

Home ranges of parthenogenetic and bisexual species in a community of *Darevskia* lizards (Reptilia: Lacertidae)

Neftalí Sillero^{a*}, Claudia Corti^b and Miguel A. Carretero^c

^aObservatório Astronómico Prof. Manuel de Barros, Centro de Investigação em Ciências Geo-Espaciais (CICGE), Faculdade de Ciências da Universidade do Porto (FCUP), Portugal;

^bSezione di Zoologia “La Specola”, Museo di Storia Naturale dell’Università di Firenze, Firenze,

Italia; ^cCampus Agrário de Vairão, CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Vairão, Vila do Conde, Portugal

(Received 2 February 2016; accepted 3 September 2016)

We analysed the home ranges of a community of *Darevskia* rock lizards composed of a bisexual species (*D. valentini*), two parthenogens (*D. armeniaca* and *D. unisexualis*), and two backcross forms between bisexual and unisexual forms. We estimated home range areas of ink-marked, GPS-located lizards using Minimum Convex Polygon (MCP) and 95% of the locations for those individuals with five or more sightings. The bisexual *D. valentini* was the species with the largest home ranges, distances travelled, and the most intersections. No differences between unisexual species and backcrosses were recorded for any comparison. In males, home range size and perimeter were related to morphological characteristics. Contrary to what has been described in allopatry, unisexual species showed smaller home ranges and fewer overlaps than sympatric bisexual species. We tentatively suggest that the presence of potential bisexual partners might increase sexual competition among parthenogenetic females while differences in habitat use should also be considered.

Keywords: Reptiles; parthenogenesis; home range; Armenia; spatial statistics; minimum convex polygon

Introduction

Home range structure and functions are quite well understood in many reptile species, especially lizards. The main function of home ranges in lizards is to maintain a reproduction area (Rose, 1981). The social systems of lacertids (and many other lizards) suggest both male and female promiscuity, weak territoriality (no more than aggression related to a certain spatial context) and the lack of female mate choice (Olsson, 1986; Olsson, Gullberg, Tegelström, Madsen, & Shine, 1994; Carazo, Font, & Desfilis, 2008, 2011). In these conditions, males with larger home ranges would be advantaged in having access to more females. Correspondingly, females would tend to save energy and diminish predation risk by maintaining home ranges more related to food and refuge availability while copulating with multiple males, but having cryptic male selection mediated by sperm competition. Several studies (Gil, Pérez-Mellado, & Guerrero, 1988; Perry & Garland, 2002; Haanel, Smith, & John-Alder, 2003a; Goodman, Echternacht, & Burton, 2005) report larger home ranges in males than in females. Moreover, home range size seems to increase with the body size (Christian & Waldschmidt, 1984;

*Corresponding author. Email: neftali.sillero@gmail.com

Haenel et al., 2003a; Verwajen & Van Damme, 2008) or social position (Griffiths, 1999), but not in all lizard species (Morrison, Keogh, & Scott, 2002).

Parthenogenetic lizards provide a model system for testing the effects of sexual and interspecific interactions on home range patterns. Although several studies on the home range have been published (Eifler, 1996; Eifler & Eifler, 1998; Galoyan, 2013), virtually nothing is known on the main spatial structure of the communities of parthenogenetic species, and particularly how they may change in the presence of bisexual species. Galoyan (2013) indicated that unisexual species have large home ranges and more overlaps than bisexual species. However, both populations studied were 600 km apart while habitats only had an overall resemblance: the lack of real sympatry resulted in problematic inferences on the effects of unisexuality on home ranges. Comparison of sympatric bisexual and parthenogenetic species is, nevertheless, crucial to provide insights into the putative competitive interactions suggested by Tarkhnishvili, Gavashelishvili, Avaliani, Murtskhvaladze, & Mumladze (2010) at a geographic level.

Therefore, the main aim of this work was to determine if the presence of bisexual species can reduce the size of home ranges and the number of overlaps of the individuals of sympatric parthenogenetic species. To test this hypothesis, we took advantage of a community of lizards in real sympatry composed of several *Darevskia* species, found in Armenia (Danielyan, Arakelyan, & Stepanyan, 2008).

The genus *Darevskia* Arribas, 1997 is a group of small lizards with a wide distribution range across the entire Caucasus, adjacent regions of Turkey, northern Iran, and the Balkans. This was the first vertebrate group where parthenogenesis was described (Darevsky, 1967) and a total of 25 bisexual species and seven parthenogenetic forms have been described (see e.g. Murphy, Darevsky, MacCulloch, Fu, & Kupriyanova, 1996; Arnold et al., 2007) although their phylogenetic relationships and taxonomy are still under discussion. In Armenia, up to eight *Darevskia* species occur in a relatively small area and frequently overlap at a local scale (Arakelyan, Danielyan, Corti, Sindaco, & Leviton, 2011): four are bisexual (*D. portschinskii*, *D. praticola*, *D. raddei-nairensis*, and *D. valentini*) and four are parthenogenetic (*D. armeniaca*, *D. dahli*, *D. rostombekovi*, and *D. unisexualis*).

