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# Habitat and microhabitat use by *Crossodactylus schmidti* (Anura: Hylodidae) in Atlantic Rainforest streams

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**Abstract**

**Habitat and microhabitat use by *Crossodactylus schmidti* (Anura: Hylodidae) in Atlantic Rainforest streams.** A combination of biotic and abiotic factors influences the habitat and microhabitat selection by anurans. To analyze the habitat and microhabitat use by adults of *Crossodactylus schmidti,* we sampled 13 streams in the Atlantic Rainforest of Iguaçu National Park, Southern Brazil, between November 2014 and August 2015. We recorded abundance data and measured structural environmental variables of the streams related to habitat selection on three occasions in each stream. Data collection occurred along a 50-meter transect in each stream. Additionally, two samplings were conducted specifically to obtain microhabitat usage data, sampling only the same three streams on each sampling. We employed Generalized Least Squares analysis to assess spatial variation in abundance as a function of environmental structural variables, considering models with and without spatial structuring. We applied the Multinomial Goodness-of-Fit Test to elucidate the types of microhabitats most utilized by the frogs. Our analysis revealed that considering or not the spatial autocorrelation in the variation in *C. schmidti* abundance, none of the predictor variables was significant. The results obtained demonstrate that the analyzed environmental variables are not important for habitat selection of *C. schmidti,* and the spatial configuration and distance among streams are not determinants for abundance distribution. At the habitat scale, this species exhibits a random distribution independent of spatial and environmental features. Regarding microhabitats, individuals were predominantly found inhabiting streams in pool areas characterized by rocky substrate or organic matter accumulation. Conservation strategies for this species should encompass the scale-dependent relationships.

**Keywords:** Brazil, Distribution, Frogs, Habitat selection, Spatial dynamics.

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**Resumo**

**Uso do habitat e micro-habitat por *Crossodactylus schmidti* (Anura: Hylodidae) em riachos da Mata Atlântica.** Uma combinação de fatores bióticos e abióticos influencia a seleção de habitat e micro-habitat por anuros. Para analisar o uso de habitat e micro-habitat por adultos de *Crossodactylus schmidti*, amostramos 13 riachos na Mata Atlântica no Parque Nacional do Iguaçu, sul do Brasil, entre novembro de 2014 e agosto de 2015. Registramos dados de abundância e medimos variáveis ambientais estruturais dos riachos relacionadas à seleção de habitat pelos anuros em três ocasiões em cada riacho. A coleta de dados ocorreu ao longo de um transecto de 50 m em cada riacho. Além disso, foram realizadas duas coletas especificamente para a obtenção de dados do uso de micro-habitat, amostrando somente os mesmos três riachos em cada amostragem. Nós empregamos a análise Generalized Least Squares para avaliar a variação espacial na abundância em função das variáveis ambientais estruturais dos riachos, considerando modelos com e sem estruturação espacial. Nós aplicamos o Multinomial Goodness-of-Fit Test para elucidar os tipos de micro-habitat mais utilizados pelas rãs. Nossa análise revelou que, considerando ou não a autocorrelação espacial na variação da abundância de *C. schmidti*, nenhuma das variáveis preditoras foi significativa. Os resultados obtidos demonstram que as variáveis ambientais analisadas não são importantes para a seleção de habitat de *C. schmidti*, e a configuração espacial e a distância entre os riachos não são determinantes para a distribuição da abundância. Portanto, na escala do habitat, esta espécie exibe uma distribuição aleatória independente das características ambientais e espaciais. Em relação aos micro-habitats, os indivíduos foram encontrados predominantemente ocorrendo em áreas de remanso dos riachos, contendo substrato rochoso ou com acúmulo de matéria orgânica. Dada a variação na seleção de habitat entre as escalas avaliadas, as estratégias de conservação para esta espécie devem levar em conta as relações dependentes da escala.

**Palavras-chave:** Brasil, Dinâmica espacial, Distribuição, Rãs, Seleção de hábitat.

## Introduction

Habitats and microhabitats exhibit variation in conditions and quality within natural ecosystems. Individuals are expected to optimize their survival and reproductive success by selecting suitable habitats and, within these environments, favorable microhabitats (Arlt and Pärt 2007). The selection of habitat and microhabitat is influenced by a combination of biotic and abiotic factors, as well as individual organism characteristics (Rosenzweig 1981, Morris 2003). Biotic factors influencing habitat selection include the presence of predators, parasites, and competitors (Binckley and Resetarits 2005, Tolvanen *et al.* 2017, Rushing *et al*. 2021), as well as the quantity and quality of food resources (e.g., Nielsen *et al.* 2010, Rushing *et al*. 2021). Regarding abiotic factors, conditions (e.g., temperature), habitat structure, and surrounding landscape also play significant roles in habitat selection (Pelinson *et al.* 2016, Marques *et al.* 2019). Individual characteristics such as sex (Chinchilla-Lemus *et al.* 2020), life stage (Wells 2007), and individual behavior (e.g., prior experience) (Liford and Cecala 2017) can influence habitat selection. Habitat selection represents a complex behavioral decision-making process directly impacting individuals' fitness (Freitas *et al*. 2016) and spatial distribution (Morris 2003).

