Tracking *Ceratophrys ornata*: a Telemetry-based Study on a Vulnerable Amphibian Species and its Conservation Implications

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Abstract.—The Argentinean Horned Frog (*Ceratophrys ornata*) is a vulnerable amphibian from the Pampas experiencing population decline. We assessed the spatial ecology in Buenos Aires Province, Argentina, during three breeding seasons (2019–2022). We fitted 37 adults with radio transmitters, recording daily locations, meteorological variables, and microhabitat characteristics. We tracked individuals during reproductively active (RAP) and inactive (RIP) periods. We estimated home ranges using the Minimum Convex Polygon and compared daily movement rates between periods and sexes. We explored the influence of meteorological variables on movement patterns using Generalized Estimating Equations. Finally, we characterized microhabitat and assessed habitat use and selection employing land use/cover layers. *Ceratophrys ornata* had a median home range of 5,800 m² during the RAP (range of values, 500–32,100 m², n = 11) and 660 m² during the RIP (23–9,320 m², n = 18). Median daily movement rates were significantly higher during the RAP (43.2 m/d, range of values, 7.7–106.7 m/d, n = 11) than the RIP (1.7 m/d, 0.3–8.7 m/d, n = 18). The probability of movement was significantly ($P < 0.05$) and positively associated with relative humidity and 5-d accumulated precipitation. Microhabitats for RAP and RIP shared similar vegetation structure but were located in different sites/substrates (ground and water). At habitat scale, individuals used grasslands and flooded grasslands. *Ceratophrys ornata* required < 4 ha for essential activities (foraging, sheltering, reproduction) and shallow flooded grasslands with dense vegetation and diverse native grasses. These findings provide the basis for *in situ/ex situ* actions to conserve remnant populations of *C. ornata*.

Key Words.—anuran; behavior; Ceratophryidae; home range; habitat; movement; radio telemetry.

Introduction

The study of animal movements reveals crucial aspects of the natural history of a species, providing essential insights into its behavioral ecology (Wells 2007; Horne et al. 2019). Among the outcomes of animal movement research is the estimation of home range, defined as the area where an animal concentrates its daily vital activities, such as foraging, sheltering, and reproduction (Burt 1943; Powell 2000). Home range size is shaped by a variety of ecological and physiological factors, including food availability, individual body size, population density, meteorological conditions, and habitat quality (McNab 1963; Wells 2007; Horne et al. 2019). These factors determine the extent of space an individual

requires, and understanding the drivers of home range size helps clarify spatial strategies and resource use.

Additionally, studies on animal movements help elucidate habitat usage and requirements across different spatial and temporal scales (Nathan et al. 2008). At fine spatial scales, a detailed understanding of the behavioral and spatial ecology of a species can shed light on important aspects of its microhabitat (Rowley and Alford 2007b). Moreover, at broader habitat scales, integrating geolocation data from telemetry tracking with geographic information systems enables the identification of key habitat types, supporting targeted conservation and restoration efforts (Varghese et al. 2022).

Amphibians are the most threatened vertebrate group, with over 40% of species worldwide at risk of

extinction (Luedtke et al. 2023; International Union for Conservation of Nature [IUCN] 2025). Several drivers of amphibian population decline and species extinctions have been identified, including habitat loss due to agricultural expansion and urbanization, pollution, climate change, emerging diseases, invasive exotic species, and overexploitation (Luedtke et al. 2023). Although this decline is global, amphibians in the Neotropics, which comprise nearly half of the amphibian species of the world, are at greatest risk, with 48% of species at risk of extinction (IUCN Species Survival Commission 2023).

The Neotropical family Ceratophryidae comprises three genera (*Ceratophrys, Lepidobatrachus, and Chacophrys*) with 11 species in total (Frost, D. 2025. Amphibian Species of the World: An Online Reference (version 6.2). Available from https://amphibiansoftheworld.amnh.org/ [Accessed 3 December 2025]). Among the species highlighted for conservation priorities is the Argentinean Horned Frog (*Ceratophrys ornata*), an iconic amphibian of the South American temperate grasslands whose original distribution included the Pampean Region in central Argentina, the departments of San José, Rocha, and Montevideo in Uruguay, and the state of Rio Grande do Sul in southern Brazil (Deutsch et al. 2024).

The global conservation status of *C. ornata* is Vulnerable (Deutsch and Agostini 2025). Regional assessments considered the species as Vulnerable in Argentina (Vaira et al. 2012) and Uruguay (Carreira and Maneyro 2019) and as Critically Endangered in Rio Grande Do Sul, Brazil (https://dados.mma.gov.br/dataset/especies-ameacadas). The species has not been recorded in Brazil since 1992 and in Uruguay since 1982, suggesting it is possibly extinct in both countries (Deutsch et al. 2024). In Argentina, the current distribution is restricted to two areas in the Pampean Region, where remnant populations are at risk due to pressure from agricultural expansion, intensive livestock farming, urbanization, and wetland loss (Agostini and Bilenca 2024; Deutsch et al. 2024).

Ceratophrys ornata stands out as the largest anuran species in the Pampean Region and exhibits sexual dimorphism. Females reach snout-vent lengths of 120–140 mm and weigh up to 500 g, whereas males measure 81–105 mm and weigh up to 200 g (Fernández and Fernández 1921; Gallardo 1974, 1987; De Vosjoli 1990). Males also possess a vocal sac characterized by dark-colored spots (Fernández and Fernández 1921; Gallardo 1974, 1987; Cei

1980). The species feeds primarily on vertebrates, especially anurans (Basso 1990).