In our study area, we carried out an intensive sampling to understand how bisexual (male and females) and unisexual (only females) species share the space and if there are differences among them in their home ranges. Unisexual female lizards are supposed to be less aggressive than bisexual females (Tarkhnishvili et al., 2010), and unisexual populations have been reported to attain higher densities than bisexual ones in similar habitats (Darevsky, 1967). Here we hypothesise that both characteristics are linked, that is, the higher densities of parthenogens when compared to bisexual species are made possible through an increment of home range overlaps while maintaining (or increasing) home range size. Therefore, in sympatry, males of bisexual species should have larger but less mutually overlapping home ranges than bisexual females. Moreover, bisexual females should still overlap less than parthenogenetic females in the same conditions. We would also expect little interference between species, and parthenogens dominating based on numbers due to their lower intraspecific aggressiveness (Tarkhnishvili et al., 2010). On the other hand, the presence of “hybrids” (= backcrosses) in this locality (Danielyan et al., 2008) suggests that at least bisexual males do not ignore parthenogenetic females. The scarcity of bisexual females seems to facilitate such backcrosses (Danielyan et al., 2008). Specifically, we aimed: 1) to describe the home ranges of *Darevskia* bisexual and parthenogenetic species at this sympatric area; 2) to describe the local spatial patterns of the home ranges for each species and sex; and 3) to infer species interactions at the spatial level.

Table 1. Sightings and captured individuals of *Darevskia* species at Kuchak (Armenia). The left part indicates the total numbers and the right part only those used to calculate the HR (individuals with more than 5 sightings). * Hybrid between *D. valentini* and *D. armeniaca*. ** Hybrid between *D. valentini* and *D. unisexualis*.

	Female	Male	Total	Female	Male	HR
Sightings						
<i>D. armeniaca</i>	75		75	61		61
<i>D. unisexualis</i>	9		9	8		8
<i>D. valentini</i>	1	34	35		34	34
Hybrid <i>val/arm*</i>	18		18	17		17
Hybrid <i>val/uni**</i>	12		12	12		12
Total	115	34	149	98	34	132
Individuals						
<i>D. armeniaca</i>	14		14	8		8
<i>D. unisexualis</i>	2		2	1		1
<i>D. valentini</i>	1	4	5		4	4
Hybrid <i>val/arm*</i>	3		3	2		2
Hybrid <i>val/uni**</i>	2		2	2		2
Total	22	4	26	13	4	17

Material and methods

Study area. The study area was located near the village of Kuchak, Armenia (44.385°N, 40.532°W, 1940 m; Figure 1), in the foothills of Mt Aragats. The study area includes several longitudinal rock outcrops alternating with grasslands and bushes (for a general aspect of the landscape see Figure 151 in Arakelyan et al., 2011). These outcrops are composed of accumulations of big rock boulders, reaching an approximate altitude of 1955 m at the highest point above ground level (1930 m). The study was conducted in one of the highest outcrops of the study area (0.34 ha; Figure 1).

Species community composition. The *Darevskia* community was composed of three species: one bisexual (*D. valentini*) and two unisexual species or parthenogens (*D. armeniaca*, *D. unisexualis*), as well as two hybrid forms or backcrosses (*D. valentini-D. armeniaca*, *D. valentini-D. unisexualis*). In this locality, hybrids are frequent between bisexual and unisexual species, producing triploid and tetraploid lizards (Danielyan et al., 2008). Individuals were determined to species level using external characteristics according to Darevsky (1967), Danielyan et al. (2008), and Arakelyan et al. (2011). According to the same references, hybrid individuals were recognised by their comparatively large size and intermediate coloration pattern. The Green Lizard *Lacerta agilis* is also present in Kuchak, although we did not observe it in our study area.

Sampling. The fieldwork was conducted between 12 and 18 June 2013, coinciding with the reproductive period (Arakelyan et al., 2011). We concentrated our sampling effort within a short time period to avoid confusing home ranges with dispersal mediated by social interactions or with seasonal changes in home ranges (Boudjemadi, Lecomte, & Clobert, 1999; Galoyan, 2013). We captured the lizards by noose (García-Muñoz & Sillero, 2010) on 12 June 2013, and marked each individual temporarily on the belly with a number using marker pen. The number belonged to a number series, unique for each sampler participating in the fieldwork (see Acknowledgements). We identified the capture site for each lizard with the number of the lizard on a plastic tape and geo-referenced it with a Trimble GPS receiver (GeoExplorer GT) with a horizontal error around 10 cm after post-processing (see below). We recorded several morphological measurements (for a detailed description see Kaliontzopoulou, Carretero, & Llorente, 2007) with a 0.01 mm precision digital calliper: snout-vent length (SVL), trunk length (TRL), head length (HL), head width

(HW), head height (HH), front foot length (FFL), and hind foot length (HFL). Tail removal has already been observed to have a negligible effect on spatial patterns in saxicolous lacertids (García-Muñoz, Ceacero, Pedrajas, & Carretero, 2011). In summary, the following data were recorded per individual: temporal number, colour code, sex, and size class (adult or subadult). For visual identification of lizards during re-sighting sampling, we marked each individual with coloured inks using a unique code consisting of three coloured dots on their back. Finally, we released them at the exact site of capture within a few hours.

We left lizards undisturbed for one day in order to ensure that they had returned to their normal activities after being captured. After that, animals were re-sighted visually between the 14 and 18 June 2013 (40 working hours in five days, with cloudy afternoons on two days). We performed 26 random routes from the beginning until the end of the lizards' diel activity around the study area in search of lizards on rocks and ground, during daylight hours and favourable climatic conditions. Routes (see Figure 1 as an example) were designed to sample the study area only once per survey to avoid pseudo-replication, allowing lizards to recover their normal activity after disturbance by the observer; and preventing lizard re-sightings being too close in time to keep independence. In fact, the minimum time between two consecutive sightings of the same lizard was one hour. In this way, the time between two consecutive sightings was higher than the minimum time to move between two consecutive positions. Consequently, a position cannot be predicted from the previous one, independent of whether the lizard effectively moves or not. We recorded the position of each lizard with the GPS receiver during 60 seconds together with substrate and air temperature, ambient humidity, and wind speed. We recorded local weather measurements with a portable meteorological station SkyMate SM-18. We corrected all GPS positions by differential GPS procedure using Trimble GPS Pathfinder office software v 5.0 and the SOPAC (Scripps Orbit and Permanent Array Center, <http://sopac.ucsd.edu>) permanent station located at Zelenchukskaya (Russia).