In amphibians, habitat and microhabitat selection play a crucial role because reproductive success and population maintenance of this group are directly linked to the surrounding environment (Murphy 2003). Among abiotic factors influencing habitat selection by adult anurans, structural features of the habitat appear to be paramount (Watson *et al*. 2003, Carisio *et al*. 2014), as they directly impact the selection of calling, courtship, and spawning sites (Parris 2001, Touchon and Warkentin 2008, Buxton and Sperry 2017). In lotic environments utilized by anurans for reproduction, width and depth serve as indicators of available habitat for individuals. In streams, a greater abundance of adult anurans is anticipated in water bodies of intermediate sizes, as these habitats are expected to exhibit greater microhabitat heterogeneity (Hopey and Petranka 1994, Parris 2001). Canopy cover is another significant variable that is associated with species adaptation to forested or open areas (Van Buskirk 2005). Light penetration directly affects primary productivity and the nutritional quality of food ingested by tadpoles (Schiesari 2006). Water flow speed is another critical variable in lotic environments because higher speeds create a noisier environment, thereby interfering more with intraspecific acoustic communication (Vielliard and Cardoso 1996) and potentially carrying away tadpoles and adults. Success in occupying lotic environments is associated with, among other factors, the need for behavioral and/or acoustic adaptations that promote intraspecific communication (Heyer *et al*. 1990, Goutte *et al*. 2013) and local permanence (Wells 2007). Lotic environments exhibit structural variation, and the selection of appropriate habitat for reproduction is expected to confer specific advantages to males in acquiring a mate and subsequently maintaining the local population.

Amphibians typically select specific locations within their habitat, known as microhabitats, to occupy, vocalize, and spawn (Buxton and Sperry 2017, Melo *et al*. 2018, Flores *et al*. 2024). The selection of microhabitats by anurans is of paramount importance for their reproductive success and overall ecological fitness. Similar to habitat selection, anurans exhibit discerning preferences for particular microhabitats based on several environmental features, including water flow speed, depth, substrate type, and vegetation structure (Eterovick 2003, Melo *et al*. 2018, Flores *et al.* 2024). The ability of anurans to selectively utilize microhabitats that best suit their ecological requirements is crucial for maximizing fitness and ensuring population persistence in heterogeneous environments (Buxton and Sperry 2017).

The family Hylodidae comprises 48 described species (Frost 2024) of diurnal frogs commonly found in forest streams (Jordão-Nogueira *et al.* 2006, Caldart *et al*. 2010, but see Caldart *et al.* 2011a). One of these species is *Crossodactylus schmidti* Gallardo, 1961, a frog occurring in southern Brazil, southern Paraguay, and northern Argentina (Caldart *et al.* 2010, Lucas and Garcia 2011, Bastiani *et al.* 2012, Frost 2024). The species is currently classified as “Least Concern” by IUCN (2023), but its population trend is declining mainly due to habitat loss, modification, and fragmentation, and pollution (IUCN 2023). *Crossodactylus schmidti* has a snout–vent length of 28 mm and 2.5 g of body mass, and it is cryptically colored. It inhabits forest streams and is considered a habitat specialist, with individuals strongly associated with well-preserved habitats (Bastiani *et al*. 2012). Males vocalize throughout the year, with monthly variation positively influenced by accumulated precipitation and air temperature (Caldart *et al.* 2016). The species occupies rocky stream habitats wherein males prefer to utilize exposed rocks for acoustic and visual communication (Caldart *et al.* 2011b, 2016). *Crossodactylus schmidti* preys on arthropods, primarily ants, beetles, and dipterans (Caldart *et al.* 2012). Conversely, it serves as prey for spiders and snakes with both diurnal and nocturnal habits (Caldart *et al*. 2011). Despite being a species with considerable ecology and natural history information available (e.g., Caldart *et al.* 2010, 2011a, b, 2012, 2016, Bastiani *et al.* 2012), studies are lacking that evaluate the relationship between habitat and microhabitat features and the occurrence of individuals of *C. schmidti*. This study addresses two questions: (1) What is the relative influence of stream environmental features on the spatial variation of abundance in *C. schmidti*? (2) Is there differential utilization of existing microhabitats within streams by adult *C. schmidti*? Understanding distribution patterns among and within habitats is crucial for establishing effective conservation measures.

