ECOSYSTEMS

Basking and retreat site selection of *Phymaturus palluma*, a rock-dwelling lizard in the Highlands of Aconcagua

NADIA VICENZI, RUBÉN MASSARELLI, NORA IBARGÜENGOYTÍA & VALERIA CORBALÁN

Abstract: Basking and retreat sites constitute a key resource in the habitat of any ectotherm. Identifying the elements that are used and modelling the microhabitat selection of species is crucial for assessing the impact of anthropogenic disturbances at the population level and, therefore, focusing on conservation efforts. We investigated how structural attributes of the microhabitat and biotic factors influence the probability of basking and retreat sites use by *Phymaturus palluma*, a rock-dwelling and viviparous lizard endemic to the Central Andes of Argentina. We measured the characteristics of a series of rocks (basking sites) and shelters (retreat sites) in the study area and compared lizard resource use versus availability using resource selection analyses (RSFs). According to our best RSF model, *P. palluma* select high and large rocks as basking sites and prefer those near their retreat sites and far from the basking sites of their neighbours. In contrast, retreat site selection is related to the length, depth, slope, and width of the shelter. Microhabitat site selection of *P. palluma* is associated with behavioural improvements such as enhancing basking capacity, reducing both intraspecific competition with neighbours and predation risk.

Key Words: crevices, microhabitat selection, high-altitude lizard, Liolaemidae, rocks.

INTRODUCTION

Habitat structure influences several aspects of the life history of an organism, as well as the species' range and abundance (Reinert 1993, Smith & Ballinger 2001, Goldsbrough et al. 2006). At a large scale, distribution is strongly related to climatic variables (Bozinovic et al. 2011), while at the local scale, microhabitat selection can help to buffer sub-optimal environmental conditions, which is essential to predict species distribution (Huey et al. 2012). Thus, resources that influence decisions about habitat use differ across spatial scales (McMahon et al. 2017). While macrohabitat is defined as the spatial area in which individuals perform all their biological functions, the term microhabitat refers to those environmental

variables (e.g., vegetation, structural aspects of rocks and shelters, biotic interactions) that influence the allocation of time and energy of the individual (i.e. that affect individual behaviour) within its macrohabitat (Morris 1987, Jorgensen 2004). Hence, microhabitat selection involves the interplay between abiotic factors, such as rock and shelter characteristics, and biotic factors such as feeding resources, intraspecific competition, and the presence of reproductive females and predators (Huey 1991, Downes & Shine 1998, Downes 2001). Given the complexity of factors that influence the establishment of species, determining the preference or avoidance of one particular habitat (or microhabitat) in relation to its availability is

needed to understand the interaction between organisms and their environment (Neu et al. 1974). Moreover, this understanding is of great importance for carrying out actions like habitat restoration, enhancing habitat suitability and other conservation actions for animal species (Huey 1991, Manly et al. 2002, Kacoliris et al. 2009, Croak et al. 2012).

Structural and thermal characteristics of the microhabitats are crucial for ectotherms, since they allow effective behavioural thermoregulation, and could consequently increase or reduce the likelihood of attaining optimal body temperature for performance (Huey et al. 2012, Stellatelli et al. 2014). Rocky outcrops represent an important resource for lizards inhabiting high mountain environments (Hertz & Huey 1981, Carrascal et al. 1992, Martin & Salvador 1996). Particularly, for rock-dwelling lizards, rocks offer high availability and diversity of microhabitats, allowing them to satisfy several ecological, physiological and behavioural requirements. For example, the thermal characteristics of rocks vary according to their size, large rocks have lower daily temperature variation compared to small rocks with the same albedo and thermal conductance (Huey et al. 1989, Huey 1991). Hence, crevices formed by large rocks are warmer compared to crevices present in small rocks during the inactivity period (Sabo 2003). Thus, rocky outcrops with variation in rocks size provide spatial thermal heterogeneity, necessary for lizards' thermoregulation. The characteristics of rocks such as size, height, and retreat access, are often found to be the most important habitat attributes affecting the occupancy and abundance of rock-dwelling lizards (Monasterio et al. 2010, Arribas 2013, Ljubisavljević et al. 2017).

Retreat site availability also represents an important resource in microhabitat selection (Block et al. 2012, Croak et al. 2012). Selecting microhabitats with easy access to retreat sites could provide an opportunity for escaping quickly and refuge from predators (Downes & Shine 1998, Block et al. 2012, Fava & Acosta 2018), and also, retreat sites with high thermal quality could diminish the cost of hiding (Cooper & Wilson 2008). Retreat sites play an important role as thermal shelters, reducing the risk of overheating when environmental temperatures are too high (Sinervo et al. 2010, Martín & Salvador 1996, Vicenzi et al. 2017, 2019, Durán et al. 2018), as well as during brumation (winter dormancy), preventing lizards from freezing when air temperatures drop below 0 °C (Bishop & Echternacht 2004).