Statistical analysis. We estimated home range areas with Minimum Complex Polygon (MCP) instead of kernel density estimation (KDE) or local convex hull (LoCoH) methods because of the low sampling size per individual (Getz et al., 2007; Laver & Kelly, 2008). Moreover, kernels may be inadequate for herpetofauna (Row & Blouin-Demers, 2006). We calculated MCPs using the package AdehabitatHR (Calenge, 2011) of the R software (R Development Core Team, 2012) and 95% of the lizards' locations (Jennrich & Turner, 1969). Home ranges were determined for individuals with five or more sightings (following Diego-Rasilla and Pérez-Mellado 2003), and removing sporadic displacements by excluding 5% of the locations or at least 1 location.

We analysed differences among lizard groups in relationship with home range size as well as perimeter using a nested ANOVA approach (2+2), with species (nested in reproductive modes: unisexual and bisexual; hybrids were included in the bisexual reproduction group) and sex as nominal groups. We also analysed the relationship between home range size and perimeter and lizard morphology with generalised linear models (GLM) using a stepwise multivariate regression model. Homoscedasticity was tested with the Bartlett test and normality was checked with the Shapiro test. Non-normal data were transformed to logarithms. We applied the Tukey test as ANOVA post-hoc analysis.

We calculated the minimum total distance travelled by each animal by joining all individual sights through a line following the temporal sequence of sightings. We used for this the function 'Convert points to lines' of QGIS 2.0. As in the previous analysis, we analysed the relationship between total distance travelled among species groups with ANOVA for parametric data, and the relationship between total distance travelled and lizard morphology with generalized lineal models (GLM) using a stepwise multivariate regression model.

We calculated the overlaps among individuals' MCPs with QGIS 2.0. We measured the proportion (%) of the size of the overlap in relation to the size of both overlapping home ranges together. We correlated the size of the overlap with the size of both overlapping home ranges together. We counted the number of HRs intersecting other HRs and the number of HRs without any intersection. Both sets of frequencies were analysed with a Pearson's χ^2 test.

Finally, we analysed differences between sexes and reproduction modes in relation to air and substrate temperatures, humidity, and wind speed (environmental data recorded for each

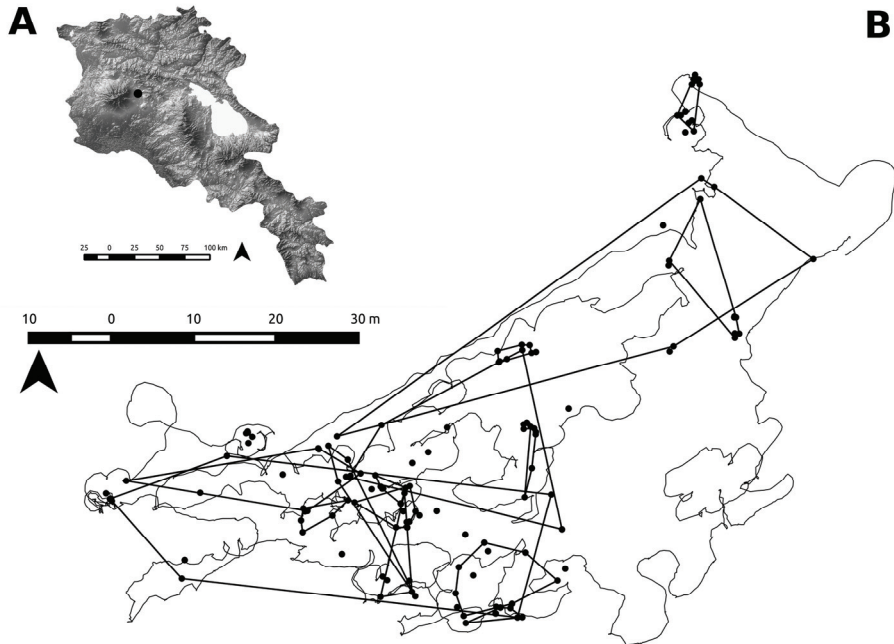


Figure 1. Location of the study area in Armenia (map A) and distribution of *Darevskia* records and their home ranges (map B). One example of the sampling tracks is shown in grey.

individual), using ANOVA for parametric data or the Kruskal-Wallis test for non-parametric data in order to test if all species groups use the space in similar ways. All analyses were performed with R software (R Development Core Team, 2012).

Results

We captured 32 individuals and recorded 149 visual recaptures from 26 lizards. After dropping nine individuals presenting fewer than five records, our working sample was restricted to 17 individuals with a total of 123 records (Table 1): eight *D. armeniaca*, one *D. unisexualis*, four males *D. valentini*, and four hybrids (two per hybrid form). Unfortunately, we could not record sufficient locations to calculate the home range of any *D. valentini* female. We calculated the MCP using 95% of each individual's locations (Figure 1). There was a low correlation between the MCP size and the number of locations (Spearman's correlation: $r=0.52$).

