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Authors: Arantes, Ísis C., Boas, Taissa C.V., and Colli, Guarino R.

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Movement and Habitat Use of Two Toad Species (Anura, Bufonidae): A Long-Term Study in a Neotropical Savanna

Ísis C. Arantes[2], Taissa C.V. Boas, and Guarino R. Colli[1]

Biology Department, University of Mississippi, Oxford, MS 38677, USA

Abstract: The movement and habitat use of amphibians provide insights into evolutionary and life history traits, as well as important conservation implications such as disease spread, invasive species control and management, and species' responses to climate change. Patterns of movement and habitat use are influenced by internal and external factors that take place across multiple spatial and temporal scales. Movement and habitat use are crucial for animals' natural history, including foraging, breeding, and thermoregulation, which impact ecological relationships and social interactions. We studied the factors affecting the movement and habitat use of two toad species in a Neotropical savanna, *Rhinella rubescens* and *R. diptycha*. We used 7 yr of capture–recapture data and spool-and-line tracking methods to investigate the factors affecting daily movement (DM), habitat area, migration patterns, and habitat use for both species. We found no difference in time spent in the study area between sexes for both species, suggesting that other factors are important in explaining the male-biased sex ratio in the populations. Both species showed site fidelity, a common pattern in terrestrial amphibians, where *R. diptycha* exhibited greater DMs, area used, and distance traveled from the reproductive site than *R. rubescens*. The area used was associated with body size, regardless of species and number of captures. The DM was associated with body size and the previous day's rainfall. Spatial segregation was primarily related to the unique climatic conditions during the reproductive periods of each species and to specific environmental traits. Reproductive behavior of *R. rubescens* occurred in the dry season, and it used more water bodies with aquatic vegetation than *R. diptycha*, which breeds during the transition from dry to wet season and uses mainly terrestrial habitats and shallow water without vegetation near the shore. Our results indicate that the reproductive behavior of *R. diptycha* is more terrestrial and involves a greater dispersal capacity than *R. rubescens*, which may explain the greater geographic distribution of *R. diptycha*. Although both species belong to the same clade (the *R. marina* group), they exhibit different movement patterns and space use, which allows their coexistence in the Brazilian Neotropical savanna.

Key words: Amphibians; Dispersal; Home range; Long-term; Microhabitat; Site fidelity

Exploring the dynamics of how animals move and use their environment can shed light on the evolution of common spatial patterns and their profound impact on animals' life history traits (Holden 2006; Börger et al. 2008; Nathan 2008). Movement and habitat use patterns are fundamental components of organisms' natural history and encompass foraging sites, breeding grounds, refuges, thermoregulation sites, dispersal capacity, migration distances, and the genetic structure within and between populations (Duellman and Trueb 1994; Wells 2007). These intricate movement patterns also serve as indicators for crucial aspects of wild population conservation, ranging from the spread of emerging diseases and the expansion of invasive species to patterns of habitat use and responses to climate change (Semlitsch 2008). Migration, dispersal, and home range emerge as prominent habitat use patterns, each intricately influenced by a variety of spatial and temporal conditions, resulting in distinct movement patterns for each species (Burt 1943; Murray 1967; Bowler and Benton 2005; Dingle and Drake 2007).

How animals utilize their environment is influenced by both spatial and temporal conditions, resulting in distinct movement patterns observed among different species (Börger et al. 2006; Giuggioli et al. 2006; Nathan et al. 2008). Migration patterns are often impacted by factors, such as food availability, climate conditions, and reproductive activity, which can cause animals to move towards or away from breeding sites (Hall 1972; Semlitsch 2008). Dispersal, on the other hand, is typically a one-way movement from the birth site to the reproductive sites of other populations, with juveniles tending to disperse more than adult migrants, and dispersal usually occurring only once in an animal's lifetime (Semlitsch 2008). The tendency of an animal to return to a previously occupied area or remain in the same area for an extended period is referred to as philopatry or site fidelity, which strongly influences migration and home range establishment (White and Garrott 1990). This behavior results in an animal becoming familiar with its environment, making it easier to access resources and avoid predators (Switzer 1997). These factors contribute to an individual's preferred space for carrying out physiological and social activities, known as its home range (Burt 1943). Home range is a common pattern of habitat use (Börger et al. 2008), and it is influenced by body size (McNab 1963; Harestad and Bunnel 1979; Kramer and Chapman 1999), habitat structure, food availability (Tufto et al. 1996; Indermaur et al. 2009), and microhabitat selection, reflecting each organism's physiological requirements (Huey 1991). These patterns are determined by processes that occur across multiple spatial and temporal scales and depend on the interaction of various internal and external factors (Börger et al. 2006; Giuggioli et al. 2006; Nathan et al. 2008).

Movement and habitat use patterns, both within and between species, have been extensively studied across a variety of taxa. However, amphibians have received relatively less attention compared to other tetrapod species (Holyoak et al. 2008; Laver and Kelly 2008). Although the number of studies has increased in the past 20 yr, most have been conducted in the Northern Hemisphere, contributing to a geographic bias and underrepresentation of countries with the highest amphibian diversity (Altobelli et al. 2022). Amphibians may be overlooked partly due to their physiological traits, such as permeable skin and ectothermy, which

[1] Present Address: Departamento de Zoologia, Universidade de Brasília, Brasília, Distrito Federal, 70910-900, Brazil

[2] Correspondence: e-mail, isisarantes@gmail.com

strongly influence their behavior and ecology (Shoemaker and Nagy 1977; Brattstrom 1979). In addition, most amphibians go through two distinct life stages: an aquatic larval stage (tadpoles) and a terrestrial adult stage, further complicating how they use and move through habitats (Wilbur 1980; Semlitsch 2008). Research has shown that amphibians typically exhibit short-range movements occasionally interspersed with longer movements throughout the day (Bellis 1965; Dole 1965; Wells and Wells 1976; Jreidini and Green 2022a). They tend to have low dispersal capacity, high site fidelity, and occupy relatively small home ranges (Blaustein et al. 1994; Smith and Green 2005; Husté et al. 2006; Caldwell and Shepard 2007; Marchand et al. 2017; Jreidini and Green 2022b). For example, terrestrial amphibians are generally nocturnal, moving through open areas at night and seeking shaded shelters during the day to control water loss (Cohen and Alford 1996; Seebacher and Alford 2002; Bartelt et al. 2004; Tozetti and Toledo 2005). heir body temperature closely follows substrate temperature, which can affect an animal's homeostasis and greatly impact how and when amphibians explore their environment (Tracy 1976). However, determining movement patterns for the entire group, particularly for conservation management strategies, is challenging due to the high variability in movement, habitat use, and home range among amphibian species, given their diverse characteristics (Lemckert 2004; Smith et al. 2005).

The spatial dynamics of tropical and subtropical species are poorly known because most studies are conducted on temperate environment species from North America and Europe (Lemckert 2004; Altobelli et al. 2022). To better understand the spatial dynamics of Neotropical anurans, we studied South American true toads belonging to the genus *Rhinella,* a large and diverse group within the Bufonidae family (Pereyra et al. 2021). Generally, species that belong to this family breed in still water, and migration is associated with movements toward reproductive aggregations where males call (Wells 2007). Larger body sizes allow long-distance movements, although the relationship between body size and home range size is not clear in bufonids (Lemckert 2004). In addition, longer distance movements are observed during rainy and humid days, creating seasonal movement patterns (Seebacher and Alford 1999; Bartelt et al. 2004; Forester et al. 2006). Furthermore, females typically travel greater distances than males (Lemckert 2004) because they are transient at breeding sites, staying only for oviposition. In contrast, males spend more time at these sites calling, which contributes to the male-biased sex ratio observed in many bufonid populations (Blair 1943; Christein and Taylor 1978).

Distinct patterns in environmental use may allow the coexistence of many species, including closely related species, which tend to be associated with similar niches because they usually have the same functional and morphological characteristics (Schoener 1974; Toft 1985; Menin et al. 2005; Holden 2006). *Rhinella diptycha* (Cope 1862) and *R. rubescens* (Lutz 1925) widely coexist in the Neotropical savannas, known as Cerrado, located in central Brazil. Both belong to the *R. marina* group, but *R. diptycha* belongs to a north-central clade composed of the larger sized species, whereas *R. rubescens* belongs to a south-central clade formed by the smaller species (Maciel et al. 2007, 2010; Lavilla and Brusquetti 2018; Pereyra et al. 2021). *Rhinella diptycha* has a broader distribution in open areas of South America than *R. rubescens*, which is mainly distributed in the southeast-central region with few records in the northeast and central-west regions of Brazil (Maciel et al. 2010; Valencia-Zuleta et al. 2017). Both *R. diptycha* and *R. rubescens* use mainly open canopy vegetation but can be found in several other types of Cerrado vegetation and thus are considered generalists with high dispersal capacities (Brandão and Araújo 2002). They are prolonged breeders (Wells 1977a; Perotti 1994), and the egg clutches are deposited in gelatinous strings (Eterovick and Sazima 2004).

Populations of *R. diptycha* and *R. rubescens* were studied by Arantes et al. (2015) and Vasconcellos and Colli (2009), who suggested that similarities in longevity, growth, sexual dimorphism, and vital rates result from high phylogenetic conservatism in the genus *Rhinella*. Differences include the timing of the breeding period, which occurred from June to September for *R. rubescens* and from the end of July to November for *R. diptycha*, with little temporal overlap (Vasconcellos and Colli 2009). The activity pattern of *R. rubescens* is almost entirely restricted to the dry season but, in *R. diptycha,* it ranges from the end of the dry season to the beginning of the rainy season (Vasconcellos and Colli 2009), as observed in other populations of these species (Moreira and Barreto 1997; Toledo et al. 2003; Prado et al. 2005). Despite morphological similarities, overlapping distribution areas, and shared phylogeny, *R. diptycha* and *R. rubescens* likely exhibit different breeding patterns to avoid temporal or spatial overlap (Vasconcellos and Colli 2009; Pereyra et al. 2021).

