



Restricted use of space in an endemic lizard of the Andes: addressing the effects of intrinsic and environmental factors

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Abstract

Spatial ecology often results from the interaction between animals' spatial use behavior and the characteristics of their environment, which can have implications for social relationships between individuals. Therefore, understanding individual spatial use is crucial to species conservation as it directly impacts population stability and species persistence. *Phymaturus* is a vulnerable genus of liolaemid lizards. In this study, we address the patterns involved in the variation of spatial use of saxicolous lizards, focusing on the endemic *Phymaturus williamsi*. We used generalized linear models to evaluate factors (intrinsic and extrinsic) that may affect lizards' use of space (home range and microhabitat). Home ranges estimated for population varied from 0.0063 to 44.36 m². This species presented the smallest home range recorded to date among Liolaemidae. Home range size varied seasonally and was not related to lizard snout-vent length. Female home ranges were significantly smaller than male and juvenile home ranges. An interesting fact is that home range size was not related to microenvironmental variables: wind speed, distance to vegetation, microhabitat used, thermoregulation condition, or shelter condition. However, home range size and microhabitat use were related to substrate temperature. This species specialized in two rock types (basaltic and feldspathic rock). We conclude that *P. williamsi* is a lizard with strict and reduced microhabitats, dependent on substrate temperature, which makes it highly vulnerable to habitat changes and requires careful habitat management. To our knowledge, this is the first study of its kind on this species and has important implications for its conservation.

Significance statement

Spatial ecology affects and is affected by almost every aspect of an individual's biology and is therefore crucial for conservation. By studying the spatial ecology of individuals during a complete activity period (from spring to autumn), we were able to obtain valuable information on how the use of space changes as the associated factors, both intrinsic or extrinsic, change for an individual. Studying home range and microhabitat use, we observe that the spatial ecology of *Phymaturus williamsi* responds to intrapopulation and seasonal and substrate temperature variables, with these being very specific for utilization of microhabitat. Therefore, we propose that this species could be threatened, due to the combination of aspects analyzed in this study and its biology. We highlight that spatial ecology provides comprehensive information that must be taken into account for the conservation and management of species and their habitats.

Keywords Argentina · Home range · Microhabitat use · Spatial use · Overlap · *Phymaturus williamsi*

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Introduction

Spatial ecology often results from the interaction between animals' spatial use behavior and the characteristics of their environment (climate, food, predators, diseases, and other abiotic and biotic environmental factors), which can have implications for social relationships between individuals (Pough et al. 2001; Hoffmann et al. 2015; He et al. 2019; Shaw 2020). As a result, different distributions of these environmental factors in space and time will translate into

different spatial and temporal availability of potential mates and the ability to monopolize them (Hoffmann et al. 2015). Each of these intraspecific interactions and abiotic factors is filtered through the individual to shape its spatial ecology (Shaw 2020). Understanding individual spatial use is crucial for species conservation, as it directly impacts population stability and species persistence (Evans et al. 2019). For example, in order to predict the consequences of anthropogenic change, it is essential to understand the capacity and motivation for the spatial use of species within complex landscapes (Evans et al. 2019). Consequently, spatial ecology affects and is affected by almost every aspect of an individual's biology (Pough et al. 2001; Shaw 2020) and reflects many fundamental ecological processes (Ousterhout and Burkhart 2017).

A relevant factor in spatial ecology is home range (hereafter, HR), defined as the total area within which an individual moves and performs its daily activities (Burt 1943; Rose 1982). HR size is a good indicator of the relationship between resource requirements and resource availability in the environment (Perry and Garland 2002; Hult and Germano 2015) and can be used to model several other processes, including an animal's cognitive map of its environment (Ousterhout and Burkhart 2017). HR size can be influenced by an individual's characteristics (e.g., size (Turner et al. 1969; Christian and Waldschmidt 1984; Van Sluys 1997), sex (Simonetti and Ortiz 1980; Rocha 1999; Robles and Halloy 2009), age (Davis and Ford 1983), social status (Jones and Droge 1980), sexual activity (Rose 1982; Stamps 1983), or trophic level (Christian and Waldschmidt 1984; Verwajen and Damme 2008). Additionally, overlap can vary according to size, sex, and different classes (=hierarchies) of individuals (Stamps 1977; Kacolis et al. 2009c). For example, in lizards, HR sizes are strongly associated with body size (Turner et al. 1969; Christian and Waldschmidt 1984) and depend, among other things, on an individual's dietary requirements and the cost of foraging (Escudero et al. 2020). The energetic hypothesis suggests that the size of the home range is related to body size and sex (Perry and Garland 2002), where larger species and males have wider home ranges (as compared to smaller species and females). In addition, lizards which are insectivores or carnivores have larger home ranges than herbivores (Christian and Waldschmidt 1984) as they need larger areas in which to search for and find their prey (Rocha 1999). Despite such a variety of factors influencing individual spatial use, it has been suggested that HR depends on habitat productivity and resource distribution, as they relate to individual energy requirements (Stellatelli et al. 2016a). Generally, lizards inhabiting highly complex habitats have smaller home ranges than those from homogeneous environments with relatively scarce resources (Perry and Garland 2002; Stellatelli et al. 2016a).

On the other hand, spatial ecology can also be understood from the microhabitat perspective. Differences in local abiotic conditions contribute to individual spatial use variation (Shaw 2020). In fact, animals are distributed in space in a non-random fashion, responding to microhabitat diversity of resources through selection strategies which increase their odds of survival (Ribeiro et al. 2009; Gómez Carella et al. 2019; He et al. 2019). The need to determine the selection or avoidance of a given microhabitat has been acknowledged as the first step in understanding ecological interactions between organisms and their surroundings (Kacolis et al. 2009b). For example, one of the main factors determining microhabitat use in ectotherms is thermoregulation, as it affects their behavioral, physiological, and ecological characteristics (Huey 1982; Angilletta et al. 2009; Sinervo et al. 2010; Block et al. 2013). To maintain their body temperature within an adequate range in the face of environmental fluctuations, lizards move between microhabitats (Vicenzi et al. 2017; Gómez Alés et al. 2021). This selective exploitation of microhabitats allows them to maintain their body temperature and thus to optimize their physiological capacities, and, as a consequence, their ecological performance (Civantos 2000).

Reptiles are suitable organisms for studying the costs and benefits of spatial use. Since they are ectothermic vertebrates, their activity patterns depend mainly on environmental temperature and opportunities for thermoregulation (Sound and Veith 2011). In lizards, the physiological benefits of thermoregulation necessarily imply costs, such as energy expenditure, when moving between warm and cool spots or increased exposure to predators (Huey 1982; Block et al. 2013). Moreover, the time invested in thermoregulation cannot be used for other activities such as reproduction, feeding, social behaviors, and territory defense (Huey 1982; Vicenzi et al. 2019). Secondly, lizards show extensive intraspecific variation in patterns of space usage (Stamps 1983; Christian and Waldschmidt 1984) and, in consequence, have often been used as model systems in ecology (Huey et al. 1983; Vitt and Pianka 1994; Perry and Garland 2002). For example, sexual differences in thermoregulatory behavior have been observed, suggesting that males and females could differ in their thermal preferences (Maia-Carneiro and Rocha 2013a, 2013b) and, therefore, in the use of different microhabitats with dissimilar thermal characteristics (Block et al. 2013).