Sizes of home ranges were significantly different between sexes but not between reproductive modes (nested ANOVA for transformed variables: sex $F1 = 9.75$, $P = 0.008$; reproduction mode $F1 = 0.13$, $P = 0.73$), with *D. valentini* males being those with the largest home ranges (Tukey test: bisexual and male/unisexual and female, $P = 0.036$; Figure 2A). The analysis of the home range perimeters showed similar results: significant differences between sexes but not between reproductive modes (nested ANOVA for transformed variables: sex $F1 = 11.70$, $P = 0.004$; reproduction mode $F1 = 0.16$, $P = 0.70$). The largest difference corresponded again to the pair *D. valentini* males/unisexual group (Tukey test: bisexual and male/unisexual and female, $P = 0.021$; Fig. 2B).

Table 2. Generalized Linear Models summary results for comparison between home range (HR) size and perimeter, and total distance travelled with *Darevskia* morphological characteristics. All data were transformed with logarithms. Home range size AIC=25.78 and 16 freedom degrees. Home range perimeter AIC=2.09 and 16 freedom degrees. Travelled distance AIC=6.68 and 16 freedom degrees.

	Coefficients	Std. Error	t value	p value
HR Size				
Intercept	2.62	8.91	0.29	0.7736
SVL	22.68	9.78	2.32	0.0374
TRL	-29.76	6.34	-4.69	0.0004
HH	6.15	3.25	1.89	0.0811
HR Perimeter				
Intercept	8.25	2.52	3.28	0.0060
TRL	-10.07	1.63	6.16	<0.0001
HH	5.27	1.39	3.80	0.0022
HFL	4.22	1.80	2.34	0.0358
Distance travelled				
Intercept	10.05	2.81	3.57	0.0031
TRL	8.36	1.75	-4.77	0.0003
HH	6.70	1.42	4.70	0.0003

GLM results showed that home range size was positively correlated with SVL and negatively with TRL (Table 2). On the other hand, home range perimeter was positively correlated with HH and HFL and negatively with TRL (Table 2). There was interaction among factors only related to home range perimeter.

We calculated the individual movements of 17 lizards (Figure 3). Total length travelled was significantly different among the sexes but not between reproductive modes (nested ANOVA for transformed variables: sex $F_1 = 12.30$, $P=0.004$; reproduction mode $F_1 = 0.04$, $P=0.85$). As with the comparison of home range size and perimeter among species, males of bisexual species (*D. valentini*) travelled more than the unisexual group (Tukey test: bisexual and male/unisexual and female, $P=0.020$; Figure 2C). GLM results showed that total length travelled depended positively on HH and negatively on TRL (Table 2). There was also interaction among factors.

The home ranges of only two individuals (two *D. armeniaca*) did not intersect with at least another individual. There were 27 intersections in total (Table 3). There were 23 overlaps involving males (18 overlaps among males and females of both reproduction modes, and four overlaps among males), and four involving only females (two between unisexual females and two between females of both reproduction modes). There was no overlap among hybrid bisexual females. The Pearson χ^2 test found highly significant differences among the intersection frequencies of both reproduction modes and sexes ($\chi^2 = 22.73$, $P < 0.001$). Therefore, male *D. valentini* was the group with more intersections. Lizards overlapped with a mean size proportion of $2.95\% \pm 3.11$ (total area of each overlapping pair). The lowest size proportion overlap was 3.11% and the largest 11.04%

Table 3. Proportion (%) of overlap and number of overlaps (in parenthesis) among bisexual males, bisexual females, and unisexual females.

		Bisexual	Unisexual		Total
		Female	Male	Female	
Bisexual	Female		8.90 (3)		8.90 (3)
	Male	2.57 (3)	12.99 (4)	3.02 (2)	18.58 (9)
Unisexual	Female	0.67 (2)	37.20 (11)	14.21 (2)	52.08 (15)
Total		3.24 (5)	59.09 (18)	17.23 (4)	79.57 (27)

(total area of each overlapping pair). The Pearson X^2 test found highly significant differences among the percent overlaps among both reproduction modes and sexes ($X^2=27.17$, $P<0.001$). The total area of MCP pairs and the intersection area were uncorrelated (Spearman's correlation: $r=0.16$).

There were no significant differences between sexes (males and females) and reproduction modes (unisexual and bisexual) in relation to environmental variables (nested MANOVA for transformed variables: Wilks lambda = 0.942, $F_1 = 1.735$, $P=0.154$; reproduction mode: Wilks lambda = 0.974 $F_1 = 0.766$, $P=0.55$; air temperature: unisexual: $23.7\pm 2.85^\circ\text{C}$; bisexual: $23.5\pm 2.46^\circ\text{C}$; substrate temperatures: unisexual species: $26.1\pm 3.78^\circ\text{C}$; bisexual species: $26.9\pm 3.81^\circ\text{C}$; humidity: unisexual species: $52.3\pm 10.16\%$; bisexual species: $51.9\pm 9.09\%$; and wind speed: unisexual species: 0.8 ± 1.49 km/h; bisexual species: 1.4 ± 1.94 km/h).