We investigated the factors that affect movement and habitat use in *R. diptycha* and *R. rubescens* to better understand their coexistence in the Brazilian Neotropical savanna. We tested the following hypothesis: (1) in both species, toads show high site fidelity but migrate to breed; (2) in both species, toads move greater distances on rainy and humid days; (3) in both species, larger individuals move greater distances and use larger areas than smaller individuals; (4) despite being closely related, the species are spatially segregated, which facilitates their coexistence; (5) in both species, males spend more time in the reproductive site than females, accounting for the male-biased sex ratio observed in the populations.

Materials and Methods

Study Area

The study was conducted in Estação Ecológica de Águas Emendadas (ESECAE), a protected area in Distrito Federal, Brazil (15°35'22"S, 47°41'47"W; datum = WGS84). We conducted the study in a wet grassland area that has undergone human-mediated alterations due to the construction of 14 pisciculture tanks and the introduction of *Brachiaria decumbens* grass in the 1980s for pasture. It comprises an area of approximately 3.2 ha at the shore of Lagoa Bonita, the largest natural pond of the Federal District (Munhoz and Ribeiro 2008). These tanks are colonized by plants of the families Cyperaceae, Xyridaceae, and Gramineae, and they are densely occupied by amphibians (Brandão and Araújo 1998). This area was incorporated into ESECAE at the beginning of 1980 (Horowitz and Jesus 2008) and is strongly impacted by human activities such as urbanization, soybean monoculture, and cattle (Brandão and Araújo 1998; Fonseca 2008). The area is in the core region of Cerrado (900 m of

altitude), a Neotropical savanna biome that is considered a biodiversity hotspot for conservation priority (Myers et al. 2000). The climate is strongly predictable and seasonal, with a wet season from October to April and a dry season from May to September; annual temperatures average 21°C, being relatively constant year-round, and relative humidity varies from 7 to 70% (Nimer 1989).

Data Collection

We monitored populations of *R. diptycha* and *R. rubescens* from October 2004 to March 2012 through weekly visits to the study area (Vasconcellos and Colli 2009; Arantes et al. 2015). Monitoring consists of rigorous inspection of land areas, tanks, and margins through visual and auditory searches with the aid of flashlights in the evening. We captured the individuals manually, measured them with a digital caliper (0.01 mm accuracy), and weighed them with a dynamometer (1 g, 5 g, and 10 g accuracy). We marked individuals larger than 60 mm by implanting a microchip (passive integrated transponder, PIT tag) in the dorsal part near the parotoid gland (Ireland et al. 2003). We sterilized the microchip implant with 70% alcohol and applied a liquid antiseptic (liquid bandage, 0.2% benzethonium chloride, and 0.75% dyclonine hydrochloride) to prevent infections at the implantation site. We recorded cloacal, air, and substrate temperature with a thermometer (0.2°C accuracy). We determined the sex of individuals based on secondary sexual characteristics, such as keratinized nuptial pads on thumbs and forearms and vocal sacs. We classified the behavior of each individual as vocalizing, active (individuals found in nocturnal activity without vocalizing), or inactive (individuals found in daytime shelters or night shelters). Starting in 2008, we measured the water depth and the distance from the individual to the nearest pond margin using a tape measure (1 cm accuracy), and in previous years, we estimated the distance to the margin visually.

We classified the habitat used according to the substrate (water or land) and microhabitat at the point where each animal was captured. We defined nine categories of microhabitat: water without vegetation (W), water with macrophytes (WM), branches in water (BW), shrubs or grass in water (SGW), bare soil (S), grass (G), shrubs or grass on soil (SGS), termite mound (T), and dead vegetation (DV). The "BW" category included shrub branches, tree trunks, and fallen leaves of the palm tree *Mauritia flexuosa*, also known as "buriti." The "DV" category included leaf litter, shrub branches, tree trunks, and fallen palm tree leaves. The "T" category included individuals found in or around termite mounds.

We used a spool of thread to track movements. Spool tracking is a highly efficient, easy-to-use, and affordable capture–tag–recapture method. It allows almost perfect location tracking and provides continuous, hour-by-hour monitoring (Tozetti and Toledo 2005). It is a technique used in several taxa, such as small mammals (Cunha and Vieira 2002; Moura et al. 2005; Vieira et al. 2005; Steinwald et al. 2006), snakes (Tozetti and Martins 2007; Tozetti et al. 2009), turtles (Stott 1987; Carter et al. 2000), and even gastropods (Pearce 1990). In amphibians, it has been used to investigate movement patterns, habitat use (Dole 1965, 1967; Duellman and Lizana 1994; Tozetti and Toledo 2005), and orientation (Dole 1968; Grubb 1970; Dole 1972; Sinsch 1988). In order not to affect the survival, reproductive success, and locomotion of individuals, the mass of the spools employed corresponded to less than 5% of the total animal mass (Heyer 1974; Tozetti and Toledo 2005), reaching a maximum length of approximately 160 m for *R. rubescens* and 400 m for *R. diptycha*. To mitigate potential behavioral changes and enhance survival, the tracking apparatus was removed after 3 d of monitoring.

From June to December 2010 and 2011, we temporaly attached a spool of cotton twine (Hiltex Ltda.) to the inguinal region of the individuals caught at night and returned them to the same capture site (Fig. 1). Spools were not left on individuals for the entire season; rather, each animal carried the spool only during its tracking interval (up to three consecutive nights). We considered the record of each individual's displacement in the environment left by the spool unwinding as a path. We delimited each path by a release starting point and an ending point, determined by the recapture of the animal with the spool or by finding the end of the broken line or the loose spool. When we found the broken line, we sought its continuation within a radius of 5 m and, if found, considered the displacement between the two ends as a straight line. We tracked each individual's displacement for up to three consecutive nights, logging tracks during the following mornings or afternoons, and logging shelter sites used in the daytime. On the last day, we removed the spool of thread apparatus to prevent skin abrasion (Muths 2003a). Thus, we recorded up to three trips and two shelters per week for each marked individual.

We recorded the geographic coordinates of the capture points from 2004 to 2011, and the spool tracks from June to December of 2010 and 2011 with a Trimble GeoExplorer 3 handheld GPS. We transferred the data to a computer through GPS Pathinder Office software (Trimble Geospatial). Afterward, we performed a differential correction and exported points to an Excel spreadsheet and paths to the format "shapefile." The differential correction process allowed us to obtain a submetric accuracy of the geographical position of the points and paths. For this, we used base files provided by the Santiago and Cintra Active Stations Network (available at https://santiagoecintra.com.br) and the Brazilian Network

FIG. 1.—A *R. rubescens* individual with the spool-and-line tracking apparatus used to determine its path of movement.

for Continuous Monitoring of GNSS Systems (available at https://www.ibge.gov.br). We constructed the figures by crossing the image of the study area with the paths and the capture points, using ArcGIS v9.3 (Environmental Systems Research Institute, Redlands, CA, USA). We obtained a high-resolution GEOEYE image (0.6 m = 1 pixel) from Google Earth, and we georeferenced the image using over 20 known points obtained in the study area.

Capture–Recapture and Length of Stay

We used the Mann–Whitney test to verify the difference between sexes in the number of captures and recaptures per individual, as well as in the length of stay at the study site. We calculated the length of stay in weeks over a year, and we designated the start of the year at the beginning of the reproductive activity, indicated by the presence of vocalizing males.

Site Fidelity

We used a binomial test with a probability of return equal to 50% to verify whether individuals occupied the same area in the study site in different years more than expected by chance (Crawley 2007). We considered the start of the reproductive season to be the beginning of each year and the occupation of the same places as the intersection between the areas of use in the different years. We utilized bivariate kernel density estimation to determine the areas of use, with the smoothing parameter given by the plug-in estimate:

$$h = 0.5\,(\sigma\,[x] + \sigma\,[y]) * n^{-1/6},$$

where σ(x) and σ(y) are the estimated variances of the x and y coordinates, and n is the sample size, using the R package adehabitat (Calenge 2006). We used a 95% density threshold to calculate the area. We used the Wilcoxon test and Spearman correlation test to investigate the linearity of paths and site fidelity within 1 yr, comparing the daily movement (DM) and the linear distance (DL) between the start and end points of each path. We calculated the path sinuosity, which corresponds to the DM divided by the DL between the start and end points, with the ArcGIS v9.3 program. Thus, the higher the sinuosity, the greater the tendency of the animal to move around the initial capture point (i.e., circular and zigzag movements; Tozetti et al. 2009). We used a binomial test with a return probability of 50% to check whether individuals returned to the same shelter on consecutive days (Crawley 2007).