Vegetation structure has a large influence on the composition and abundance of reptile assemblages (Pelegrin & Bucher 2012). It plays an important role in behavioural thermoregulation providing thermal heterogeneity and buffering hot and cold temperatures, which ultimately can restrict lizards' activity time (Sunday et al. 2014, Grimm-Seyfarth et al. 2017). Moreover, several studies in Liolaemidae lizards have shown how the presence of native shrubs favours physiological performance and thermoregulatory behaviour (Stellatelli et al. 2013, 2014). Vegetation also represents a palliative against the predation of lizards (Stamps 1983, Block et al. 2012), acting as an antipredatory shelter (Block et al. 2012), influencing escape tactics (Cooper 1998, Kacoliris et al. 2010), favouring crypsis (Schulte et al. 2004, Block et al. 2012), and offering visual cover that prevents detection by predators while lizards move through their habitat (Kacoliris et al. 2009, Pietrek et al. 2009). Furthermore, in herbivorous species, the structure and composition of vegetation represent the availability of feeding resources (Vitt & Caldwell 2008). Thus, vegetation cover could represent an essential resource for the thermal, feeding and antipredatory needs of lizards. In this study, we

assessed different microhabitat features and biotic factors that could influence the selection of basking and retreat sites by *P. palluma*, and the results may important for the conservation management of the species. We predicted that *P. palluma* lizards would select: 1) basking sites consisting of high rocks near their retreat sites and vegetative forage to diminish their predation risk, but distant from basking sites used by their neighbours to avoid territorial contests; and, 2) retreat sites formed by deep and long crevices in large rocks to avoid predation.

MATERIALS AND METHODS

Study species and area

Phymaturus palluma is a viviparous, rock-dwelling and herbivorous lizard endemic to the rocky outcrops of the Central Andes of Argentina, which belongs to the Liolaemidae family (Cei 1986). They live in small groups, composed of one territorial male, one or more females, and juveniles (Videla 1982) which share different microhabitat resources, such as basking sites, shelters and forage sites (Figure 1, Videla 1982, Vicenzi et al. 2019). As other cold-climate lizards, *P. palluma* activity period is restricted to austral spring and summer, during which lizards

thermoregulate by shuttling between rocks directly exposed to the sun and rock crevices (Vicenzi et al. 2019). Rock crevices are used as retreat sites for brumation during the autumn-winter period, and as thermal and antipredatory retreat sites during the activity period. Like other species of the genus *Phymaturus*, *P. palluma* is considered particularly vulnerable to climate change because of the prediction of substantial reductions in the available habitat over the species' current distributional range in the next 50 years (Sinervo et al. 2010, Vicenzi et al. 2017).

The study was conducted in the Vacas Valley in Aconcagua Provincial Park (32.8453°S, 69.7619°W, WGS84, 2500 m asl), Mendoza, Argentina. The site belongs to the Altoandina phytogeographic province and is characterized by a cold semiarid climate, according to Köppen classification.

Fieldwork

We selected a study area (200 × 60 m) where microhabitat characteristics were determined. This relatively flat area was characterized by bare soil interspersed with rocks and typical vegetation, such as the shrub genera *Tetraglochin* and *Ephedra*, and the grasses *Poa* and *Stipa* (Figure 2, Méndez et al. 2006). Three

Figure 1. a) Female (lizard at the left of the figure) and male of *Phymaturus palluma* sharing a basking site. **b)** Male, females and juveniles sharing a retreat site.

200-m transects, parallel and 20-m apart, crossed the study area. Microhabitat variables were measured in 100-m^2 quadrats located 10-m apart along each transect. We measured a total of 25 quadrats in the study area, and, within each one, we measured the features of all potential basking sites as well as retreat sites present.

The selected population for these analyses were previously studied during the years 2013-2015, for behaviour and home range research (Vicenzi et al. 2019, N. Vicenzi, unpublished data). This data allowed us to recognize lizards groups and their adjacent neighbours. In addition, based on direct observation of *P. palluma* lizards, during 2013-2015 sampling period, N.V. registered *Tetraglochin alatum, Ephedra sp.,* greater burnet (*Acaena magellanica*), field bindweed (*Convolvulus arvensis*), alfalfa (*Medicago sativa*), and dandelion (*Taraxacum officinale*) as food items of the population (N. Vicenzi, unpublished data). All this data was used to define the biotic variables of the microhabitat selection.

For basking sites, we measured rock height, orientation, slope, and size. We defined three size categories of rocks: (i) small, < 0.1 m^3; (ii) medium, 0.1 to 0.6 m^3; and (iii) large, > 0.6 m^3,

Figure 2. Photograph of rocky outcrops used by the *Phymaturus palluma* in Punta de Vacas Valley, Mendoza, Argentina.

taking into account the variability and frequency of different sizes of rocks present in the study site. The rock size was calculated as the product among rock height, width, and length. We also registered distance to the nearest retreat site, distance to water, distance to the nearest neighbour-lizard basking site, and distance from the closest plant that lizards would use for foraging.

