aeet
ASOCIACIÓN ESPAÑOLA
DE ECOLOGÍA TERRESTRE

Ecosistemas 32 (2): 2425 [Mayo-Agosto 2023]
https://doi.org/10.7818/ECOS.2425

MONOGRÁFICO: Ecología del Movimiento: del análisis individual a la provisión de servicios ecosistémicos

Editores: Eneko Arrondo, Zaida Ortega y Juan Manuel Pérez-García

ARTÍCULO DE INVESTIGACIÓN

ecosistemas
REVISTA CIENTÍFICA DE ECOLOGÍA Y MEDIO AMBIENTE

ISSN 1697-2473
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disponible en www.revistaecosistemas.net

Jumping between narrow banks: social spacing of the stream-dwelling montane frog, *Crossodactylus trachystomus* (Hylodidae)

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> Recibido el 15 de julio de 2022 - Aceptado el 21 de marzo de 2023

Como citar: Wachlevski, M., Passos, D., Eterovick, P.C 2023. Jumping between narrow banks: social spacing of the stream-dwelling montane frog, *Crossodactylus trachystomus* (Hylodidae). *Ecosistemas* 32(2): 2425. https://doi.org/10.7818/ECOS.2425

Jumping between narrow banks: social spacing of the stream-dwelling montane frog, *Crossodactylus trachystomus* (Hylodidae)

Abstract: Spacing patterns among individuals can reveal many ecological and behavioral features, such as responses to resource availability and social organization. The study of the amphibian movements still constitutes a gap in the knowledge of the animal ecology, and the general issues of the patterns of home range are poorly known to date. Herein, we evaluated the social spacing of a small stream-dwelling frog (*Crossodactylus trachystomus*), an endemic species from the Espinhaço mountain range in southeastern Brazil. We found that *C. trachystomus* shows one of the smallest home ranges among anurans, indicating a high philopatry level. We also showed that the home range size did not differ between females and males, neither was influenced by individual body size, which reveals a possible limitation for the use of larger home ranges in riparian systems. The distribution of home ranges showed high overlap among adult males, suggesting a weak territorial behavior or a possible "dear enemy effect" for this species. Beyond expanding the knowledge about the spatial ecology and behavior of the genus *Crossodactylus*, our outcomes contributed to the understanding of space use and the social organization of frogs, revealing spatial patterns that can be expected for other stream-dwelling frog species.

Keywords: Anura; home range; spatial overlap; site fidelity

Saltando entre bancos angostos: espaciamiento social de la ranita de arroyos montanos, *Crossodactylus trachystomus* (Hylodidae)

Resumen: Los patrones de espaciamiento entre individuos pueden revelar muchas propiedades ecológicas y de comportamiento, como las respuestas a la disponibilidad de recursos y la organización social. El estudio del movimiento de los anfibios aún constituye un vacío en el conocimiento de la ecología animal, y las cuestiones generales de los patrones de área de campeo son poco conocidos hasta la fecha. Aquí, evaluamos el espacio social de una pequeña rana que habita en arroyos (*Crossodactylus trachystomus*), una especie endémica de la cordillera del Espinhaço en el sudeste de Brasil. Encontramos que *C. trachystomus* muestra una de las áreas de campeo más pequeñas entre los anuros, lo que indica un alto nivel de filopatría. También mostramos que el tamaño del área campeo no tuvo diferencia entre hembras y machos, ni fue influenciado por el tamaño corporal individual, lo cual revela una posible limitación para la formación de áreas de campeo más grandes en sistemas ribereños. La distribución de las áreas de campeo mostró una alta sobreposición entre los machos adultos, lo que sugiere una conducta no territorial o un posible "efecto del enemigo querido" para esta especie. Más allá de ampliar el conocimiento sobre la ecología y el comportamiento del género *Crossodactylus*, nuestros resultados contribuyen a la comprensión del uso del espacio y la organización social de los anuros, revelando patrones espaciales que podrían ser parecidos en otras especies de ranas que habitan en arroyos.

Palabras Clave: Anura; área de campeo; sobreposición espacial; fidelidad al sitio

Introduction

In the animal ecology, the movement patterns have profound implications in multiple hierarchical levels, such as individual fitness, population dynamics, and species distribution (Brown and Orians 1970; Nathan et al. 2008). Specifically, the home range is a key topic about space use in ethological studies (e.g. Börger et al. 2008; Spencer 2012). Historically, the home range is conceived as the area where an individual habitually thrives and performs its main activities related to survival, growth, and reproduction (Burt 1943; Wells 2007). The home range includes food, refuges, and mates, being useful to express individual responses to resource availability, intra and interspecific interactions, as well as to reveal properties of social organization, being thus applicable to delineate conservation strategies (e.g. Knapp and Owens 2005; Formica et al. 2010). However, the understanding of movement and spatial patterns still faces deep knowledge gaps (Holyoak et al. 2008; Nathan et al. 2008).