## Materials and Methods

### *Study Area*

The study was conducted in Iguaçu National Park (INP), a conservation unit located in the western region of the state of Paraná, southern Brazil (25°05'–25°41' S, 53°40'–54°38' W; Figure 1). The INP covers 185,265 ha across five municipalities: Céu Azul, Foz do Iguaçu, Matelândia, São Miguel do Iguaçu, and Serranópolis do Iguaçu. The vegetation comprises Semideciduous Seasonal Forests, Mixed Ombrophilous Forests, and Alluvial Pioneer Formations of the Atlantic Rainforest (Souza *et al.* 2017). Specifically, in the area where the present study was conducted, the vegetation is predominantly Mixed Ombrophilous Forest. The climate in the region is classified as Cfa (temperate and humid) according to Köppen's classification (Alvares *et al.* 2013), with four well-marked seasons. Precipitation is evenly distributed throughout the year, with no dry season, and a higher volume of rainfall in the summer, resulting in an annual precipitation total of around 1800 mm (Nitsche *et al.* 2019). The average annual temperature varies between 20°C and 22°C, with summer averaging 26°C and winter averaging 17°C (Nitsche *et al.* 2019).

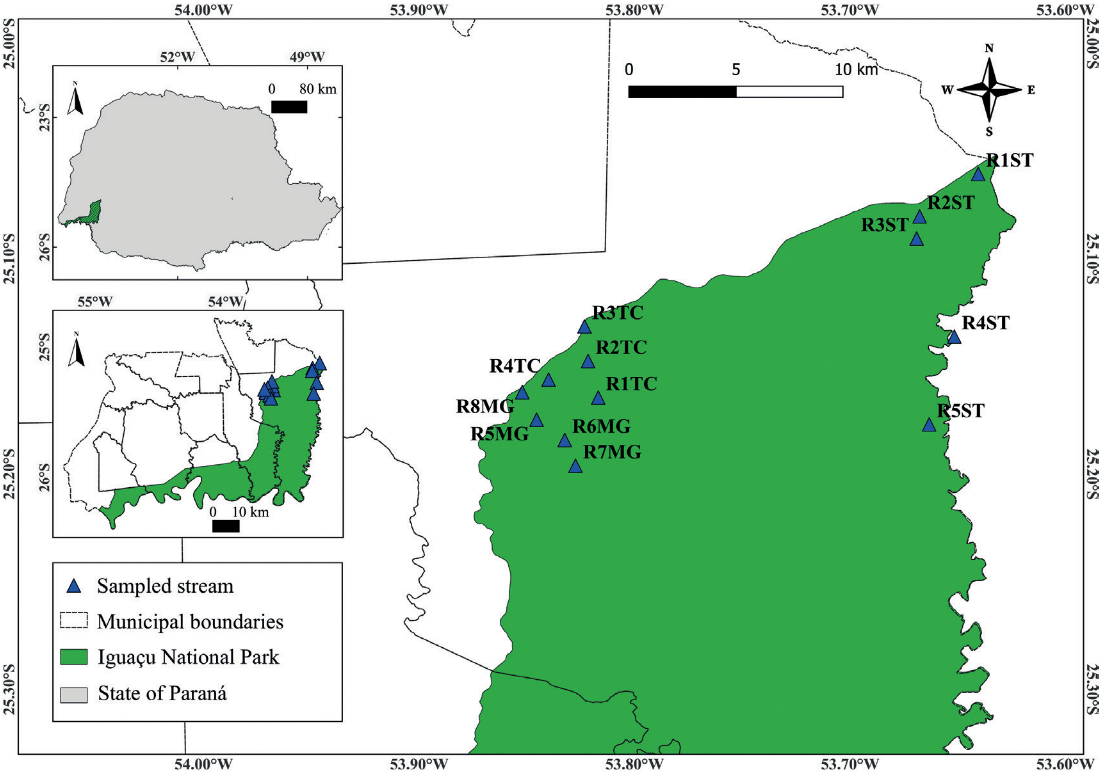

**Figure 1.** Map showing the location of Iguaçu National Park (green area) in the state of Paraná in southern Brazil and the distribution of sampling units at Iguaçu National Park (blue triangles). In detail, the distribution of sampling units (blue triangles) represents the location of each sampled stream. Each acronym represents a specific stream.

### *Habitat Data*

We sampled 13 streams in primary forest of the INP, all of which were situated within Araucaria Moist Forest areas in the municipality of Céu Azul (Table 1; Figure 1). We chose to sample only small to medium-sized streams (first to third order) (Caldart *et al.* 2016) because no specimens of *Crossodactylus schmidti* were found in larger streams in previous monitoring efforts in INP (e.g., Iguaçu River) (M. V. Garey pers. obs.). We conducted our sampling during daylight and twilight periods (8:00 to 19:00 h). We established a 50-m transect in each stream, considering that this transect size has already been used in other studies with amphibians (e.g., Hazell *et al*. 2004, Wassens *et al*. 2013). The transect was permanently established upstream of the access point to the water body to minimize the impacts of researchers' presence on anurans and water. We sampled each transect three times: the first between November and December 2014, the second in January 2015, and the third in August 2015. The definition of sampling events was conducted considering climatic conditions (i.e., forecasted light rain on sampling days) and logistics. Two samplings were performed during the warmer and rainier period, while another occurred during the cooler and less rainy period. This decision was made due to uncertainty regarding whether the studied population would follow the same pattern reported for another population of the species in a more southern region (Caldart *et al.* 2016).