Spatial Distribution

To examine interspecific variations in the area of highest intensity of use, we focused on: (1) year-round patterns, (2) patterns specific to the reproductive period, and (3) potential intraspecific differences between the reproductive and nonreproductive periods. We used an adaptation of the overlap index $HR_{i,j}$, which is the ratio of the area i overlapped by area j, and $HR_{j,i}$, which is the proportion of area j overlapped by area i (Kernohan et al. 2001):

$$HR_{i,\,j} = A_{i,\,j}/A_i \text{ and } HR_{j,\,i} = A_{i,\,j}/A_j\,.$$

In analysis 1 (year-round patterns), $A_{i,j}$ = interspecific overlap area in area usage, A_i = *Rhinella rubescens* area usage, and A_j = *R. diptycha* area usage. In analysis 2 (specific to the reproductive period), $A_{i,j}$ = area of interspecific overlap in the reproductive period, A_i = area usage of *R. rubescens* in the reproductive period, and A_j = area usage of *R. diptycha* in the reproductive period. In analysis 3 (differences between periods), $A_{i,j}$ = area of intraspecific overlap between the reproductive and nonreproductive periods, A_i = area usage in the reproductive period, and A_j = area usage in the nonreproductive period. *HR* ranges from zero (when there is no overlap between areas) to one (when one area is completely overlapped by another). To calculate the areas with the highest intensity of use, we used the 50% fixed kernel density method estimated using ad hoc smoothing parameters. The 50% kernel is the area where the density of 50% of the records is more concentrated, being defined as the core area, i.e., with the highest intensity of use and highest activity (e.g., Blundell et al. 2001; Indermaur et al. 2009; Stradiotto et al. 2009). The analyses were conducted using the R package adehabitat (Calenge 2006).

Daily Movement

The DM is defined as the total distance traveled during the night, measured in meters. In amphibians, the median tends to provide a better estimate of the DMs of a population, given the common pattern characterized by many short movements and few long movements, forming a positive asymmetric distribution. In such cases, the mean is influenced by the tail and therefore has a higher value than the median (Bellis 1965; Wells and Wells 1976; DeVore et al. 2021; Pašukonis et al. 2022; Spießberger et al. 2023; Jreidini and Green 2024). We analyzed linear models to identify the main factors that explain the variation in DM. We identified the best model by manual stepwise model selection. The independent variables were species (*R. diptycha* vs. *R. rubescens*), sex (male vs. female), snout–vent length (SVL), body mass, reproductive period (the period between the first and last record of males vocalizing or couples in range), season (warm and rainy vs. cold and dry), total daily precipitation, total previous day precipitation, minimum air temperature, average air temperature, maximum air temperature, and relative humidity. Climate variables were obtained from the ESECAE Weather Station, located approximately 10 km from the study area. We used model averaging to verify the relative importance of the independent variables and obtain coefficient estimates of models with Akaike weights greater than zero using the R package MuMIn (Barton 2012). In this analysis, we eliminated variables that were highly correlated ($r > 0.95$): maximum and minimum temperature and humidity. We used only 163 out of 170 observations due to missing data. To test whether DM was associated with body size and the total previous day's precipitation, regardless of species, we used a covariance analysis (Crawley 2007). The species variable was considered as a covariate because *R. rubescens* and *R. diptycha* have different body sizes (Arantes et al. 2015) and different breeding seasons (Vasconcellos and Colli 2009).

Home Range

For anurans, the calculation of home range generally does not consider the reproductive site and migration area, referring to the area used only in the nonreproductive period (Lemckert 2004). We calculated the area occupied by one individual using all capture points obtained during the 7 yr of data collection, including points collected in the reproductive site

and the living area, and defined it as the home range. We used covariance analysis to test whether home range was associated with body size, regardless of species and number of catches. We considered the largest body size recorded for each individual and calculated the area of use with the R package adehabitat (Calenge 2006), using the 95% fixed kernel density method estimated using ad hoc smoothing parameters. For the analysis, we considered only individuals with five or more recapture points registered with GPS.

Habitat Use

We evaluated habitat use by analyzing microhabitat and substrate choice (land or water), the distance from the capture point to the nearest pond margin, and the depth of the water. We performed a logistic regression using manual stepwise model selection to identify the key factors that influenced habitat use. The logistic regression error follows the binomial distribution, and the method to estimate parameters is ensured by maximum likelihood. Thus, at each step of the procedure, the most important variable is the one that produced the largest change in the likelihood logarithm relative to the model that does not contain the variable (Quinn and Keough 2002). Because this project encompassed many years of data collection, the early stages and periods of personnel transition were associated with substantial missing data. Accordingly, for this analysis, we excluded data from 2004, 2007, and January–July 2005 due to the large number of missing values for some independent variables. The sample number was reduced from 1274 to 835 observations. In this new set of data, the missing values (less than 20% of the observations for each variable) were replaced using the multivariate imputation by chained equations technique with the R package mice (Van Buuren and Groothuis-Oudshoorn 2011). Independent variables included were species (*R. diptycha* vs. *R. rubescens*), sex (male vs. female), SVL, body mass, behavior (active vs. inactive vs. vocalizing), sexual maturity (juvenile vs. adult), period of the day (day vs. night), reproductive period (period between the first and last recording of male vocalizing or couples in amplexus), population reproductive activity (number of recorded male vocalizing on the day of capture), season of the year (warm and rainy vs. cold and dry), total daily precipitation, total previous day precipitation, wind speed, relative humidity, minimum, average, and maximum air temperatures, air and substrate temperatures recorded at capture time, and cloacal temperature.

We performed a multinomial logistic regression to investigate the factors that explained the choice of microhabitat using the R package mlogit (Croissant 2011). Independent variables were species, time of day, sex, season, and air and substrate temperature. We analyzed three models using as reference variables "water with macrophytes," "bare soil," and "water without vegetation," given the largest number of observations in these categories. The "dead vegetation" microhabitat was removed from the analysis due to the small number of observations ($n = 4$).

We analyzed linear models as described above to identify the main factors that explained the variance in the distance to the nearest pond margin and in the water depth. The pond margin is set as zero; positive values represent distances on land, and negative values represent distances on water. As described in the data collection section, habitat use was classified according to substrate choice (water or land) and microhabitat characteristics, which served as the independent variables in our analysis of distance to the nearest pond margin. In addition, margin distance was also included as an independent variable in depth analysis. A total of 735 records were obtained for margin distance and 248 for depth. We replaced the missing values for independent variables, which corresponded to less than 20% of the observations for each variable, using the multivariate imputation by chained equations technique using the R package mice (Van Buuren and Groothuis-Oudshoorn 2011).

The manual stepwise model selection consisted of adding the most important variable and removing nonsignificant variables from the null model. We used the Akaike information criterion (AIC) to select the best model. The best model is the one with the lowest AIC value (Quinn and Keough 2002). We obtained the significance of the regression models using a chi-square test by comparing the complete model with the null model. Significant differences between the models indicate the relationship between the independent variables and the response variable (Quinn and Keough 2002; Tabachnick and Fidell 2007).

Comparison with Other Anurans

To contextualize the observed movement patterns of *R. diptycha* and *R. rubescens*, we compared our findings on DM and home range with data available from a few selected studies on anuran and Bufonidae movement. This comparison provides a general perspective on how the movement behavior of these species relates to patterns reported for other anurans. This comparison included studies that employed various methods, such as spool tracking, mark–recapture, and radiotelemetry, to quantify movement patterns and home range sizes during both nonreproductive and reproductive periods. We extracted key parameters from these studies, including estimates of DM and home range size. Studies were selected for their methodological clarity and sampling effort and covered a range of habitat types to provide a comprehensive comparative perspective.

Statistical Analyses

All statistical analyses in this study were performed using R v4.0.2 (R Core Team 2020). The significance level used in the hypothesis tests was 5%.

RESULTS

Over 7 yr, we conducted a total of 327-night visits to the study area, where we captured 219 individuals of *R. rubescens* (19 adult females, 191 adult males, 1 adult not sexed, and 8 juveniles), totaling 266 recaptures, and 179 individuals of *R. diptycha* (17 females, 90 males, 5 adults not sexed, and 67 juveniles), totaling 477 recaptures. We obtained 430 GPS coordinates for *R. rubescens* and 597 for *R. diptycha*. During the 56 diurnal visits, we recorded 67 shelters and 88 routes for 35 *R. rubescens* individuals and 68 shelters and 82 routes for 16 *R. diptycha* individuals.

Capture–Recapture and Length of Stay

There was no difference in the average number (mean ± SD) of captures per individual according to sex for either species (*R. rubescens*, males = 2.4 ± 2.2; females = 1.7 ± 1.5; $W_{202} = 1{,}388.5$, $P = 0.096$; *R. diptycha*, males = 5.1 ± 7.5; females = 6.1 ± 6.5; $W_{105} = 901.5$, $P = 0.22$).

There was no sex-based difference in the average length of stay (weeks per year) in the study area for either species (*R. rubescens*, males = 3.7 ± 4.3 wk; females = 2.9 ± 4.2 wk; W_{235} = 1,949.5, P = 0.135; *R. diptycha*, males = 5.4 ± 7.2 wk; females = 8.5 ± 7.8 wk; W_{142} = 1,716, P = 0.064).

Site Fidelity

Both species showed annual site fidelity (Fig. 2A), with 72% of *R. rubescens* (n = 18) and 90% of *R. diptycha* (n = 21) individuals occupying the same sites at different years (binomial test, $P < 0.05$). The paths presented high average (mean ± SD) sinuosity (*R. rubescens* = 18.94 ± 46.29, median = 4.38, n = 88; *R. diptycha* = 17.62 ± 33.21, median = 5.33, n = 79). The DM was greater than the DL between the start and end points (Fig. 2B; *R. rubescens*, DM = 60.31 ± 35.09 m; DL = 14.03 ± 15.06 m; V_{87} = 3,916, $P < 0.001$; *R. diptycha*, DM = 109.71 m ± 80.54; DL = 21.91 ± 20.43 m; V_{74} = 2,850, $P < 0.001$), and there was a weak correlation between them (*R. rubescens*, r_s = 0.23, P = 0.03; *R. diptycha*, r_s = 0.51, $P < 0.001$). Among individuals with two consecutive records of using a day shelter, 68% of *R. rubescens* (n = 22) and 70% of *R. diptycha* (n = 27) used the same shelter, and the observed values were significantly different than the expected (binomial test, $P < 0.05$).