Ceratophrys ornata is rarely encountered and only active during reproduction, which lasts for a few days and occurs under very particular meteorological conditions (Cei 1980; Gallardo 1987). During the non-breeding season, individuals are terrestrial and fossorial and may spend months buried, forming a desiccation-resistant cocoon (McClanahan et al. 1976; Cei 1980). Additionally, low population densities make it even more difficult to detect in the field. Its scarcity and secretive nature have restricted natural history studies to anecdotal and observational accounts of behavior, often based on a limited number of captive individuals (Obst et al. 1988; Duellman and Lizana 1994). Comprehensive long-term monitoring of behavior and movements of free-ranging *C. ornata* is notably lacking, significantly impeding conservation planning efforts.

Recent advances in telemetry, including miniaturization and enhanced reliability, have encouraged its use in the study of amphibian movements. Challenges to amphibian telemetry persist, however, and studies on Neotropical species remain scarce (Altobelli et al. 2022). To date, there have been few studies of movements of Ceratophryidae species (Duellman and Lizana 1994), and none have employed radio telemetry.

In response to the conservation needs of *C. ornata*, we have employed radio telemetry in a remnant free-ranging population in Argentina to fill critical information gaps. These include the estimation of home range and daily movement, the analysis of the effect of meteorological variables on individual movement, the characterization of microhabitat, and the assessment of habitat use and selection. We also discuss the conservation implications of these findings to promote decision-making for *in situ/ex situ* conservation actions.

Materials and Methods

Study area.—We conducted this study in the northern portion of the Atlantic Coast of Buenos Aires province, Argentina, in General Lavalle (Fig. 1). Encompassing 7 km², the study area hosts one of the remaining populations of the species and is located in the Flooding Pampa, an ecological unit within the Pampean Region (Soriano 1991). This ecological unit is characterized by temporary water accumulation due to its elevation and topography (Marino 2008). The climate is temperate and sub-
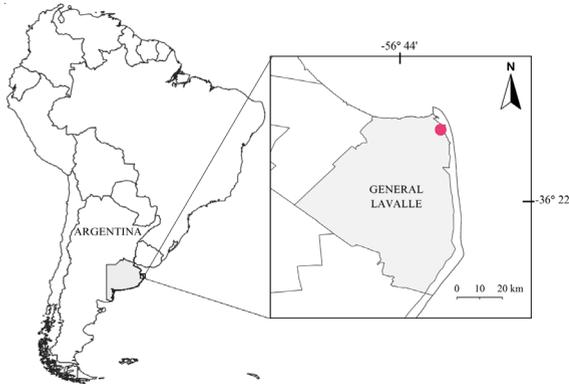
FIGURE 1. Study site location in General Lavalle (Buenos Aires Province, Argentina) highlighted by a pink circle.

humid, with mean monthly temperatures ranging from 13° to 23° C (Sala et al. 1986; Bilenca and Miñarro 2004). Annual precipitation varies between 750 and 900 mm (Sierra et al. 1993), with rainfall occurring throughout the year but often concentrated between November and April. The topography is mostly flat, with slight variations in slope that cause differences in soil and vegetation communities, influenced by the duration of flooding. The region is predominantly grasslands, composed mainly of Poaceae species. Native species dominate, though naturalized species are also present (Sala et al. 1986; Bilenca et al. 2018).

Field surveys.—We conducted surveys between 2019 and 2022 during the breeding season (September-March) of *C. ornata* (Cei 1980). For most amphibian species, the breeding season provides the best opportunity to study movement patterns, as most movements and interactions with other individuals are linked to reproductive activities (Wells 1977, 2007; de Oliveira et al. 2016). This is particularly true for *C. ornata*, which breeds explosively for only a few days under very particular meteorological conditions (Cei 1980; Deutsch 2024). Additionally, *C. ornata* appears to remain buried for extended periods and is active only during reproductive events (Gallardo 1974). For this study, we defined two periods within the breeding season: the reproductively active period (RAP), characterized by the presence of choruses of at least four individuals, indicating active reproduction; and the reproductively inactive period (RIP), corresponding to intervals between RAPs, when individuals were not reproductively active and remain hidden or partially buried.

After heavy rainfall, we captured adult specimens through active searches using standardized amphibian monitoring techniques (Heyer et al. 1994). We then fitted adults with VHF radio transmitters (model TXC-007T; Telenax Wildlife Telemetry, Playa del Carmen, Quintana Roo, México), weighing 3–4 g, which represented < 5% of the body weight of an individual, in accordance with established telemetry guidelines (Kenward 2001). We attached the transmitters to each individual, following Bartelt and Peterson (2000), and incorporated silicone straps. We previously tested the technique on captive specimens under laboratory conditions to ensure that the harness and transmitters did not injure the animals (Fig. 2). Additionally, we determined the sex of each individual based on the presence of secondary sexual characteristics (pigmented vocal sac and dark nuptial pads of males), size, and vocalizations (Cei 1980; Gallardo 1987). We conducted general health assessments when we attached transmitters and at least once during the monitoring period to ensure that the transmitters were not causing any adverse effects. If a transmitter was lost, we searched for a new individual to outfit with a transmitter, as described above. We tracked individuals with a TR-4 receiver (Telonics, Mesa, Arizona, USA) and a three-element Yagi antenna (ELVCOM, Ciudad Autónoma de Buenos Aires, Argentina).

We divided the daily movement of each individual into three observation blocks: morning (0600–1400), afternoon (1400–2200), and night (2200–0600). We recorded data from night movement at 0600, morning movement at 1400, and afternoon movement at 2200. The timing varied slightly (by 1–2 h) due to changes in sunrise and sunset times during the study period (early spring to late summer), which could affect amphibian activity (Jaeger and Hailman 1981; Hatano et al. 2002). We began collecting data 24 h after transmitter outfitting to avoid any potential behavioral effects caused by the deployment of the transmitters (Rowley and Alford 2007a). At each detection, we recorded the location and straight-line distance to the previously recorded location using an eTrex 32x GPS unit (Garmin, Olathe, Kansas, USA). Additionally, we recorded air temperature (°C), relative humidity (%), wind speed (km/h), and atmospheric pressure (hPa) *in situ* using a Kestrel 5000FW portable weather station (Nielsen-Kellerman Co., Boothwyn, Pennsylvania, USA). Finally, we recorded the accumulated precipitation for each observation period (mm/8 h) and accumulated precipitation over 5 d (mm/5 d), both obtained from the nearest weather station located 10 km from the study site (https://www.weathercloud.net/). We

FIGURE 2. Radio transmitter outfitting of Argentinean Horned Frogs (*Ceratophrys ornata*) under controlled captive conditions and field tracking in Buenos Aires Province, Argentina. (Photographs A and B by Sofia Perrone and C by Damián Fidanza).

recorded environmental data for each location (three times a day).