We collected data on the abundance of *C. schmidti* (response variable) and environmental variables describing habitat structure (predictor variables) in each stream transect. Two researchers sampled the transects for 30 min each, totaling an hour of search effort per transect per sampling campaign. During the diurnal and nocturnal searches, all encountered adult individuals were counted. Adults were defined as having SVL > 20 mm (Bastiani *et al.* 2012). The species abundance in each stream was considered equal to that of the campaign where the highest number of individuals was recorded in each stream. This procedure was adopted to mitigate the risk of overestimating abundance due to recounting individuals between different campaigns, as individuals were not marked. However, we know that the population size in each stream is larger than our observations suggest (see Greener *et al*. 2017), and that males and females may only visit the breeding site occasionally (Boyle *et al.* 2021). Considering that the visual encounter survey probably represents only a portion of the population's abundance, this limitation should be kept in mind.

We measured five environmental variables in each transect to characterize the habitat: maximum depth, width, water flow speed, predominant substrate type, and percentage of canopy cover (Table 1). We recorded environmental variables every 10 m in each transect, with six samples per stream per campaign. Water flow speed and percentage of canopy cover were measured at the middle of the stream. Maximum depth and substrate type were assessed across the entire width of the stream at each abiotic variable collection point. Maximum depth and stream width were measured in centimeters using a tape measure. We estimated water flow speed (cm/s) using the floating object method (Kauffman *et al.* 2009), where we recorded the time (s) taken for a 2-cm diameter Styrofoam ball to travel one meter. We visually classified substrate type into one of seven categories: bedrock (rock outcrop), boulder (larger rock fragments > 8 cm), coarse gravel (2–8 cm), fine gravel (1–2 cm), organic matter (i.e., leaves and stems), clay, and sand. Canopy cover was estimated by capturing photographs of the canopy with a Fujifilm FinePix XP10 camera positioned horizontally at a standardized height (approximately 140 cm above ground level). We converted the obtained images to binary black ("not sky") and white ("sky") and analyzed the proportion of white pixels in each photo, representing an estimate of visible canopy fraction or the percentage of canopy openness

**Table 1.** The abundance of individuals of *Crossodactylus schmidti*, structural environmental characteristics, and the location of the 13 lotic water bodies sampled in Iguaçu National Park, western Paraná state, Brazil. Values are presented as mean ± standard deviation (range). Wfs = Water flow speed (cm/s). Sw = Stream width (cm). Cc = Canopy cover (%).

| Stream | Abundance | Wfs | Sw | Depth (cm) | Substrate | Cc | Latitude | Longitude |
|---|---|---|---|---|---|---|---|---|
| R1ST | 13 | 22.47 ± 17.38<br>(12.18–46.08) | 75 ± 36<br>(34–159) | 10 ± 5<br>(5–26) | Clay | 0.61 ± 0.08<br>(0.41–0.73) | -25.060555 | -53.640555 |
| R2ST | 8 | 12.89 ± 18.80<br>(0.00–37.03) | 100 ± 67<br>(30–308) | 8 ± 3<br>(3–16) | Clay and organic matter | 0.63 ± 0.07<br>(0.63–0.75) | -25.080277 | -53.667777 |
| R3ST | 7 | 33.33 ± 31.17<br>(19.04–78.74) | 178 ± 152<br>(62–720) | 8 ± 3<br>(3–17) | Boulder | 0.60 ± 0.12<br>(0.38–0.79) | -25.090555 | -53.669166 |
| R4ST | 1 | 30.49 ± 42.76<br>(13.25–100) | 257 ± 151<br>(66–486) | 6 ± 2<br>(3–11) | Boulder | 0.65 ± 0.04<br>(0.59–0.72) | -25.136111 | -53.651666 |
| R5ST | 6 | 15.80 ± 25.66<br>(0.00–55.86) | 121 ± 45<br>(41–179) | 9 ± 7<br>(1–23) | Boulder | 0.68 ± 0.05<br>(0.57–0.76) | -25.176944 | -53.663333 |
| R1TC | 0 | 10.65 ± 35.85<br>(2.85–68.49) | 204 ± 81<br>(102–370) | 18 ± 10<br>(5–38) | Coarse gravel | 0.67 ± 0.03<br>(0.61–0.76) | -25.164444 | -53.816944 |
| R2TC | 20 | 22.94 ± 37.74<br>(12.79–82.64) | 142 ± 106<br>(16–411) | 5 ± 3<br>(1–13) | Clay and organic matter | 0.69 ± 0.05<br>(0.62–0.79) | -25.147500 | -53.821666 |
| R3TC | 57 | 10.34 ± 19.79<br>(5.38–49.02) | 77 ± 19<br>(43–121) | 11 ± 5<br>(5–19) | Clay | 0.66 ± 0.05<br>(0.56–0.76) | -25.131388 | -53.823333 |
| R4TC | 16 | 9.70 ± 10.15<br>(3.90–27.70) | 120 ± 60<br>(16–272) | 9 ± 3<br>(6–16) | Clay and organic matter | 0.64 ± 0.06<br>(0.56–0.74) | -25.156111 | -53.840000 |
| R5MG | 6 | 44.64 ± 52.96<br>(22.42–142.86) | 439 ± 233<br>(170–985) | 20 ± 14<br>(3–56) | Boulder | 0.54 ± 0.09<br>(0.39–0.68) | -25.174722 | -53.845555 |
| R6MG | 50 | 13.02 ± 58.70<br>(4.01–109.89) | 256 ± 113<br>(84–490) | 14 ± 6<br>(6–28) | Bedrock | 0.61 ± 0.05<br>(0.53–0.69) | -25.184166 | -53.832500 |
| R7MG | 49 | 11.38 ± 11.84<br>(4.13–32.05) | 206 ± 174<br>(78-650) | 12 ± 6<br>(5–25) | Coarse gravel and clay | 0.67 ± 0.06<br>(0.55–0.75) | -25.196111 | -53.827500 |
| R8MG | 8 | 9.31 ± 16.01<br>(3.71–40.00) | 143 ± 85<br>(37—329) | 9 ± 4<br>(2–16) | Boulder | 0.68 ± 0.07<br>(0.52–0.78) | -25.161944 | -53.852222 |