Spatial Distribution

Although widely distributed throughout the study area (Fig. 2C), individuals of both species concentrated their activities in different areas during the year ($HR_{i,j}$ = 0.27; $HR_{j,i}$ = 0.23; Fig. 2D) and were completely segregated during the reproductive season ($HR_{i,j}$ = 0; $HR_{j,i}$ = 0). *Rhinella rubescens* presented low segregation between the reproductive season and the rest of the year, with a distance of 25 m between the centroids of the two areas ($HR_{i,j}$ = 0.75; $HR_{j,i}$ = 0.55; Fig. 2E). In contrast, *R. diptycha* used segregated areas with a distance of 93 m between the centroids ($HR_{i,j}$ = 0; $HR_{j,i}$ = 0; Fig. 2F).

Daily Movement

DM in *R. rubescens* ranged from 2.72 m to 153.68 m, with a median of 52.08 m; in *R. diptycha*, it ranged from 0 to 347.34 m, with a median of 92.17 m (Fig. 3A). The model selection analysis indicated that the variation in DM was best explained by the species and the total previous day precipitation ($F_{2,160}$ = 16.05, $P < 0.001$, r^2 = 0.17). However, the model averaging indicated that mass and body size were also important (Table 1). The DM in *R. rubescens* was lower than in *R. diptycha* (W_{168} = 2,240, $P < 0.001$; Fig. 3A). The covariance analyses showed that there was no interaction between species with the total previous day's precipitation ($F_{1,166}$ = 0.01, P = 0.9) and with the SVL ($F_{1,165}$ = 2.44, P = 0.12). DM was positively related to the total previous day's precipitation for both species ($F_{1,166}$ = 10.88, $P < 0.01$; Fig. 4A) and with body size for *R. rubescens* ($F_{1,165}$ = 18.90, $P < 0.001$; Fig. 4B).

Home Range

The home range size (mean ± SD) of *R. rubescens* was smaller than *R. diptycha* (t_{62} = –4.96, $P < 0.001$; *R. rubescens* = 5.541 ± 10.054 m^2; *R. diptycha* = 20.043 ± 20.390 m^2; Fig. 3B). The covariance analysis showed that there was no interaction between species, SVL, and the number of captures ($F_{1,56}$ = 0.92, P = 0.3), and larger individuals occupied larger areas, regardless of species (Fig. 4C), and the number of captures ($F_{1,56}$ = 33.44, $P < 0.001$).

Habitat Use

The logistic regression indicated that substrate choice (land or water) was significantly explained by the variables used (χ^2_{26} = 1,207.74, $P < 0.001$), and from all selected variables, the reproductive activity was the least significant variable (Tables 2 and 3). The multinomial logistic regression analysis indicated that the model significantly explained the use of microhabitats (χ^2_{42} = 1,215.8, $P < 0.001$; McFadden r^2 = 0.39). During the day, the animals used more shrubs or grass in the water, and at night, they instead used water with macrophytes, water without vegetation, bare soil, and grass (Fig. 5A). Aquatic microhabitats, which had higher temperatures when compared to the air temperature, were more often used on colder nights than terrestrial microhabitats. *Rhinella rubescens* more often used water bodies with macrophytes, shrubs, grass, and twigs, while *R. diptycha* more often used water without vegetation, shrubs, or grass on land, termite mounds, grass, and bare soil (Fig. 5B). The individuals used more water with macrophytes and water without vegetation in the cold and dry season, and shrubs or grass in the water or soil, termite mounds, grass, and bare soil during the hot and rainy season (Fig. 5C). Males used more water without vegetation and shrubs or grass on land, while females used more bare soil and grass (Fig. 5D).

The variables species and microhabitat explained the distance to the pond margin observed for individuals found on land ($F_{7,290}$ = 76.08, $P < 0.001$, r^2 = 0.65), in water ($F_{7,429}$ = 28.1, $P < 0.001$, r^2 = 0.31; Tables 4 and 5), and the water depth ($F_{7,240}$ = 20.15, $P < 0.001$, r^2 = 0.37; Tables 5 and 6; Fig. 6).

Comparison with Other Anurans

When comparing our results with selected studies of other anurans, the DM varied greatly and ranged on average from 3.9 to 109 m depending on the technique used. *Anaxyrus americanus* had the lowest and *R. diptycha* had the highest DM (Table 7), whereas *R. rubescens* presented intermediate values of DM with 60 m on average. These comparisons highlight that *R. diptycha* demonstrates unusually high mobility and spatial use relative to other anuran species, while *R. rubescens* occupies an intermediate position. The home range area values varied from 163.3 to 246,000 m^2, with *R. ocellata* having the smallest and *A. boreas* having the largest home ranges (Table 8). *Rhinella diptycha* had a relatively large home range size when compared to other anuran species, while *R. rubescens* exhibited mid-range values within its genus (Table 8). These values underscore the considerable variation in home range size across anuran species, which seems to result from differences in species ecology, reproductive timing, environmental context, and methods used to estimate DM and home range data. Overall, these patterns suggest species-specific differences in spatial ecology among anurans, with implications for habitat use, for dispersal potential, and for conservation management.

Discussion

This study focused on how sympatric populations of *R. rubescens* and *R. diptycha* explore their Neotropical savanna environment. We found no sex-based differences in

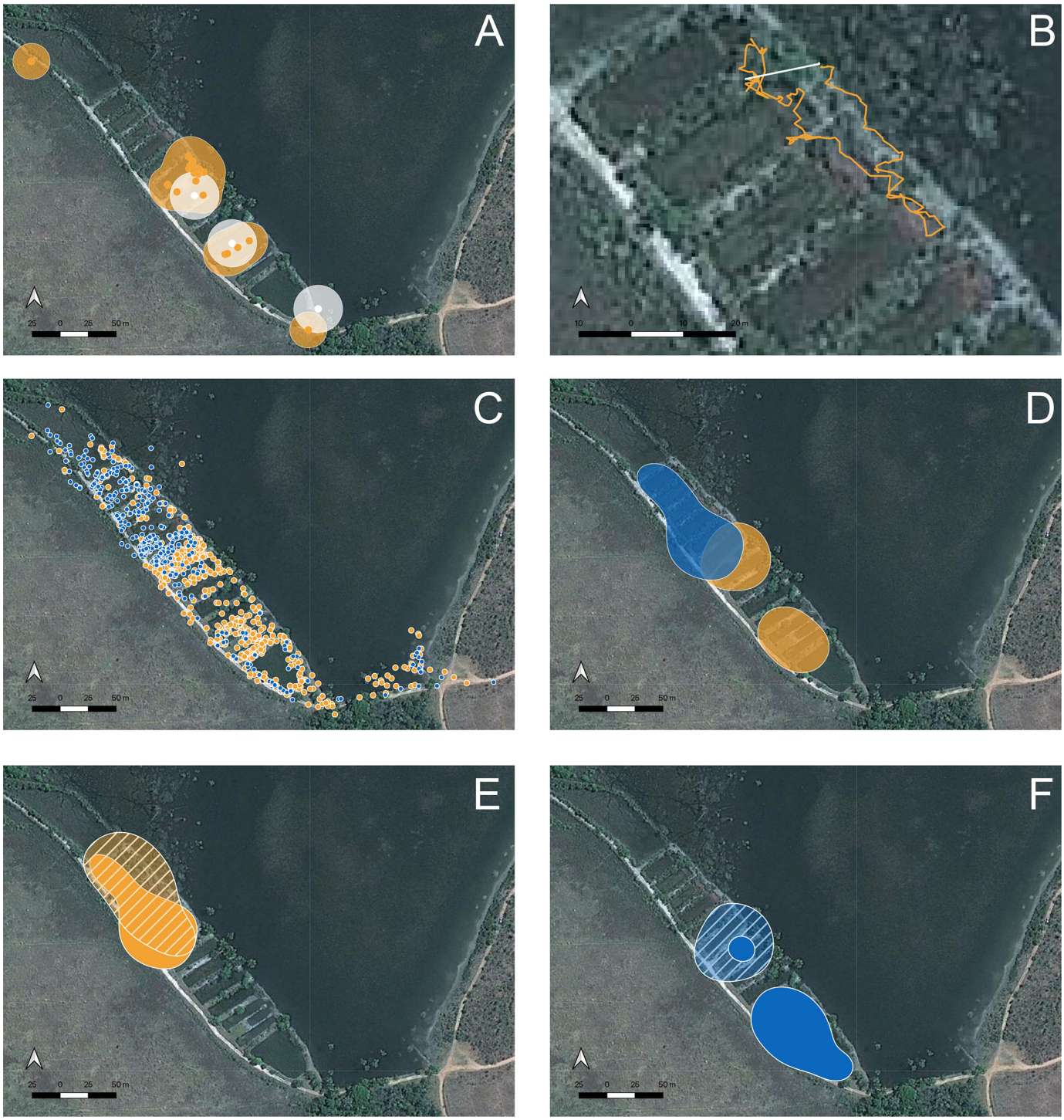

FIG. 2.—The study site comprised an area of approximately 3.2 ha at the shore of Lagoa Bonita, a large natural pond in ESECAE, a protected area in Distrito Federal, Brazil. (A) An example of overlap between areas occupied by an individual of *R. diptycha* in 2006 in orange and 2007 in white. (B) An example of the DM in orange and the DL between the start and end points in white for an individual of *R. diptycha*. (C) Distribution of the geographical points recorded for *R. rubescens* in blue and *R. diptycha* in orange. (D) Area with the highest intensity of use for *R. rubescens* in blue and *R. diptycha* in orange. (E) Area with the highest intensity of use during the reproductive period in orange and nonreproductive period in hatched pattern for *R. rubescens*. (F) Area with the highest intensity of use during the reproductive period in blue and nonreproductive period in hatched pattern for *R. diptycha*.