Discussion

Our results provide the first evidence of differences in home range and dispersal between parthenogenetic and males of bisexual *Darevskia* living in sympatry. The sign of such differences was nevertheless unexpected, with the bisexual *D. valentini* displaying higher mobility than the sympatric parthenogens *D. armeniaca* and *D. unisexualis*. Certainly, the low number of backcrosses and mainly the scarcity of bisexual females of *D. valentini* (otherwise real as reported by Danielyan et al., 2008) prevented some comparisons. Nevertheless, our conclusions are statistically supported. As such, the males of the bisexual species *D. valentini* were the group with the largest home range (either in size or perimeter), with the largest distances travelled, and with more intersections. These results are typical for species with a soft territoriality, where territory is only defended when an individual tries to enter into an already occupied spot. Unfortunately, there is no information on the relative size of the home ranges of males and females within other *Darevskia* species. There were no differences between unisexual species and hybrid bisexual females. Females of both groups are socially active, as proved by the presence of hybrids (Danielyan et al., 2008). Home range and lizard morphology were remarkably linked, for example home range size depended positively on snout-vent length (SVL) but negatively on trunk length (TRL), while home range perimeter depended positively on HH and hind foot length (HFL) and negatively on TRL. Moreover, the total length travelled depended positively on HH and negatively on TRL. In other words, individuals with large bodies, high heads, short trunks, and long hind feet had home ranges with larger sizes and perimeters. These morphological characteristics correspond to the overall morphology of male lacertids (Kaliontzopoulou et al., 2006;

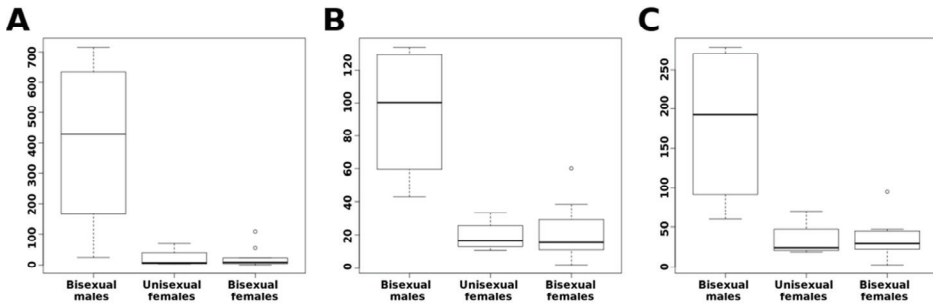


Figure 2. Home ranges (A), perimeter (B) and individual movements(C) per species group. The plots give the means \pm SD. Each graph gives the means for bisexual males (left), unisexual females (middle) and bisexual females (right).

Kaliontzopoulou et al., 2012), and thus to *D. valentini* (Danielyan et al., 2008). Consequently, as *D. valentini* males are the sex with the largest home ranges and distances travelled, this is also the species with more overlaps (a total of 23, mainly with females). Moreover, males of bisexual species presented a low proportion of overlapping areas (12.99 %) and a low frequency (only 4) of intersections among them. Darevsky (1967) suggested micro-habitat segregation between *Darevskia* species. However, in the mixed community inhabiting Kuchak we failed to find any environmental differences of the locations attributable to species, sexes or reproductive modes.

Males *D. valentini* have larger home ranges, and moves more to be able to overlap more females (in our sample, only parthenogens and hybrid females). In agreement with this, we frequently found unisexual and hybrid females in the study area with copulation marks (in the inguinal region, pers. obs), suggesting continuous hybrid production (Danielyan et al., 2008). Even if we assume that there may be polyploid hybrids resembling *D. valentini* males, the scarcity of *D. valentini* females compared with males observed both in this study and in that by Danielyan et al. (2008) cannot be attributed to sampling bias and is intriguing. Such a skewed sex ratio may be a response to karyological incompatibilities, particularly due to Haldane's rule (Haldane, 1922): "When in the F1 offspring of two different animal races one sex is absent, rare, or sterile, that sex is the heterogametic one". In other words, the absence of *D. valentini* females seems genuine while the group of *D. valentini* males might be inflated by cryptic hybrids.

Many studies have already shown that male lizards have larger home ranges in order to overlap with more females (e.g. Lewis & Saliva, 1987; Ruby & Dunham, 1987; Melville & Swain, 1999; Verwajen & Van Damme, 2008; Pérez-Buitrago, Sabat, & McMillan, 2010), although some species show no such differences (Boag, 1973). Indeed, Rose (1981) stated that the main function of home ranges in male lizards is to maintain a reproduction area, not for feeding purposes. This is to be expected in multiple mating polygynous communities (Morrison et al., 2002). Female reproductive success depends on resource distribution, while male reproductive success is limited primarily by access to potential mates (Stamps, Losos, & Andrews, 1997; Mahrt, 1998; Haenel et al., 2003b). In fact, females with less reproductive success, and males with poor body condition disperse more as they have greater difficulty in establishing a territory (Olsson, Gullberg, & Tegelstroem, 1997).

The only previous work about *Darevskia* home ranges stated that parthenogenetic species have larger home ranges and overlap more than females of bisexual species due

