



Resource segregation in two herbivorous species of mountain lizards from Argentina

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Lizard assemblages may experience resource partitioning in the spatial, trophic or temporal dimensions of their niche. Niche segregation does not always imply competition, and the role of interspecific competition is better understood when the response of species to the presence or absence of other species is evaluated. The aim of this study is to determine daily activity patterns and food consumption in two phylogenetically related species (*Phymaturus roigorum* and *P. payunia*). These saxicolous and herbivorous species live in sympatry in the volcanic region of Payunia, in central-west Argentina. One of these species can also be found in allopatry, allowing comparative studies on their lifestyle. We evaluated the temporal daily patterns of both species and their diet overlap. Although competition is not evident between the species studied here, it is shown that selectivity towards different plant species and the time schedule of foraging are the primary mechanisms that promote the coexistence of these lizards. Daily basking activity, however, was similar in both species.

Key words: activity pattern, food segregation, Payunia region, *Phymaturus*

INTRODUCTION

For the past four decades, ecologists have been interested in investigating how species with similar requirements can coexist in a given place. Resource partitioning patterns and character displacement between sympatric species were proposed as mechanisms to minimise competition (e.g., Schoener, 1974a; Losos, 2000). Pianka (1969) proposed that species can divide resources along three major dimensions: food, habitat and time. However, niche segregation does not always imply competition (Wahungu et al., 2004), since other causes, such as predation and extrinsic or intrinsic constraints on an organism's performance may bring about resource partitioning (Joern, 1979; Toft, 1985; Luiselli, 2007). For example, James & M'Closkey (2002) found that sympatric species of phrynosomatine lizards differ in their microhabitat use, but after observing the absence of aggressive behaviour, these authors concluded that this segregation is not due to interspecific competition. Thus, the role of interspecific competition is better understood when the research is made in the presence and absence of particular species (Schluter & McPhail, 1992; Taper & Case, 1992; Radtkey et al., 1997; Melville, 2002).

Several studies carried out in lizard assemblages reveal that resource partitioning occurs mainly along microhabitat (space) and temporal axes (Melville & Swain, 1997; Howard & Hailey, 1999; Leal & Fleishman, 2002; Wahungu et al., 2004; Luiselli, 2007). When

niche dimensions interact, some authors proposed that differences in time budget are frequently attributed to avoidance of food competition by insectivorous lizards (Pianka, 1969, 1973; Schoener, 1974a, b; Pianka, 1975; Simon & Middendorf, 1976; Pianka, 1980). Although some terrestrial lizard species have shown diet partitioning (Pianka, 1973; Akani et al., 2002; Hardy & Crnkovic, 2006; Carretero et al., 2006), most of these studies involve mostly insectivorous (and omnivorous) species, and frequently prey size is responsible for this segregation (Schoener, 1974a). Resource partitioning among strictly herbivorous lizard species, however, still remains understudied. Luiselli (2007) proposed that reptiles living in extreme climates have populations under the carrying capacity of the system, preventing exploitative competition because trophic resources are not limited. However, we believe that in rocky mountain habitats vegetation cover is usually low, and those more nutritive items could be limiting for herbivorous lizards inhabiting these kinds of systems.

In general, the activity patterns of animals could be described as unimodal or bimodal, though these patterns may vary depending upon the species. Patterns can also vary among different populations of the same species living in different climatic conditions, habitat structure or geographic locations, or even in the same site, but in different seasons (Radder et al., 2005; Pelegrin et al., 2013). Additionally, Carothers (1983) postulated that differences in activity times are more related to thermoregulatory constraints. As thermal

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inertia increases with body size, smaller individuals (or juveniles) are active earlier in the day than larger ones (or adults). Although this was demonstrated for size classes within a single species (Middendorf, 1979; Carothers, 1983), it may also be valid for closely coexistent species with different sizes.