According to Nathan et al. (2008), the paradigm of movement pattern of amphibians involves at least five individual movement phases and nine distinct modes. However, most studies have focused on tadpole movements (e.g. Pacheco et al. 2019), while juvenile dispersal has received some attention in recent decades (e.g.

Semlitsch 2008), and even less is known about space use patterns in adults (Pittman et al. 2014). We basically know that amphibians use the space in a very different way from other terrestrial animals, presenting one of the smallest home ranges among vertebrates (Wells 2007). However, studies on the general determinants of home range patterns in amphibians remains to be addressed. The extension of home ranges is influenced by body size in the amphibians (Mathis 1991; Henrique 2016), as it has already been demonstrated for other tetrapods (e.g. McNab 1963; Armstrong 1965; Turner et al. 1969). Moreover, in view of the general trend of sexual dimorphism biased toward females larger than males, added to the prevalent epigamic sexual selection operating among amphibians (Wells 2007), as well as active defense of spatial resources reported for many species (Muths 2003; Poelman and Dicke 2008), we can also expect that intersexual divergences in home range size arise after maturity (Muths 2003; Valenzuela-Sánchez et al. 2014). Furthermore, regarding social organization, it is plausible to assume that the intrasexual overlap of the home range would be less intense among territorial species (Roithmair 1992; Werner et al. 2010).

The South American frogs belonging to the family Hylodidae are stream-dwelling diurnal species with continuous reproduction (e.g. Weygoldt and Carvalho-e-Silva 1992; Almeida-Gomes et al. 2007; Wachlevski et al. 2008; Machado et al. 2016; Caldart et al. 2019), that could express territoriality through acoustic and visual signals (Wögel et al. 2004; Hartmann et al. 2005; Caldart et al. 2014; Sá et al. 2016). The hylodids are usually abundant, and show relatively sedentary habits (e.g. Narvaes and Rodrigues 2005), features that make them suitable models to study use of space. Notwithstanding, although hylodids comprise 48 species in four genera (*Crossodactylus*, *Hylodes*, *Megaelosia* and, *Phantasmarana* - Frost 2021), the movements and home range of the group is only known for *Hylodes dactylocinus* (Narvaes and Rodrigues 2005). Thus, it is reinforced the necessity of provide information on space usage of others hylodids in order to reach a broad comprehension on the spatial ecology of stream-dwelling frogs as a whole.

Crossodactylus trachystomus (Reinchardt and Lütken 1862) is a small diurnal stream-dwelling frog, and endemic from Espinhaço mountain range in southeastern Brazil (Pimenta et al. 2015). It is a highly selective species regarding microhabitat usage, both within and among streams (Afonso and Eterovick 2007; Wachlevski et al. 2008). Adults of *C. trachystomus* usually live close to shallow water, with calling males showing high preference for fast current and sandy substrates (Wachlevski et al. 2008). This latter feature is attributed to the construction of submerged nests, which are excavated in the sandy bottom (Weygoldt and Carvalho-e-Silva 1992; Wachlevski et al. 2008). Males of *C. trachystomus* also exhibit acoustic and visual displays that can be directed towards rivals (MW personal observation). Considering these behavioral peculiarities, its relative abundance and ease of sampling, herein we researched the social spacing of *C. trachystomus*. Specifically, we aimed to evaluate the intersexual differences and morphological influences on home range size, as well as patterns of home range overlap within and between sexes. In view of distinct sexual dimorphism and sexual roles of females and males among frogs of the genus *Crossodactylus*, we hypothesized that females of *C. trachystomus* would have larger home ranges than males, and predicted that the home range size would be positively influenced by the body size (length and body mass) due to inherent energetic constraints on larger individuals. Moreover, as most hylodid frogs show territorial habits, we also expected that home range overlapping would be lower between individuals of the same sex than in intersexual pairs.

Methods

Study site

We conducted this study at the Reserva Particular do Patrimônio Natural (RPPN) Santuário do Caraça (20^{0}05’37”S, 43^{0}29’59”W; 1293 m a. s. l.), Catas Altas municipality, Minas Gerais state, Southeastern Brazil. The protected area has 11 233 ha and is located at the Espinhaço mountain range, with vegetation including elements of the Cerrado and the Atlantic Forest biomes (Giulietti and Pirani 1988; Giulietti et al. 1997). The average annual temperature is 15°C (Andrade 2000). The climate is seasonal, with a dry season extending from April to September and a rainy season, from October to March, and 2048 mm of average annual rain (Canelas and Bertolucci 2007). The specific studied site comprised a section of a permanent stream (Cascudos stream) bordered by riparian Atlantic Forest. The bottom of the stream is sandy with scattered rocks. The width of the studied section ranges between 2 and 6 m, and the depth, from 3 to 100 cm.