For retreat sites, including natural crevices in rocks and spaces between the bottom of rocks and the substrate, we measured the depth, inclination (using a manual clinometer), length, orientation and width of the shelter, and the size of the rock containing the retreat sites.

A total of six field trips with five-days of duration were conducted in January and March 2015 (sampling period). Four visual surveys per day (at 9.00h, 11.00h, 14.00h and 16.00h) were conducted during the activity period of the lizards, and the use of sites for basking and retreats were recorded. Once a resource unite (rock or shelter) was used by one lizard, the rock was permanently marked to avoid repeated measures (pseudoreplication) at a later time or in another field trip. Thus only the first record of use of a basking or retreat site by a lizard was included in the analysis. Each survey was conducted along the located quadrats along the transects which were walked in opposite directions and without following a consecutive order (for example 3, 1, 2), to avoid disturbing lizards in adjacent transects.

In addition, during December 2015 and January 2016 (a total of 35 days), almost one year after the first survey, the operative temperature (T$_e$, *sensu* Bakken 1992) in a sample of basking and retreat sites used by the lizards were measured to evaluate the thermal resources. We placed six physical models (Hertz et al. 1993, Bakken & Angilleta 2014) calibrated for *P. palluma* (for details, see Vicenzi et al. 2017 and

Corbalán et al. 2013) above basking sites formed by each size-class of rocks as well as inside retreat sites located in small, medium and large rocks. We programmed the data loggers to record temperatures every 15 min., and we measured each rock and crevice for seven days. For the analyses of basking sites, we compared 7-day mean T_e hourly recorded for each rock (N = 15) during the activity period of *P. palluma* (9.00 to 17.00 h). For the analyses of retreat sites, we also compared the 7-day mean T_e per hour recorded in crevices (N = 15) inside small rocks, medium rocks, and large rocks, during activity period (9.00 to 17.00 h) and during inactivity time (17.00 to 8.00 h).

Statistical analysis

We used resource selection functions (RSFs), which are mathematical functions that integrate the joint contribution of multiple predictor variables that influence animal use in a given time and area (Manly et al. 2002, Boyce 2006). RSFs provided estimates that were proportional to the probability of use (Manly et al. 2002). Our measurements were made at the population level, which means that individual information, such as sex, body size or age, was not taken into account in the analyses. Thus, the experimental design used to determine the existence of microhabitat selection corresponded to Type I, according to Manly et al. (2002). Each rock and shelter within the 25 quadrats studied represented a resource unit. Each rock represented a resource unit for the basking sites analyses, whereas each shelter represented a resource unit for the retreat sites analyses. Resource units were categorized as "used" when we registered the presence of a lizard in the unit during the sampling period, and "available" when the resource unit could potentially be encountered by a lizard, but we did not register

any lizard using it within the sampling period analyzed (Manly et al. 2002, Lele et al. 2013).

We generated two different RSFs, one for basking sites and one for retreats (Manly et al. 2002, Goldstein et al. 2010, Lele et al. 2013). The first one was employed to estimate the relative probability of lizards selecting a basking site given its size, slope and height, and its distance to a retreat site, to a neighbour basking site, and to vegetation. The second RSF was generated to estimate the relative probability of lizards selecting a retreat site given its depth, inclination, length, orientation, width and the size of the rock that formed the site. Each RSF was obtained using general linear models (GLMs), with a binomial distribution (where "used" was encoded as 1, and "available" as 0). With the first observation of a basking or retreat site used by a lizard, the resource unit was assigned a value of 1, and subsequent records of use of this basking or retreat site were not registered. We worked at population level, thus each resource unit was analysed once. We started our analyses with a global model that included all variables. To avoid overfitting, because our sample size was small, model comparisons were based on the corrected Akaike Information Criterion (AICc) and were conducted with the function dredge of MuMIn package in R (Legendre & Legendre 1998, Burnham & Anderson 2002). According to this function, models are ranked according to their AICc values, and the model with the lowest AICc is considered the best, whereas those with an AICc value difference less than 2 compared to the AICc value of the best model are considered models with substantial support (Burnham & Anderson 2002). To check multicollinearity in the data, we calculated both with the Pearson correlation test and the variance inflation factors (VIFs). These values were below the traditional thresholds (r < 0.7 and VIF < 5, respectively), suggesting no significant collinearity between

the variables (Sokal & Rohlf 1995, Chatterjee et al. 2000). Finally, we estimated the selection ratio (values > 1 indicate preference and values < 1 avoidance), the relative probability of use, standard errors and confidence intervals (CIs) for each variable in the final model.