per point (Smith and Ramsay 2018). We analyzed the images using Image J software (Abramoff *et al.* 2004).

### *Microhabitat Data*

We conducted two campaigns to collect data on the microhabitats used by adult *C. schmidti* in the streams of Iguaçu National Park. The first sampling was conducted in April, and the second in September 2014. For this sampling, we selected only three of the 13 streams, and we traversed transects of these three streams during both campaigns. We selected the streams for convenience, prioritizing those with easier access and shorter walking time to reach the sampling point, and ensuring they were at least 1 km apart from each other. Along the stream transect, we characterized the occurrence location (i.e., the microhabitat used) of each adult individual recorded based on seven variables: (i) position of the individual concerning the stream (i.e., inside or outside of the water), (ii) distance of the individual from the stream margin (cm), (iii) type of microhabitat (i.e., pool, riffle, or fast-flowing), (iv) substrate type (i.e., rock, coarse gravel, fine gravel, organic matter, or sand), (v) stream width (cm), (vi) maximum depth (cm), and (vii) water flow speed in the microhabitat (cm/s).

### *Statistical Analysis*

We applied the Variance Inflation Factor (VIF) to evaluate the presence of multicollinearity among habitat environmental variables from the 13 sampled streams. A variable with a VIF value higher than three was deemed multicollinear (Zuur *et al*. 2009). The variable “substrate type” was excluded from subsequent analyses due to multicollinearity. Following the removal of this variable, the remaining variables showed no signs of multicollinearity. Subsequently, these remaining variables were standardized using Z-scores, ensuring that all variables had a mean of zero and a standard deviation of one (Legendre and Legendre 2012). This standardization procedure was implemented due to the variables being measured in different units.

We conducted Generalized Least Squares (GLS) analysis to assess the variables associated with the variation in abundance of *C. schmidti* across the streams. This method addresses both heteroscedasticity and residual autocorrelation (Pinheiro and Bates 2000), but it does not account for variation in detection probability (Mazerolle *et al.* 2007). We chose this approach because GLS models allow for explicit incorporation of spatial autocorrelation by adjusting a variance-covariance matrix to fit the data characteristics better (Dormann *et al*. 2007). Since autocorrelation is a significant source of bias, the explicit modeling of spatial autocorrelation is expected to substantially enhance the accuracy of abundance distribution predictions (Guélat and Kéry 2018). To incorporate spatial structure, we included latitude and longitude data obtained at the center of each stream transect. We tested one non-spatial model and four models with different potential spatial correlation structures: spherical, exponential, Gaussian, and rational quadratics (Zuur *et al.* 2009). The selection of the most predictive model for abundance variation was based on three criteria: (1) models with ΔAICc less than 2.0, (2) inclusion in the set of best-supported models with combined Akaike weights of 0.70 (70% confidence set), and (3) relative likelihood higher than 0.7 (Burnham and Anderson 2002, Burnham *et al.* 2011). Spatial autocorrelation in model residuals was quantified using Moran’s I test (Dormann *et al.* 2007). These analyses were conducted using R version 4.2.2 (R Core Team 2022) with the nlme (Pinheiro and Bates 2023) and qpcR (Spiess 2018) packages.