To characterize the microhabitat, we placed a 2 × 2 m quadrant around each animal (Dodd 2009) and recorded the microhabitat characteristics at each detection during the tracking period (three times a day). We photographed the ground at each site from a height of 1.5 m to estimate vegetation cover. Additionally, we obtained vegetation height using a measuring tape. For all specimens found on the ground, we estimated the percentage of the exposed substrate and the percentage of the substrate covered by vegetation from the photographs using *Canopeo* software (Patrignani and Ochsner 2015). For specimens found in water, we estimated the percentage of exposed substrate and the substrate covered by vegetation (emergent and submerged plants) as previously described, and vegetation height from the bottom of the water body (cm) and we recorded water depth (cm) with a measuring tape. We measured water quality parameters of pH, total dissolved solids (ppm), and temperature (°C), using a Hanna VCx3 multiparameter meter (Hanna Instruments, Woonsocket, Rhode Island, USA). At each location, we identified plants to the genus or species level using available literature (Roitman et al. 2012).

Data analysis.—To estimate the home range of *C. ornata* individuals during the breeding season, we calculated a 95% Minimum Convex Polygon (MCP), using geographic coordinate data from all locations and the adehabitatHR package (Calenge and Fortmann-Roe 2023). We used the MCP method because of the relatively short tracking durations and limited relocation points per individual. This approach allows the inclusion of a larger number of individuals, providing a more representative and reliable estimate of home range size than methods requiring more extensive data per individual, such as Kernel Density Estimators (Seaman et al. 1999; Row and Blouin-Demers 2006). We calculated the home range of male and female individuals for RAP and RIP separately. To ensure a representative estimation of home range, we included only individuals with a minimum of five data points, with at least three discrete locations (Calenge and Fortmann-Roe 2023). For each period, we compared the sizes of home ranges for females and males using the non-parametric Wilcoxon Rank-sum Test for independent samples. To compare home range size between periods, we used the non-parametric Wilcoxon Signed-rank Test for paired samples, including only those individuals with locations in both periods. We presented the median and range values instead of means to provide a more reliable and representative description of central tendency, due to the high variability in home range size among individuals.

To assess daily movement, we summed the straight-line distances covered by each individual between

TABLE 1. Number of female and male Argentinean Horned Frogs (*Ceratophrys ornata*) individuals tracked (n = 29), and the number and duration of reproductive events during the three breeding seasons in Buenos Aires Province, Argentina. No individual was monitored in more than one breeding season. Abbreviations are F = females, M = males, NRE = number of reproductive events, and DRE = duration of each reproductive event in days.

Breeding season dates	F	M	NRE	DRE (d)
September 2019 - March 2020	0	3	3	10, 2, 1
September 2020 - March 2021	9	4	2	4, 7
September 2021 - March 2022	4	9	1	10

consecutive locations within the observation blocks (morning, afternoon, and night) and divided the total by the number of tracking days (variable expressed as rate). We determined median daily movement rates of males and females for RAP and RIP. To assess differences in daily movement rates between sexes within each period as well as between periods, we used the statistical tests previously described. Additionally, we used descriptive statistics to explore individual movement across daily observation periods (morning, afternoon, and night). We calculated the median distances covered by each individual for each daily observation block.

To analyze the relationship between the movement of *C. ornata* and meteorological variables, we used Generalized Estimating Equations (GEEs) to fit marginal Generalized Linear Models and address temporal correlation in the location data (Zuur et al. 2009), employing the geepack package (Højsgaard et al. 2006). We used separate models for RAP and RIP. To avoid the skewed distribution with extreme values and a high proportion of zeros, we transformed the distance data into a dichotomous variable. We considered distances greater than 0 m as movement (1), while distances equal to 0 m were considered as no movement (0). The models were fitted using a binomial distribution with a logit link function to estimate the probability of movement. We included air temperature (°C), relative humidity (%), wind speed (km/h), atmospheric pressure (hPa), accumulated precipitation (mm/8 h), and accumulated precipitation over the last 5 d (mm/5 d) as explanatory variables. The models included individuals as a random factor to address repeated measures from the same individual (Zuur et al. 2009). We identified collinear covariates using the GVIF (Variance Inflation Factor) function within the package car (Fox and Weisberg 2018). We then used a stepwise procedure to remove covariates with the highest GVIF values (> 5). We based model selection on the Quasi-likelihood under the Independence

Model Criterion (QIC), a modification of Akaike's Information Criterion suitable for GEE models, available through the package MuMln (Bartoń 2022). We employed a backward stepwise selection procedure to obtain the minimum adequate model from the full model, which included all predictor variables. We evaluated model performance with confusion matrices (Fielding and Bell 1997) using Receiver Operating Characteristic (ROC) curves and Area Under the Curve (AUC) calculations (Boyce et al. 2002), using the package ROCR (Sing et al. 2005).

To assess the habitat use and selection, we conducted a spatial analysis using annual land use/cover (LULC) layers (2019–2022; https://pampa.mapbiomas.org) and QGIS version 3.32 (https://qgis.org/). The layers were composed of several habitat types/categories: closed forest and shrubland, forest plantation, grassland, non-vegetated area, open forest, pasture, temporary crop, water body, and wetland (locally known as flooded grassland). We used the 2020 LULC layer, as there were no substantial changes in land use or cover extent within the study area during the period analyzed.