capture–recapture rates and length of stay in the study area. Both species showed high annual site fidelity, consistently occupying the same locations across different years. Spatial distribution analyses revealed that both species were widely dispersed in the study area, with activities concentrated during the reproductive season. DM patterns varied, with *R. diptycha* covering greater distances compared to *R. rubescens*, which exhibited smaller home range sizes. The interaction of species, sex, and environmental factors played a crucial role in influencing habitat use, providing a detailed understanding

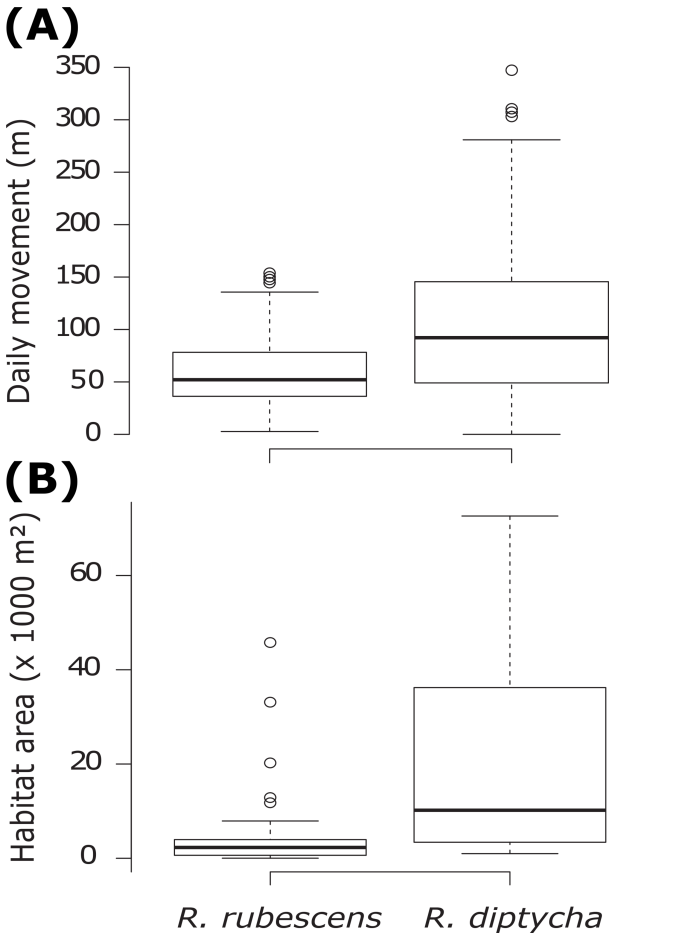

FIG. 3.—Boxplots illustrating DM (A) and habitat use (B) for *R. rubescens* and *R. diptycha* in ESECAE in Distrito Federal, Brazil.

of the ecological dynamics leading to the behavior of both species.

We found that there were no differences between sexes in the average number of captures and length of stay in the study area for *R. rubescens* and *R. diptycha*. Note that the length of stay was assessed throughout the year and not just in the

TABLE 1.—Results of the manual stepwise model selection and model averaging to identify variables that explain DMs of *R. rubescens* and *R. diptycha* from an area in ESECAE, Distrito Federal, Brazil. Estimate = coefficients of the best model. Coefficient average of 44 models with a weight higher than zero. Importance = sum of the Akaike weight of all models in which the parameter of interest is present in the model.

Variables	Estimate	Coefficient average	Importance
Intercept	56.71	187.24	
Species: *R. diptycha*	42.90	56.20	0.91
Mass		0.34	0.88
SVL		–2.09	0.82
Total previous day precipitation	29.85	28.47	0.68
Average relative humidity		0.62	0.50
Season: warm and rainy		5.78	0.32
Sex: male		–9.78	0.31
Total daily precipitation		–9.62	0.31
Average temperature		3.92	0.27
Period: reproductive season		–0.63	0.26

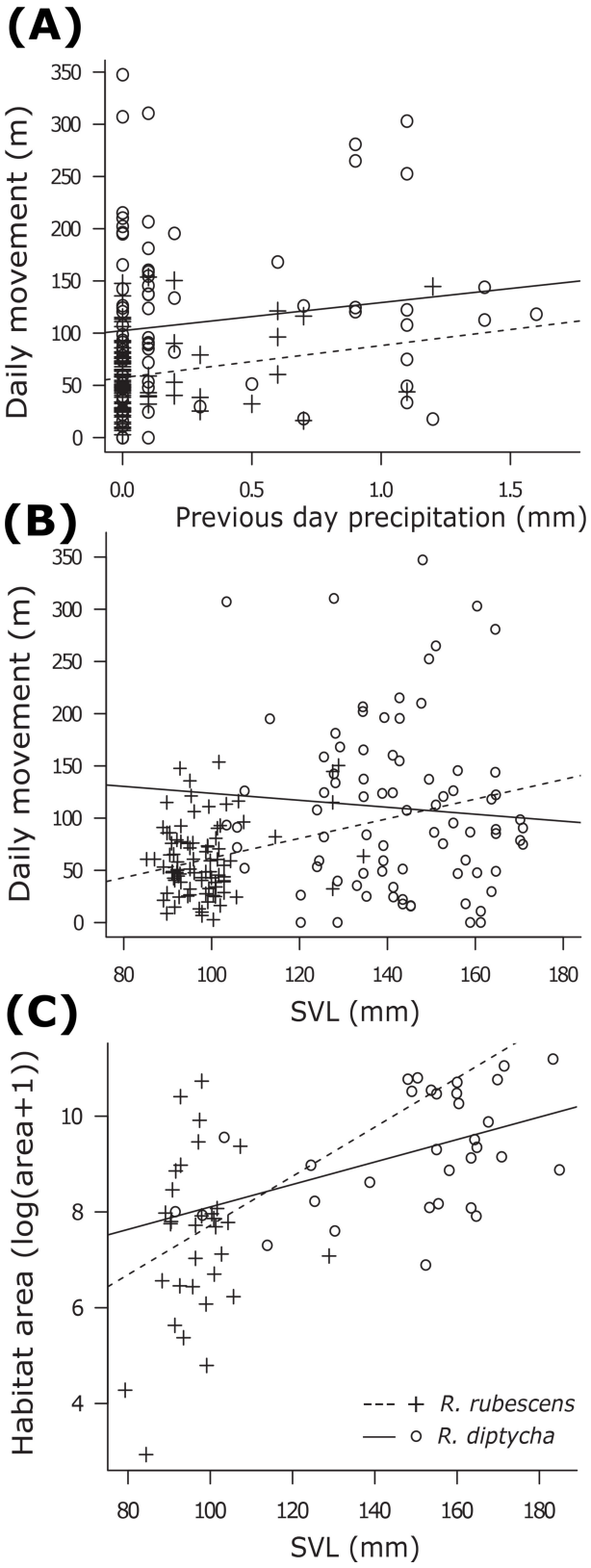

FIG. 4.—Relationship between DM and the total previous day's precipitation (A), body size (B), and habitat use (C) for each species in ESECAE, a protected area in Distrito Federal, Brazil.

TABLE 2.—Results of the logistic regression analyzing the variables that explain the substrate choice of *R. rubescens* and *R. diptycha* from an area in ESECAE, Distrito Federal, Brazil. Estimate = coefficients of the best-supported model (M1) identified during manual stepwise selection. M1–M3 = models with non-zero Akaike weights. Mean = model-averaged coefficient across all models (the similarity to the Estimate column reflects the strong weight of M1). Importance = sum of the Akaike weights of models in which the variable appeared. Negative coefficients indicate a higher probability of selecting water, whereas positive coefficients indicate a higher probability of selecting land. The bottom rows report model degrees of freedom (df), log-likelihood, corrected Akaike Information Criterion (AICc), AICc difference (ΔAICc), and model weight for the three best-supported models.

Variables	Estimate	M1	M2	M3	Mean	Importance
Intercept	7.86	7.86	7.43	6.78	7.82	
R. diptycha	1.63	1.63	1.62	1.71	1.63	1.00
Warm and rainy season	1.87	1.87	2.16	1.96	1.88	1.00
Substrate temperature	–0.46	–0.46	–0.48	–0.48	–0.46	1.00
Cloacal temperature	–0.31	–0.31	–0.32	–0.31	–0.31	1.00
Air temperature	0.35	0.35	0.38	0.36	0.35	1.00
Night	2.00	2.00	2.00	2.15	2.00	1.00
Male	–1.04	–1.04	–1.10		–1.04	0.99
Reproductive activity	–0.12	–0.12		–0.12	–0.12	0.96
df		9	8	8		
Log-likelihood		–282.59	–286.76	–288.02		
AICc		583.40	589.70	592.22		
ΔAICc		0.00	6.29	8.82		
Weight		0.95	0.04	0.01		

reproductive period. Thus, individuals may have established home ranges after the reproductive period, leading to an equal length of stay between the sexes. In contrast, in Woodhouse's Toads, *Anaxyrus woodhousii,* males tend to stay longer at reproductive sites to maximize the number of mates because they can reproduce more than once in the same year, whereas females produce only one clutch each year (Woodward 1982, 1984). In addition, a positive correlation between length of stay and mating success has been demonstrated in many species (e.g., Murphy 1994; Given and Montgomery 2002; Jofré et al. 2005). Taken together, the lack of sex differences in number of captures and length of stay in our study, along with similarities in the likelihood of recapture and survival between the sexes and the absence of temporary emigration (Vasconcellos and Colli 2009), suggests that the observed sex ratio genuinely reflects a higher number of males than females in these populations studied.