In South America, *Phymaturus* is a genus of liolaemid lizards that contains more than 60 species distributed throughout southwest (Lobo et al. 2016; Jara et al. 2019). However, the genus is conservative in many aspects of its life history and has a narrow ecological range (Corbalán and Debandi 2013; Vicenzi et al. 2017). All *Phymaturus* species are herbivorous, saxicolous, and viviparous, and inhabit cold and extreme environments of the Andes in Argentina and

Chile (Cruz et al. 2009; Lobo et al. 2016; Valdecantos et al. 2019). Moreover, the reproductive output of *Phymaturus* species is low; females have biennial reproductive cycles and small clutch sizes ($n=2$) (Boretto et al. 2007; Cabezas Cartes et al. 2010). In addition, most individuals within a species require between 7 and 9 years to reach sexual maturity (Boretto et al. 2015; Piantoni et al. 2006). These species, with limited dispersal capacities and confined to specialized habitats within restricted distribution ranges, are particularly vulnerable (Abdala et al. 2012) and susceptible to the effects of global warming (Ibargüengoytía and Casalins 2007; Sinervo et al. 2010; Vicenzi et al. 2017; Jara et al. 2019). *Phymaturus williamsi* is an endemic lizard of the Andes in Calingasta in the San Juan province of Argentina (Lobo et al. 2013) (Fig. 1a). This species has specialized morphological characteristics which allow it to live in rocky areas (Ceï 1986). Despite vulnerability of the genus, *P. williamsi* is currently categorized as a species of “Least Concern” by the IUCN Red List of Threatened Species, with low priority for conservation (Abdala 2016). However, little is known about this species and the determinants of its spatial ecology remain an enigma.

For these reasons, here, we address the patterns involved in the variation of spatial ecology of *Phymaturus williamsi* in the Argentinean Puna. In particular, we determine the effect of intrinsic factors (sex, age, body size), microhabitat features (structure, sun exposure), microenvironment variables (substrate temperature, wind speed), and seasonality on home range size. We explore patterns of overlap among sexes and age classes. Additionally, we compare the microhabitat use of individuals among pre-reproductive, reproductive, and post-reproductive periods, addressing associations with microenvironmental variables and intrinsic factors. We hypothesize that the harsh conditions of the Puna habitat and this lizard’s condition as herbivorous and saxicolous will limit spatial use by *P. williamsi*. Thus, these lizards will establish relatively smaller home ranges compared to other

Liolaemidae. We also predict that *P. williamsi* males will have larger home ranges than females.

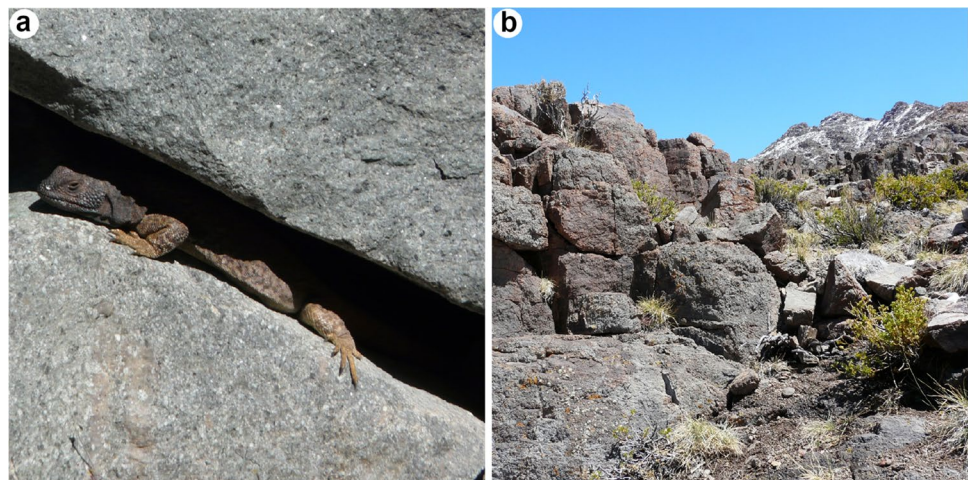
Materials and methods

Study area and fieldwork

We carried out this study in Quebrada Vallecito, located in the Andes Mountains, 40 km west of the town of Calingasta in the San Juan province of Argentina ($31^{\circ}11,021''S$; $69^{\circ}42,015''W$, ~3000 m above sea level). The area has a cold and dry climate, with a mean annual temperature around $4.6^{\circ}C$ (annual temperature range $20.38^{\circ}C$), a mean annual minimum temperature of $-5.39^{\circ}C$, and a mean annual maximum temperature of $14.99^{\circ}C$; annual rainfall is 154 mm (Gómez Alés et al. 2021). In winter, accumulations of snow limit access to the site, so specimen collection can only take place from spring to early autumn (Cabezas Cartes et al. 2010). The area’s vegetation is typical of that of the phytogeographic province of the Puna and is made up of shrublands of *Artemisia mendozana*, *Fabiana denudata*, *Adesmia piniifolia*, *Adesmia horrida*, *Esphedra multiflora*, and *Esphedra breana*, as well as cacti, such as *Maihuenopsis glomerata* or *Lobivia formosa*, and isolated grasslands of the genera *Stipa* and *Javana* in the understory (Márquez et al. 2016).

We conducted field work during March, October, and December 2011 and April 2012. This period includes spring, summer, and autumn, comprising the pre-reproductive, reproductive, and post-reproductive periods, respectively (Castro et al. 2018). The search for individuals took place for seven consecutive days between 10 am and 7 pm, the timeframe of lizard activity. Within the study area, we marked a grid (2500 m^2) on an area with typical vegetation and rocky outcrops adequate for *P. williamsi* (Fig. 1b) and subdivided the grid into 5×5 m quadrants, measured with a laser rangefinder (Bushnell, Elite 1600, precision of ± 1 m)

Fig. 1 (a) Female adult *Phymaturus williamsi* in basalt rock crevice. (b) Representative image of one of the rocky outcrops used by the lizards in Quebrada Vallecito, San Juan, Argentina



(e.g., Robles and Halloy 2009). We assigned each vertex of the quadrant a number (columns) and a letter (row) (adapted from Gil et al. 1989). We performed sampling under all the weather conditions, except for rainy weather.