We determined habitat use by overlapping the geographic coordinates of individuals with the LULC layer, which allowed us to identify the corresponding land use/cover category. We informed habitat use as the percentage of individual locations of each use/cover category. To explore habitat selection, we used the observed percentage of each category for both periods and compared it with the expected percentage of habitat availability (under the assumption of random habitat use). This calculation was carried out within the 7 km² study area. For the comparison between periods, we used Wilcoxon Rank-sum Test for independent samples.

For all analyses, we used only data from individuals with more than one day of radio tracking. We performed all statistical analyses using R version 4.2.1 (R Development Core Team 2024). We used a significance level of α = 0.05 for statistical tests.

RESULTS

We fitted 37 individuals with transmitters and successfully tracked 29 of them. These included 13 females, weighing 291–400 g, and 16 males, weighing 112–173 g. The remaining eight individuals lost their transmitters within 24 h and were therefore excluded from the dataset (Table 1). The duration of monitoring for each individual ranged from 1 to 143 d, depending on how long the radio transmitters
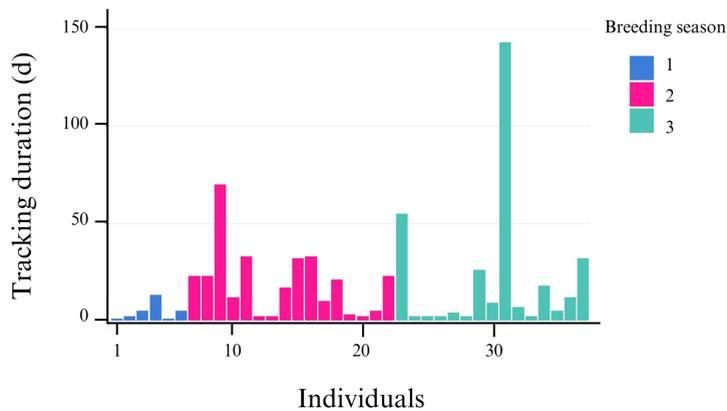
FIGURE 3. Tracking duration of 37 Argentinean Horned Frogs (*Ceratophrys ornata*) individuals during three breeding seasons in Buenos Aires Province, Argentina. Each bar corresponds to a single individual.

remained active and attached to the animals (Fig. 3).

Home range.—We determined home ranges of 23 individuals that met the criteria adopted for the MCP. Home range size varied considerably among individuals (Fig. 4), ranging from 500 to 32,100 m^2 (median = 5,800 m^2, n = 11) during the RAP and from 23 to 9,320 m^2 (median = 660 m^2, n = 18) during the RIP (Fig. 5). No significant differences were found between sexes during the RAP (W = 19.5, P = 0.464; n = 11) or the RIP (W = 30, P = 0.408; n = 18). We tracked six individuals in both the RAP and RIP but found no significant differences in home range size between them (V = 5; P = 0.312; n = 6; Fig. 6).

Daily movement.—Using a data set of 23 animals, we found that during the RAP, individuals covered significantly greater daily distances compared to the RIP (V = 21; P = 0.031; n = 6). Daily movement rate ranged from 7.7 to 106.7 m/day (median = 43.2 m/day; n = 11) during the RAP and from 0.3 to 8.7 m/day (median = 1.7 m/day, n = 18) during the RIP (Fig. 7). Median daily movement did not differ between sexes in either RAP (W = 7, P = 0.380; n = 11) or RIP (W = 33, P = 0.550; n = 18). When exploring movement across observation blocks (morning, afternoon, night), median distances covered by individuals in both periods were higher at night than in the morning or afternoon (Table 2).
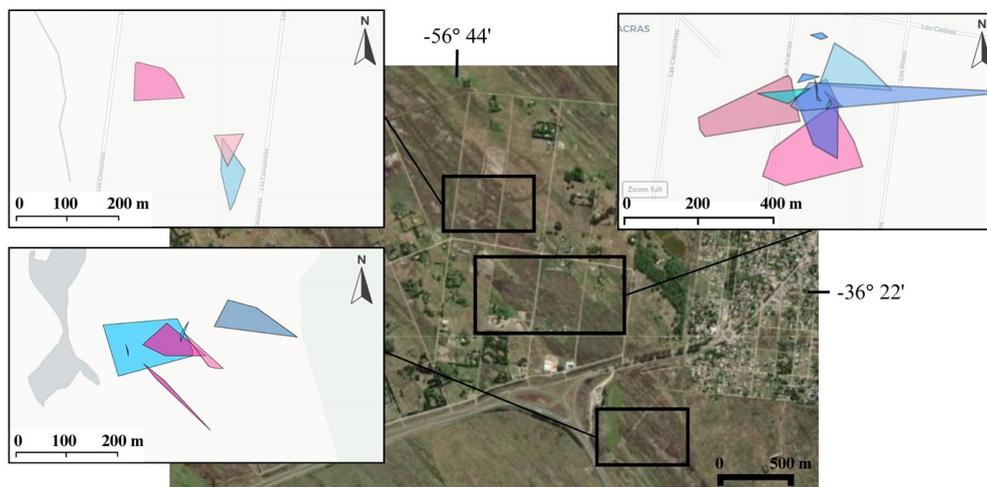