Sampling procedures

We placed a grid composed of 96 quadrats of 2 x 2 m (totaling 384 m^2) along a section of the Cascudos stream and carefully searched for adults and juveniles of *C. trachystomus*. At the first capture, all the frogs had the snout-vent length (SVL) measured with calipers (to 0.01 mm), and the body mass with a dynamometer (to 0.1 g). All the individuals were marked by toe clipping (Waichman 1992), through the excision of a single distal phalange, and when two phalanges needed to be excised, they were never taken from the same member. Toe-clipping is a useful and very safe marking method in mark–recapture studies with anurans (e.g. Phillott et al. 2011; Corrêa et al. 2013). We continuously recaptured healthy marked frogs throughout the study period. We assigned the sex of adult individuals by the presence of vocal sacs in males or by the exhibition of calling behavior, and the detection of mature oocytes under the transparent belly in females.

We monitored the occurrence of marked individuals in the grid during three- to five-day-trips conducted each month from March 2004 to February 2005. We made daily searches in the morning and in the afternoon, during the activity period of the species. We used different pathways systematically to monitor the grid along the sampling days in each month, to avoid spatial-temporal dependence of records. The position of each recaptured individual was estimated in metric units based on its position according to axes X and Y at the margins of the grid.

We used the method of Minimum Convex Polygon (Mohr 1947) to estimate home range sizes (in m^2). This method delimits a polygon by interconnecting the most external points of a set of spatial positions (Hayne 1949). We excluded the 5% most extreme points of each individual to avoid incorporating localities rarely visited. Although there are other methodological alternatives, the Minimum Convex Polygon method remains the most frequently used to estimate home ranges in different animal groups (Laver and Kelly 2008) and it is suggested as the most suitable for estimating reptile and amphibian home ranges according to Row and Blouin-Demers (2006). We generated an accumulation curve to relate the home range size estimates (natural log transformed) with the number of sightings, and to define, therefore, the minimum threshold of spatial records (Rose 1982). Based on this curve, we identified the number of sightings from which the size of the home ranges showed the smallest increases in relation to the number of recaptures.

Statistical analysis

Before the statistical analyses, we inspected the data regarding the conformity with normal distribution by Shapiro-Wilk tests, and in relation to homoscedasticity between groups by Levene’s tests. When the data did not fit a normal distribution, we applied nonparametric tests. We used Student t-tests to evaluate the intersexual differences in SVL and home range size, whilst for the differences in body mass between females and males we used a Wilcoxon test. In addition, we assessed the relationship between home range size and number of sightings, and between home range size and body length by Pearson correlations. Meanwhile, the relationship between home range size and body mass was assessed by Spearman rank correlation.

We assigned a level of significance α = 0.05 for all analyses, and the descriptive statistics are presented as mean ± standard deviation. We conducted all statistical analyses and graphic illustrations in R v.4.1.0 (R Core Team 2021), using the packages *adehabitatHR* (Calenge 2006) and *rgeos* (Bivand and Rundel 2013), following the code *HunteR* (Passos et al. 2015; https://github.com/NeoLiBE/NeoLiBE/), for automated estimation of home range size and calculation of overlap percentages.

Results

We captured and marked 102 individuals of *Crossodactylus trachystomus* along 12 months, including 34 females (33%), 56 males (55%), and 12 (12%) juveniles. Of this total, we recaptured 75 (74%) individuals at least once, averaging 6.1 ± 5.4 (2 - 31) records per individual, totaling 482 spatial localities. The cumulative curve of the home range size in relation to the number of recaptures showed a decrease of variation in the estimates after seven records (**Fig. 1**). Based on this threshold, the estimates recovered an area on average 10% larger than estimates based on six records and only 2% smaller than estimated with eight records. Thus, we assigned seven records as the minimum threshold of recaptures per individual to estimate home range size. Considering this cutoff, we obtained the estimates of home range for 22 individuals (29% of recaptured ones), consisting of seven females, 14 males, and a juvenile. There was no significant correlation between these 22 estimates of home range size and the maximum number of individual records (Pearson correlation - r = 0.28; *P* = 0.21).

The studied population of *C. trachystomus* showed significant sexual dimorphism in the SVL (Student-t; t = 14.27; df = 88; *P* < 0.01) and body mass (Wilcoxon test = 1821.5; df = 88; *P* < 0.01), with the body size of females (SVL = 25.14 ± 1.16 mm; body mass = 1.55 ± 0.23 g; n = 34) larger than males (SVL = 21.94 ± 0.94 mm; body mass = 1.14 ± 0.13 g; n = 56). However, the home range size between females (1.98 ± 1.88 m², n = 7) and males (1.57 ± 2.07 m², n = 14) did not significant differ (Student-t; t = 1.27; df = 19; *P* = 0.22; **Fig. 2**). The average of the home range size was 2.7 ± 4.6 m² (n = 22), and it ranged from 0.1 to 24.0 m². The home range size was not influenced by the SVL of the individuals (Spearman rank correlation - rho = 0.07; df = 20; *P* = 0.76; **Fig. 3a**) neither by the body mass (Spearman rank correlation - rho = -0.01; df = 20; *P* = 0.98; **Fig 3b**). The only juvenile individual, with enough recaptures, presented a home range size with 3.14 m², an area larger than 75% of those estimated for females and males (**Fig 3**).