We performed random transects using the technique of visual encounter surveys (Heyer et al. 1994; Robles and Halloy 2009). Sampling was carried out by two observers standing 5 m apart (Frutos et al. 2007; Frutos and Belver 2007). Observations were made in independent unidirectional transects, avoiding visits to any location twice. In this way, we ensured that we are able to capture individual variability in spatial use while preventing repeated observations of the same individual (Pérez i de Lanuza and Carretero 2018). Using the mark-recapture method (Krebs 1999), we captured individuals by hand or noose on rocky outcrops and marked them with a toe-clipping numerical code for their permanent identification (Kacoliris et al. 2009a; Paulissen and Meyer 2000). We also marked the lizards with their corresponding identification number using non-toxic white paint (Grimm-Seyfarth et al. 2018) for their remote identification. For each record, we registered the following variables: date, spatial location on the grid, substrate temperature (with laser gun Benetech GM320), wind speed (measured with a Kestrel electronic anemometer), distance to nearest vegetation (where the maximum was a 60-cm radius from the capture site; using a tape measure), SVL (with digital caliper), and sex (determined based on external secondary characteristics) (Cei 1993). In addition, we classified individuals into adult or juvenile age classes, according to the shortest SVL recorded for reproductive individuals (females or males) available in the literature, as follows: female: 82.42 mm (82.42–101.78 mm; $n=18$) and male: 83.48 mm (83.48–104.50 mm; $n=28$); while juvenile SVL varied between 52.76 and 82.70 mm ($n=21$) (Cabezas Cartes et al. 2010). Subsequently, animals were released at the same capture site.

To record the spatial distribution of the lizards with respect to the characteristics of the microhabitat, we determined the type of substrate (feldspathic rock (Fr), basaltic rock (Br), or bare soil (Bs)). The rocks were differentiated by their mineralogy, type of fragmentation, and texture, which give them different thermal properties. We searched the three substrate types (Crump and Scott 1994) thoroughly, and when an individual was found, we recorded thermoregulating condition: whether sunlight shone on more (sun) or less (shade) than half of the body; shelter condition: whether the lizard had its entire body hidden in a shelter (crevice) or completely outside the shelter (exposed); and plant species found less than 60 cm from the capture site. In addition, substrate temperature and wind speed above ground were measured every time a lizard was spotted, using a laser gun (Benetech GM320) and an electronic anemometer (Kestrel). These microenvironmental variables are important to

understand as they directly affect this lizard's thermoregulation. It was not possible to record data blindly because our study involved observation of focal animals in the field.

Statistical analyses

We estimated HR areas with the minimum convex polygon (MCP) (Rose 1982), suggested as the most appropriate method for herpetofauna (Winck et al. 2011) because it is easy to apply, it is less prone to home range overestimation, and it can be applied to small sample sizes (Olsen et al. 2011; Downs et al. 2012). The area within the polygon is an estimation of the space used by the individual (Rose 1982). We plotted and linked the capture points of the same individual, and this area represents the minimum HR. Because the MCP method is sensitive to outliers, their inclusion in the area can result in overestimates of true home ranges (Hult and Germano 2015). These outliers can result from exploratory displacements of an animal rather than a displacement needed for survival and reproduction or may even result from translocation by a predator bird, or from sampling errors. Following Hult and Germano (2015), we examined our data and found that only one of the sampled lizards had an atypical point (the home range of this lizard was 30 times larger than the average home range of the species). Therefore, we decided not to consider this exceptionally large home range and included 100% of the subsequent MCP for all HR estimations. We calculated and graphed the HR and overlap area between the HR of *P. williamsi* using Biotas software (Frutos et al. 2007; Kacoliris et al. 2009c) with a minimum of three observations per individual (Rose 1982). This minimum number of sightings was obtained following the Rose criteria (1982), which selects the number of points needed to describe 80% of the ultimate HR area. We work with the maximum number of sightings per individual, that is, one data point per individual in the analyses. Thus, we constructed data area curves using the number of sightings versus the accumulated mean home range for all individuals and determined that an average of 3 sightings explained 80% of the estimated home range size. Home range area increases with the number of sightings of an individual (Tinkle 1967; Rose 1982). This positive correlation disappears as the number of sightings increases and the home range of an individual becomes more completely described (Tinkle 1967; Rose 1982; Christian and Waldschmidt 1984). Thus, we estimate a minimum of 3 sightings as the smallest sample size at which the number of sightings was found to be non-correlated with home range sizes ($r=0.127$; $P=0.42$) (Rose 1982; Stelatelli et al. 2016a).

We conducted all analyses and created all graphics with R statistical software, version 3.4.4 (R Core Team 2018). We tested assumptions of normality and homogeneity of variance with the one-sample Kolmogorov–Smirnov test and

with the Levene test, respectively. Means are given with ± 1 standard error (SE) and a significance of $\alpha=0.05$ was used. We carried out parametric tests when data followed normality assumptions and homogeneity of variance, and non-parametric equivalent tests when such assumptions were not met (Sokal and Rohlf 1995; Crawley 2013). Additionally, we assessed multicollinearity using pairwise correlation tests, subsequently eliminating all the variables with correlation coefficients higher than 0.70 (Sokal and Rohlf 1995). We generated all the candidate models in the R package MASS (Bartoń 2013) and selected the best model (i.e., the most parsimonious) using the Akaike information criteria (AIC; see Burnham and Anderson 2004). All models were simplified using backward elimination of non-significant terms and model assumptions were tested in all cases. For each model, we evaluated data dispersion and the distribution of residual values (Crawley 2013).

To analyze the HR of these lizards, we performed two generalized linear models with a negative binomial distribution using the log link function. In the first model, HR size was the response variable, while sampling month, SVL, sex, and age were the predictor variables. In the second model, we tested five environmental predictor variables: wind speed, distance to vegetation, substrate type, thermoregulating condition, shelter condition, and substrate temperature. We eliminated the variable “shelter condition” since it was correlated ($r>0.70$) with “thermoregulating condition” (Sokal and Rohlf 1995). To compare whether HR size for sex and age groups changed throughout the year (between months), we performed Kruskal–Wallis tests and subsequently carried out multiple comparison tests.

To analyze microhabitat use, only individuals without recaptures were considered. We then performed a third linear generalized model with a negative binomial distribution and log link function (Crawley 2013). We considered the number of individuals (counts) occupying each category of the variables. We eliminated the variable “thermoregulating condition” since it was correlated ($r>0.70$) with “substrate temperature” (Sokal and Rohlf 1995). Lizard frequency was the response variable as a function of sampling month and sex, in relation to the following variables: wind speed, substrate temperature, substrate type, and shelter condition. To assess the presence of plant species in microhabitats, we performed chi-squared tests.

Results

Home range in relation to month, SVL, sex, and age

We obtained the HR size for 42 individuals throughout the entire study period (Fig. 2). Population average home range size was 8.12 m^2 (range: 0.0063–44.36, SE = 1.61 m^2). For

these individuals, the mean number of sightings was 4.04 (range: 3–7, SE = 1.06). Regarding sampling month, HR in March was significantly higher than in October ($Z = -4.42$, SE = 0.44, $P < 0.0001$), April ($Z = -2.68$, SE = 0.35, $P = 0.007$), and December ($Z = -2.40$, SE = 0.30, $P = 0.016$). Following that trend, HR in April was significantly higher than in October ($Z = -2.13$, SE = 0.48, $P = 0.033$), but did not significantly differ from that of December ($Z = 0.63$, SE = 0.34, $P = 0.53$) (Fig. 3a). HR size was not related to SVL ($P > 0.1$). The best model for explaining such a variation had a weight of 50.75%.