FIGURE 4. Home range (Minimum Convex Polygon, 95%) of females (pink, n = 9) and males (blue, n = 14) of Argentinean Horned Frogs (*Ceratophrys ornata*) in the study area in Buenos Aires Province, Argentina. Some of the estimated home ranges are not visible due to polygon overlap, small size, and adjustments in map scale. Background map from CartoDB Positron (Carto, New York, New York, USA) and Esri World Imagery tiles (Esri, Redlands, California, USA).
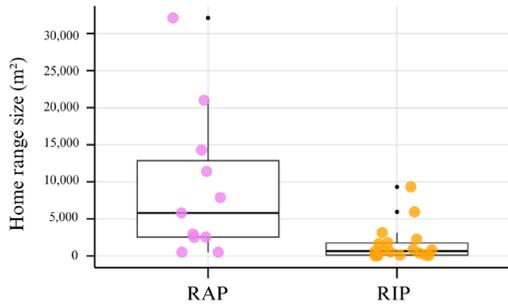
Figure 5. Median home range size (Minimum Convex Polygon, 95%) in the reproductively active period (RAP; n = 11) and the reproductively inactive period (RIP; n = 18) during the breeding season of Argentinean Horned Frogs (*Ceratophrys ornata*) in Buenos Aires Province, Argentina. Six individuals were tracked in both periods. The lower and upper ends of the boxes represent the first and third quartiles. The horizontal line in the boxes represents the medians for the values. The whiskers represent the maximum and minimum range (excluding outliers, which are represented by black dots).

Movement and meteorological variables.—Based on observations of 23 tracked individuals, the results showed that, among the meteorological variables initially considered, only accumulated precipitation over the previous 5 d was retained in the final GEE model for the RAP. It was significantly and positively associated with the probability of movement of individuals ($W = 9.27$; df = 9; $P = 0.002$; AUC = 0.66). For the RIP, the final model included accumulated precipitation over the last 5 d ($W = 16.12$; df = 15;

Table 2. Daily movement of 23 Argentinean Horned Frogs (*Ceratophrys ornata*) in Buenos Aires Province, Argentina. Values are median (range) during the reproductively active period (RAP) and the reproductively inactive period (RIP). Six individuals were tracked during both periods.

	Distance covered (m)		
	Morning	Afternoon	Night
RAP (n = 11)	12.8 (0.0–61.0)	9.8 (0.0–83.0)	22.0 (0.0–181.0)
RIP (n = 18)	0.5 (0–6.8)	0.8 (0.0–9.0)	2.3 (0.0–17.2)

$P = 0.018$) and relative humidity ($W = 5.59$; df = 15; $P < 0.001$; AUC = 0.61), both positively associated with the probability of movement.

Microhabitat.—This characterization was based on field observations of the entire set of 29 tracked individuals. The microhabitats of females and males did not appear to differ spatially in either of the periods evaluated. There was, however, a clear shift in microhabitat type: during the RAP, most individuals were located in aquatic environments, while during the RIP, they were found on land (Fig. 8). The microhabitat of *C. ornata* during both periods was characterized by a similar vegetation structure with a high vegetation cover and a predominance of the herbaceous stratum (Table 3). Reproductively active microhabitat was characterized by low-lying areas prone to water accumulation, leading to the formation of shallow, temporary ponds with an average depth
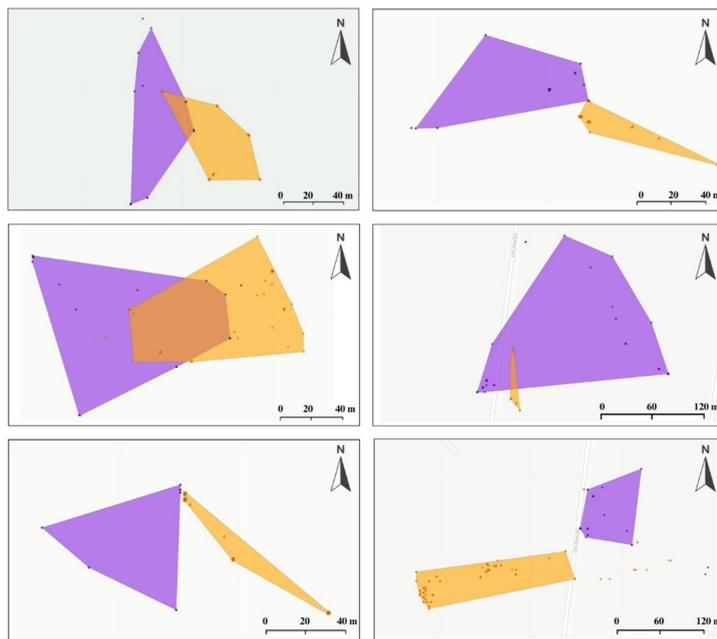

Figure 6. Home range sizes (Minimum Convex Polygon, 95%) and locations (points) in the reproductively active period (RAP, purple) and reproductively inactive period (RIP, orange) during the breeding season of Argentinean Horned Frogs (*Ceratophrys ornata*) in Buenos Aires Province, Argentina. Each panel shows the home ranges of one of the six individuals included in the comparison. The corresponding figure for all 23 individuals is available in Supplemental Information file (Fig. S1).

TABLE 3. Microhabitat variables (mean ± standard error) registered for 29 Argentinean Horned Frogs (*Ceratophrys ornata*) tracked in Buenos Aires Province, Argentina. Abbreviations are n = number of individuals, VC = vegetation cover, BSC = bare soil coverage, VH = vegetation height, D = water depth, TDS = total dissolved solids, WT = water temperature.