We used the k-fold cross-validation technique to assess the predictive power of each RSF. We split our data into two groups using the sample function in R (Wiens et al. 2008). Seventy-five percent of our data was used to generate the training data ("model-training"), and 25% was used to generate the testing data ("model-validation"). The GLM was set using the training data, and estimated coefficients were used to predict values for the testing data set. Predicted values were separated into 10 equal-sized categories or bins, scaled between the minimum and maximum values. Then, using a Spearman rank correlation, comparison by bin of the frequencies of predicted values for the test data to the frequencies of observed values was done to evaluate model performance (Boyce et al. 2002, Sawyer et al. 2009, Eads et al. 2011).

To explore the existence of differences in thermal attributes of basking and retreat sites, we compared the hourly mean T_e of each rock size using an Repetead Measures ANOVA for parametric data and a Friedman test for non-parametric data. All statistical analyses were conducted in R (R Core Team 2018). The assumptions of normality and homogeneity of variance were checked, using Shapiro-Wilk's and Bartlett's tests, respectively. Means are presented with a ± standard error (SE). Alpha was set to 0.05 for statistical significance.

RESULTS

Basking sites

We recorded and characterized 301 rocks, 121 of which were considered to be used by individuals

of *P. palluma*, whereas 180 remained available. Only three RSF models had a Δ AICc ≤ 2 (Table I). The three models included rock height, distance to crevice and distance to the nearest neighbour rock as explanatory variables. Basking sites used by lizards were 56.9 ± 3.3 cm high, 68.5 ± 10.7 cm from the retreat site, and 789.3 ± 32 cm from the neighbour rock (Figure 3). Basking sites that remained available were 42.5 ± 1.9 cm high, 110.6 ± 8.5 cm from the retreat site, and 705.3 ± 22.4 cm from the neighbour rock (Figure 3). Based on the top model (Table II; Figure 4), the odds of relative probability of selection increased 1.61% for every 1-cm increase in rock height, and 0.1% for every 1-cm increase in distance from neighbour rock; and diminished 0.44% for every 1-cm increase in distance from retreat site. Lizards also showed a higher probability of selecting large rocks (148.11%), despite their low availability (Figure 5). Our model validation confirmed good fit between observed and predicted counts for the final model, with a Spearman rank correlation value of 0.78.

Retreat sites

Of the 158 recorded and characterized retreat sites, 64 were considered to be used by individuals of *P. palluma*, whereas 94 remained available. Four RSF models had a Δ AICc ≤ 2 (Table I). All models included the length and width of the retreat site as explanatory variables. Retreat sites used by lizards were 4.14 ± 0.2 cm wide, 23.2 ± 0.2 cm long, 0.91 ± 0.1 rad of inclination, and 37.6 ± 1.7 cm deep (Figure 3). Retreat sites that remained available during the sampling period were 5.6 ± 0.3 cm wide, 19.2 ± 1.4 cm long, 0.95 ± 0.07 rad of inclination, and 25.2 ± 1.2 cm deep (Figure 3). Based on the top models (Table II; Figure 4), the odds of relative probability of selection increased 4.3% for every 1-cm increase in retreat site length and 2.1% for every 1-cm increase in depth. The probability of selection

Table I. The three best models of basking sites selection and the four best models of retreat sites for *Phymaturus palluma*. Model parameters (K), AICc for each model, differences between the model with the lowest AICc and each model (ΔAICc) and Akaike Weight.

Microhabitat	Model	K	AICc	ΔAICc	Weight
Basking site	Size + Height+ Distance to retreat site + Distance to neighbour	5	377.20	0.00	0.4
	Height + Distance to retreat site + Distance to neighbour	4	378.54	1.3	0.21
	Size + Height + Distance to retreat site + Distance to neighbour + Distance to vegetation	6	379.29	2.09	0.14
Retreat Site	Width + Length	2	200.7	0.00	0.27
	Width + Length + Inclination	3	200.8	0.08	0.26
	Width + Length + Inclination + Depth	4	201.3	0.69	0.20
	Width + Length + Depth	3	202	1.24	0.15

diminished 26.58% for every 1-cm increase in retreat site width and 35.1% for every radian increase in inclination. Only the model that considered length, width, depth, and inclination of the retreat site as explanatory variables confirmed a medium fit between observed and predicted counts, with a Spearman rank correlation value of 0.52.

Thermal characterization of basking and retreat sites used by lizards

During the activity time of lizards (from 09.00 to 17.00 h), the T_e of the rocks used as basking sites varied according to the size of the rock and hour. Small rocks were the hottest (mean = 38.91°C), medium rocks had an intermediate temperature (mean = 33.8°C), and large rocks were the coldest (mean = 31.87°C; RMANOVA: $F_{rock\ size\ 2, 34}$ = 379.66, P < 0.001; Bonferroni Test $t_{Small - Medium}$ = 5.11, $t_{Small - Large}$ = 7.04, $t_{Large- Medium}$ = 1.93, P < 0.001). Differences among hours were also statistical significant ($F_{hour\ 8, 34}$ = 35.93, P < 0.001), as the interaction of rock size and hour of the day (Table III; $F_{rock\ size-\ hour\ 16, 34}$ = 12.89, P < 0.001).