We also observed site fidelity in *R. rubescens* and *R. diptycha*, where individuals used the same sites in different years. Site fidelity is common in pond breeding terrestrial amphibians (Smith et al. 2005), with high fidelity to reproductive sites and terrestrial refuges (Reading et al. 1991; Sinsch 1992; Lemckert and Brassil 2000; Gamble et al. 2007). The tracked routes in our study indicated that routine movement was mainly characterized by nonlinear movements near the point of capture, consisting of turns and use of the same shelter or nearby shelters on consecutive days. In *A. americanus,* the use of the same shelter was also observed over several days (Forester et al. 2006), and high fidelity was also observed in another toad, *Epidalea calamita* (Sinsch 1992). The high fidelity is likely related to environmental stability. Philopatry in adult amphibians may have evolved given the advantage of using a known location with favorable and relatively stable resources (Semlitsch 2008). Thus, individuals accumulate greater reproductive success and survival simply by using the same site each year (Johnson and Gaines 1990).

Animals migrate in search of resources that vary in space and time, and amphibians usually have a seasonal migration both toward and away from breeding sites, which are associated with water bodies or moist environments (Dingle and Drake 2007; Semlitsch 2008). *Rhinella diptycha* exhibits migration behavior associated with reproductive aggregations, following a similar pattern found for most Bufonidae species (Lemckert 2004). This pattern, however, is unclear for *R. rubescens*, which appeared to remain relatively close to the breeding site throughout the year, as well as for *R. ocellata,* which does not migrate (Caldwell and Shepard 2007). The seasonality of reproductive migrations is presumably the result of the contrast between the seasonal availability of water, food for the tadpoles, favorable environmental conditions for terrestrial migration, foraging resources, and suitable habitats for hibernation during winter and aestivation during the dry season (Semlitsch 2008). If the individuals of a species do not exhibit migratory behavior, the necessary resources for the species will likely be available in the regions adjacent to the breeding area, and it is advantageous to stay close to the reproductive site throughout the year. *Rhinella rubescens* and *R. diptycha* are reproductively active primarily during the cold and dry seasons, when the high risk of desiccation limits terrestrial movement. As a result, individuals are less likely to leave breeding ponds during this period, as migration over land is generally associated with heavy rainfall (Semlitsch 2008). However, in this study, eight linear paths away from the reproductive site were recorded for *R. rubescens*, which characterizes migratory movements (Forester et al. 2006), and

TABLE 3.—Frequency of the categorical variables, mean and standard deviation of the continuous variables that were selected in the logistic regression according to the use of water or land as a substrate by *R. rubescens* and *R. diptycha*. Reproductive activity represents the number of calling males in the study site.

Variables		Water	Land	Total
Species	*R. rubescens*	312	69	381
	R. diptycha	165	289	454
Season	Cold and dry	394	106	500
	Warm and rainy	83	252	335
Time of day	Day	83	52	135
	Night	394	306	700
Sex	Female	21	114	135
	Male	456	244	700
Air temperature (°C)		17.4 ± 5.5	21.0 ±3.3	
Substrate temperature (°C)		22.7 ± 2.6	22.2 ± 2.2	
Cloacal temperature (°C)		21.8 ± 2.7	21.8 ± 2.3	
Reproductive activity		4.4 ± 4.6	0.9 ± 2.0	

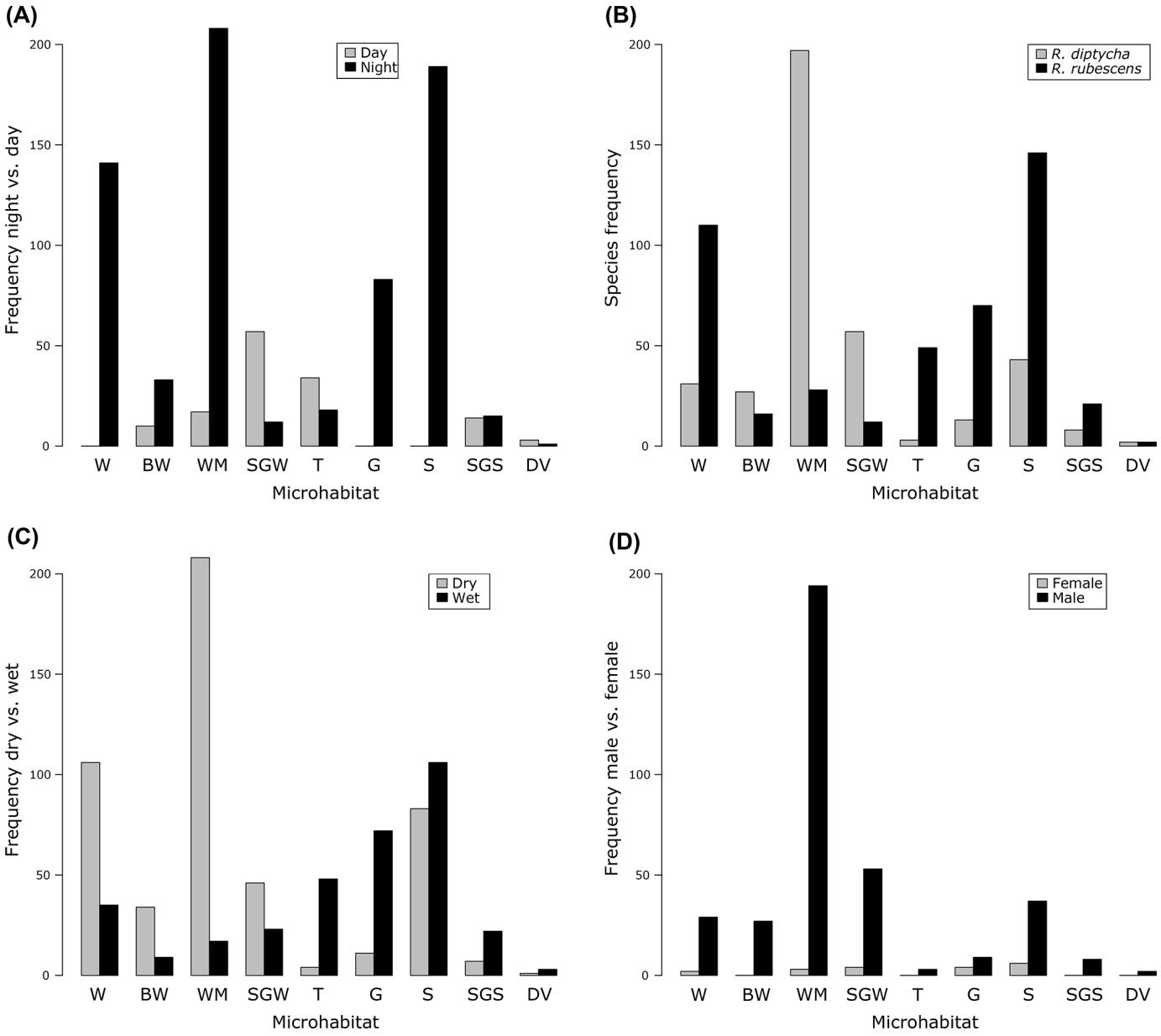

FIG. 5.—Frequency of individuals in each microhabitat category according to the period of the day (A; night vs. day), species (B), wet and dry seasons (C), and sex (D). Microhabitats are coded as follows: W = water without vegetation, BW = branches in water, WM = water with macrophytes, SGW = shrubs or grass in water, T = termite mound, G = grass, S = bare soil, SGS = shrubs or grass on soil, and DV = dead vegetation.

it might indicate that some individuals migrate to other places beyond the study area. In addition, most of the linear paths occurred in water, allowing long-distance movement during the cold and dry seasons. Migration distance from reproductive sites varies widely among amphibian species, ranging from 30 to 1,600 m with an average of approximately 290 m (Semlitsch and Bodie 2003; Lemckert 2004), and in many species, only a small proportion of adults make long-distance movements. These longer movements are often made by females (Bartelt et al. 2004; Forester et al. 2006), which may be related to the fact that females are the larger sex in most amphibian species (Shine 1979).

The average DM of *R. rubescens* and *R. diptycha* was quite high compared to that found in other anuran species (Table 7). Our findings suggest that the spool tracking technique is an effective tool for quantifying DMs, although it presents limitations when tracking distances greater than approximately 400 m or durations longer than 3 d. In contrast to radiotelemetry, which typically underestimates movement by measuring DLs between consecutive locations, the spool tracking method captures more detailed and realistic movement paths (Lemckert and Brassil 2000; Tozetti and Toledo 2005; Forester et al. 2006; Tozetti et al. 2009). Therefore, terrestrial amphibians may move more than currently reported, since most studies on animal movement use DL (Smith and Green 2005).

DM observed in this study was most influenced by species, SVL, mass, and total previous day precipitation. *Rhinella rubescens* is smaller than *R. diptycha,* which can explain the variation in DM between the species. In addition, we found that larger individuals moved longer distances when compared with smaller individuals, albeit with a weak correlation

TABLE 4.—Results of the manual stepwise selection model analyzing variables that explain the distance to the pond margin of individuals found on land and water. Estimate = coefficients of the best model. On land, the microhabitat reference variable was "shrub or grass," and on water, the variable was "water without vegetation." On land, the negative coefficient represents greater proximity to the pond margin, while on water, the positive value represents greater proximity to the pond margin.