The HR for females (mean = 3.98, SE = 0.82 m^2 , $n = 19$) was significantly lower than that of juveniles (mean = 14.99, SE = 5.78 m^2 , $n = 8$) ($Z = 3.07$, SE = 0.34, $P = 0.002$) and males (mean = 9.71, SE = 2.79 m^2 , $n = 15$) ($Z = 2.88$, SE = 0.28, $P = 0.004$). No significant differences were found between males and juveniles ($Z = 0.692$, SE = 0.3554, $P = 0.48872$) (Fig. 3b). The HR for females varied significantly among sampling months ($H_{3,19} = 8.77$, $P = 0.03$). The test a posteriori showed that such differences occurred between March and October (Multiple K-W comparison test (M, O) = 2.89, $P = 0.02$) (Table 1). On the other hand, the mean HR size for males and juveniles did not significantly vary among sampling months ($H_{3,16} = 1.36$, $P = 0.71$; $H_{2,7} = 3.92$; $P = 0.14$, respectively).

Overlap

The mean HR overlap percentage was $4.73 \pm 2.07\%$. During the sampling months, the HR overlap percentage varied significantly ($H = 4.13$, $P = 0.04$), with higher percentages in March (mean = 9.72, SE = 4.37%, $n = 10$) and lower percentages in October (mean = 0.17, SE = 0.15%, $n = 2$) (Fig. 2). Considering sexes and age class, we obtained 23 pairs of HR overlap. The highest percentage of HR overlap corresponded to the intersection between the HR of males and juveniles, followed by that between females. The HR overlap between the two sexes (M-F) was low in relation to the other values (1.05%). The overlap between males was also low (0.80%) (Table 2). During breeding season (December to early April), males overlapped with up to three females, while during subsequent seasons, we only registered one intersexual overlap (Fig. 2).

Home range in relation to environmental variables

HR size in the different months was not dependent on wind speed, distance to vegetation, substrate type, thermoregulating condition, or shelter condition ($Z \geq 1.3$, $P > 0.19$ in all the cases). However, HR size exhibited a significantly positive relationship with substrate temperature ($Z = 3.58$,

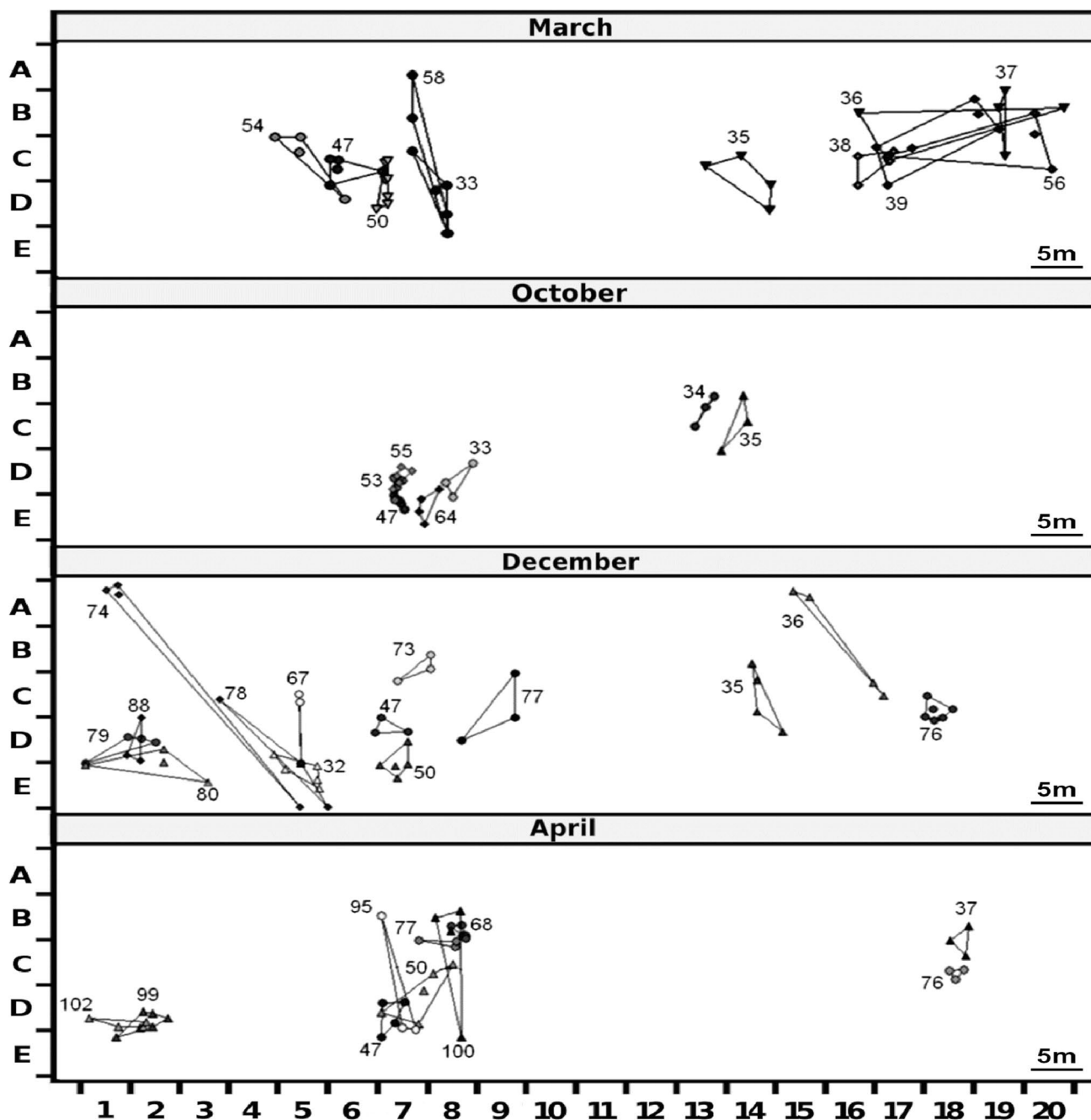


Fig. 2 Individual home ranges of adult females (circles), adult males (triangles), and juveniles (diamonds) of *Phymaturus williamsi* in Calingasta, San Juan, Argentina, between 2011 and 2012, as determined by the minimum convex polygon (MCP) method. Each lizard home

range is labeled with its identification number. The representation of the study area (2500m²) for each month is subdivided into a grid with 5×5 m quadrants. Each vertex of the quadrant is represented by a number (columns = x-axis) and a letter (rows = y-axis)

SE=0.24, $P=0.0003$) (Fig. 3c). The best model for explaining that variation had a weight of 23.65%.

Microhabitat use

The use of rocks was greater than 90% in all months (March: 92.5%, October: 100%, December: 95.9%, and

April: 95.2%). Except for during March, basalt rock was the microhabitat most used by lizards. In March and December, lizards were mainly found exposed to the sun, while in October, they were observed both in the sun and in the shade, and both exposed and in crevices in equal proportions. In April, they were more frequently found in the shade or in crevices (Table 3).