During the activity time of lizards, the T_e of the crevices used as retreat sites varied according to the size of the rock and the hour of the day small rocks had the hottest crevices (mean = 30.01°C), medium rocks had crevices with an intermediate temperature (mean = 23.86°C), and large rocks had the coldest (mean = 21.19°C; RMANOVA: $F_{rock\ size\ 2, 34}$ = 319.87, P < 0.001; Bonferroni Test $t_{Small - Medium}$ = 6.15, $t_{Small - Large}$ = 8.82, $t_{Large- Medium}$ = 2.67, P < 0.001). Differences among hours were also statistical significant ($F_{hour\ 8, 34}$ = 81.71, P < 0.001), as the interaction of rock size and hour of the day (Table III; $F_{rock\ size-\ hour\ 16, 34}$ = 41.39, P< 0.001). During the inactivity period (from 18.00 to 8.00 h), the T_e of the crevices was also related to the size of the rock and the hour of the day. Small rocks had the coldest crevices (median = 18.11°C), medium rocks had crevices with an intermediate temperature (median = 20.09°C), and large rocks had the hottest (median = 20.28°C; Friedman Repeated Measures Analysis of Variance on Ranks, $\chi2_{2, 495}$ = 603.36, P < 0.001; Bonferroni Test $t_{Small - Medium}$ = 0.69, $t_{Small - Large}$ = 0.87, $t_{Large- Medium}$ = 1.56, P < 0.001).). Difference among hours in each crevice were also statistical significant (Friedman Test Repeated Measures Analysis of Variance on Ranks, $\chi2_{44, 495}$ = 1343.7, P < 0.001).
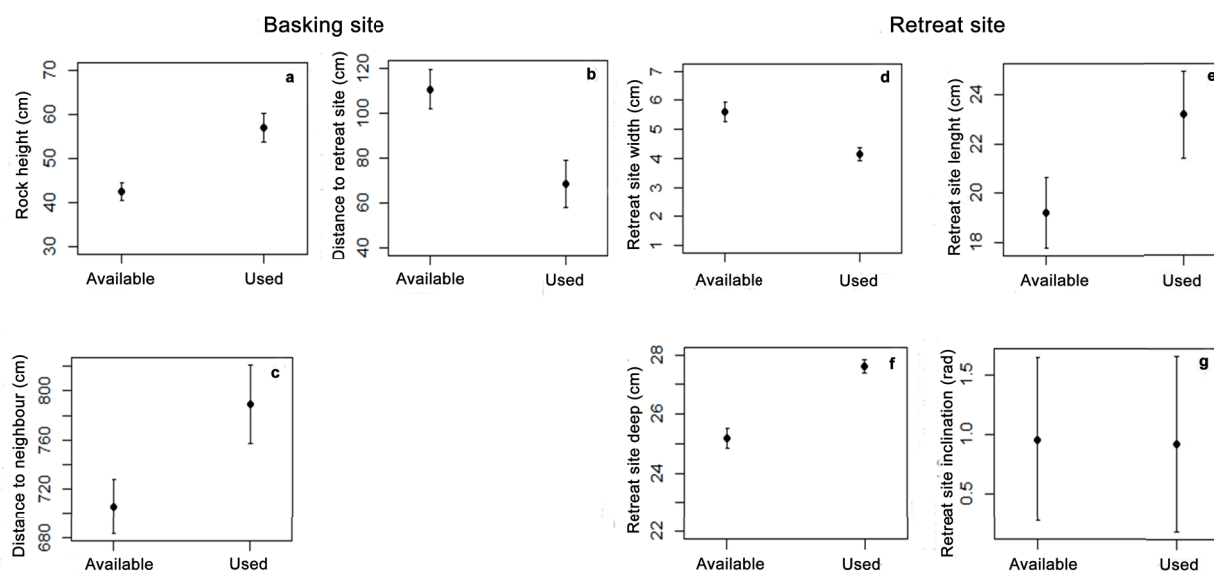
Basking site

Retreat site

Figure 3. Mean and standard error plot of available versus used resource units for basking sites and retreat sites. For basking sites a) Rock height (available = 42.5 ± 1.9 cm; used = 56.9 ± 3.3 cm); b) Distance to retreat site (available = 110.6 ± 8.5 cm, used = 68.5 ± 10.7 cm) and c) Distance to neighbour perch (available = 705.3 ± 22.4 cm, used = 789.3 ± 32 cm). For retreat sites d) Retreat site width (available = 5.6 ± 0.3 cm; used = 4.14 ± 0.2 cm); e) Retreat site length (available = 19.2 ± 1.4 cm; used = 23.2 ± 0.2 cm); f) Retreat site deep (available = 25.2 ± 1.2 cm; used = 37.6 ± 1.7 cm) and, g) Retreat site inclination (available = 0.95 ± 0.07 rad; used = 0.91 ± 0.1 rad).