	Ground		Water	
	Females	Males	Females	Males
Reproductively Active Period (RAP)				
n	5	9	5	9
VC (%)	83.8 ± 4.4	95.7 ± 1.8	80.5 ± 2.4	88.0 ± 2.2
BSC (%)	16.2 ± 4.4	4.3 ± 1.8	19.5 ± 2.4	12.0 ± 2.2
VH (cm)	52.5 ± 5.7	46.5 ± 7.2	42.8 ± 4.5	55.7 ± 5.0
D (cm)	–	–	12.6 ± 1.7	18.1 ± 1.7
pH	–	–	7.3 ± 0.1	7.3 ± 0.1
TDS (ppm)	–	–	1.3 ± 0.1	1.2 ± 0.1
WT (° C)	–	–	16.8 ± 0.3	16.5 ± 0.4
Reproductively Inactive Period (RIP)				
n	7	10	2	0
VC (%)	92.9 ± 0.6	88.9 ± 1.0	95.0 ± 5.0	–
BSC (%)	7.1 ± 0.6	13.3 ± 1.2	5.0 ± 5.0	–
VH (cm)	82.1 ± 1.9	53.2 ± 1.8	32.5 ± 7.5	–
D (cm)	–	–	6.0 ± 2.0	–
pH	–	–	7.3 ± 0.2	–
TDS (ppm)	–	–	1.5 ± 0.1	–
WT (° C)	–	–	14.8 ± 0.8	–

of no more than 18 cm (Fig. 8). These areas were dominated by emergent hydrophytes such as Spiny Rush (*Juncus acutus*), bulrush (*Schoenoplectus* spp.), and Perennial Glasswort (*Salicornia ambigua*). In contrast, reproductively inactive microhabitat was found in slightly elevated areas (height not exceeding 1.5 m elevation; Fig. 8), dominated by grasses including Saltgrass (*Distichlis spicata*), paspalum (*Paspalum* spp.), pampas grass (*Cortaderia* spp.), and sacaton grass (*Sporobolus* spp).

Habitat use and selection.—The two most representative habitat types in terms of extent in the study area were grasslands (81.1%) and flooded grasslands (16.7%). The presence of other land cover/uses categories was marginal: non-vegetated area, pasture, and forest plantation (< 1.0% each), and closed forest and shrubland, open forest, temporary crop, and water body (< 0.0001% each; Fig. 9). *Ceratophrys ornata* only used the predominant habitat types: grassland (RAP = 12.62 ± [standard error] 7.16%, RIP = 34.41 ± 9.85%, n = 29) and flooded grassland (RAP = 87.38 ± 7.16%, RIP = 76.53 ± 9.85%, n = 29). Regarding habitat selection, there was a strong selection for flooded grassland in both periods ($W = 75$, $P = 0.270$, n = 29; Fig. 10).

DISCUSSION

Our study provides new insights into the natural history of *C. ornata*, with a focus on adult movement patterns, microhabitat description, and habitat use/selection. Through extensive sampling over three breeding seasons, we fitted 37 adult individuals and
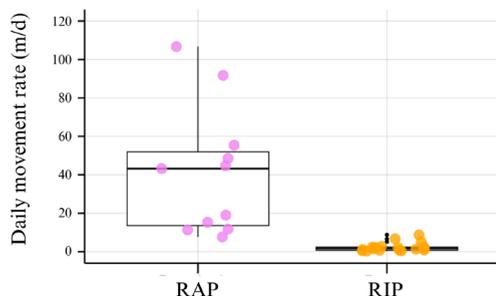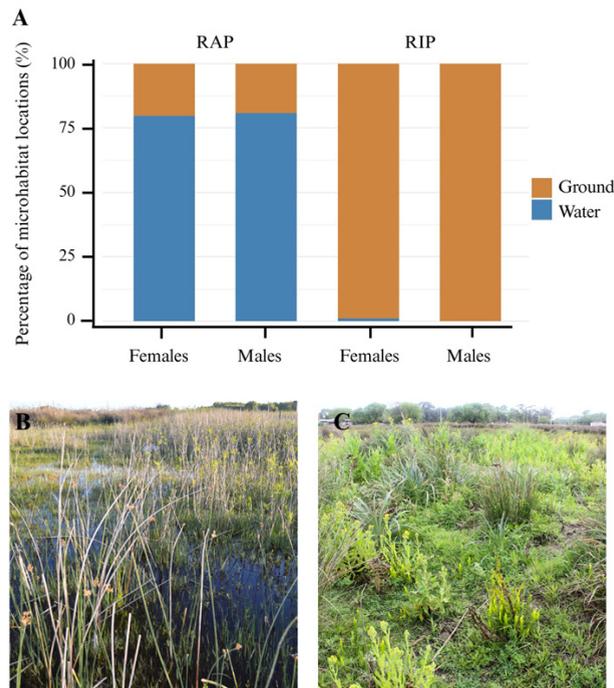
FIGURE 7. Median daily movement rates in the reproductively active period (RAP, n = 11) and the reproductively inactive period (RIP, n = 18) during the breeding season of Argentinean Horned Frogs (*Ceratophrys ornata*) in Buenos Aires Province, Argentina. Six individuals were tracked in both periods. Explanation of the box plot is in Figure 5.

FIGURE 8. Microhabitat of Argentinean Horned Frogs (*Ceratophrys ornata*) in Buenos Aires Province, Argentina. (A) Percentage of microhabitat locations (ground and water) of females (n = 13) and males (n = 16) in the reproductively active period (RAP) and reproductively inactive period (RIP). (B) Microhabitat during the reproductively active period. (C) Microhabitat during the reproductively inactive period. (Photographed by Camila Deutsch).

successfully tracked 29. Radio telemetry proved to be an effective method for conducting the first study on native populations of this threatened amphibian, even though this technique posed several challenges. Low species abundance limited the number of individuals that could be tracked, and the globose body shape of *C. ornata* required adjustments to transmitter attachment methods. Although transmitter loss occurred in all individuals at some point, we applied adjustments for attachment techniques and improved both tracking duration and sample size.

Home range.—Median values of individual home ranges of *C. ornata* obtained in this study are consistent with those reported for anuran species with similar body sizes to *C. ornata* (Lemckert 2004; Wells 2007). Nonetheless, maximum home range values were higher than those reported for most species of similar size (species from Bufonidae and Ranidae families; Lemckert 2004). Given the high variability in home range size, expanding research to include other local populations of *C. ornata* and species across the Ceratophryidae could provide valuable insights into the potential relationship between body size and home range size.