The Payunia region in central Argentina is an extra-Andean mountain system where two endemic and phylogenetically related lizards of the *Phymaturus* genus occur. These species occupy volcanic rocks and belong to two different clades (or species groups) within the genus, have different body size (*P. roigorum* is larger than *P. payunia*), and both are herbivorous and viviparous (Corbalán & Debandi, 2013). When coexisting, they may be observed basking over the same rock and sharing microhabitats for refuge (Corbalán & Debandi, unpub. data). A recent study showed that thermal requirements (preferred temperature) are similar in both species (Corbalán et al., 2013), reinforcing the conservative nature of several characteristics of this genus (Cei, 1986; Cruz et al., 2009; Debandi et al., 2012; Corbalán & Debandi, 2013).

The aim of this study is to assess temporal and trophic niche dimensions in these two species (*P. roigorum* and *P. payunia*) in sympatric and allopatric situations, in order to determine whether coexistence of these species is mediated by resource segregation along these niche axes. Because populations of *P. payunia* were always found coexisting with *P. roigorum*, it was not possible to make comparisons in this species and only *P. roigorum* was studied under both situations.

MATERIALS AND METHODS

The study was carried out at La Payunia Reserve, southern Mendoza Province, Argentina. It is situated 140 km east of the Andes Cordillera, and presents a volcanic landscape. The weather in the region is arid and cold, influenced by winds from the Pacific Ocean (Capitanelli, 1972; Candia et al., 1993). Winters are rainy and snowy, and summers are dry (Candia et al., 1993). Under these conditions lizards most likely remain inactive during cold months. The Payunia region constitutes a transitional area between the phytogeographical provinces of Monte and Patagonia, and several plants and animals belonging to each province are present, as well as endemic forms (Candia et al., 1993; Corbalán & Debandi, 2008). Only two species of the genus *Phymaturus* occur in the La Payunia Reserve, the larger *P. roigorum* (adult snout–vent length 99.97 ± 5.85 mm) and the smaller *P. payunia* (84.31 ± 5.04 mm; Corbalán & Debandi, 2013). The flattened body shape of both species helps them to take refuge in the crevices of rocks. These species are endemic to the Payunia region, and the distribution range of *P. roigorum* is broader than that of *P. payunia*. While *P. roigorum* can be found in allopatry or in syntopy with *P. payunia*, this later species was only found in syntopy with *P. roigorum*.

We chose three rocky promontories inside the reserve to observe the daily activity of lizards, including basking and foraging behaviour. Two sites (S1 and S2) were located on the north slope of Payún Matrú volcano

($36^{\circ}20'56.9''$ S, $69^{\circ}14'25.8''$ W, 2372 m a.s.l.), and are 380 m apart. The remaining site (S3) was located at the base of the Payún Liso volcano ($36^{\circ}29'$ S, $69^{\circ}22'$ W, 2111 m a.s.l.), 20 km away from S1 and S2 (see Corbalán & Debandi, 2013 for more details). *Phymaturus payunia* was only present at S2 and S3, whereas *P. roigorum* was present at all three sites, so we refer to site S1 as allopatric, and to sites S2 and S3 as sympatric. At each site we established a grid of 10x20 m and all lizards present were permanently marked with jewellery beads sutured through the tail (Fisher & Muth, 1989), and then released at the capture site. We marked a total of 12 *P. roigorum* individuals at S1, 9 *P. roigorum*, 19 *P. payunia* at S2, and 7 *P. roigorum* and 5 *P. payunia* at S3. Four marked individuals of *P. payunia* and one of *P. roigorum* at S1 were not observed again during the sample period, and thereby we considered them transients.

Three days of sampling with similar weather conditions were conducted at S1 in November 2008 (spring) and three days in January 2009 (summer). Similar sampling effort was conducted at S2. Four days of sampling were conducted at S3 in January 2009. Two points of observation were located at opposite sides of the grids in order to have visual access to all rocks simultaneously, avoiding disturbance to the study animals. Two observers switched places at the surveillance point in the middle of the day, alternating points every day. Observations of activity were recorded using two kinds of binoculars (Sigma 8x40 ZWPF, Sigma Corporation, Japan, and Tasco 12x25, #178RB, China) from 0900 hours (official Argentinean time) until the time when all individuals retreated to crevices, at about 1900 (see Corbalán & Debandi, 2013 for considerations on mean local time). Throughout each day, we recorded activity behaviour and plant consumption during 10 minute intervals, separated by 5 minutes of resting. However, for statistical analyses we re-grouped the data in periods of one hour.