The occurrence frequencies of adults of *C. schmidti* in microhabitats with different structural environmental features were compared using the Multinomial Goodness-of-fit Test (McDonald 2014). We evaluated three microhabitat characteristics: (i) the position of the individual concerning the stream, (ii) the type of microhabitat, and (iii) the substrate type. This test involves assessing the fit of a probabilistic model to a set of observed data when sample size is small (McDonald 2014).

## Results

We observed adult *Crossodactylus schmidti* in 12 of the 13 sampled streams, totaling 361 individuals. In streams occupied by *C. schmidti*, an average of 20.08 ± 19.97 individuals were found, ranging from 1 to 57 individuals per stream. These streams had a water flow speed of 18.95 ± 11.14 cm/s (range: 9.32–44.64), a maximum width of 167.46 ± 81.16 cm (range: 74.94–334.98), a maximum depth of 10.02 ± 4.07 cm (range: 4.49–20.05), and canopy coverage of 64 ± 4% (range: 54–69) (Table 1). Tadpoles of *C. schmidti* were observed in all streams where adults were found. Males engaged in vocalization activities were recorded, indicating utilization of these habitats as breeding sites.

Among the four models evaluated in the GLS analysis, both the non-spatial and Gaussian Correlation Structure models performed equally well in predicting the spatial variation in the abundance of *C. schmidti* in streams of the Atlantic Rainforest (Table 2). In the non-spatial model, only the intercept was significant, suggesting that none of the variables was individually important in explaining the abundance data without considering spatial autocorrelation. In the model with a Gaussian autocorrelation structure, none of the environmental variables were significant (Table 3), indicating that the abundance distribution of *C. schmidti* in streams is independent of both environmental and spatial factors.

Within the analyzed habitats, individuals predominantly occupied microhabitats within the stream, mainly in pool areas (54.16%), followed by riffle areas (37.5%) and fast-flowing sections (8.33%) ($p = 0.0013$, exact multinomial test, Appendix I). Individuals were observed to prefer microhabitats mainly composed of rock substrate (33.33% of cases) or organic matter (33.33%), with clay areas being less frequently occupied (8.33%) ($p < 0.00001$). During observations, adults were mostly found alone (75% of observations), with two adults present in the same microhabitat 25% of the time (Appendix I). Individuals were consistently found within the stream at an average distance of 23.41 ± 35.10 (0–130) cm from the margin. In these microhabitats occupied by adults, the stream had an average width of 136.75 ± 48.86 (45–228) cm, depth of 4.77 ± 2.70 (1–12) cm, and water flow speed of 19.60 ± 21.76 (0–86.96) cm/s.

## Discussion

Adults of *Crossodactylus schmidti* were found in 92% of the rocky streams sampled in Iguaçu National Park. The spatial variation in the abundance of *C. schmidti* was equally explained by the model that does not consider spatial autocorrelation and by the model considering the spatial structuring of abundance. When considering or disregarding spatial structure, we found that none of the environmental variables was associated with spatial variation in the abundance of *C. schmidti*. This result suggests that individuals were randomly distributed in relation to the measured variables. The absence of a relationship observed in the model without spatial structure does not imply that there is no habitat selection by the species. Instead, selection may be predominantly influenced by environmental variables not considered in the present study, such as physicochemical characteristics of the water and biotic variables. For example, individuals of *C. gaudichaudii* Duméril and Bibron, 1841 are more likely to be found in streams with higher water temperatures and lower pH (Pereira-Ribeiro *et al.* 2023). Unfortunately, we were unable to assess physicochemical characteristics due to the lack of a multiparameter probe. Furthermore, anurans generally avoid habitats with potential predators and competitors (Buxton and Sperry 2017, Van Buskirk and Smith 2021).

**Table 2.** Outputs of the five models, one with a non-spatial structure and four with different correlation structures, for analyzing the relationship between the abundance of *Crossodactylus schmidti* and the environmental variables of the streams. ΔAICc = difference in Akaike's Information Criteria; Weight = weights of Akaike's Information Criteria; Relative likelihood = demonstrate the probability of one model being in favor over the other.

| | ***df*** | **AIC** | **ΔAIC** | **Weight** | **Relative likelihood** |
|---|---|---|---|---|---|
| Non-spatial | 6 | 94.2959 | 0.0 | 0.4224 | 1.0000 |
| Gaussian | 8 | 95.7291 | 1.4321 | 0.2063 | 0.7884 |
| Spherical | 8 | 96.4412 | 2.1453 | 0.1445 | 0.3420 |
| Rational quadratics | 8 | 96.5476 | 2.2517 | 0.1370 | 0.3244 |
| Exponential | 8 | 97.3947 | 3.0989 | 0.0897 | 0.2124 |