Although our analyses did not reveal significant differences in home range sizes between periods, the median and range values during the RAP were higher than those observed during the RIP. Consistently, we found high rates of daily movements performed by the individuals for this period. The lack of significant differences in home range size may, therefore, be explained by the small sample size and the high variation in tracking durations.

Previous studies have shown that anuran females tend to have larger home ranges and move greater distances than males (Ovaska 1992; Muths 2003; Rowley and Alford 2007b). This is often attributed to morphological, behavioral, and/or physiological differences between the sexes (Pilliod et al. 2002; Muths 2003; Bartelt et al. 2004; Rowley and Alford 2007b). Although body size in *C. ornata* is sexually dimorphic, we found no differences in home range size between females and males. There is no evidence of reproductive migration in *C. ornata* (Deutsch 2024), as breeding and non-breeding microhabitats are located close to each other: a finding that we confirmed in our study. Additionally, both sexes hunt similarly (Obst et al. 1988; Duellman and Lizana 1994) and likely show similar movement
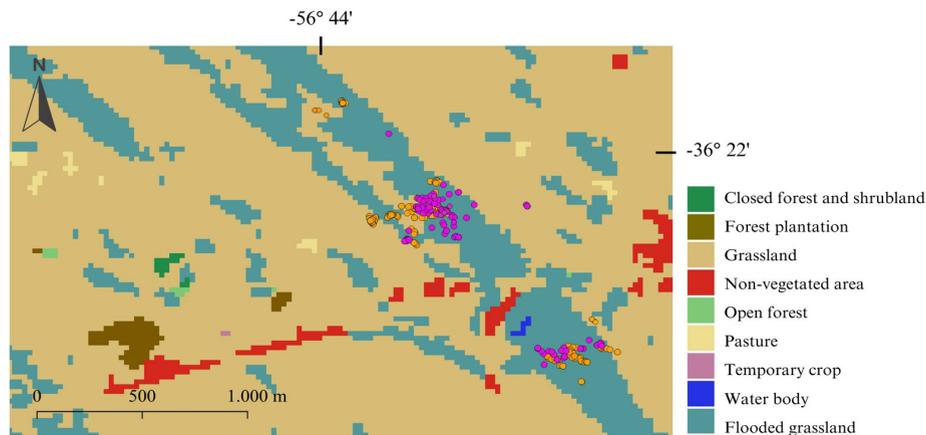
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FIGURE 9. Land use/cover and locations (points) for Argentinean Horned Frog (*Ceratophrys ornata*) individuals in the reproductively active period (purple, n = 14) and reproductively inactive period (orange, n = 21) in Buenos Aires Province, Argentina.

patterns, minimizing any sex-related differences in displacement for energy requirements.

Daily movement.—Our results indicated that *C. ornata* covers greater distances during the RAP than during the RIP. This supports previous evidence that most movements and interactions among amphibians are primarily driven by reproductive behaviors (Wells 1977, 2007; de Oliveira et al. 2016). During the RAPs, *C. ornata* individuals were highly active, moving extensively not only to find mates but also during amplexus, which can last several days (Deutsch 2024). In contrast, during the RIPs, they exhibited reduced movement but remained active. This finding challenges the widely held notion, supported by observational studies from several authors, that the species is active only during reproductive events (Cei 1980; Gallardo 1987). Notably, we observed that individuals continued to feed during the RIPs as well. As a sit-and-wait ambush predator (Obst et al. 1988; Duellman and Lizana 1994), the species appeared able to meet its energy needs without extensive movement during the non-reproductive periods.

Consistent with home range estimates, daily movements of *C. ornata* individuals did not differ between the sexes. Because both females and males use similar RAP and RIP microhabitats and move toward water bodies for mating and oviposition, the distances covered to reach reproductive sites are likely similar for both sexes. Additionally, males of
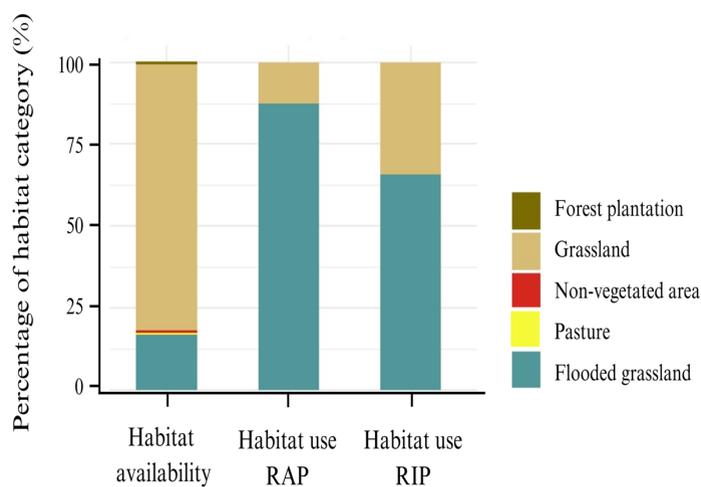

FIGURE 10. Habitat availability and habitat use by Argentinean Horned Frogs (*Ceratophrys ornata*) during the reproductively active period (RAP, n = 14) and reproductively inactive periods (RIP, n = 21) in Buenos Aires Province, Argentina. The left bar shows the percentage of each habitat (land use/land cover) category available in the study area (> 0.0001%). The right two bars indicate the mean percentage of *C. ornata* locations within each habitat category.

C. ornata did not travel extensively to find calling sites. This may reflect the proximity of microhabitats to each other in both periods.

Distances covered by individuals of *C. ornata* tend to be greater at night, consistent with most amphibian species of temperate grasslands (Cei 1980; Duellman and Trueb 1986; Wells 2007). Nocturnal movement in amphibians is widely regarded as a strategy to avoid desiccation and reduce predation risk (Duellman and Trueb 1986; Wells 2007); however, movement was also observed during the day, primarily during the RAP. These movements likely corresponded to amplexus activity, during which the species consistently moves for oviposition. Additionally, reproduction typically occurs on days with heavy rainfall (see discussion below), which reduces exposure to sunlight and high temperatures.