In order to characterise environmental conditions during emergence from crevices and activity of lizards, we recorded temperature of crevices, rock surface and air at heights of 2 cm and 1 m above the soil surface throughout the entire sampling period for each grid. Data were recorded every 5 minutes using an Onset HOBO weather micro-station.

Temporal segregation

We recorded three types of activity: *sun basking* (when individuals were exposed to full sun), *covert basking* (when individuals were totally or partially hidden by the shade cast by vegetation or rocks, or alternation between sun and shade exposure) and *foraging*. Additional notes of aggressive behaviour (like chasing or biting) among individuals were also recorded.

As our main interest was determining differences in daily patterns of activity between species or, in the case of *P. roigorum*, between sympatric and allopatric sites, the data was analysed looking for significance in the interaction between hours and species or between hours and sites. We counted all active individuals over 1 hour periods throughout the day. Values for each day were treated as replicates for the entire sampling season

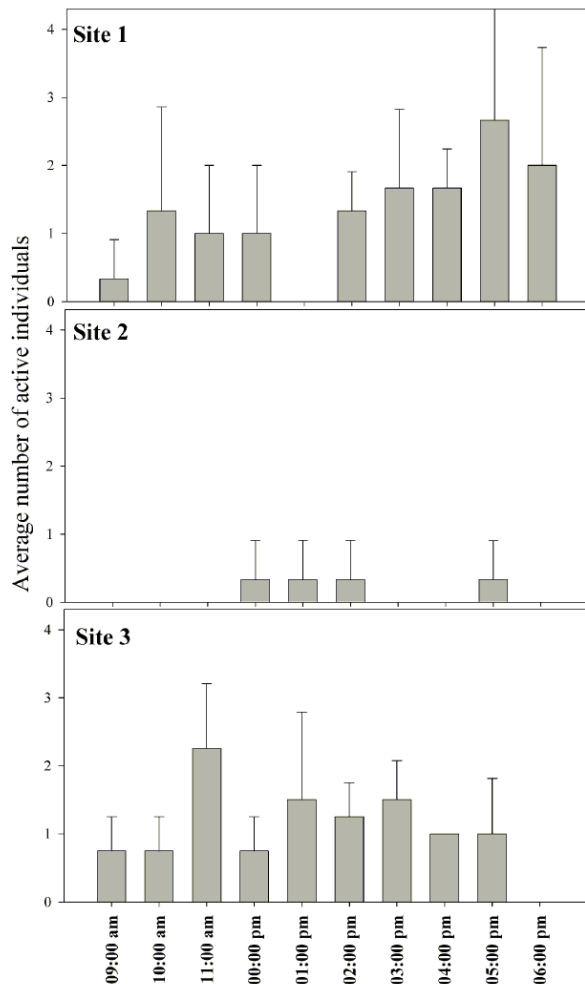


Fig. 1. Covert basking activity of *Phymaturus roigorum* during summer in allopatry (Site 1) and sympatry (Sites 2 and 3). Number of individuals for each hour period was averaged among days of sampling, and standard deviation is indicated by bars.

at each study site. Firstly, a global analysis was made to evaluate total activity (without discriminating among different activities). After that, each different activity (sun basking, covert basking and foraging) was treated separately. The data were analysed using Generalised Linear Models (GLM's) with Poisson errors and logarithms as link function (Crawley, 2007). Hours, species and sites were the explanatory factor variables, and the total number of individuals per hour in each activity (total activity, sun basking, covert basking and foraging), were the response variables in the analyses.

For each response variable, the interaction between hours and species in sympatry were tested for: site S2 in spring (November), site S2 in summer (January) and site S3 in summer. Similarly, the interaction between hours and sites was tested for *P. roigorum* in spring (between sites S1 and S2) and summer (among all three sites). Interactions were tested using likelihood tests using nested models. Tests were assessed using χ^2 in all cases, except when the data showed overdispersion, in which case the models were fitted using quasipoisson errors and the *F* statistic to test the interaction. All the analyses were made using R software, v.3.01 (R Development Core Team, 2008).