Fig. 3 Home range size of *Phymaturus williamsi* (between 2011 and 2012) in the Andes Mountain Range, Calingasta, Province of San Juan, Argentina. Representation of means and standard errors (\pm SE): home range (a) according to month; (b) according to sex and age class. (c) Relationship between home range and substrate temperature, showing the trend and 95% confidence interval. The relationship was obtained using GLM with a negative binomial distribution

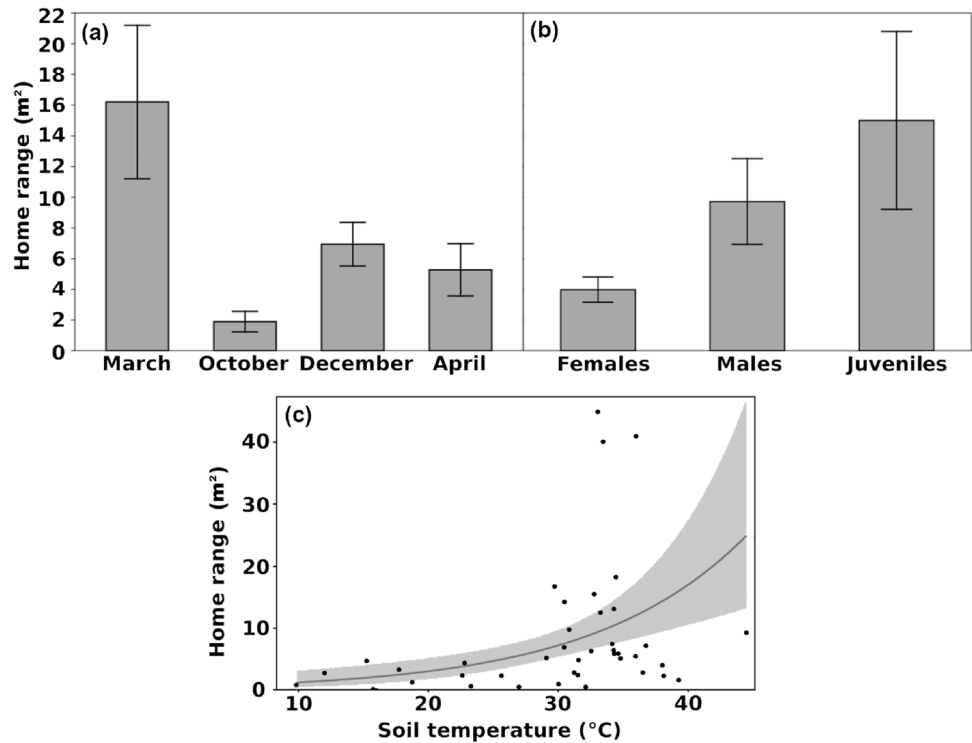


Table 1 Snout-vent length and home range size of *Phymaturus williamsi*, sampled between March 2011 and April 2012 in Calingasta, San Juan, Argentina

Months	Snout-vent length (mm)				Home ranges (m ²)			
	<i>n</i>	Mean \pm SE	Minimum	Maximum	<i>n</i>	Mean \pm SE	Minimum	Maximum
March	34	96.73 \pm 2.84	58.00	116.00	11	16.20 \pm 4.99	1.68	44.36
Females	14	103.36 \pm 1.79	90.00	114.00	4	7.65 \pm 0.73	6.32	9.73
Males	11	107.63 \pm 1.92	97.00	116.00	4	20.31 \pm 9.10	1.68	44.36
Juveniles	9	68.78 \pm 2.21	58.00	77.00	3	28.5 \pm 11.54	5.47	40.54
October	17	93.59 \pm 4.30	56.00	115.00	7	1.89 \pm 0.66	0.0063	4.73
Females	10	100.50 \pm 2.01	92.00	115.00	4	1.10 \pm 0.75	0.0063	3.29
Males	3	107.66 \pm 4.10	100.00	114.00	1	4.73	-	-
Juveniles	4	65.75 \pm 5.73	56.00	78.00	2	2.07	1.34	2.80
December	42	87.597 \pm 3.08	57.00	116.00	14	6.94 \pm 1.42	0.50	18.05
Females	19	99.58 \pm 2.23	79.00	112.00	6	4.50 \pm 1.72	0.05	12.47
Males	8	104.37 \pm 2.57	97.00	116.00	5	7.99 \pm 2.16	5.14	16.59
Juveniles	15	63.47 \pm 1.63	57.00	77.00	3	10.06 \pm 4.39	2.88	18.05
April	27	96.63 \pm 2.91	53.00	115.00	10	5.26 \pm 1.70	0.58	15.35
Females	16	100.81 \pm 2.19	81.00	110.00	5	2.71 \pm 1.26	0.58	6.95
Males	7	104.00 \pm 2.39	96.00	115.00	5	7.82 \pm 2.86	2.35	15.35
Juveniles	4	67.00 \pm 5.55	53.00	80.00	-	-	-	-

Mean \pm standard error (SE) and sample size (*n*) are presented

The best model for explaining the frequency of *P. williamsi* included 3 significant variables (substrate type, substrate temperature, and sex). The variables month, wind, and shelter conditions did not show significant interactions with the other variables. The use of basalt rock was higher than that of bare soil ($Z = -4.10$, $SE = 0.33$, $P < 0.00001$), but did not significantly differ from the use of feldspathic rock ($Z = -0.58$, $SE = 0.16$, $P = 0.56$). Following that trend, the use of feldspathic rock was higher than the use of bare

soil ($Z = 3.75$, $SE = 0.34$, $P = 0.0001$). The frequency of males had a significant relationship with substrate temperature ($r^2 = 0.30$, $P = 0.01$), while the frequency of females and juveniles did not show a trend in relation to this variable ($r^2 = 0.0002$, $P = 0.94$; $r^2 = 0.002$, $P = 0.86$, respectively) (Fig. 4). Based on this, males were statistically different from females ($Z = 2.08$, $SE = 0.20$, $P = 0.037$) and juveniles, albeit marginally non-significant ($Z = -1.83$, $SE = 0.24$, $P = 0.066$).

Table 2 Percentage overlap based on home ranges of *Phymaturus williamsi* in Calingasta (San Juan, Argentina) during 2011 and 2012

Overlap	<i>n</i>	Mean ± SE	Minimum	Maximum
F-F	4	6.89 ± 6.49	0.01	26.34
M-M	3	0.80 ± 0.38	0.20	1.20
F-M	5	1.05 ± 0.44	0.0005	2.35
F-J	2	0.65 ± 0.33	0.32	0.98
M-J	6	9.02 ± 6.44	0.36	40.87
J-J	3	6.03 ± 4.72	0.07	15.35

Regarding the acronyms: Sample size (*n*), standard error (SE), and range of percentage overlap (Minimum–Maximum). Comparisons are for females (F), males (M), and juveniles (J)

Within the rock promontory, 41.1% of *P. williamsi* detections occurred in microhabitats with the presence of *E. multiflora*, followed by *Proustia cuneifolia* with a frequency of 21.4% ($\chi^2_{11} = 539.76$, $P < 0.0001$). In all seasons, these two plant species were more frequent in microhabitats used by the lizards (Table 3) (March: $\chi^2_{11} = 144.45$, $P < 0.0001$; October: $\chi^2_{11} = 102.43$, $P < 0.0001$; December: $\chi^2_{11} = 198.98$, $P < 0.0001$; and April: $\chi^2_{11} = 140.39$, $P < 0.0001$).

