls; calls of male 2 were not synchronized with advertisement call of male 1. Afterwards, this male 1 jumped close to male 2, and remained there for a few seconds partially submerged and ca. of 20 cm from him. The male 1 changed his posture, leaving his vocal sacs out of the water, and again emitted advertisement call and simple and complex territorial calls inflating both vocal sacs, moving his arm as before. After a few seconds, this male jumped to the other side of the stream and started response the male 2 emitting advertisement and simple and complex territorial calls.

On July 13, 2022, at 3:52 p.m. (air temperature = 16.8 °C; water temperature = 15.1 °C), a male chased away another individual after visualized him in his territory. The resident male (SVL = 30.32 mm; body mass = 1.94 g) emitted advertisement calls and territorial calls with notes A and B. All calls were directed to the intruder male (SVL = 26.48 mm; body mass = 1.23 g); the resident male immediately turned his body and took a few steps forward over a rock inside the stream channel and just below a small waterfall as soon as he saw the intruder. Soon after, the resident male emitted advertisement calls and then jumped close to the intruder individual, at which point he emitted advertisement and territorial calls, in addition to visual signals (moving the toes). The intruder remained stationary and only moved after the resident

male approached him: the intruder turned his back to the resident male in a fleeing posture. The males remained stationary for ca. of one minute and we ceased observation.

The territorial call also preceded a physical combat between males, which we observed on February 21, 2022, at 7:05 p.m (air temperature = 18.9°C, water temperature = 21.1 °C). One male emitted territorial calls with notes A, inflating only its right vocal sac, which was directed to another male. The male emitted nine territorial calls with combinations of notes A ca. 10 cm distant from the other male, which was partially submerged in the water and did not move at all. The calling male then jumped onto the other, hitting him in the dorsum and head with his hind legs. The males were not captured.

We observed territorial calls emitted in a courtship context. The courtship event occurred on November 23, 2021 from 4:53 a.m. to 5:20 a.m. (nighttime to twilight; mean water temperature = 16.3 °C, mean air temperature = 15.3 °C), while conspecific nearby males were emitting advertisement and territorial calls. The focal male did not synchronize his calls with those emitted by the neighbors, overlapping them. Initially, the male was positioned in front of the female and facing away from her. Both male and female were 40 cm above the water flow and on the tip of a partially decomposed log at approximately 15 cm of each other. The male emitted call a series of 13 simple and complex territorial calls. Between calls, the male moved twice as if he was adjusting himself on the spot. The first time, he lifted his body along with his arm while in the second he moved quickly and slightly to the side. The female then jumped and positioned herself ca. 5 cm behind the male, which ceased calling and remained still for about 45 s. The male then jumped into the water and after ca. 30 seconds he returned partially submerged on a fallen trunk below where it was before the jumps. Then, the female moved her body and head towards the male, which emitted notes A inflating only the left vocal sac (closer to the female) and positions himself to the side of the female ca. 40 cm distant. The female again jumps where the male was while the male again jumps into the water after a few seconds. As the male realized that the female had not jumped into the water with him, he climbed back up the fallen branch and positioned himself on the side of the female and at ca. of 5 cm. The male emitted notes A and B inflating both vocal sacs while nearby males were emitting notes A and advertisement calls. After that, he emitted two notes A, the female changed her posture and turn around to the male. In this moment, she tilted her head towards the male, who emitted AA and AAA combinations of notes only inflating his right vocal sac close to the female. Then, he takes steps forward and emitted a combination AA. The male jumps back into the water trying touch the female and remained submerged; he was soon followed by the female, where the individuals interacted by means of tactile signals.

3.4 DISCUSSION

Males of *Hylodes perere* emitted at least two types of calls, namely the advertisement and territorial call. In addition, the territorial calls are shown to be variable, and can be simple or complex, including various possible combinations of notes A and B. The social context seems to be decisive in the emission of these calls, which are more emitted when other individuals are present, in calling activity and closest of each other within the stream. We also found that these calls can be emitted in male-male and male-female interactions.