Trophic segregation

We recorded (by direct observation) plants consumed by each species throughout the day in every grid, and when possible, we distinguished among leaves, fruits and flowers.

We determined diet overlap between both species at each sympatric site using Pianka's index (Pianka, 1973):

$$O_{jk} = \frac{\sum p_{ij} p_{ik}}{(\sum p_{ij}^2 \sum p_{ik}^2)^{1/2}}$$

where p_i is the frequency of occurrence of plant item i in the diet of species j and k (Pianka, 1973). Pianka's index varies between 0 (no overlap) to 1 (total overlap).

To calculate this index, we used the EcoSim software v.7 (Gotelli & Entsminger, 2006). We chose the RA2 randomisation algorithm available in the software (niche breadth relaxed/zero states retained). This algorithm was chosen because we felt that zeros represented utilisation constraints that were imposed by forces other than species interactions, as in the case of *Ephedra chilensis* (Ephedraceae), a plant species with hard stems never consumed by the smaller lizard species, *P. payunia*. The data on relative plant availability were used to calculate Pianka's index by selecting the "user-defined" option.

Availability of plant species was assessed throughout 7 vegetation transects 10 m long separated by 3 m in each grid using the intercept method (Krebs, 1999). This method consists in recording those plant species that intercept a 1 m long vertical stick every 30 cm along each transect. These transects were set up after the observation periods. The identification of plant species was made by A. Dalmasso and R. Candia at the IADIZA Institute, based on a field herbarium.

In order to evaluate whether lizard species select different food items, the total observed frequencies of food items consumed by each species at each site and date were compared with those expected from the relative plant availability using the *G* test in InfoStat software (InfoStat, 2009). This test was calculated both in sympatric and allopatric grids. However, in sympatric grids, this analysis was made only for January, since in November we only recorded 36 data on consumption of *Fabiana punensis* by *P. payunia* and one record of consumption of *E. chilensis* by *P. roigorum* at S2, and no data were available for S3. Once we found significant differences between consumed food and plant availability, we calculated Bailey's index (Cherry, 1996) for each food item to evaluate preference, avoidance or indifference. Bailey's index computes confidence intervals for multinomial proportions using Bonferroni's inequality, and provides the best combination of low error and interval length (Cherry, 1996). Only plant items with relative frequencies of use or availability above 5% were considered in the analyses (Mosca Torres & Puig, 2010).

RESULTS

During each sampling period, temperatures in crevices remained almost constant throughout the day (Mean=14.18±1.37°C and 20.04±3.49°C in November

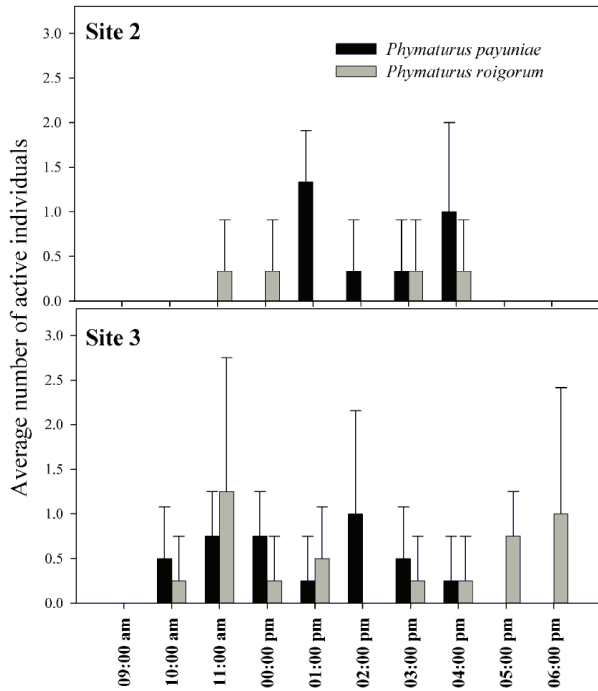


Fig. 2. Foraging activity of *Phymaturus roigorum* and *P. payuniaie* during summer in sympatry (Sites 2 and 3) in the Payunia region. Number of individuals foraging in each hour period was averaged among days of sampling, and standard deviation is indicated by bars.

and January, respectively), and both lizard species began activity when external temperatures (air and rocks) began to exceed the temperature of crevices. In the afternoon, the individuals of both species retreated into the crevices when air temperature 1 m above ground dropped to below 21°C, although the temperature of rocks stayed higher for longer time.