Regarding social spacing, 14 (64%) of 22 individuals with estimated home range, showed spatial overlap with at least one neighboring individual (**Fig. 4**). Considering these individuals, we recorded 12 home range overlapped in the studied population (**Fig. 4**). Most of overlaps (67%) occurred among pairs of males (eight of 12 home ranges overlaps, involving nine different males), followed by between pairs of females (17%, two of 12 home range overlaps, involving four females); meantime there was only an overlap between a female and a male (8%, one of 12 home range overlaps), and another between a female and a juvenile (8%, one of 12 home range overlaps). The percentage of home ranges overlap among the pairing types were: male-male (27.7 ± 29.1%; 3.3 - 100.0%), female-female (43.4 ± 46.8%; 2.4 - 100.0%), female-male (6% of female' area and 38% of male' one), and female-juvenile (3% of female' area and 24% of juvenile' one).

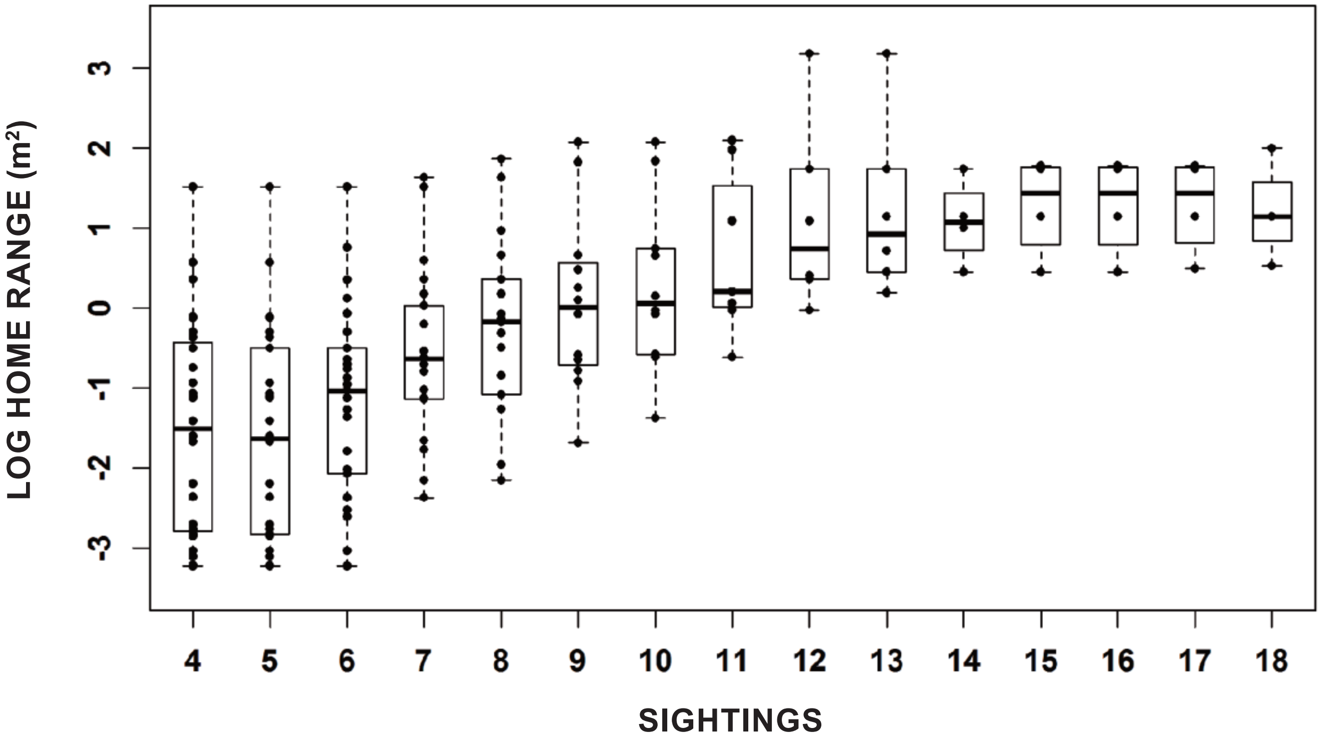

Figure 1. *The relationship between home range size (m² in* $\log_e$*) and the number of sightings of Crossodactylus trachystomus from the RPPN Santuário do Caraça, Catas Altas municipality, Minas Gerais state, southeastern Brazil.*

Figura 1*. Relación entre el tamaño del área de campeo (m² en* $\log_e$*) y el número de avistamientos de Crossodactylus trachystomus de la RPPN Santuário do Caraça, municipio de Catas Altas, estado de Minas Gerais, sudeste de Brasil.*