The aggressive call of *Hylodes perere* is here considered a territorial call (TOLEDO et al., 2015) because males indeed remain in their territories for weeks or months and chase away intruders (chapter 1; our results). This subcategory of aggressive call is emitted exclusively by males of territorial species and, as the name suggests, the main function is the defense of the territory (WELLS, 2007; TOLEDO et al., 2015). Individuals use territories as calling sites to attract females and oviposition, in addition of development of the tadpoles (this study). Thus, individuals who show site fidelity and successfully defend their territories of other males can increase their fitness because they can increase the chances of survival and reproduction (WELLS, 2007). Specifically for *Hylodes perere*, as observed for other *Hylodes* (NARVAES; RODRIGUES, 2005; de SÁ et al., 2015), males construct underwater chambers as oviposition sites that can be selected by females (R. A. F. Turin, unpublished data), which explains why the territory is crucial for increasing male reproductive success. Remaining in the same territory could also be associated with the abundance and heterogeneity of escape sites against predators, because calling males are exposed (RYAN; TUTTLE; TAFT, 1981; ALMEIDA et al., 2021). Males of *H. perere* usually jumped into the water when we tried to capture them, where they hid for a while, then cautiously returned to the surface, head first and then the whole body (R. A. F. Turin, personal observations); hiding by submersion was also reported for *H. amnicola*, *H. dactylocinus*, *H. japi* and *H. caete* (POMBAL; FEIO; HADDAD, 2002; NARVAES; RODRIGUES, 2005; de SÁ et al., 2015; MALAGOLI et al., 2017). The banks also serve as escape sites, including soil, rock crevices or associated vegetation, as well as fallen vegetation within the water and undercut banks. Indeed, some studies with herpetofauna have shown that male knowledge about their territories is adaptive (SCHWARTZ; BAIRD; TIMANUS, 2007; SONNLEITNER et al., 2020). Besides, the territory ensures the necessary condition for the permanence of the adult individuals as higher air humidity and hydration (HATANO; ROCHA;

VAN SLUYS, 2002; WELLS, 2007; SILVA et al., 2012), because high gradient streams include small waterfalls and rapids, which produce splash zones at short distances in terrestrial environment (HADDAD; GIARETTA, 1999; NUNES-DE-ALMEIDA et al., 2016) and may be crucial to adult frogs with diurnal activity (HATANO; ROCHA; VAN SLUYS, 2002; MACHADO et al., 2016). In addition, individuals may remain at ground level or near the water surface when active, but individuals may also occupy higher microhabitat sites while inactive as *H. dactylocinus* and *H. nasus* (NARVAES; RODRIGUES, 2005; MACHADO et al., 2016).

The fact that individuals emitted territorial calls in light and dark periods of the day and on different microhabitats demonstrate their importance for the social interactions of *H. perere*. Species of this genus are predominantly diurnal (HEYER et al., 1990; MALAGOLI et al., 2017). However, nocturnal vocalizations occurred occasionally in *H. phyllodes*, *H. amnicola*, *H. sazimai*, *H. caete*, and regularly in *H. japi*, *H. meridionalis* and *H. magalhesi* (HEYER et al., 1990; POMBAL; FEIO; HADDAD, 2002; LINGNAU et al., 2013; de SÁ et al., 2015; MALAGOLI et al., 2020; MUSCAT et al., 2020). Silva and Benmaman (2008) described *H. perere* as a species with diurnal and nocturnal activity because males emitted calls in both periods. However, these authors did not specify the type of the vocalizations emitted at night as well as other studies on the nocturnal vocalization's activity of species of *Hylodes*, with exception of Alencar et al., (2012) to *H. phyllodes*. Here, we found that both advertisement and territorial calls are emitted during both periods of the day in *H. perere*: while the advertisement calls are predominantly emitted at daylight, at twilights and occasionally at nighttime (chapter 1), the territorial calls are emitted with a strong dependence on the social context and can be emitted at any period of the day (table 1).