Total activity

When all activities were considered jointly, daily patterns did not differ between species at S2 during spring ($F=0.29$, $df=10, 54$, $p=0.97$) or summer ($\chi^2 = 8.06$, $df=9$, $p=0.52$), nor at S3 during summer ($\chi^2= 10.91$, $df=9$, $p=0.28$). These results indicate that both species are active in the same proportion along the day in different seasons and sites. When comparing the daily activity pattern of *P. roigorum* at different sites, there were no statistically significant interactions between hours and sites during spring ($\chi^2=3.75$, $df=9$, $p=0.92$, one sympatric and one allopatric site) or summer ($\chi^2=9.12$, $df=18$, $p=0.95$, two sympatric and one allopatric site), indicating that the daily activity pattern of this species is not affected by the presence of *P. payuniaie*.

Sun basking

Analysing each activity separately, we found that individuals of both species showed a similar daily pattern when basking in full sun, since there were no significant interactions between hours and species at S2 during spring ($\chi^2=5.71$, $df=9$, $p=0.85$) or summer ($\chi^2=5.15$, $df=9$, $p=0.82$), nor at S3 during summer ($\chi^2=11.49$, $df=9$, $p=0.24$). Moreover, the daily pattern of sun basking of *P. roigorum* was similar among sympatric and allopatric

sites, since there were no interactions between hours and sites during spring ($\chi^2=5.60$, $df=9$, $p=0.77$, one sympatric and one allopatric site), nor during summer ($\chi^2=17.93$, $df=18$, $p=0.45$, two sympatric and one allopatric site). These results indicate that the presence of *P. payuniaie* does not modify the time at which *P. roigorum* basks in full sun.

Covert basking

As with sun basking, the daily pattern of shade use was similar between species, since interactions between hours and species were not significant at S2 during spring ($\chi^2=13.27$, $df=10$, $p=0.20$) or summer ($\chi^2=12.13$, $df=9$, $p=0.20$), nor at S3 during summer ($\chi^2=8.79$, $df=9$, $p=0.45$).

For *P. roigorum*, the daily pattern of shade use was similar between sites S1 and S2 during spring ($\chi^2=6.47$, $df=9$, $p=0.69$) but slightly different among all three sites during summer ($\chi^2=29.76$, $df=18$, $p=0.039$). Despite the significant interaction between hours and sites, the presence of *P. payuniaie* did not affect shade use by *P. roigorum*, since differences can be attributed to the low frequency of this behaviour at S2, and not to differences between sympatry-allopatry situations (Fig. 1).

Foraging

The foraging pattern throughout the day was similar in both species at S2 during spring ($\chi^2=3.88e-8$, $df= 9$, $p=1$)