Table II. The best model of basking site and retreat site selection for *Phymaturus palluma*. Coefficients, standard error (SE), selection ratio (>1 selected resource, <1 avoided resource), probability of selection (%), probability (P) and confidence intervals (CI) with 0.95 of significance.

| Microhabitat	Variable	Coefficient	SE	Selection ratio	Probability of selection	P (>|z|)	CI lower	CI upper
Basking site	Rock Intercept	0.02	0.45	1.02	1.62	**<0.05**	0.004	0.03
	Small rock	-1.52	0.01	0.21	-78.07	0.12	-2.43	-0.65
	Medium rock	-0.24	0.32	0.78	-21.53	0.45	-0.87	0.38
	Large rock	0.91	0.63	2.48	148.12	0.15	-0.31	2.19
	Retreat site	-0.004	0.001	0.99	-0.44	**<0.05**	-0.007	-0.002
	Neighbour rock	0.001	0.0004	1.01	0.1	**<0.05**	0.0001	0.002
Retreat site	Intercept	0.68	0.51	-		0.5	-0.68	1.3
	Width	-0.32	0.08	0.73	-26.58	<0.05	-0,5	-0.16
	Length	0.04	0.01	1.04	4.3	<0.05	0.004	0.06
	Inclination	-0.4	0.27	0.65	35.1	0.1	-0.98	0.08
	Depth	0.02	0.01	1.02	2.1	0.2	-0.01	0.05
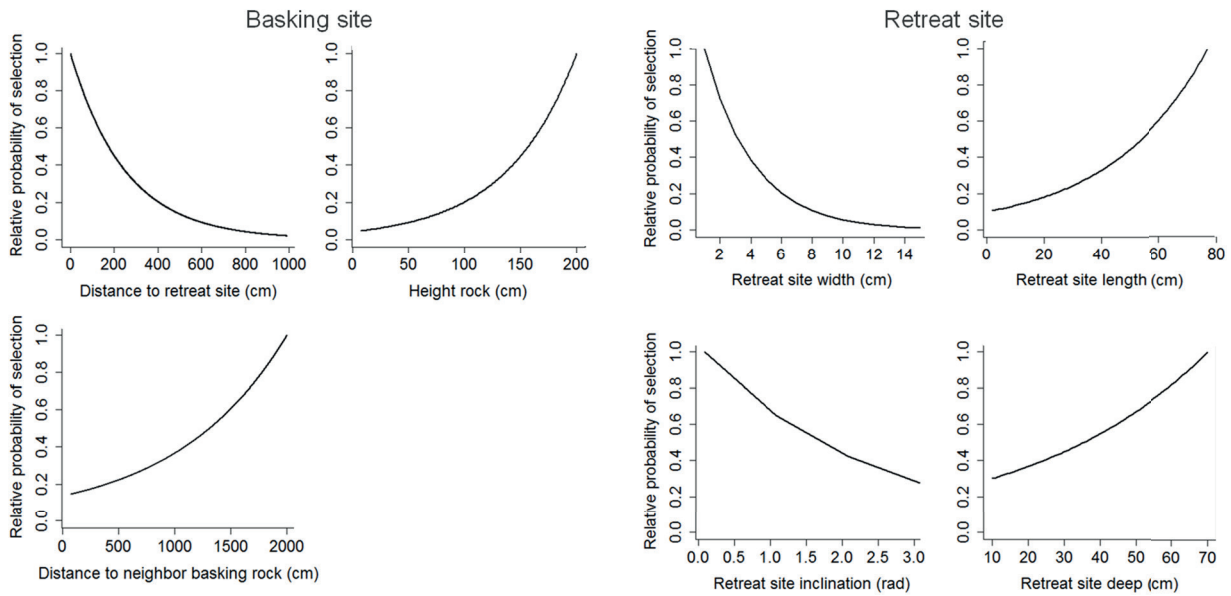
Figure 4. Plots showing the relative probability of basking site selection and retreat site selection of *Phymaturus palluma* assuming all other variables were held constant at their respective median, for the most important variables in the RSF models with a Δ AICc ≤ 2.

DISCUSSION

The selection of basking and retreat sites by *P. palluma* was influenced by abiotic features of the rocks and shelters, such as size and structure and by biotic factors, such as distance to conspecifics. Consistent with our predictions, *P. palluma* selected basking sites formed by high and large rocks, near retreat sites and far from the basking sites of their neighbours, whereas retreat sites selected were formed by narrow, depth and long shelters.