Territorial calls are typically directed towards a visible intruder male or at neighbors who are signaling, but also may be emitted in the absence of conspecific males because it also serves in the male interspacing (TOLEDO et al., 2015; de SÁ; ZINA; HADDAD, 2016). The more active and close individuals, the more complex the repertoire used by *H. perere*, including the use of complex and simple territorial calls, as well as advertisement calls. Only territorial calls were emitted with control of paired bilateral vocal sacs, when males inflate one of them at short distances to other individuals, as also found for *Hylodes. japi*, *H. meridionalis*, *H. heyeri*, *Crossodactylus timbuhy* and *Staurois guttatus* (de SÁ; ZINA; HADDAD, 2016; ELIAS-COSTA; FAIVOVICH, 2019; FURTADO et al., 2019; STRUETT; CONFETTI; LEIVAS, 2021; LACERDA et al., 2022). Within *Hylodes*, territorial calls are generally shorter than advertisement calls, emitted at higher rates, and in presence or simulation of neighboring males (WOGEL; ABRUNHOSA; WEBER, 2004; HARTMANN; HARTMANN; HADDAD, 2006;

LINGNAU; BASTOS, 2007). Simple and complex territorial calls were described to *H. regius* (de SÁ; LYRA; HADDAD, 2020), *H. uai* (NASCIMENTO; POMBAL; HADDAD, 2001), *H. japi* (de SÁ; ZINA; HADDAD, 2016) and *H. asper* (HADDAD; GIARETTA, 1999), but other than our study, the combination of note types were detailed only in *H. regius*. The use and function of this territorial call variability is unclear within the genus but seems to be related to the emphasis of signal information in short-range in *H. perere*. The territorial calls tended to be less intense than advertisement calls (chapter 1), which makes it more efficient in close interactions (BECKERS; SCHUL, 2004; de SÁ; ZINA; HADDAD, 2016), as does also the use of visual signals in this context (de SÁ; ZINA; HADDAD, 2016). In male-male interactions, notes B were more frequent, which makes it more aggressive. Furthermore, the note types of the territorial call are also emitted in courtship context in *H. perere*, especially the notes A, which was used by male to guide the female towards the oviposition site at short distance (R. A. F. Turin, unpublished data). Similarly, de Sá, Zina and Haddad (2016) found that both note types were emitted in courtship context in *H. japi*, although they also recorded the advertisement and courtship call in this context.

We described the territorial calls of *H. perere*, and detailed the emissions of each note type that forms simple and complex calls, which is rare for the genus. We highlight that social contexts may determine the patterns of emission of these calls, which happened predominantly in male-male interactions, but also in other contexts, such as during courtships, influencing its reproduction. This becomes of particular importance for a Data Deficient species such as *H. perere*, given studies that show that species with this type of classification are more likely to face threats (BORGELT et al., 2022). We emphasize the need for future studies of closely-related species to comprehend evolution communication in frogs, which can also combine their vocal repertoire with other types of signals, such as visual, tactile and chemical signals and, as a consequence, display multimodal communication (AMÉZQUITA; HÖDL, 2004; STARNBERGER; PREININGER; HÖDL, 2014; BRUNETTI et al., 2015; de SÁ; ZINA; HADDAD, 2016; FURTADO et al., 2019).

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COMITÊ DA BACIA HIDROGRÁFICA AFLUENTES MINEIROS DOS RIOS PRETO E PARAIBUNA - CBHAMRPP. **Complementação e finalização do plano integrado de recursos hídricos da Bacia Hidrográfica do Rio Paraíba do Sul - PIRH-OS e elaboração dos planos de recursos hídricos das Bacias Hidrográficas afluentes - Produto Final 05**: Plano diretor de recursos hídricos da Bacia Hidrográfica dos afluentes mineiros dos Rios Preto e Paraibuna. Resende: CBHAMRPP, 2021.