**Table 3.** The models' outputs were derived from the analyses of spatial variation in the abundance of *Crossodactylus schmidti* by environmental variables of streams in the Atlantic Rainforest of Iguaçu National Park. SE = standard error.

| | **Estimate** | **SE** | ***t*-value** | ***p*-value** |
|---|---|---|---|---|
| *Non-spatial* | | | | |
| Intercept | 19.1345 | 5.9474 | 3.2173 | **0.0123** |
| Water flow speed | -15.6946 | 11.1079 | -1.4130 | 0.1954 |
| Width | 4.2976 | 9.4307 | 0.4557 | 0.6607 |
| Deep | -2.5034 | 9.2745 | -0.2699 | 0.7941 |
| Canopy cover | -7.3951 | 10.0225 | -0.7379 | 0.4817 |
| *Gaussian* | | | | |
| Intercept | 19.1251 | 8.3516 | 2.2899 | 0.0513 |
| Water flow speed | -11.6149 | 7.0416 | -1.6495 | 0.1377 |
| Width | 2.0765 | 9.5453 | 0.2175 | 0.8332 |
| Deep | -4.9967 | 5.2347 | -0.9545 | 0.3678 |
| Canopy cover | -8.4582 | 6.7685 | -1.2496 | 0.2467 |

Habitat selection by anurans, particularly for breeding sites, tends to be strongly associated with the structural environmental features of water bodies (Welch and MacMahon 2005, Carisio *et al*. 2014, Thomas *et al.* 2019). Studies on stream-dwelling anurans have observed the importance of environmental and structural stream features such as water velocity, substrate type, depth, and width of the stream in species occurrence and abundance (e.g., Eterovick 2003, Oliveira and Eterovick 2010). In the present study, it was not possible to demonstrate the existence of preferential habitat selection by *C. schmidti* because the variation in the abundance of this species was independent and random with respect to environmental features. Despite anurans being considered organisms with limited dispersal capability (Smith and Green 2005, Wells 2007), the inclusion of spatial autocorrelation in the abundance models did not alter the result of statistical analysis. Caution must be exercised in the conclusions because GLSs do not take into account some factors that may affect abundance data collection. For example, the visual encounter survey often records lower abundances than are actually present in the stream when compared to other methods (e.g., removal sampling) (Greener *et al.* 2017), individuals may only visit the breeding site occasionally (Boyle *et al.* 2021), differences in individual detection among collectors, climatic and environmental variations that may occur between data samples, and the recounting of individuals (Mazerolle *et al.* 2007). In our study, all samples were taken by the same researchers, and individual counting was done jointly; thus, this factor did not result in bias in our study. However, environmental and structural variations may have caused bias. We observed in the field that structural variations in streams between data samples were small. Climate variation within the same campaign was also small (e.g., temperature and humidity), likely having little influence on the counting of individuals of *C. schmidti,* but variation between campaigns was more significant, which may have influenced the recorded abundance (Caldart *et al.* 2016). The recounting of individuals in the same stream or between streams in the same campaign probably did not occur due to the distance between streams and the search always being conducted against the water flow. Between campaigns, the recounting of an individual may have occurred, but with a low probability due to the limitation in the dispersal capacity of anurans (Smith and Green 2005).

At the microhabitat scale, we observed that adults of *C. schmidti* preferentially occur in stream interiors, particularly in shallow areas with rocky substrates or organic matter accumulation located in pools. The utilization of these microhabitat types by the population in Iguaçu National Park coincides with observations from other populations of *C. schmidti* (Caldart *et al.* 2010, Bastiani *et al*. 2012) and in other populations of the genus *Crossodactylus* (Almeida-Gomes *et al.* 2007, 2012). *C. schmidti* occupies these microhabitats for calling and visual communication (Almeida-Gomes *et al.* 2007, Caldart *et al.* 2010), where individuals remain partially submerged or at water level (Caldart *et al.* 2010; present study). Rocky substrates used as calling sites are strategically important in predation risk situations, including for tadpoles, because they allow easy access to water and small underwater chambers (Caldart *et al.* 2010) or even burrows located on stream banks (Pimenta *et al*. 2008). This species uses underwater chambers as spawning sites (Haddad *et al*. 2013); thus, the presence of adults in these locations may be influenced by the availability of suitable oviposition sites. Another advantage of using rocky microhabitats may be increased visibility for visual communication behaviors, which is common in many species of this genus (Caldart *et al.* 2010). The secondary use of pool microhabitats by individuals of *C. schmidti* coincides with reports for individuals of *C. trachystomus* (Reinhardt and Lütken, 1862) (Pimenta *et al.* 2008). According to Pimenta *et al.* (2008), individuals of the genus *Crossodactylus* tend to avoid occupying fast-flowing areas, especially during periods of heavy rainfall, prioritizing marginal areas with lower water volume. The preference for pool areas may be related to the energetic cost of remaining in swift-flowing areas, reducing the risk of being washed away during rainy periods. Another potential explanation is related to acoustic communication, as ambient noise can mask and interfere with acoustic communication (Goutte *et al.* 2013), which tends to be less pronounced in pool areas.