Movement and meteorological variables.— As ectotherms highly susceptible to desiccation (Duellman and Trueb 1986), amphibians are highly dependent on humidity (Bellis 1962; Boquimpani-Freitas et al. 2007; Wells 2007). This dependency is further pronounced, as precipitation triggers reproductive events in most amphibian species (Duellman and Trueb 1986; Bertoluci and Rodrigues 2002; Boquimpani-Freitas et al. 2007), and the larval cycle generally occurs in water (Duellman and Trueb 1986). We found a significant association between the movement of individual *C. ornata* and accumulated rainfall during the RAPs. This is consistent with existing literature (Cei 1980), including a recent field study showing that *C. ornata* reproduction is triggered by at least 55 mm/5 d of accumulated rainfall (Deutsch 2024). We also found that high relative humidity and an increase in cumulative rainfall were both associated with greater movement of individuals in the RIPs. Contrary to previous studies (Gallardo 1974), these results continue to support the notion that individuals remain active, likely feeding or seeking shelter, and move during humid and rainy days, even when not breeding.

Microhabitat and habitat use and selection.—At the microhabitat scale, *C. ornata* individuals were associated with densely vegetated areas dominated by an herbaceous stratum composed of native species. The *C. ornata* individuals bred in low-lying areas prone to water accumulation and sought refuge in areas near water bodies that are less prone to flooding during RIPs. Our results align with previous studies, indicating that remnant populations of *C. ornata* were associated with native grasslands characterized by minimal disturbance and grazing pressure (Perrone et al. 2022; Agostini and Bilenca 2024; Deutsch et al. 2024). These areas include salt-tolerant native species such as *Salicornia ambigua* and low-forage-value species (low palatability) that experience minimal impact from cattle grazing (Roitman et al. 2012).

At the habitat scale*, C. ornata* showed a clear selection for flooded grasslands, with grasslands also selected, though less frequently. Our results align with previous studies conducted on the distribution of the entire species, which reported that *C. ornata* tended to occur near flooded grassland patches (Deutsch et al. 2024). In contrast to the patterns observed at the microhabitat scale, our results do not reveal a difference in habitat selection between the reproductively active and inactive periods. This can be explained by the fact that the type of habitat selected by the species corresponds to seasonally flooded grassland plains (Soriano 1991). These ecosystems represent temporarily inundated areas influenced by elevation and topography, resulting in highly dynamic and heterogeneous environments. Consequently, this type of habitat can simultaneously offer both flooded and non-flooded microhabitats, which the species appears to use differentially depending on its reproductive activity. The variability of such environments may, therefore, prevent differences in habitat selection from becoming apparent unless analyzed at a finer, microhabitat scale. Hence, integrating studies across multiple spatial scales is essential to characterize the ecological requirements of the species accurately and to inform effective conservation strategies.

Conservation and management implications.— The estimated home range (and daily distances covered) for *C. ornata* suggests that individuals at our study sites need < 4 ha to carry out vital activities, e.g., foraging, seeking refuge, and reproduction. This relatively small home range, compared to other animal groups (e.g., Schoener 1968; Milton and May 1976; Harestad and Bunnell 1979; Lindstedt et al. 1986), could facilitate *in situ* conservation by limiting the area required to sustain populations. A broad network of small refuges, including patches of privately owned, low-impact productive lands as well as public lands (e.g., municipal and provincial reserves), could support the regional conservation of the species. Alternatively, the small home range size and limited movement of *C. ornata* could have negative

conservation implications. Habitat fragmentation alters anuran movement patterns (Gibbs 1998; Cushman 2006; Husté et al. 2006) and constitutes a major threat to amphibians worldwide (Luedtke et al. 2023). In our study area, recent urbanization for tourism (Celsi et al. 2016) has fragmented habitat and degraded wetlands, many of which have been drained, channelized, or leveled (Benzaquén et al. 2017). This fragmentation could isolate local populations and increase the risk of inbreeding (Reh and Seitz 1990; Keller and Waller 2002; Cushman 2006). Land use planning, incorporating both terrestrial and aquatic ecosystems, should ensure connectivity of breeding areas where remnant populations of *C. ornata* still occur. Given the vital role of these ecosystems in the reproduction of *C. ornata*, mitigation should be implemented at local and regional levels (Agostini et al. 2021; Agostini and Bilenca 2024).

Our study is also germane to ongoing *ex situ* management within the Giant of the Pampas conservation project, including the rescue and relocation of at-risk individuals (Deutsch et al. 2017; Deutsch 2024). Based on our findings, we recommend prioritizing relocations to shallow wetland sites with substantial vegetation cover and low levels of livestock grazing and urban disturbance. Finally, ongoing conservation initiatives are working to advance grassland preservation and biodiversity through sustainable cattle management, with collaborative actions across various stakeholders. Particularly, the initiative Alianza del Pastizal (BirdLife International, Cambridge, UK) and conservation projects in the buffer zone of Campos del Tuyú National Park (Fundación Vida Silvestre Argentina, Ciudad Autonóma de Buenos Aires, Argentina, and National Parks Administration, Argentina) offer critical opportunities for safeguarding remnant grassland along the northern Buenos Aires Atlantic Coast. While these efforts have predominantly focused on terrestrial habitats, they could provide essential support for *C. ornata* if extended to include wetland ecosystems within the conservation framework. Therefore, we propose fostering cooperative efforts among non-governmental organizations, the agricultural production sector, and government agencies (e.g., National Parks Administration, Buenos Aires Provincial Ministry of Environment, and local municipalities like La Costa and General Lavalle) to ensure the viability of remnant populations of *C. ornata*.

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