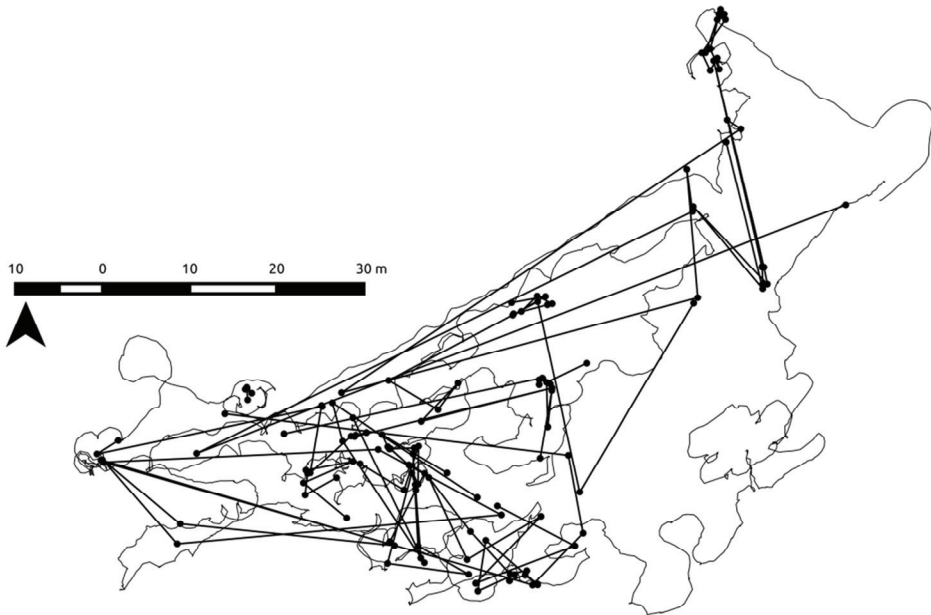


Figure 3. Map with the distances travelled by all *Darevskia* lizards. One example of the sampling track is shown with a thin black line.

to their lower aggressiveness (Galoyan, 2013). Our results can be only partially compared to those by Galoyan (2013) who studied an allopatric population of the parthenogen *D. armeniaca* and compared the results of Tsellarius and Tsellarius (2005, 2006) for the bisexual *D. braueri* from a distant locality, but with a similar biotope. In a forest environment, Galoyan (2013) reported home range sizes of $104.8 \pm 35.23 \text{ m}^2$ for adult *D. armeniaca*, very far from our value of $9.31 \pm 9.37 \text{ m}^2$ for *D. armeniaca*. Our value is more similar to the lizards classified by Galoyan (2013) as wanderers (37.3 ± 4.68). Galoyan (2013) also found large overlaps among females (seven and nine lizards in two years, with 93.7 ± 6.14 and 96.7 ± 3.76 of overlapping percentage) while we found only four pairs of unisexual species and hybrids overlapping with lower proportions. Eifler and Eifler (1998) also found a high degree of overlapping in the parthenogenetic teiid *Aspidoscelis uniparens*. However, we found unisexual species with smaller home ranges and with fewer overlaps than the bisexual ones. These contrasting results might be caused by the syntopic presence of bisexual species (in our case, *D. valentini*). Our system can be considered as the typical study of the home ranges of one particular bisexual species (Perry and Garland, 2002), but here all females corresponded to other unisexual species or to their hybrids (Danielyan et al., 2008). We tentatively attribute our results to the presence of potential bisexual partners, which might increase sexual competition among parthenogenetic females since bisexual reproduction is also available for them (as proved by the existence of hybrids).

Additionally, habitat structure may also have an effect. On the one hand, the open habitat of our study area providing unrestricted basking opportunities contrasts with that described by Galoyan (2013) where lizards would be forced to overlap on the scarce sun patches in an area dominated by forest. Moreover, differential habitat selection between species has been reported for Armenia (Arakelyan et al., 2011), with *D. valentini* tend-

ing to occupy meadows and grassland, *D. unisexualis* steep rocky exposures, and *D. armeniaca* being intermediate in habitat use. If this holds true here, we may at least expect a more aggregated distribution of *D. unisexualis* associated with rocky outcrops and, hence, home range overlap being more likely. Whatever the case, our results for the bisexual species are in accordance with Rose's (1981) main conclusions, who considers that the main function of home ranges on male lizards is to maintain a reproduction area while on female lizards it is exclusively a foraging area. However, the pattern found in parthenogenetic species suggests a shift in the presence of a bisexual species.

Although our study is constrained by the low sample sizes resulting from a concentrated period of observation, we believe that more time would not have shown different results because of the proportions of the different categories here compared. Indeed, long-term studies may even increase the uncertainty on home range estimation. In particular, home ranges are not static but can change through time (e.g. in a seasonal sequence; Boudjemadi et al., 1999, Vignoli, Vuerich, & Bologna, 2012; Galoyan, 2013). Thus, pooling observations recorded during long periods may result in incorrect inferences on individual resilience and, ultimately, in home range overestimation. Only a high record density across short periods will increase the quality of home range estimation, a recommendation which can be extended to most home range studies. Remarkably, each reproduction mode and sex group had similar home range sizes and responded in the same way to the several variables analysed. The coherence of our results must be taken as a sign of reliability. More sampling time would certainly increase the number of locations per individual, but not the number of individuals, while social dispersal would disturb home range estimations (Boudjemadi et al., 1999, Vignoli et al., 2012). The low density of the bisexual species at Kuchak is noteworthy and is especially marked for females. We randomly captured only five individuals of *D. valentini* against 21 individuals of parthenogens and hybrids, which could be in accordance with the suggestions of outcompetition by parthenogens (Tarkhnishvili et al., 2010).

When comparing the current results with those in the literature, it is important to take into account that our study was not focused on individuals regardless of the location (i.e. radio-telemetry studies; Powell & Mitchell, 2012), but on individuals living within a study area. Certainly, some lizards may partially move outside the study area and then they will have smaller MCP values. Classifying individuals as residents, wanderers, and passers-through (Galoyan, 2013) would be arbitrary. As lizards were not monitored outside the study area, there is no guarantee that their home ranges extend outside it or that some were simply predated (pers. obs.). These methodological aspects (time and method of monitoring, size of the study area) should be better defined for future home range studies.

The lack of GIS layers hampered a proper spatial analysis of the distribution of home ranges, namely for testing the importance of some environmental variables as limiting factors (Sillero & Gonçalves-Seco, 2014). Future studies must enhance recapture probabilities by renewing the visual marks or use other types of visual marks with a longer durability. Certainly, *Darevskia* rock lizards constitute optimal model organisms for determining the function of home ranges and of the factors involved. Further studies are necessary to compare other *Darevskia* communities with the same or different species in order to obtain more general inferences.