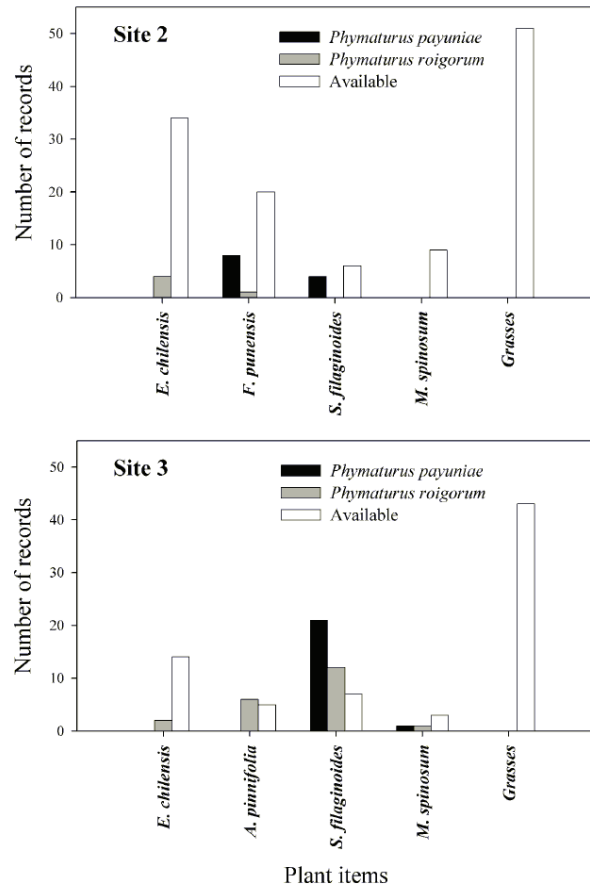


Fig. 3. Food selection during the summer (January) for *Phymaturus roigorum* and *P. payuniaie* in sympatry in the Payunia region.

and summer ($\chi^2=8.77$, $df=9$, $p=0.45$), but differed at S3 during summer ($\chi^2=17.70$, $df=9$, $p=0.038$). This significant interaction between hours and species at S3 suggests that *P. payuniaie* has a unimodal pattern with highest frequency during midday, while *P. roigorum* shows a bimodal pattern of foraging with highest frequency in the morning and late afternoon: 1700–1800; Fig. 2). Nevertheless, on several occasions individuals of both species were seen feeding on the same plant at the same time. In these cases, one individual began to eat, and then the other individual followed, indicating an imitation behaviour.

For *P. roigorum*, there were no differences among sympatry-allopatry situations. Interaction between hours and sites was not significant during spring ($\chi^2=3.56e-8$, $df=9$, $p=1$) or summer ($\chi^2 = 19.22$, $df=18$, $p=0.37$).

Trophic segregation

Plant cover was low in all three habitats, varying between 40–50%, of which 17–28% was represented by grasses. Direct observations indicated that the plant items consumed are similar for both species, with the exception of *Ephedra chilensis*, which is consumed only by *P. roigorum*. In summer (January), diet overlap of *P. roigorum* and *P. payuniaie* based on Pianka's index was different for both sympatric sites. While at S2, the overlap was 0.18, at S3 it was 0.80. In spring, at S2 we obtained 36 records of consumption of *Fabiana punensis* (Solanaceae) and one record of *Tetraglochin alatum* (Rosaceae) for *P. payuniaie*, and only one record of *E. chilensis* for *P. roigorum*. Then, the low frequency of observations for *P. roigorum* in this period did not allow us to calculate diet overlap between these lizard species.

When it was possible to distinguish the part of the plant consumed, we found that flowers made up the highest proportion for both species (68% in *P. roigorum* and 90% in *P. payuniaie*, respectively).

Taking into account the availability of each plant species in each grid and the plants consumed by each lizard species, we found selectivity in *P. payuniaie* in both grids (S2: $G=33.82$; $df=4$; $p<0.0001$, and S3: $G=60.53$; $df=4$; $p<0.0001$). In sympatry, *P. roigorum* showed selectivity only at S3 ($G=37.81$; $df=4$; $p<0.0001$), whereas no selectivity was found for S2 ($G=7$; $df=4$; $p=0.14$). In allopatry, this species showed selectivity both in November ($G=27.35$; $df=6$; $p=0.0001$) and January ($G=29.34$; $df=6$; $p=0.0001$).

Bailey's test indicated that *P. payuniaie* showed preference for *F. punensis* at S2 and for *Senecio filaginoides* (Asteraceae) at both S2 and S3 during summer (Fig. 3). This species also showed avoidance of *E. chilensis* and grasses in both grids. *Mulinum spinosum* (Apiaceae) was indifferent for this species at S2. Preference by *F. punensis* at S2 was also evident in spring, since this item was almost the only food consumed for *P. payuniaie*. Because no selectivity was found for *P. roigorum* at S2 using G test, food preference in sympatry was only evaluated at S3. At this site, this species showed preference for *S. filaginoides* and *Adesmia pinnifolia* (Fabaceae), as well as avoidance of grasses. *Ephedra chilensis* was indifferent for this species in this grid