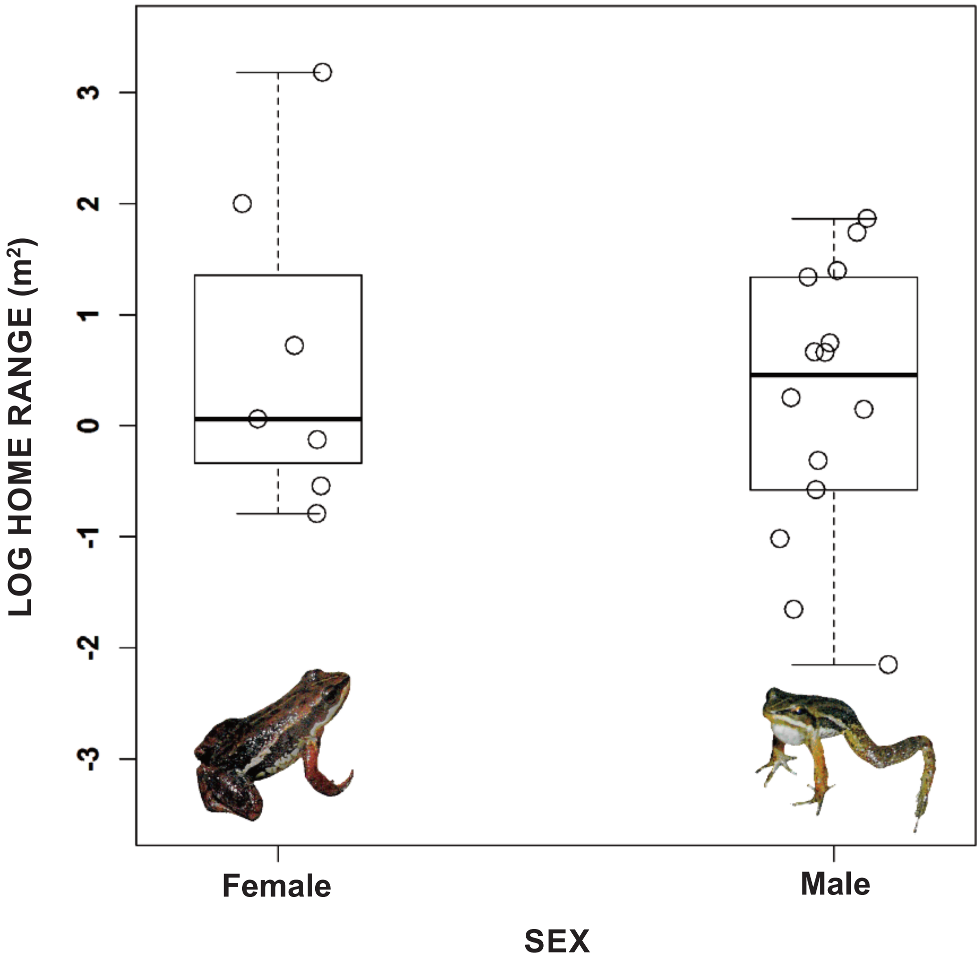

Figure 2. Home range size (m² in $\log_e$) of female and male adults of <u>Crossodactylus</u> <u>trachystomus</u> from the RPPN Santuário do Caraça, Catas Altas municipality, Minas Gerais state, southeastern Brazil.

Figura 2. Tamaño del área de campeo (m² en $\log_e$) de hembras y de machos adultos de <u>Crossodactylus</u> <u>trachystomus</u> de la RPPN Santuário do Caraça, municipio de Catas Altas, estado de Minas Gerais, sudeste de Brasil.