	Land			Water		
Variables	Estimate	*t*	*P*	Estimate	*t*	*P*
Intercept	0.96	3.209	<0.01	–2.26	–2.73	<0.01
R. diptycha	–0.52	–2.765	<0.01	0.97	4.05	<0.001
Warm and rainy season	0.62	3.640	<0.001			
Termite mound	4.66	14.793	<0.001			
Branches in water				–2.1	–6.92	<0.001
Water with macrophytes				–0.8	–3.64	<0.001
Reproductive season				–0.54	–2.34	<0.05
Substrate temperature				0.07	2.07	<0.05
Total daily precipitation				–0.03	–2.11	<0.05

between size and distance. We also found that individuals, regardless of species, exhibited increased movement on days following higher precipitation levels. This highlights the significant role that humidity and precipitation play in influencing amphibian movement patterns (DeVore et al. 2021). Seasonal patterns of activity and movement mainly related to soil moisture and precipitation were also found in *A. americanus* (Forester et al. 2006), *A. boreas* (Bartelt et al. 2004), and *R. marina* (Seebacher and Alford 1999), which moved mostly during rainy or humid days. Terrestrial anuran species generally lack morphological or physiological adaptations to decrease evaporative water loss, unlike arboreal species (Wygoda 1984). Conversely, they rely on the ability to absorb water from the soil quickly, an important adaptation that allows them to move away from water bodies under damp soil conditions (Walker and Whitford 1970). Moreover, the relationship with the total previous day's precipitation was also small, which implies the importance of other factors that were not measured, like the actual soil moisture (Seebacher and Alford 1999), the internal status of individuals (Börger et al. 2008), the foraging strategy (Strussmann et al. 1984), and the temporal reproductive pattern of the species associated with intraspecific competition (Wells 1977b). In line with this, long-term research on *Anaxyrus fowleri* demonstrated that even when numerous intrinsic (e.g., body size, sex, and age) and extrinsic (e.g., population density and environmental variables) factors were considered, none significantly explained variation in DM distances (Jreidini and Green 2022a). Together, these findings emphasize that while environmental moisture is a key driver of amphibian movement, stochastic processes and individual variability also play an important role in shaping their movement.

The average home range area utilized by both species was larger than the average home range area found for most of the Bufonidae species (Table 8), and this is attributed to the larger body size of *R. rubescens* and *R. diptycha* in comparison to most species in this family. While comparing our results with other studies may provide valuable insights into the size of the home range for *R. rubescens* and *R. diptycha*, we acknowledge that discrepancies in the species' body size, time frame, methodologies, and techniques employed in these studies may impact the validity of our comparisons. Notably, most studies calculated the home range area considering only activity centers during the nonreproductive period (Lemckert 2004). In light of these variations, it is clear that for conservation actions aimed at sustaining amphibian populations in the long term, it is crucial to account for the entire area occupied, including both activity centers and migratory routes throughout both breeding and non-breeding seasons. The covariance analysis showed that the habitat area increased with larger body size, regardless of species, suggesting that body size is an important predictor of an individual's home range area and that larger individuals tend to explore a larger area when searching for resources. The relationship found between

TABLE 5.—Distance from the pond margin and water depth in meters for all categorical variables included in the best models (mean ± standard deviation).

Variables		Distance from margin on land (m)	Distance from margin in water (m)	Water depth (m)
Species	*R. rubescens*	1.44 ± 1.68	–1.93 ± 2.06	0.32 ± 0.16
	R. diptycha	1.64 ± 2.17	–0.35 ± 0.69	0.13 ± 0.10
Season	Cold and dry	0.65 ± 1.3	–1.61 ± 1.98	
	Warm and rainy	2.07 ± 2.23	–0.35 ± 0.67	
Activity	Reproductive		–1.63 ± 1.98	
	Nonreproductive		–0.26 ± 0.43	
Time of day	Day		–0.83 ± 1.28	0.24 ± 0.15
	Night		–1.52 ± 1.97	0.31 ± 0.17
Water without vegetation			–0.37 ± 0.76	0.17 ± 0.11
Shrub or grass in water			–0.53 ± 1.20	0.21 ± 0.11
Branches in water			–2.97 ± 3.21	0.21 ± 0.13
Water with macrophytes		0.60	–1.98 ± 1.75	0.34 ± 0.17
Shrubs or grass on land		1.04 ± 1.73		
Grass		1.44 ± 1.5		
Bare soil		0.74 ± 1.05		
Termite mound		5.7 ± 1.2		
Dead vegetation		1.58 ± 2.95		

TABLE 6.—Results of the manual stepwise model selection revealing the variables that explain the variation in the water depth. The estimate is the coefficient of the best model, and the microhabitat of reference was water without vegetation.

Variables	Estimate	*T*	*P*
Intercept	0.57	6.85	<0.01
Species: *R. diptycha*	–0.11	–3.79	<0.01
Minimum air temperature	–0.02	–5.03	<0.001
Distance from margin	–0.02	–3.58	<0.001
Night	–0.07	–2.68	<0.01
Shrubs or grass	–0.08	–1.36	0.17
Branches in water	–0.08	–1.30	0.19
Macrophytes	0.06	1.03	0.30

body size and area utilized is essentially associated with energy requirements, and larger amphibian species require larger amounts of resources and therefore use larger areas to maintain themselves (McNab 1963; Harestad and Bunnel 1979; Kramer and Chapman 1999). Although the relationship was positive, it was also weak, suggesting the importance of other factors in explaining the variation in amphibian home range area size. It is known that body size is a general indicator of the area occupied by an organism (Biedermann 2003); however, it is not an accurate way to predict the home range size required by a species, given the intraspecific variation in area for the same body size range. Therefore, food availability and habitat structure might better contribute to predicting the habitat area used than individual characteristics in amphibians (Indermaur et al. 2009).

The sympatric populations of *R. rubescens* and *R. diptycha* show both spatial and temporal segregation, which helps them coexist in the Neotropical savannas (Vasconcellos and Colli 2009). The partitioning of ecological niches among species, known as niche segregation, is explained by two evolutionary mechanisms: coadaptive processes driven by competition (Schoener 1974) and distinct evolutionary adjustments leading to niche differentiation (Toft 1985). The strength of competition among species may be related to the level of overlap in the use of a limiting resource. In this case, the species tend to diverge, reducing resource overlap to avoid competition (Lehtinen 2005). Then, different morphological, physiological, and behavioral adaptations may have arisen among species due to their distinct evolutionary histories. Both species belong to the *R. marina* group but are nested in different clades. *Rhinella diptycha* belongs to a large-sized species clade with a wide distribution in South America, while *R. rubescens* belongs to a smaller-sized species clade and is found in central-south regions that experience cooler climates (Maciel et al. 2010; Vallinoto et al. 2010; Valencia-Zuleta et al. 2017; Pereyra et al. 2021). Therefore, the geographical distribution and evolutionary relationships of these species may suggest that temporal segregation is linked to conserved ancestral characteristics. This may explain why *R. rubescens* reproduces during the cold and dry season, as the species is less tolerant of high temperatures and temperature variations in both its adult and larval stages (Wells 2007). Variation in thermic limitations was observed for two sympatric species in the genus *Rana*, which reflects and reinforces segregation between reproductive periods (Cook and Jennings 2007). Additionally, *R. rubescens* reproduces in streams, and tadpoles have behavioral and morphological characteristics adapted to life in streams (Eterovick and Sazima 1999; Eterovick 2003;

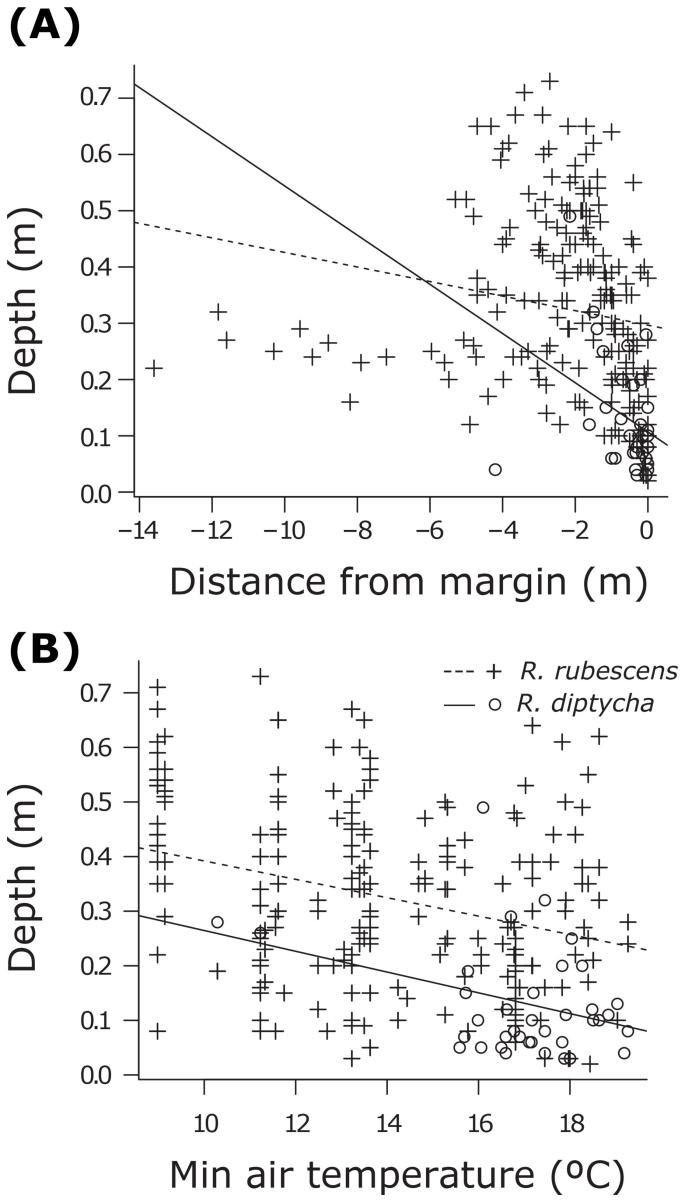

FIG. 6.—Relationship between water depth and distance to pond margin (A) and minimum air temperature (B) for each species. The zero value represents the pond margin.