Acknowledgements

We thank Marine Arakelyan and students of Yerevan State University for helping in fieldwork and lizard identification. Animal captures were covered by the agreement between CIBIO and

Yerevan State University within the framework of the Gulbenkian Foundation project. No lizards or their habitats were damaged during this study.

Funding

This work was partially funded by FCOMP-01-0124-FEDER-007062 Fundação para a Ciência e a Tecnologia under the projects HOUSE PTDC/BIA-BEC/102280/2008 and PTDC/BIA-BEC/101256/2008; by the project “Biodiversity, Ecology and Global Change” co-financed by North Portugal Regional Operational Programme 2007/2013 (ON.2 – O Novo Norte), under the National Strategic Reference Framework (NSRF), under the European Regional Development Fund (ERDF); and by the project “Preserving Armenian biodiversity: Joint Portuguese-Armenian program for training in modern conservation biology” of the Gulbenkian Foundation (Portugal).

Disclosure Statement

No potential conflict of interest was reported by the authors.

References

- Arakelyan, M., Danielyan, F., Corti, C., Sindaco, R., & Leviton, A. E. (2011): *Herpetofauna of Armenia and Nagorno Karabakh*. San Francisco: Society for the Study of Amphibians and Reptiles.
- Arnold, E. N., Arribas, O., & Carranza, S. (2007): Systematics of the Palearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa*, 1430, 1–86.
- Boag, D.A. (1973). Spatial relationships among members of a population of wall lizards. *Oecologia*, 12, 1–13.
- Boudjemadi, K., Lecomte, J., & Clobert, J. (1999): Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. *Journal of Animal Ecology*, 68, 1207–1224.
- Calenge, C. (2011): *Home range estimation in R: the adehabitatHR Package*. R package vignette. <https://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf>.
- Carazo, P., Font, E., & Desfilis, E. (2008): Beyond “nasty neighbours” and “dear enemies”? Individual recognition by scent marks in a lizard (*Podarcis hispanica*). *Animal Behaviour*, 76, 1953–1963.
- Carazo, P., Font, E., & Desfilis, E. (2011): The role of scent marks in female choice of territories and refuges in a lizard (*Podarcis hispanica*). *Journal of Comparative Psychology*, 125, 362–365.
- Christian, K.A., & Waldschmidt, S. (1984): The relationship between lizard home range and body size: a reanalysis of the data. *Herpetologica*, 40, 68–75.
- Danielyan, F., Arakelyan, M., & Stepanyan, I. (2008): Hybrids of *Darevskia valentini*, *D. armeniaca* and *D. unisexualis* from a sympatric population in Armenia. *Amphibia-Reptilia*, 28, 487–504.
- Darevsky, I. S. (1967): *Rock lizards of the Caucasus (systematics, ecology and phylogenesis of the polymorphic groups of rock lizards of the subgenus Archaeolacerta* [Translation in English]. Leningrad: Nauka.
- Diego-Rasilla, F. J., & Pérez-Mellado, V. (2003): Home range and habitat selection by *Podarcis hispanica* (Squamata, Lacertidae) in Western Spain. *Folia Zoologica*, 52, 87–98.
- Eifler, D. A. (1996): Experimental manipulation of spacing patterns in the widely foraging lizard *Cnemidophorus uniparens*. *Herpetologica*, 52, 477–486.
- Eifler, D. A., & Eifler, M. A. (1998): Foraging behavior and spacing patterns of the lizard *Cnemidophorus uniparens*. *Journal of Herpetology*, 32, 24–33.
- Galoyan, E. (2013): Joint space use in a parthenogenetic Armenian rock lizard (*Darevskia armeniaca*) suggests weak competition among monoclonal females. *Journal of Herpetology*, 47, 97–104.