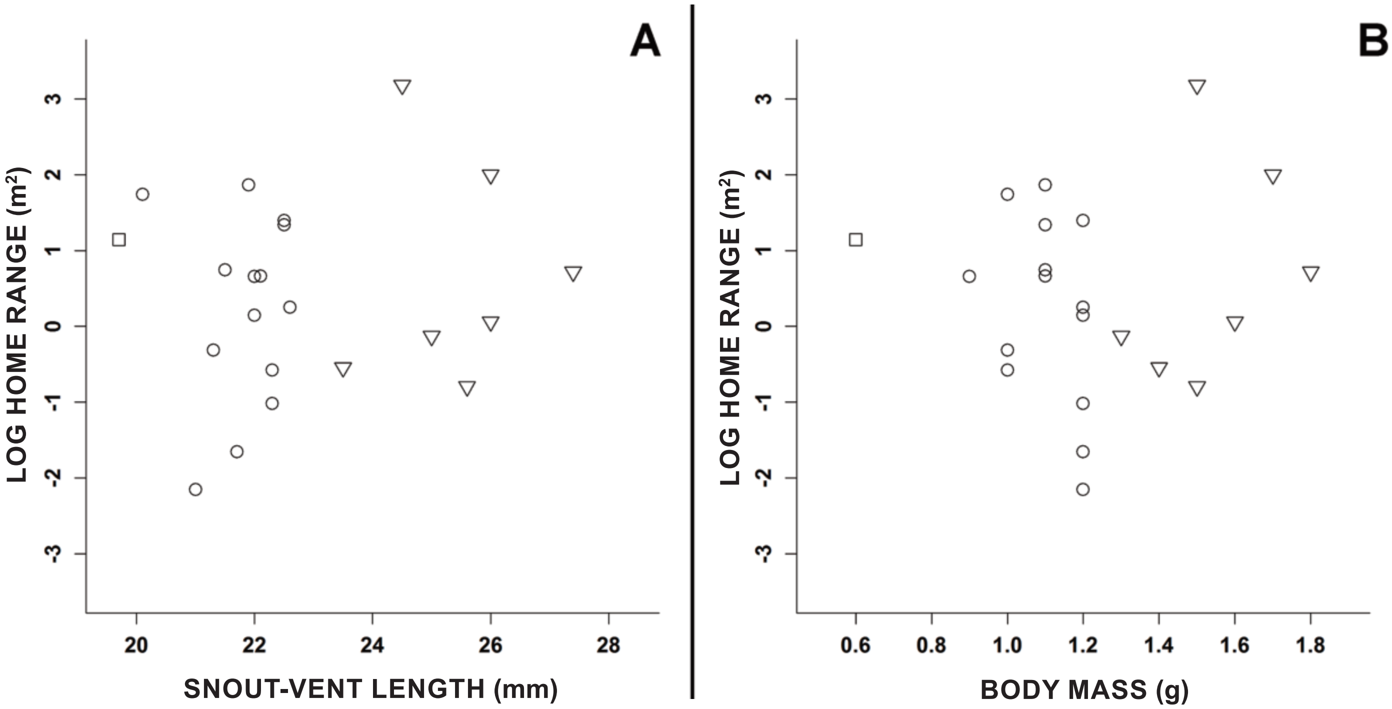

Figure 3. *Relationship between home range size ($\log_e$ transformed) and snout-vent length, (**A**) and between home range size ($\log_e$ transformed) and body mass (**B**) of <u>Crossodactylus</u> <u>trachystomus</u> from the RPPN Santuário do Caraça, Catas Altas municipality, Minas Gerais state, southeastern Brazil. Different symbols refer to females (triangles), males (circles), and a juvenile (square).*

Figura 3. *Relación entre el tamaño del área de campeo ($\log_e$ transformado) y la longitud hocico-cloaca (**A**) y entre tamaño del área de campeo ($\log_e$ transformado) y masa corporal (**B**) de <u>Crossodactylus</u> <u>trachystomus</u> en la RPPN Santuário do Caraça, municipio de Catas Altas, estado de Minas Gerais, sudeste de Brasil. Diferentes símbolos se refieren a hembras (triángulos), machos (círculos) y un juvenil (cuadrado).*