The relative probability of selection of basking sites of *P. palluma* increased 148.12 % when the rock was large (more than > 0.6 m³). Several studies have demonstrated that the rock dimension is an important component of the selection of microhabitats (Huey 1991, Kearney 2002, Quirt et al. 2006, Ljubisavljević et al. 2017). In high-mountain lizards, such as *P. palluma*, the selection of certain features of basking sites could optimize thermoregulatory opportunity (Huey 1982, Van Damme et al. 1989),

which is important because it enables lizards to reach body temperatures near the preferred temperature range, despite the extreme and variable air temperatures. In our study site, large rocks were colder than small ones, and both medium and large rocks exhibited mean
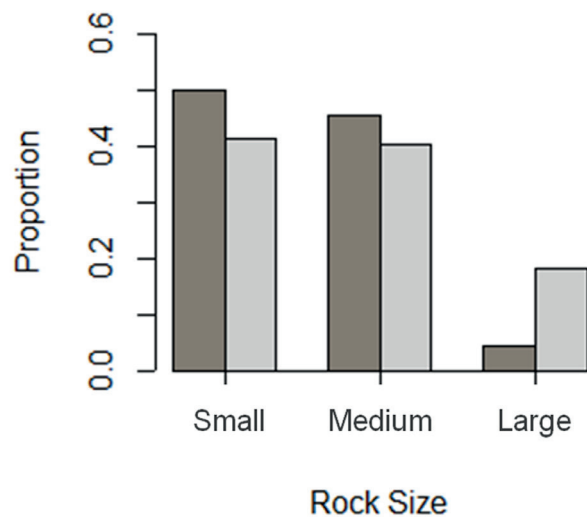

Figure 5. Histogram of proportions of Available versus Used basking sites according to the type of rock (small, medium and large).

temperatures, 33.8°C and 31.87°C respectively, below the set point of preferred temperature of the species (34.24-36.11°C, Vicenzi et al. 2017), whereas temperature of small rocks showed a mean of 38.91°C, near the critical maximum for the species (41.18°C, Vicenzi et al. 2017). Thus, by selecting large rocks, lizards could avoid overheating, and consequently, reduce the costs of thermoregulation. However, rock features which could optimize the heat gain of lizards by solar radiation, such as orientation and slope of the perch (Muth 1977, Ribeiro et al. 2009), did not influence basking site selection.

The advantage of selecting higher rocks that facilitates vigilance, and therefore enabling lizards to scan the environment more effectively and detect other individuals (Avery 1991), could also be a disadvantage, as it may increase their conspicuousness, especially to predators (Zucker 1986, Radder et al. 2005). One way to reduce predation risk is basking near retreat sites. Our results demonstrated that the probability of selection of basking sites by *P. palluma* increases when rocks have available

retreat sites at a minimum of 1 m distance, as was observed in *Iberolacerta monticola* and *Podarcis hipanica* (Martin & Salvador 1996, Diego-Rasilla & Perez-Mellado 2003). This could reduce predation risk (Carrascal et al. 1992), especially during the early morning when locomotor performance of lizards is low (Van Damme et al. 1989, Carrascal et al. 1992). Previous studies registered that in the mornings, *P. palluma* uses sun exposed crevices to start basking behaviour, which gives the lizards the opportunity to increase their body temperature without exposing themselves to predators (Vicenzi et al. 2019). During the day, however, the selection of basking sites near retreat sites could also be related to thermoregulation needs, such as avoiding overheating risk during the summer. Several studies about thermoregulation in *Phymaturus* species have shown that these lizards thermoregulate shuttling between rocks and rock crevices (Durán et al. 2018, Vicenzi et al. 2019), thus short distances between basking and retreat sites could diminish thermal risks. In addition, this thermoregulatory behaviour

Table III. Operative temperature (Mean ± SE) of small, medium and large rocks and crevices within each of them per hour during activity period of *Phymaturus palluma*.

Hour	Small rock (°C)	Medium rock (°C)	Large rock (°C)	Crevice within small rock (°C)	Crevice within medium rock (°C)	Crevice within large rock (°C)
9.00	31.59 ± 0.86	27.15 ± 0.72	24.31 ± 0.61	21.35 ± 0.59	16.43 ± 0.39	17.4 ± 0.37
10.00	36.91 ± 0.96	30.79 ± 0.85	28.05 ± 0.78	29.62 ± 0.81	17.78 ± 0.38	18.32 ± 0.39
11.00	40.96 ± 0.84	33.54 ± 0.85	31.18 ± 0.84	33.58 ± 0.83	19.65 ± 0.41	19.40 ± 0.41
12.00	43.15 ± 1.03	35.09 ± 0.79	33.35 ± 0.91	32.93 ± 0.79	23.39 ± 0.74	20.62 ± 0.42
13.00	43.38 ± 1.32	36.24 ± 0.95	34.46 ± 1.02	32.51 ± 0.87	24.98 ± 0.71	21.92 ± 0.51
14.00	43.06 ± 1.23	36.96 ± 0.91	35.4 ± 0.99	32.28 ± 0.89	26.33 ± 0.65	22.75 ± 0.5
15.00	40.61 ± 1.3	36.74 ± 0.87	35.35 ± 0.94	31.02 ± 0.88	27.72 ± 0.65	23.26 ± 0.46
16.00	38.43 ± 1.01	35.52 ± 0.89	33.97 ± 0.92	29.5 ± 0.7	28.93 ± 0.66	23.5 ± 0.47
17.00	32.13 ± 0.9	32.19 ± 1.1	30.78 ± 1.01	27.27 ± 0.61	29.52 ± 0.76	23.50 ± 0.48