- García-Muñoz, E., Ceacero, F., Pedrajas, L., & Carretero, M.A. (2011): Tail tip removal for tissue sampling has no short-term effects on microhabitat selection by *Podarcis bocagei*, but induced autotomy does. *Acta Herpetologica*, 6, 223–227.
- García-Muñoz, E., & Sillero, N. (2010): Two new types of noose for capturing herps. *Acta Herpetologica*, 5, 259–263.
- Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J., & Wilmers, C. C. (2007): LoCoH: Nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS One*, 2, e207.
- Gil, M., Pérez-Mellado, V., & Guerrero, F. (1988): Estructura del hábitat y dominios vitales en *Podarcis hispanica* (Steindachner, 1870). *Miscellanea Zoologica*, 12, 273–281.
- Goodman, R. M., Echternacht, A. C., & Burton, F. J. (2005): Spatial ecology of the endangered iguana, *Cyclura lewisi*, in a disturbed setting on Grand Cayman. *Journal of Herpetology*, 3, 402–408.
- Griffiths, A. D. (1999): Demography and home range of the frillneck lizard, *Chlamydosaurus kingii* (Agamidae), in northern Australia. *Copeia*, 1999, 1089–1096.
- Haenel, G. J., Smith, L. C., & John-Alder, H. B. (2003a): Home-range analysis in *Sceloporus undulatus* (Eastern fence lizard). I. Spacing patterns and the context of territorial behavior. *Copeia*, 2003, 99–112.
- Haenel, G. J., Smith, L. C., & John-Alder, H. B. (2003b): Home-range analysis in *Sceloporus undulatus*. II. A test of spatial relationships and reproductive success. *Copeia*, 2003, 113–123.
- Haldane, J. (1922): Sex ratio and unisexual sterility in hybrid animals. *Journal of Genetics*, 12, 101–109.
- Jennrich, R. I., & Turner, F. B. (1969): Measurement of non-circular home range. *Journal of Theoretical Biology*, 22, 227–237.
- Kaliontzopoulou, A., Adams, D. C., Meijden, A., Perera, A., & Carretero, M. A. (2012): Relationships between head morphology, bite performance and ecology in two species of *Podarcis* wall lizards. *Evolution and Ecology*, 26, 825–845.
- Kaliontzopoulou, A., Carretero, M. A., & Llorente, G. A. (2006): Patterns of shape and size sexual dimorphism in a population of *Podarcis hispanica* (Reptilia: Lacertidae) from NE Iberia. Pp 73–89. In: Corti, C., Lo Cascio, P., & Biaggini, M. (Eds.), *Mainland and insular lacertid lizards: a Mediterranean perspective*. Firenze: University Press.
- Kaliontzopoulou, A., Carretero, M. A., & Llorente, G. A. (2007): Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. *Journal of Morphology*, 268, 152–165.
- Laver, P. N., & Kelly, M. J. (2008): A critical review of home range studies. *Journal of Wildlife Management*, 72, 290–298.
- Lewis, A. R., & Saliva, J. E. (1987): Effects of sex and size on home range, dominance, and activity budgets in *Ameiva exsul* (Lacertilia: Teiidae). *Herpetologica*, 43, 374–383.
- Mahrt, L. A. (1998): Territorial establishment and maintenance by female tree lizards, *Urosaurus ornatus*. *Journal of Herpetology*, 32, 176–182.
- Melville, J., & Swain, R. (1999): Home-range characteristics of an alpine lizard, *Niveoscincus microlepidotus* (Scincidae), on Mtn Wellington, Southern Tasmania. *Wildlife Research*, 26, 263–270.
- Morrison, S. F., Keogh, J. S., & Scott, A. W. (2002): Molecular determination of paternity in a natural population of the multiply mating polygynous lizard *Eulamprus heatwolei*. *Molecular Ecology*, 12, 535–545.
- Murphy, R. W., Darevsky, I. S., MacCulloch, R. D., Fu, J., & Kupriyanova, L. A. (1996): Evolution of the bisexual species of Caucasian rock lizards: a phylogenetic evaluation of allozyme data. *Russian Journal of Herpetology*, 6, 18–31.
- Olsson, M. (1986): Spatial distribution and home range size in the Swedish sand lizard (*Lacerta agilis*) during the mating season. Pp. 597–600. In: Z. Roček (Ed.), *Studies in Herpetology*. Prague: Societas Herpetologica Europea.
- Olsson, M., Gullberg, A., & Tegelström, H. (1997): Determinants of breeding dispersal in the sand lizard, *Lacerta agilis*, (Reptilia, Squamata). *Biological Journal of the Linnean Society*, 60, 243–256.

- Olsson, M., Gullberg, A., Tegelström, H., Madsen, T., & Shine, R. (1994): Rewards of “promiscuity”. *Nature*, 372, 230.
- Pérez-Buitrago, N., Sabat, A. M., & McMillan, W. O. (2010): Spatial ecology of the endangered Mona Island iguana *Cyclura cornuta stejnegeri*: does territorial behavior regulate density? *Herpetological Monographs*, 24, 86–110.
- Perry, G., & Garland, T. (2002): Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. *Ecology*, 83, 1870–1885.
- Powell, R. A., & Mitchell, M. S. (2012): What is a home range? *Journal of Mammalogy*, 93, 948–958.
- R Development Core Team. (2012). R: *A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Rose, B. (1981): Factors affecting activity in *Sceloporus virgatus*. *Ecology*, 62, 706–716.
- Row, J. R., & Blouin-Demers, G. (2006): Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia*, 2006, 797–802.
- Ruby, D. E., & Dunham, A. E. (1987): Variation in home range size along an elevational gradient in the iguanid lizard *Sceloporus merriami*. *Oecologia*, 71, 473–480.
- Sillero, N., & Gonçalves-Seco, L. (2014): Spatial structure analysis of a reptile community with airborne LiDAR data. *International Journal Geographical Information Science*, 28, 1709–1722.
- Stamps, J. A., Losos, J. B., & Andrews, R. M. (1997): A comparative study of population density and sexual size dimorphism in lizards. *American Naturalist*, 149, 64–90.
- Tarkhnishvili, D., Gavashelishvili, A., Avaliani, A., Murtskhvaladze, M., & Mumladze, L. (2010): Unisexual rock lizard might be outcompeting its bisexual progenitors in the Caucasus. *Biological Journal of the Linnean Society*, 101, 447–460.
- Tsellarius, A. Y., & Tsellarius, E. Y. (2005): Space use pattern and mating system of Rock Lizard – *Lacerta saxicola* (Reptilia, Sauria) [in Russian]. *Modern Herpetology*, 3, 99–110.
- Tsellarius, A. Y., & Tsellarius, E. Y. (2006): Forming and defense of individual space of Rock Lizard males (*Lacerta saxicola*, Sauria). 2. Territory and territorial relations [in Russian]. *Russian Journal of Zoology*, 85, 73–83.
- Verwajen, D., & Van Damme, R. (2008): Wide home ranges for widely foraging lizards. *Zoology*, 111, 37–47.
- Vignoli, L., Vuerich, V., & Bologna, M. A. (2012): Experimental study of dispersal behavior in a wall lizard species (*Podarcis muralis*, Sauria, Lacertidae). *Ethology, Ecology, Evolution*, 24, 244–256.