We found that adults of *C. schmidti* occur in forested streams within Iguaçu National Park, exhibiting a complex spatial structure. The species can be considered specialized in forest environments (Caldart *et al.* 2010, Bastiani *et al.* 2012), but generalist in terms of the streams it inhabits, as it occupies a wide range of streams. Furthermore, they can be considered specialists in the type of microhabitat they occupy, as they consistently inhabit similar microhabitats across different streams. These patterns may be related to the behavioral and reproductive adaptations of the species, such as specialized vocalization adapted to the typical noises of this environment (Caldart *et al.* 2011b), visual communication strategies (Caldart *et al.* 2010), and efficient escape behaviors against predation. Future studies could benefit from the inclusion of additional populations, evaluation of oviposition sites, microhabitat choice by tadpoles, and other variables that might play a significant role in habitat selection for this species, such as physicochemical variables of the water. It is crucial for future studies to consider broader spatial and temporal scales by expanding the transects to incorporate greater within-stream variability and the gradient of stream features that this species can inhabit. Simultaneously addressing spatial autocorrelation and imperfect detection by sampling unmarked individuals across multiple sites or observing individual behaviors—such as using photographic documentation of pattern variations to estimate population size, track migration, and assess the likelihood of individuals utilizing different microhabitats—could provide a better understanding of potential threats faced by this species.

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**Appendix I.** *Microhabitats used by individuals of* Crossodactylus schmidti*, along with their respective environmental features and the positioning of individuals in relation to streams. The data were obtained from 24 microhabitats within the streams of Iguaçu National Park, southern Brazil.*

| Micro-habitat | Abundance | Position | Water flow speed (cm/s) | Width (cm) | Depth (cm) | Substrate | Type | Distance from shore (cm) |
|---|---|---|---|---|---|---|---|---|
| 1 | 1 | Outside | 28.82 | 95 | 8 | Coarse and fine gravel | Riffle | 0 |
| 2 | 1 | Outside | 28.49 | 93 | 12 | Rock | Riffle | 10 |
| 3 | 1 | Outside | 4.17 | 200 | 7 | Organic matter and coarse gravel | Pool | 103 |
| 4 | 2 | Inside | 0.00 | 190 | 7 | Sand | Riffle | 98 |
| 5 | 2 | Inside | 0.00 | 63 | 8 | Sand | Pool | 8 |
| 6 | 1 | Inside | 0.00 | 86 | 7 | Organic matter | Pool | 10 |
| 7 | 1 | Inside | 28.09 | 104 | 6 | Organic matter | Pool | 7 |
| 8 | 1 | Inside | 2.73 | 154 | 1 | Organic matter | Pool | 2 |
| 9 | 1 | Outside | 55.25 | 45 | 3 | Rock | Riffle | 4 |
| 10 | 1 | Outside | 4.04 | 155 | 6 | Rock | Pool | 8 |
| 11 | 1 | Outside | 15.65 | 160 | 3 | Rock | Pool | 5 |
| 12 | 2 | Inside | 14.04 | 170 | 3 | Organic matter | Pool | 15 |
| 13 | 1 | Outside | 23.53 | 228 | 5 | Organic matter | Pool | 35 |
| 14 | 1 | Inside | 40.65 | 70 | 5 | Sand and fine gravel | Riffle | 30 |
| 15 | 1 | Inside | 25.91 | 210 | 2 | Rock and sand | Riffle | 130 |
| 16 | 1 | Inside | 0.00 | 153 | 3 | Organic matter | Pool | 17 |
| 17 | 1 | Outside | 86.98 | 145 | 4 | Rock | Riffle | 30 |
| 18 | 2 | Inside | 0.00 | 150 | 3 | Organic matter | Pool | 3 |
| 19 | 1 | Outside | 39.37 | 76 | 3 | Fine gravel | Riffle | 8 |
| 20 | 1 | Inside | 24.21 | 144 | 2 | Rock | Fast-flowing | 7 |
| 21 | 2 | Inside | 0.00 | 181 | 3 | Rock | Pool | 8 |
| 22 | 1 | Outside | 10.24 | 150 | 8 | Rock | Fast-flowing | 5 |
| 23 | 2 | Inside | 38.31 | 127 | 2 | Rock and organic matter | Riffle | 5 |
| 24 | 1 | Inside | 0.00 | 133 | 3 | Organic matter | Pool | 14 |

**Appendix II.** *Six of the 13 streams sampled in Iguaçu National Park for the study of the population of* Crossodactylus schmidti *(***A–F***), along with photographs of individuals in various microhabitats within the streams (***G–J***).*