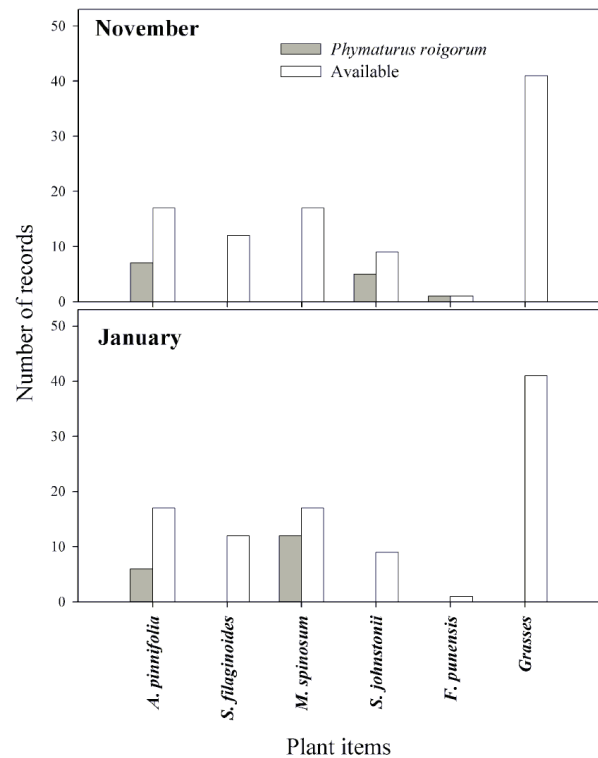


Fig. 4. Food selection by *Phymaturus roigorum* in spring (November) and summer (January) in the allopatric site (Site 1).

(Fig. 3). In allopatry, *P. roigorum* preferred *A. pinnifolia* and *Schinus johnstonii* (Anacardiaceae) in November (avoiding *M. spinosum*), but it preferred *A. pinnifolia* and *M. spinosum* in January. This species avoided grasses on both dates at this site, and showed indifference towards *F. punensis* (Fig. 4).

DISCUSSION

Several authors emphasise the importance of body size in interspecific interference competition, where larger individuals have superiority in aggressive encounters, then being superior in competitive interactions (Miller, 1967; Rand, 1967; Schoener, 1975; Melville, 2002; Langkilde & Shine, 2004). In our study we observed aggressive behaviour by some individuals in chasing other individuals on six occasions, three times between females (*P. roigorum* chasing *P. payuniaie*), twice between individuals of different sexes (males of *P. roigorum* chasing females of *P. payuniaie*), and only one time between males (*P. roigorum* chasing *P. payuniaie*). Although these encounters were found from the larger (*P. roigorum*) to the smaller (*P. payuniaie*) sized species, their low frequency (six times in about 1,600 minutes of observation in sympatric grids) does not provide enough evidence to conclude that competition between species is operating in this system. Moreover, we frequently observed individuals of both species feeding on the same plant or sharing rocks for basking without showing any aggressive behaviour. However, other stressful interactions could exist. We observed on several occasions head bobbing displays in both lizard species that could

be interpreted as aggressive signalling (Lovern & Jenssen 2003), as occurs with species of the related genus *Liolaemus* (Martins et al., 2004). Due to the complexity of visual displays, specific studies on behaviour are needed to understand their significance. Other indirect measures for evaluating competition are the character displacement shown by the species when they are in the presence of competitors (Losos, 2000; Melville, 2002). We could not evaluate character displacement in the smaller species (*P. payunia*) in the presence of the larger one (*P. roigorum*), because we never found a site where the species live in allopatry. We were able, instead, to evaluate this parameter for *P. roigorum* in allopatric and sympatric situations. We found that, in the presence of *P. payunia*, males of *P. roigorum* are larger in size than those males living in allopatry (Mean±SD LHC: 104.48±4.3 mm vs 97.97±4.9 mm; $F_{1,36}=16.32$, $p<0.001$). However, to conclude character displacement, differences must be genetically based (Losos, 2000), and no data are available to address this issue. However, this difference in size is probably more related to habitat quality and fitness of individuals than to its dominance over *P. payunia*. It is possible that our sympatric sites have a higher proportion of suitable thermal microsites and food availability than the allopatric site, where plants such as *F. punensis* and *E. chilensis* were absent or with very low availability. Thus, more mature and stronger males occupy better patches, displacing immature males to poorer patches. If the hypothesis of habitat quality is correct, it can also explain the absence of *P. payunia* in poor habitats, and the higher density of this species at S2, where *F. punensis* is more abundant than other plant species. However, determinations of habitat quality and source-sink systems are more complex and it is necessary to evaluate other parameters linked to fitness (Lidicker, 1995; Loeb, 1999; Wheatley et al., 2002; Corbalán et al., 2006).