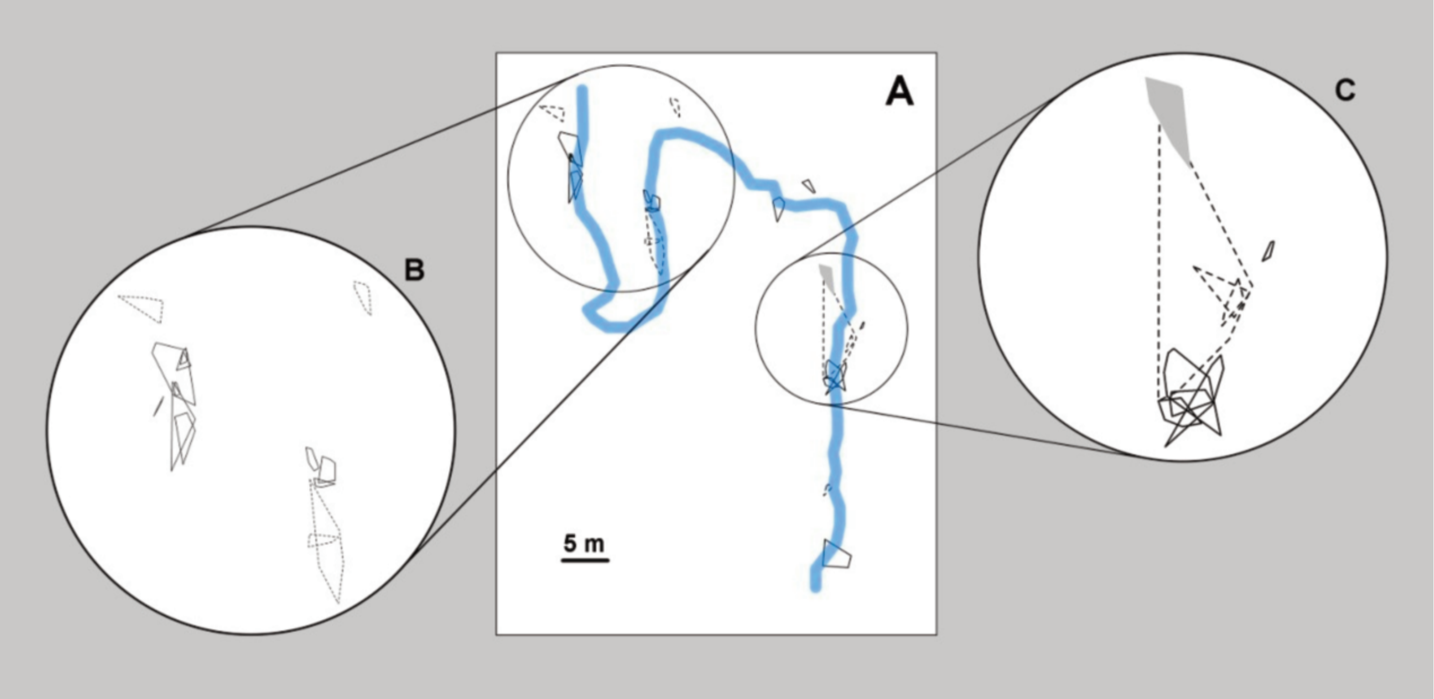

Figure 4. *Spatial organization of Crossodactylus trachystomus from the RPPN Santuário do Caraça, Catas Altas municipality, Minas Gerais state, southeastern Brazil. Polygons represent the home range areas of females (dashed outline), males (solid outline) and a juvenile (filled gray). Riverbed of the Cascudos stream in blue (**A**). Details highlight regions of intrasexual (**B**) and intersexual (**C**) home range overlap.*

Figura 4. *Organización espacial de Crossodactylus trachystomus en la RPPN Santuário do Caraça, municipio de Catas Altas, estado de Minas Gerais, sudeste de Brasil. Los polígonos representan el área de campeo de las hembras (líneas punteadas), de los machos (líneas continuas) y de un juvenil (relleno en gris). Cauce del arroyo Cascudos en azul (**A**). En destaque, están los locales de mayor sobreposición del ámbito de hogar intrasexual (**B**) e intersexual (**C**).*

Discussion

Home range size did not differ between sexes in *Crossodactylus trachystomus*, although such intersexual differences are relatively common among ectotherms (e.g. Haenel et al. 2003a, 2003b), including amphibians (e.g. Muths 2003; Poelman and Dicke 2008). Contrary to our hypothesis, female home ranges were not larger than those of males. Similar home ranges between sexes could be related to little or no sexual dimorphism (i.e., sexes with similar body sizes), as already suggested for lizards (Warrick et al. 1998; Kerr and Bull 2006). However, considering energetic needs, differences between sexes could be expected in species that females are larger than males, as *C. trachystomus* (Pimenta et al. 2015). In addition to sexual dimorphism, we expected females to have larger home ranges than males due to: 1) females of Hylodidae cover large areas looking for mates (e.g. Narvaes and Rodrigues 2005; Sá et al. 2016); and 2) hylodid males select and defend small specific sites where build nests for oviposition (Haddad and Giaretta 1999; Caldart et al. 2014). However, although the females of many anuran species have larger home ranges than males (e.g. Muths 2003; Wells 2007; Poelman and Dicke 2008), it is also known that the home range size of females may greatly vary through the breeding season (Fischer et al. 2020). For instance, females of *Allobates femoralis* are usually sedentary in small home ranges but can increase their area in 30% during breeding events, when they move in search for mates and oviposition sites (Fischer et al. 2020). We found mature females of *C. trachystomus* during the whole study period, corroborating other studies that found prolonged breeding for hylodids (e.g. Weygoldt and Carvalho-e-Silva 1992; Narvaes and Rodrigues 2005; Caldart et al. 2019). Thus, as our sampling included all the reproductive period of *C. trachystomus*, the reason for the small home ranges in both sexes may reside in the limited availability of suitable habitats for the species at the studied stream. If on the one hand, natural history attributes of hylodids males (as site fidelity or territoriality) might explain their small home range sizes, as aforementioned, the same seems not to be true for females. Thus, it is more plausible to assume that a common ecological pressure operates on males and females spacing behavior. In direction, as *C. trachystomus* occurs exclusively in small permanent streams (Pimenta et al. 2008; 2015) and both of sexes shows high selectivity in the use of microhabitats (Wachlevski et al. 2008), individuals are usually found aggregated in restricted portions of the habitat, which can limit the magnitude of space explored by females and males.

The body size of individuals did not influence home range size of *C. trachystomus*. Several authors have stated that the home range increases with body size taking into account the energetic demands (e.g. McNab 1963; Mace and Harvey 1983). The energetic demand has indeed been listed as a primary factor influencing home range size in several vertebrate groups for instance: birds (Armstrong 1965), lizards (Turner et al. 1969) and mammals (Harestad and Bunnell 1979). Based on the available knowledge on anuran space use, larger species tend to explore larger areas in order to fulfill their feeding requirements (Wells 2007; Henrique 2016). However, contrary to theoretical predictions, the positive relationship between home range size and body size often does not occur at an intraspecific level in ectotherms, as observed in different families of lizards (e.g. Phrynosomatidae - Haenel et al. 2003b; Liolaemidae - Kacoliris et al. 2009; Tropiduridae - Ribeiro et al. 2009) and anurans (e.g. Bufonidae - Forester et al. 2006; Ranidae - Ra et al. 2008; Dendrobatidae - Brown et al. 2009). A possible explanation for this trend is the limited range of size within species when compared to those among species (Passos unpubl. data), revealing that mechanisms acting on different taxonomic hierarquic levels are not necessarily the same (Gompper and Gittleman 1991). In the case of *C. trachystomus*, that seems to prefer the sandy margins of the streams, the role of the relatively low availability to suitable microhabitats cannot be ruled out, as it may limit the acquisition of larger home ranges.