Afonso and Eterovick 2007). This might explain the reproductive activities during the dry season because it could be advantageous to reproduce in the drought when the stream current speed is lower, allowing the eggs and tadpoles to develop without being carried by the current.

The analysis of linear models indicated that species was a determining factor in all variables related to habitat use and that spatial segregation between *R. rubescens* and *R. diptycha* is associated mainly with the climatic conditions during the highest activity period of each species. Logistic regression analyses clearly showed the importance of substrate in controlling body temperature and evaporative water loss, with aquatic microhabitats being selected during colder periods and by the species *R. rubescens*, and terrestrial microhabitats during warmer periods and by *R. diptycha*. The specific heat of water is greater than that of the earth, which makes it a better environment during cold and dry seasons, especially at

TABLE 7.—Estimates of DM in anurans (mean ± standard deviation or standard error).

Species*	DM (m)	Technique	Observation
R. rubescens	60.31 ± 35.09 (SD)	Spool tracking	Reproductive and post-reproductive seasons (July to December).
R. diptycha	109.71 ± 80.54 (SD)	Spool tracking	Reproductive and post-reproductive seasons (July to December).
R. marina (1, 7)	0–62	Spool tracking	Most months, except for the driest months, the DM was near zero. (7)
	37.4 ± 14.1 (SE)	Radiotelemetry	Reproductive season.
A. boreas (2)	39.2 ± 7.8 (SE)	Radiotelemetry	Males and females, respectively. Reproductive and post-reproductive
	38.9 ± 0.3 (SE)		seasons (May to August).
A. americanus (3)	3.9 ± 4.6 (SD)	Radiotelemetry	81% of the females. Post-reproductive season. Variation during 3 d
	1.5 ± 2.1 (SD)	Spool tracking	for six females. Post-reproductive season.
Epidalea calamita (4)	20 ± 41 (SD)	Radiotelemetry	Males and females, respectively. Variation in the average movement
	51 ± 60 (SD)		for 7 individuals during breeding and 11 individuals during post-reproductive season.
Mixophyes iteratus (5)	13.2 ± 10.9 (SD)	Spool tracking	Average DM during the reproductive season.
	8.3 ± 7.8 (SD)	Radiotelemetry	
Leptodactylus labyrinthicus (6)	28.4 ± 47.6 (SD)	Spool tracking	Males and females, respectively. Reproductive season.
	48.7 ± 61.1 (SD)		

* References: (1) Seebacher and Alford (1999); (2) Bartelt et al. (2004); (3) Forester et al. (2006); (4) Miaud et al. (2000); (5) Lemckert and Brassil (2000); (6) Tozetti and Toledo (2005), (7) DeVore et al. (2021).

night. Terrestrial environments are best used in the hot season and at the beginning of the rains, conditions that offer lower thermic limits and moisture, allowing for better exploitation of this environment. Studies on other species reveal an association between microhabitat selection and temperature and humidity conditions (Tracy et al. 1993; Seebacher and Alford 2002), as well as the importance of substrate temperature in controlling body temperature (Tracy 1976). Still underscoring the importance of climatic conditions in substrate choice, we also observed that biotic variables, such as sex differences and population reproductive activity, are less important. These variables, however, confirm the greater likelihood of finding individuals in the water when reproductive activity is higher and finding more males than females, as observed in *A. boreas* (Bartelt et al. 2004), which is expected by the type of reproduction in puddles and choir formation (Wells 2007).

Clear differences were observed in aquatic microhabitat use between the species. While *R. rubescens* was restricted to macrophytes and branches farther from the margins, *R. diptycha* was typically found in shallow, open areas near the margins of the water. In water, individuals select microhabitats in response to local differences in temperature, which may vary with depth, distance to shore, and vegetation. In addition, microhabitat selection may be related to reproductive behavior, such as the choice of vocalization and oviposition sites (Wells 2007). On land, both species used bare soil and grass more often during nocturnal activity, showing no difference in microhabitat preference. However, *R. diptycha* moved further from the margins, a characteristic that was associated with termite mounds used as a day shelter. During nocturnal activity, anurans use open areas or low vegetation cover, environments that facilitate prey encounters (Yu et al. 2010). While there is a preference towards open areas, it is interesting to note that males exhibit a higher presence on exposed soil or grass compared to females. This aligns with the findings in *A. boreas*, where females tended to utilize more exposed soil in shrub-covered sites, while males showed a preference for exposed soil without any vegetation cover (Bartelt et al. 2004). We expected females to use more protected environments than males, considering the reproductive strategy between the sexes. However, as males reach smaller body sizes (Arantes et al. 2015) and are therefore more susceptible to water loss (Wells 2007), we can understand the use of shrubs or grass on the ground as protection against desiccation.

During the day, individuals chose shaded environments more than exposed ones, a behavior that is expected in amphibians to avoid evaporative water loss (Tracy 1976).

TABLE 8.—Average home range size estimates for species in the Bufonidae family (mean ± standard deviation). Home range corresponds to the post-reproductive centers of activity. Habitat use area includes the center of activity and the migration routes. RP = reproductive period; NRP = nonreproductive period; MCP = minimum convex polygon; CMR = capture–mark–recapture.

Species*	Area (m²)	Observation	Technique	Method
R. diptycha	20,042 ± 20,390	Habitat use area	CMR and spool tracking	95% fixed kernel
R. rubescens	5,541 ± 10,054	Habitat use area	CMR and spool tracking	95% fixed kernel
R. ocellata (1)	163.3 ± 35.9	RP	CMR	MCP
A. boreas (2)	246,000 (females)	Habitat use area in 1 yr	Radiotelemetry	95% adaptive kernel
	58,298 (males)			
A. americanus (3)	687.9 ± 293.5	Home range	Radiotelemetry	95% fixed kernel
Epidalea calamita (4)	5,000 (BP)	Median value of RP (reproductive	Radiotelemetry	MCP
	65,000 (NBP)	site) and during NRP (habitat use area)		
Bufo bufo (5)	570 ± 872	Home range	Radiotelemetry	95% fixed kernel
B. japonicus (5)	220 ± 159	Home range	Radiotelemetry	
Bufotes viridis (6, 7)	2456 ± 3946	Home range	Radiotelemetry	95% fixed kernel
	74.36 ± 35.30	Activity ranges	Telemetry and accelerometer	MCP

* References: (1) Caldwell and Shepard (2007); (2) Muths (2003b); (3) Forester et al. (2006); (4) Miaud and Sanuy (2005); (5) Kusano et al. (1995); (6) Indermaur et al. (2009), (7) Spießberger et al. (2023).

However, there was a difference between species: individuals of *R. rubescens* used water with shrubs or grass and generally remained submerged or burrowed on the margin (under vegetation or ground with their heads up), whereas individuals from *R. diptycha* took refuge in termite mounds or on the ground under bushes or grass. Terrestrial anurans utilize various types of shelters to avoid desiccation, high temperatures, and predators, including dense vegetation, fallen trunks, plant roots, their own or other animal-built holes, rock cavities, or dead vegetation (Griffin and Case 2001; Semlitsch and Bodie 2003; Rosset and Alcalde 2004; Forester et al. 2006; Yu et al. 2010). However, records of water as a shelter, as observed in *R. rubescens,* are not common. The preference for specific types of shelter varies in response to seasonal changes (Seebacher and Alford 1999). In the case of *R. marina*, the selection of shelters is closely related to the need to reduce water loss rates. Particularly, the species exhibits an interesting strategy, using holes as shelters during the dry season and opting for dry grass in the rainy season (Schwarzkopf and Alford 1996). This adaptive behavior highlights the species' ability to adjust its shelter choices based on the specific environmental demands of different seasons.

The species studied were widely distributed throughout the study area but concentrated their activities in different sites. The differences in the distribution of the two species may be explained by habitat characteristics. *Rhinella rubescens* was mostly found in areas with dense aquatic vegetation and thick vegetation along the margins. In contrast, *R. diptycha* occurred more often in places with sparse vegetation, shallower water during dry periods, and more open ground cover. This explains the segregation in the habitat used by the species since the results showed the preference for deeper water and vegetation for *R. rubescens* and water without vegetation and bare soil for *R. diptycha*. Furthermore, suitable conditions for tadpole development might depend on the tank's habitat characteristics.

Conclusion

DM was characterized by winding movements, using the same or nearby shelters on consecutive days, and with few linear movements. Thus, it is less limited than currently thought, as most techniques use the DL between consecutive points, which underestimates the actual movement of animals. The spool tracking technique successfully represented the effective distance traveled by an individual.

The patterns of movement and habitat use varied between species. In common, they presented high site fidelity, and DM was associated with rainfall, a common pattern in terrestrial amphibians. Additionally, the length of stay in the study area was the same between males and females. Body size was a good factor in predicting the size of the home range area, while routine movements also depended on the species. Spatial segregation was mainly related to different climatic conditions of the reproductive period of each species and the environmental heterogeneity of the study area. *Rhinella diptycha* presented greater DM, migration distance, and area of use than *R. rubescens*. These results suggest that *R. diptycha* is a more terrestrial species with greater dispersal capacity than *R. rubescens*, which may explain the greater geographical distribution of the former. Although they belong to the same group (*R. marina*) and have similarities in various aspects of biology and population dynamics, they had different patterns in movement and habitat use, which makes coexistence possible. Moreover, the spatial relationships of *R. rubescens* and *R. diptycha* suggest little or no interspecific competition.

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