of *Phymaturus*, could explain why distance to vegetation was not influence basking site selection.

Retreat sites were selected according to their attributes, such as length, depth, slope, and width. The flattened body morphology and the spiny tail of all *Phymaturus* species are associated with adaptative advantages of retreating into narrow rocky crevices where they are protected from predators (Debandi et al. 2012). Thus, the selection of long crevices could facilitate the quicky access of lizards to crevices, whereas the selection of deep and narrow crevices with low slope could help to avoid *Agriornis* birds predation, the main predator of *P. palluma* (Videla 1982). Some retreat site features, such as orientation and rock size, could influence the thermal regime of the shelter (Kearney 2002). Despite the operative temperature inside crevices being highly related to rock size, this characteristic did not influence the selection by individuals of *P. palluma*, in contrast to the results by other authors for in *Sceloporus occidentalis* (Sabo 2003) and *Oedura lesueurii* (Croak et al. 2008). This result suggests that predator avoidance is more important than thermal requirements when *P. palluma* lizards select retreat sites, at least during the activity time periods (from 9.00 to 17.00 h), as was observed by Downes & Shine (1998), in the habitat selection experiment carried out in the gecko *Oedura lesuerii*. During the night, crevices in large rocks attain higher T_e (median= 20.08°C) than small ones (median= 18.11°C), and large rocks likely represent better refuges both during summer nights and during the winter. Unfortunately, we could not evaluate selection of retreat sites during these periods. Further research should include a profound thermal characterization of the microhabitat related to the thermal biology of the individuals, such as the implications of the biotic interactions in the population since these factors are likely to affect microhabitat selection.

The knowledge of microhabitat features allows the identification of key resources impacting population persistence, and is crucial for conservation management (Ljubisavljević et al. 2013), especially for species with specific microhabitat requirements, such as those belonging to the genus *Phymaturus* (Abdala et al. 2012, Debandi et al. 2012). Our study strongly reinforces the important role of the structure and morphology of the rocks and shelters for the selection of basking and retreat sites on rock-dwelling lizards. Rocky outcrops offer thermal heterogeneity, necessary not only to enhance thermoregulation but also to prevent lizards from overheating. Particularly, for *P. palluma*, a species whose current habitat is predicted to be reduced by 86% over the next 50 years (Vicenzi et al. 2017), the results of this study may contribute to management decisions based on the characteristics of the basking and retreat sites selected by *P. palluma*, to conserve future sites thermally suitable for the species and also to enhance basking and retreat site availability in current degraded habitat.

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NADIA VICENZI[1,2]

https://orcid.org/0000-0001-7309-7294

RUBÉN MASSARELLI[3]

https://orcid.org/0000-0001-7738-2439

NORA IBARGÜENGOYTÍA[4,5]

https://orcid.org/0000-0002-1959-2718

VALERIA CORBALÁN[1]

https://orcid.org/0000-0002-3977-392X

[1]Instituto Argentino de Investigaciones en Zonas Áridas, Consejo Nacional de Investigaciones Científicas y Técnicas (IADIZA-CONICET), Av. Ruiz Leal s/n, 5500 Ciudad de Mendoza, Argentina

[2]Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Cuyo, Padre Contreras 1300, 5500 Ciudad de Mendoza, Argentina

[3]Dirección de Recursos Naturales Renovables, Secretaría de Ambiente y Ordenamiento Territorial, Av. L. Peltier 351, 5500 Ciudad de Mendoza, Argentina

[4]Instituto de Investigaciones en Biodiversidad y Medioambiente, Consejo Nacional de Investigaciones Científicas y Técnicas (INIBIOMA-CONICET), Quintral 1250, 8400 Río Negro, Argentina

[5]Departamento de Zoología, Centro Regional Universitario Bariloche, Universidad del Comahue, Quintral 1250, 8400 Río Negro, Argentina

Correspondence to: **Nadia Vicenzi**
 E-mail: navicenzi@gmail.com

Author contributions

NV, VC and NRI conceived and designed research; NV and RM performed research and analyzed data; NV wrote the paper; and VC, NRI and RM helped revise the manuscript.