Most individuals with enough recaptures shared some portion of their home ranges with at least one other individual. Contrary to our expectations, home range overlaps were larger within than between sexes. In territorial species, is it expected that individuals of the same sex (usually males) segregate spatially, defending their territories from intruders (Martins 1994; Sheldahl and Martins 2000). This seems to be the case in some stream-dwelling species of family Hylodidae (e.g. Haddad and Giaretta 1999; Caldart et al. 2014). However, despite the relatively low percentage of home range overlap among males of *C. trachystomus*, the frequency of home range overlap among males was higher than among females. These results suggest a relatively high tolerance among conspecifics regarding use of space, which is important to understand the social organization of the species. In part, this can be explained by the higher density of males (1.6 males:1 female) in the studied population, but it may also suggest that there is no or weak defense of resources among males, implying a possible non-territoriality. Moreover, we cannot rule out the possibility of occurring a “dear enemy” phenomenon in *C. trachystomus*, a condition in which territorial males are more tolerant to conspecific neighbors than unfamiliar ones (e.g. Bee 2003; Chuang et al. 2017). In contexts of limited distribution of preferential resources, individuals may tolerate higher densities with consequent increase in home range overlap, even among individuals of the same sex (e.g. Ruby 1986; Clobert et al. 1994; Poelman and Dicke 2008). In this way, if by one side the spatial restriction of small streams (Almeida-Gomes et al. 2014) could limit the home range size of stream-dwelling frogs, on the other side, the microhabitat heterogeneity within them could determine the arrangement of home ranges (Wachlevski et al. 2008). Especially in the case of *C. trachystomus*, the availability of microhabitats with specific features (water flow, low depth, and sandy bottom) may explain the high intrasexual frequency and percentage of home range overlap at specific sections of the stream. At the same site, while males could be looking for suitable conditions to nest building, females could be searching for good mates and proper places to lay their eggs.

The use of space by *C. trachystomus* characterizes the species as philopatric according to our outcomes, with individuals spending the whole year in the same portion of stream bed. Hylodids are recognized as stream inhabitants (Heyer et al. 1990; Silva and Benmaman 2008), but their distribution and use of space within streams is poorly known (Narvaes and Rodrigues 2005). During our study, we found most individuals of *C. trachystomus* always close to the same point where we first sighted them, some even after ten months after the first capture, suggesting site fidelity (Narvaes and Rodrigues 2005; Fisher et al. 2020). Although juvenile individuals seemed to cover more extension, which probably reflected in lower recapture rates, one juvenile was recaptured throughout eight months before becoming adult, indicating that even juveniles may remain for long periods at the same area. After 18 recaptures, already as an adult, this individual moved to another site and was found calling close to a shallow water section with sandy bottom, a typical reproductive site of *C. trachystomus* (Wachlevski et al. 2008).

In summary, our findings on space use by *C. trachystomus* revealed one of the smallest home range sizes among anurans (see Narvaes and Rodrigues 2005; Henrique 2016; Neu et al. 2016) and a philopatric behavior likely to involve site fidelity. We also found that home range size did not differ between sexes nor was it influenced by body size of individuals, possibly related to limited availability of microhabitats for stream-dwelling frogs. The distribution of home ranges showed higher intrasexual than intersexual overlap and indicated high tolerance among males, suggesting a lack or weak territoriality or even a “dear enemy” effect. Our findings expand the knowledge on spacing patterns of a group of frogs highly sensitive to habitat loss and fragmentation (Welsh et al. 1998), and so, much more vulnerable to extinction (Almeida-Gomes et al. 2014). Thus, while less specialized anuran species could show different patterns of space use, the features evidenced here for *C. trachystomus* could be common to other stream dwelling frogs.

Acknowledgements

We are grateful to K. Kopp, I.M. Barata and P. Fatorelli for help during fieldwork. We thank C.A.B. Galdino and C.F.D. Rocha for suggestions in a previous version of the manuscript, T. S. Campos and M. Vallejos for translation of sections in Spanish, the staff of the RPPN Santuário do Caraça for permits and logistics, the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis/Instituto Chico Mendes de Conservação da Biodiversidade for permits (IBAMA/ICMBio 128/2004). MW received fellowship the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), PCE thanks to the Fundo de Incentivo à Pesquisa (FIP) of the Pontifícia Universidade Católica de Minas Gerais for financial support and to the Conselho Nacional de Desenvolvimento Científico e Tecnológico for a Productivity grant (309513/2020-0).

Author’s contributions

Milena Wachlevski: conceptualization, project administration, investigation, literature review, validation, data curation, writing, visualization, review and edition; Daniel Passos: literature review, data curation, formal analysis, visualization, validation, writing, review and edition; Paula C. Eterovick: conceptualization, literature review, writing, review and edition, funding acquisition.

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