Discussion

In this study, we define the spatial ecology of *P. williamsi* and its relationship to different variables for the first time. In accordance with our predictions, this species had the smallest HR as compared to other Liolaemidae: 20.7–1192.6 m² in *Phymaturus flagellifer* (Habit and Ortíz 1994; Celedón

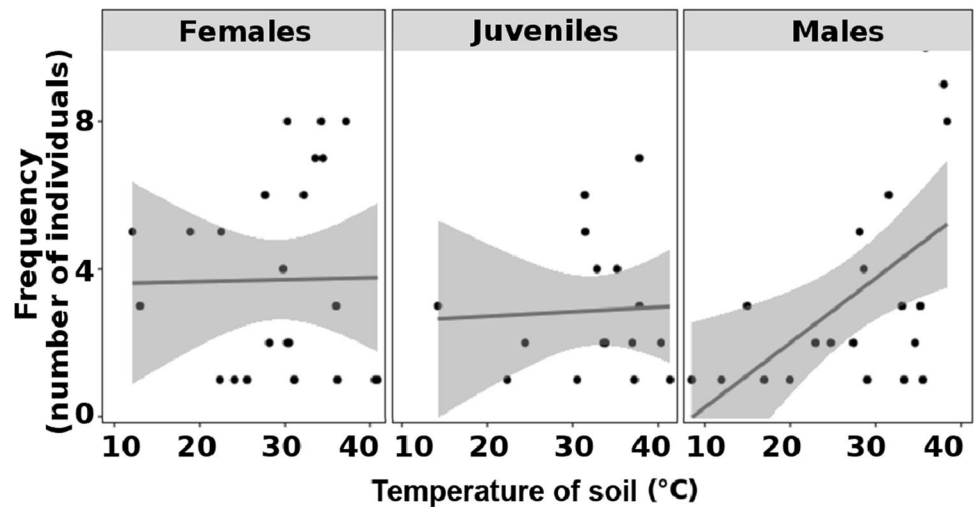
Neghme et al. 2005), 22.3–59.8 m² in *L. lutzae* (Rocha 1999), 25.55–130.57 m² and 31.5–161.5 m² in *Liolaemus quilmes* (Halloy and Robles 2002; Robles and Halloy 2009), 40.7–140.4 m² in *Liolaemus koslowskyi* (Frutos and Belver 2007), 42.1–70.91 m² in *Liolaemus melanops* (Frutos et al. 2007), 54.96–39.87 m² in *L. multimaculatus* (Kacoliris et al. 2009c), 79.44–257.90 m² in *Liolaemus espinozai* (Cabrera and Scrocchi 2012), 37.8 m² in *Liolaemus wiegmanni* (Stellatelli et al. 2016b), and 63.8–387.3 m² in *Liolaemus xanthoviridis* (Escudero et al. 2020). This can be attributed to differences in diet, as carnivores (i.e., insectivores) have larger HR compared to omnivores and herbivores (Schoener 1968; Perry and Garland 2002; Namgail et al. 2014; Shaw 2020). *P. williamsi* is a generalist herbivore species (Castro et al. 2013), which would explain the smaller HR compared to other *Liolaemus* species with insectivore-omnivore diets (Rocha 1996, 1998; Perry and Garland 2002; Frutos et al. 2007; Kacoliris et al. 2009c; Stellatelli et al. 2016b). Additionally, productivity and resource distribution in the habitat are other factors which influence HR (Stellatelli et al. 2016a). Unlike the aforementioned *Liolaemus*, most of the *Phymaturus* species are restricted to isolated rocky promontories (Ceí 1986, 1993). Consequently, the availability of rocky habitats with crevices limits the range of potential environments to be inhabited by this genus (Debandi et al. 2012; Vicenzi et al. 2017), which would explain the lower HR for *P. williamsi*. In turn, this could explain the differences with *P. flagellifer*, (herbivorous and saxicolous; Habit and Ortíz 1994), which inhabits a different Andes habitat, perhaps presenting differences in the size of the rocks, number of crevices, temperature, and food available. These

Table 3 Microhabitat use by individuals (frequency in %) of *Phymaturus williamsi* in Calingasta, San Juan, Argentina (between 2011 and 2012)

	March 2011	October 2011	December 2011	April 2012
<i>Br</i>	44.6	69.2	59.6	63.3
<i>Fr</i>	44.6	30.8	35.9	33.3
<i>Bf</i>	10.8	0	4.5	3.4
Sun	82.1	0.5	67.5	43.3
Shade	17.9	0.5	32.5	56.7
Exposed	89.3	0.5	70.8	33.3
Crevices	10.7	0.5	29.2	66.7
<i>Adesmia pinifolia</i>	5	0	0	1.5
<i>Artemisia mendozaana</i>	0	5.1	2.6	12.5
<i>Ephedra multiflora</i>	43.7	43.9	36.8	35.9
<i>Erodium cicutarium</i>	1.2	0	0	0
<i>Fabiana denudata</i>	1.2	6.2	0	0
<i>Graminea</i>	18.7	8.2	18.4	10.9
<i>Lobivia sp.</i>	1.2	0	0	0
<i>Mahuenopsis glomerata</i>	1.2	0	0	0
<i>Proustia cuneifolia</i>	12.5	17.3	36.8	29.7
<i>Schinus fasciculata</i>	6.2	2.0	2.6	1.6
<i>Sena aphila</i>	1.2	6.1	0	0
<i>Tetraglochin alatum</i>	7.5	11.2	2.6	7.8

Comparisons are for basaltic rock (*Br*), feldspathic rock (*Fr*), bare floor (*Bf*), Sun/Shade condition, shelter condition (Exposed/Crevices), and plant species (found at less than 60 cm around the capture site)

Fig. 4 Relationship between frequency and substrate temperature (between sex and age classes) of *Phymaturus williamsi* between 2011 and 2012 in the Andes Mountain Range, Calingasta, Province of San Juan, Argentina. The shaded area represents 95% confidence interval. The relationships were obtained using GLM with a negative binomial distribution



factors are considered some of the most important for determining size of home range in *Phymaturus* (Habit and Ortiz 1994; Debandi et al. 2012).

Seasonal HR variation in *P. williamsi* could be explained in relation to seasonal climate changes (Rose 1982; Christian et al. 1983; Perry and Garland 2002; Sillero et al. 2016), since environmental temperatures strongly influence the capacity of lizards to patrol, monitor, or thermoregulate (Sound and Veith 2011). In ectotherms, when thermal availability is outside the preferred body temperature range, the cost of thermoregulation can be high and lizards must retreat to their shelters (Sinervo et al. 2010; Cabezas Cartes et al. 2014) to avoid risk of death. In fact, when temperatures are extreme, individuals decrease their HR due to their physiological restrictions (Ibargüengoytía et al. 2008). Thus, with the low temperatures (mean = 12.30, SE = 5.48 °C) and precipitation registered in October, lizards did not move and remained in their crevices most of the time. On the other hand, during March, higher HR probably results from energetic requirements (Schoener 1983; Christian and Waldschmidt 1984). Climatic conditions in high-mountain areas force this species to undergo long hibernation stages (Cabezas Cartes et al. 2010); in consequence, *P. williamsi* accumulates reserves to survive the winter, increasing its foraging area during late summer and early autumn (Wone and Beauchamp 2003).