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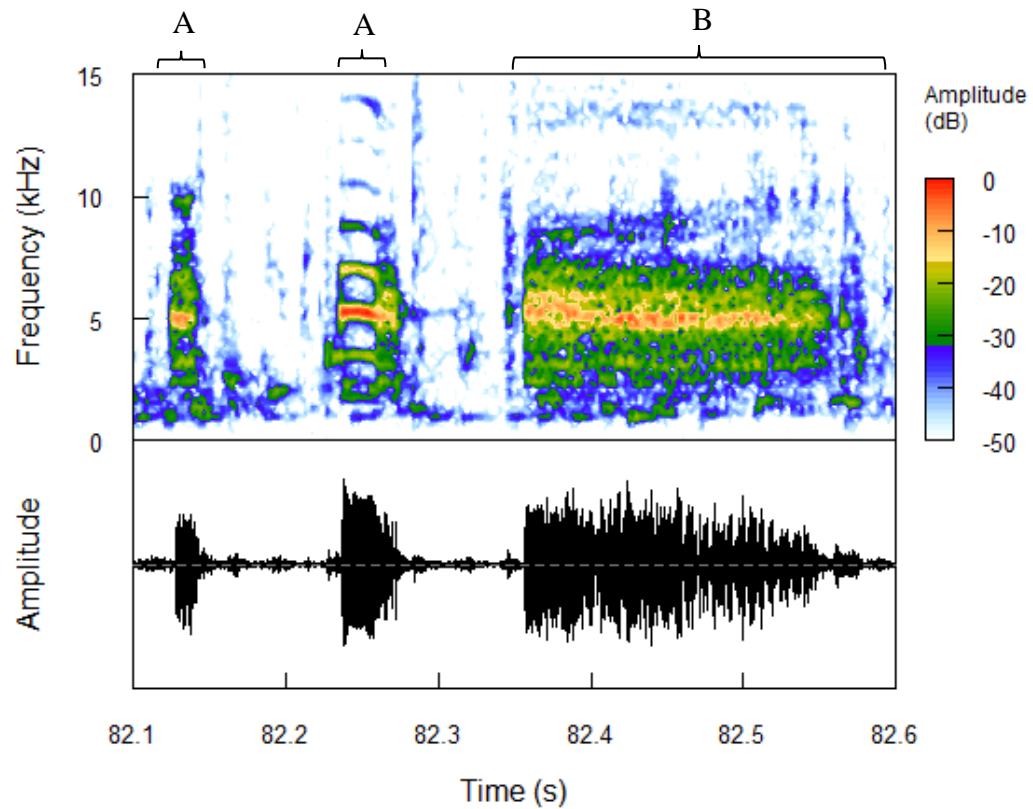
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FIGURES

Figure 1 - Example of a complex territorial call of *Hylodes perere* from the municipality Santa Bárbara do Monte Verde, southeastern Brazil. The combination of three notes are note A, note A, and note B. Water temperature = 14.9 °C ; air temperature =15.9 °C; male SVL = 27.72 mm



Fonte: Elaborado pelo autor (2022).

TABLES

Table 1 - Emission of territorial calls in *Hylodes perere*, municipality of Santa Bárbara do Monte Verde, southeastern Brazil, separated by recorded males (1 to 15), including period of emission

| Male number | N | Note A | Note B | A/B Ratio | Daytime, nighttime or twilight |
|-------------|----|--------|--------|-----------|--------------------------------|
| 1 | 23 | 58 | 9 | 6.44 | D |
| 2 | 19 | 38 | 6 | 6.33 | T |
| 3 | 10 | 28 | 0 | 0 | N |
| 4 | 10 | 8 | 5 | 1.6 | D |
| 5 | 10 | 34 | 0 | 0 | T |
| 6 | 10 | 6 | 6 | 1 | D |
| 7 | 10 | 13 | 6 | 2.16 | N |
| 8 | 13 | 31 | 4 | 7.75 | N |
| 9 | 12 | 36 | 2 | 18 | D |
| 10 | 10 | 16 | 5 | 3.2 | D |
| 11 | 10 | 10 | 6 | 1.66 | T |
| 12 | 10 | 29 | 1 | 29 | D |
| 13 | 10 | 25 | 2 | 12.5 | T |
| 14 | 10 | 14 | 5 | 2.8 | T |
| 15 | 10 | 17 | 4 | 4.25 | D |

Fonte: Elaborado pelo autor (2022).