When time use for basking is evaluated in both species living in sympatry, and between different situations (sympatry and allopatry) in *P. roigorum*, we found no evidence of niche segregation. According to our results, both species can be considered to have a unimodal activity, either entirely or discriminated between sun basking and covert basking. Both lizard species began activity at the same time (when temperatures of air and rocks began to exceed the temperature of crevices) and retreated into the crevices at the same time (when air temperature 1 m above the ground dropped below 21°C). However, previous studies indicated that differences in basking behaviour are evident when the lengths of basking periods are evaluated (Corbalán & Debandi, 2013). *Phymaturus roigorum* shows longer periods of basking (including periods of more than 3 hours), while the basking periods of *P. payunia* are shorter (10–40 min; Corbalán & Debandi, 2013), so we must be cautious in drawing conclusions about the use of time in species with a behavioural thermoregulation.

Foraging activity, instead, showed differences between species at one of the two sympatric sites, demonstrating a unimodal pattern in *P. payunia* and a bimodal pattern in *P. roigorum*. This result is interesting, because this

segregation time was found at the site where diet overlap was high. The plant item that both species consumed in common was *S. filaginoides*, for which flowers were preferred by both species of lizards. The rest of the plant species were preferred differently which is also evidenced by the low diet overlap found at S2. *Fabiana punensis* was strongly preferred by *P. payunia* in S2, being almost the only plant item consumed in spring by this species. Probably at this time, *F. punensis* is more palatable or soft enough for consumption than other vegetal species. Plants such as *E. chilensis* and grasses were avoided by this lizard species in both sympatric grids. *Phymaturus roigorum* also avoided grasses, but selected *A. pinnifolia* at S3 and consumed *E. chilensis* in both sympatric grids. *Adesmia pinnifolia* was also preferred by *P. roigorum* at the allopatric site (S1), as well as *S. johnstonii*. Because the latter species was present only at this site, diet comparison between sympatric and allopatric situations was not possible for *P. roigorum*. Studies carried out on other *Phymaturus* species of the *palluma* group also found *Adesmia* and *Ephedra* in stomachs of individuals (Videla, 1983; Araya-Díaz, 2007; Castro et al, 2013), indicating that these plant genera are important components of the diet of several species of *Phymaturus* lizards from this clade. The absence of *Ephedra* in the diet of the smaller species *P. payunia* could be attributed to the hard stems of this plant. We never observed *P. payunia* eating *A. pinnifolia*, but we observed an individual climbing a bush, probably intending to eat. So, if this plant species can be consumed by this lizard, it most likely does not represent an important item in its diet.

Until now, no studies on niche segregation have been carried out on *Phymaturus* species. In fact, most studies on lizards evaluating resource partitioning involve insectivorous or omnivorous species (Akani et al., 2002; Hardy & Crnkovic, 2006; Carretero et al., 2006). This study demonstrated that in these strictly herbivorous species, diet segregation is the niche axis that better explains their coexistence. Moreover, the low percentage of plant availability at all sites could suggest that this resource is limited in this arid environment, especially considering that flowers are the part of the plants most consumed by lizards and that they are available only for a short period of time. Further studies assessing nutritional content of new leaves, flowers and fruits of different plant species and their availability in habitats occupied and non occupied by *P. payunia* may help understand the restricted distribution of this species.

Because of their endemism and their conservative characteristics (thermal requirements, viviparity and rock specificity) both these species are considered vulnerable in the list of threatened species from Argentina (Corbalán, 2012a, 2012b; Abdala et al., 2012). Taking into account the human activities carried out in the region, especially oil extraction and mining, knowledge of ecological requirements as well as identification of limiting resources are essential for conservation planning and maintenance of biodiversity.

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