On the other hand, it is widely accepted that individual size is related to HR size (e.g., Fox et al. 1981; Christian and Waldschmidt 1984; Perry and Garland 2002; Haenel et al. 2003); however, in *P. williamsi*, SVL was not related to HR size. This is in agreement with that reported for other Liolaemidae, such as *L. koslowskyi* (Frutos et al. unpublished results), *L. melanops* (Frutos et al. 2007), *L. multimaculatus* (Kacoliris et al. 2009c), *Liolaemus espinozai* (Cabrera and Scrocchi 2012), and *L. wiegmanni* (Stellatelli et al. 2016b) and raises questions about the generality of this hypothesis.

Social factors can also lead to great variations in lizards' use of space (Stamps 1977; Rose 1982; Schoener and Schoener 1982; Stellatelli et al. 2016a), e.g., due to individual differences in habitat familiarity (He et al. 2019). In this sense, as we expected, in *P. williamsi*, the average HR of males was more than twice that of females. However, males did not significantly differ from juveniles. Intersexual differences have also been observed in several lizard species (e.g., Turner et al. 1969; Rose 1982; Schoener and Schoener 1982; Stamps 1983; Rocha 1999; Perry and Garland 2002; Frutos and Bolver 2007; Frutos et al. 2007; Germano 2007; Kacoliris et al. 2009c; Robles and Halloy 2009; Cabrera and Scrocchi 2012; Stellatelli et al. 2016a, b). In the genus *Phymaturus*, there is only information about intersexual HR size variations for *P. flagellifer* in Chile, with an average HR of 203.5–343.4 m² for males and 8.4–445.7 m² for females (Habit and Ortiz 1994). Intersexual HR differences might be explained by a combination of behavior, ecology, and physiology. For example, Miles et al. (2000) and Salido and Vicente (2019) propose that female lizards (especially those who are pregnant) run slower than males under a predation threat. Cooper et al. (1990) suggest that gravid lizards of some species achieve decreased conspicuousness by decreasing activity and remaining close to refuges. Thus, smaller HR in *P. williamsi* females might be explained by such scarce movement displacements, since remaining near crevices allows them to shelter easily. Similar results were reported for *P. flagellifer* females, which also had smaller HR (e.g., 8.4 m² HR in area 1), limited to only one rock (Habit and Ortiz 1994). On the other hand, it is likely that a combination of energy requirements and territoriality explains higher HR in males and juveniles as compared to female HR. Thus, dominant males might need HR which are large enough to meet their energy and mating demands (Simonetti and Ortiz 1980; Rocha 1999;

Frutos and Bolver 2007; Kacolis et al. 2009c; Vidal et al. 2010; Halloy et al. 2013; Stellatelli et al. 2016a, b; He et al. 2019), while juveniles might have to travel greater distances in search of food as they are displaced from areas occupied by other dominant males.

Additionally, dominance hierarchies and territorial defense are related to the overlap between individuals (Kacolis et al. 2009c). In populations with territorial behavior, low or no HR overlap is expected. Therefore, the low overlap observed in *P. williamsi* supports the idea of territorial defense in this species (Krekorian 1976; Rose 1982; Halloy and Robles 2002; Wone and Beauchamp 2003), mainly in males (overlap lower than 1%), with only two cases observed (one in March and one in April). This suggests exclusivity among males, who tend to defend exclusive areas in order to have access to females (following to Rocha 1999). This pattern has been reported in other lizard species, such as *Tropidurus itambere* (Van Sluys 1997), *L. lutzae* (Rocha 1999), *Tropidurus torquatus* (Ribeiro et al. 2009), *L. quilmes* (Robles and Halloy 2010), and *Microlophus tigris* (Ruiz et al. 2017). These results, in addition to a higher frequency of female-male overlap, a home range of larger size of males and a sex ratio biased towards females 2.03: 1 ($\chi^2_1 = 10.23$, $P = 0.001$) (AVE unpublished data), could indicate that *P. williamsi* has a polygynous mating system (following to Perry and Garland 2002). It would be interesting to address territoriality and its mating system in future studies.

Within their population, lizards can modify their HR seasonally. Male lizards, for example, can increase their HR during breeding season to find receptive females (e.g., Rose 1982; Stamps 1983; Rocha 1999, Shaw 2020). However, our results suggest that males maintained their HR, even during the warm season when greater mating activity would be expected (Castro et al. 2018). Females, instead, showed significant differences between March and October. This might have been caused by thermoregulatory behavior in response to thermal restrictions when temperatures were too low, as occurred in October, in agreement with that reported in Perry and Garland (2002). Our results showed the opposite trend of that found for *L. quilmes*, in which female HR did not vary throughout the two study years, while male HR was significantly higher during the reproductive period compared to the corresponding post-reproductive seasons (Halloy and Robles 2002). On the other hand, the higher HR overlap percentage in March agrees with that suggested by Cabezas Cartes et al. (2010) and Castro et al. (2018), who propose that mating in *P. williamsi* occurs in late summer and early autumn, for which a higher relative overlap would be expected in that period. In fact, during the summer, males overlapped with up to three females, while after mating season, we registered only one intersexual overlap.

On the other hand, HR overlap could also be related to parental care. However, in *P. williamsi*, no parental care has

been observed (Victorica and Acosta 2020). We recorded only two cases of overlap between females and juveniles (area less than 1 m²), dismissing the hypotheses of behavioral parental care, unlike other Liolaemidae (e.g., *Phymaturus antofagastensis* and *P. punae*, Cabezas Cartes et al. 2018; *Phymaturus calcogaster* and *Liolaemus multicolor*, Halloy et al. 2013; *L. huacahuasicus*, Halloy and Halloy 1997). However, some authors found a particular form of parental care through the presence of intra-abdominal yolk in newborn individuals of *P. punae* (Boretto et al. 2007), *P. antofagastensis*, *Phymaturus cf. palluma* (Cabezas Cartes et al. 2010), and *Phymaturus zapalensis* (Boretto and Ibagüengoytía 2009). This strategy might indicate a certain independence of juveniles at birth and could consequently explain the scarce overlap between females and juveniles detected in *P. williamsi*.

An interesting fact is that in *P. williamsi*, HR size was not related to the microenvironmental variables of wind speed, distance to vegetation, microhabitat used, thermoregulating condition, or shelter condition. However, HR size showed a positive relationship with substrate temperature. It is known that in ectotherms, the availability of adequate microhabitats for thermoregulation is one of the most important factors influencing activity patterns, habitat selection, and spatial distributions (Wilms et al. 2011). In this context, we believe that *P. williamsi* regulates its temperature seasonally, travelling between sites with different substrate temperatures according to its requirements, as do other *Phymaturus* species (Ibagüengoytía et al. 2008; Corbalán et al. 2013; Gómez Alés et al. 2017).