Table 2 - Combinations of notes type A ($n = 362$) and type B ($n = 60$) of 177 territorial calls measured across 15 individuals of *Hylodes perere*, municipality of Santa Bárbara do Monte Verde, southeastern Brazil. N represents the number of territorial calls with the mentioned combination of notes or single notes

| Combinations of notes or single notes | N | % |
|---------------------------------------|----|-------|
| A | 5 | 2.75 |
| AA | 39 | 21.42 |
| AAA | 57 | 31.31 |
| AAAA | 22 | 12.08 |
| AB | 13 | 7.14 |
| AAB | 10 | 5.5 |
| ABB | 1 | 0.55 |
| B | 35 | 19.23 |

Fonte: Elaborado pelo autor (2022).

Table 3 - Acoustic variables of the territorial calls of *Hylodes perere* in the municipality of Santa Bárbara do Monte Verde, southeastern Brazil, as measured from 15 individuals. Acoustic parameters include the mean, standard deviation, and range (the latter in parenthesis). *N* represents the number of measurements of each note type and the number of territorial calls (simple or complex). See text for full variable names

| Acoustic parameters | Note A <i>N</i> = 362 notes | Note B <i>N</i> = 60 notes | Overall (entire territorial call) <i>N</i> = 177 calls |
|---|-----------------------------------|----------------------------------|---|
| Dominant frequency (KHz) | 5.314 ± 0.497 (2.928- 6.546) | 5.001 ± 0.504 (3.100 – 6.201) | 5.269 ± 0.509 (2.928 – 6.546) |
| Frequency 5% (KHz) | 3.984 ± 1.101 (1.205 – 6.201) | 3.296 ± 0.938 (1.205 – 4.995) | 3.884 ± 1.105 (1.205 – 6.201) |
| Frequency 95% (KHz) | 6.301 ± 0.894 (4.134 - 10.852) | 6.692 ± 0.817 (5.340 – 8.441) | 6.359 ± 0.895 (4.134 – 10.852) |
| Call duration (s) | 0.03 ± 0.01 (0.01 - 0.06) | 0.19 ± 0.05 (0.05 - 0.30) | 0.24 ± 0.08 (0.02 – 0.45) |
| Interval between territorial calls within a series (s) | - | - | 2.62 ± 2.53 (0.48 - 28.26) |
| Call rate (calls within a series of 10 territorial calls per min) | - | - | 25.63 ± 6.37 (14.55 - 37.14) |
| Sound pressure level (dB) | - | - | 70.2 ± 5.95 (58 - 77) |

Fonte: Elaborado pelo autor (2022).

4 FINAL CONSIDERATIONS

This is the first study to investigate simultaneously frog movements and adaptations to geophony in a mark-recapture approach. Consequently, we were able to demonstrate that anurans in noisy natural environments adjust their vocal parameters (call plasticity) instead of reallocating to less noisy sections of streams. Males of *Hylodes perere* remained over weeks and months in their territories.

Sexual selection is likely crucial in this system, favoring males that are able to detect other individuals and that better adjust their call efficiency. Besides, territory defense, to which territorial calls largely contribute, is likely advantageous for *H. perere* for survival and especially reproduction.

The territorial calls of *Hylodes perere* is complex and composed of two distinct notes (A and B). Notes were emitted alone or together in eight possible combinations and depending on the social contexts. Conspecific males interacted by emitting advertisement and territorial calls in short and long distances, but also interact with females in courtship behavior. We confirmed that communication in the species is complex, with likely visual signals in some occasions (bimodal communication).

Our work will aid in research of the communication evolution within the family with contributions in the investigation of the concomitant environmental and sexual selective pressures in species that communicate in noisy environments such as *Hylodes* species. In addition, our descriptive results might help better evaluate this Data Deficient species and contribute to the knowledge of the environment in which it lives, the highly endangered Atlantic Rainforest.