In *Phymaturus*, great uniformity in the use of space is observed, with an exclusive use of rocky habitats (e.g., Cei 1986, 1993; Espinoza et al. 2004; Ibagüengoytía 2005; Boretto and Ibagüengoytía 2006; Ibagüengoytía et al. 2008; Debandi et al. 2012; Vicenzi et al. 2017). However, recent studies showed that even in these habitats there are differences among species of the genus (Debandi et al. 2012). For example, certain species of the palluma group were positively related to sunlight availability, bare soil, isotherm, and slope (Corbalán and Debandi 2013). In the case of *P. williamsi*, it is specialized in two well-differentiated rock types (*Br* and *Fr*), using crevices as shelters to avoid lethal levels of sun radiation and predators (Fava and Acosta 2018; Fava et al. 2018). Bare soil as microhabitat was not utilized by lizards and might always be used as a passage site. These results are in agreement with those found by other authors who suggest that *Phymaturus* species prefer volcanic rocks (Debandi et al. 2012; Corbalán et al. 2013; Corbalán and Debandi 2014; Gómez Alés et al. 2017). The morphological characteristics of the genus, such as its flattened body and spiny tail, provide them with evolutionary advantages for sheltering in rocky crevices (Debandi et al. 2012). Thus, the availability of rocks with crevices might

limit suitable habitat types for the species. We suggest that this hypothesis be taken into account in future studies on microhabitat use of *P. williamsi*.

Among the environmental microhabitat variables, we find that the number of individuals of *P. williamsi* was significantly related to substrate temperature. This is not surprising, as temperature is an important microhabitat variable for many lizards (e.g., Ibarzüengoytía and Cussac 2002; Vidal et al. 2010; Gómez Alés et al. 2017; Stellatelli et al. 2017). It is known that *P. williamsi*, like other *Phymaturus* species (Vidal et al. 2010; Corbalán and Debandi 2013; Gómez Alés et al. 2017; Vicenzi et al. 2017, 2019), absorbs thermal energy from the substrate through thigmothermy and alternates this strategy with heliothermy according to the environmental thermic conditions (A. Laspiur unpublished data). However, we found intrapopulation variation in such relation, with only males showing a positive relationship with substrate temperature, differing from females not showing this trend. This might be due to a compromise in males between time assigned to social interactions and time assigned to thermoregulation, a situation that does not occur in females (Dunham et al. 1989). Males are exposed to higher temperatures, since they participate in territorial behaviors such as patrolling and controlling intruders (Vicenzi et al. 2019). In contrast, females avoid high temperatures and thermoregulate with higher precision to keep a stable temperature for the adequate development of embryos, for example (Gómez Alés et al. 2017; Stellatelli et al. 2018). This also occurs in *P. patagonicus* females, which have higher heat control than males, implying a physiological control on heat gain and loss (Ibarzüengoytía 2005).

On the other hand, smaller lizards are more sensitive to heat exchange, since they have a low surface to volume ratio (Stellatelli et al. 2018). As such, *P. williamsi* juveniles might be more sensitive than males to overheating when substrate temperature is high, avoiding the risk of death through behavioral thermoregulation. This could explain the absence of a positive relationship between juveniles and substrate temperature. Likewise, juveniles of *P. cf. palluma* were more sensitive than adults to high summer temperatures (Eisenberg and Werning 2012). Another possibility is to consider thermal environment as a resource; thus, juveniles would be exposed to less thermally suitable microhabitats, due to their exclusion by dominant males from more thermally suitable microhabitats (Maia-Carneiro and Rocha 2013a; Delaney and Warner 2016). In fact, HR size of *P. williamsi* juveniles was similar to that of adult males, suggesting high displacement rates of juveniles which would expose them to thermal variations. Intraspecific differences in microhabitat use have been reported for other Liolaemidae, such as *Phymaturus palluma*, *Liolaemus nigroviridis*, and *L. lutzae* (Carothers et al. 1998; Vidal et al. 2010; Maia-Carneiro and Rocha 2013a, 2013b). However, for species of similar

environments, such as *Liolaemus parvus* and *Phymaturus extrilidus*, intraspecific differences in microhabitat use were not registered (Gómez Alés et al. 2017).

The *P. williamsi* lizards used microhabitats composed of combinations of 12 plant species of the 19 species recorded in the study area (Castro et al. 2013). However, the microhabitats used were characterized by the presence of only two dominant plant species: *E. multiflora* and *P. cuneifolia*. Like other species of lizards, *P. williamsi* seems to show a greater use of microhabitats with low vegetation (e.g., Vega 2001; Kacoliris et al. 2008, 2009b, 2010; Valdecantos et al. 2013; Peñalver Alcázar et al. 2016). Dias and Rocha (2004) suggest that the height of the vegetation in microhabitats has ecological implications related to body size and activity period which can facilitate the coexistence of sympatric species. Plants can provide protection against extreme surface temperatures (Kacoliris et al. 2008, 2010; Pietrek et al. 2009). In our study, it is possible that plants provide protection by reducing lizards' exposure to solar radiation. However, there is evidence that species specialized in certain habitats, such as *Phymaturus*, do not identify vegetation cover as a refuge due to their adaptation to the use of rocky crevices in the habitat (Pietrek et al. 2009). On the other hand, lizards can select plants according to their diet (Rocha et al. 2000; Beck and Jennings 2003; Corbalán and Debandi 2014), so *P. williamsi* could use microhabitats with the presence of these two plant species according to its food requirements. In fact, plants of the genus *Ephedra* are an important component of the diet of *P. williamsi* (Castro et al. 2013), as is the case of other species of *Phymaturus* (Debandi et al. 2012; Corbalán and Debandi 2014) such as *P. palluma* (Videla 1982) and *P. antofagastensis* (Acosta et al. 2008). It would be interesting to test these relationships in future studies.

We conclude that several factors interact to determine spatial ecology in this species, including individual characteristics (sex and age) and extrinsic factors such as seasonality, temperature (substrate), and habitat structure. Our data indicate that *P. williamsi* has the lowest home range among Liolaemidae recorded to date and uses highly restricted and specific microhabitats (basaltic and feldspathic rocks, with shrubby vegetation, avoiding open spaces with bare substrate or disaggregated soil). This rare lizard, with a small population size (AVE et al., unpublished data), occurs in delicate balance with its habitat, and as such any alteration of its environment exposes it to high vulnerability (Abdala et al. 2012). Therefore, we consider that this species could be highly vulnerable due to the combination of aspects analyzed in this study with its life history. In this sense, we consider that spatial ecology provides comprehensive information that must be taken into account for the conservation and management of species and their habitats, in light of the

increasing fragmentation of habitats and increasing risks of extinction with progressively warming climates.

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Author contribution All authors contributed to the study conception and design. AEEV and JCA collected data. AEEV and GAF performed the analyses. AEEV, GAF, and JCA wrote the manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available as electronic supplementary material.

Code availability Not applicable.

Declarations

Ethical approval This research was authorized by the Secretaría de Medio Ambiente, Dirección de Conservación y Áreas Protegidas, Provincia de San Juan (permits issued: R056) and complies with the ASIH/HL/SSAR Guidelines for Use of Live Amphibians and Reptiles, as well as the regulations detailed in Argentinean National Law #14346. All protocols in the field, including the capture and handling of animals, were approved by the Department of Biology Committee of the National University of San Juan, Argentina.

Conflict of interest The authors declare no competing interests.

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