Acta Herpetologica 13(2): 155-163, 2018
DOI: 10.13128/Acta_Herpetol-22830

Short term spatial structure of a lizard (*Darevskia* sp.) community in Armenia

Neftalí Sillero[1,*], Elena Argaña[1], Susana Freitas[2,3], Enrique García-Muñoz[2], Marine Arakelyan[4], Claudia Corti[5], Miguel A. Carretero[2]

[1] *CICGE Centro de Investigação em Ciências Geo-Espaciais, Faculdade de Ciências da Universidade do Porto (FCUP), Observatório Astronómico Prof. Manuel de Barros, Alameda do Monte da Virgem, 4430-146, Vila Nova de Gaia, Portugal. *Corresponding author.* E-mail: neftali.sillero@gmail.com
[2] *CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus de Vairão, Rua Padre Armando Quintas, Nº 7. 4485-661 Vairão, Vila do Conde, Portugal*
[3] *Department of Animal and Plant Sciences, The University of Sheffield, Sheffield S10 2TN, UK*
[4] *Faculty of Biology, Yerevan State University, Alek Manoogian 1, 0025, Yerevan, Armenia*
[5] *Museo di Storia Naturale dell'Università di Firenze, Sezione di Zoologia "La Specola", Via Romana 17, 50125 Firenze, Italia*

Submitted on: 2018, 6th March; revised on: 2018, 18th September; accepted on: 2018, 30th September
Editor: Simon Baeckens

Abstract. Factors driving the spatial patterns of communities of sedentary organisms are still poorly understood. In this context parthenogenetic animals are useful to test the contribution of sexual and interspecific interactions on spatial patterns. As such, mixed communities of asexual and sexual species are expected to be spatially organized as a single sexual species, with sexes randomly distributed and mutually independent. During the reproductive period, we determined the instantaneous spatial structure in a community of *Darevskia* rock lizards from Armenia composed of one sexual species (*D. valentini*), two asexual species (*D. armeniaca*, *D. unisexualis*), and their hybrids. We also analysed the specific composition of clusters and the species segregation by habitat. We used the Ripley's K distance function to measure clustering spatial patterns, and the Delaunay's triangulation to identify the clusters and their specific composition. We estimated the spatial segregation among species by calculating the overlap between species pairs, by comparing pairwise distances from males to other males and from males to females, and by comparing the frequencies of both sexes and reproduction modes (asexual and sexual) in plant cover and height using log-linear models. Species displayed a clustered spatial structure, with parthenogens (mainly *D. armeniaca*) or their hybrids in all clusters. Females and males were concentrated in areas with medium plant cover. *D. armeniaca* and *D. valentini* were the species with the highest overlap. Males were closer to males than to females. This community displays an instantaneous spatial pattern resembling a population of a single sexual species. Spatial statistics offer new insights to analyse the spatial structure of species communities.

Keywords. Armenia, *Darevskia*, GIS, local distribution patterns, spatial statistics.

INTRODUCTION

The analysis of the short-term spatial structure within a community of species with low dispersal allows understanding how individuals share the space and modify their home ranges depending on the presence of other species (competitors, predators, prey items) or other environmental factors (temperature, shelters) (Sillero and Goncalves-Seco, 2014; Sillero and Gomes, 2016). Contrary to home range analyses on the spatial needs of single individuals, species distribution analysis focuses on the presence of one or more species in a particular geograph-

ISSN 1827-9635 (print)
ISSN 1827-9643 (online)

© Firenze University Press
www.fupress.com/ah

ical area characterized by certain environmental variables (mainly climate) at coarse scales (regional or continental) (Sillero et al., 2014; Sillero and Gomes, 2016). Linking both analytical levels, community spatial distributions can identify the main environmental factors with a high spatial resolution, applying techniques of species distribution studies to the same scale of home ranges but during short time periods and with a different purpose. Namely, the community spatial distribution approach aims at providing a snapshot of the multispecies spatial patterns at a local scale. As such, species' interactions can be revealed without collecting repeatedly individual data (as required for home range studies).

Species within a community can be distributed randomly, regularly, or in clusters (Gorton et al., 1979; Frost and Bergmann, 2012). Random distributions are typical of non-territorial or non-competing species living in habitats with abundant and widespread resources. The probability of finding an individual is the same across the study area and independent from the presence of other individuals. Species can be regularly distributed when individuals avoid being mutually close (due competition or territoriality) and resources are evenly distributed. Species appear clustered when the resources are irregularly distributed, hence, the probability to find either a second individual near the first or areas without individuals is higher than expected by random. Clustering is the most frequent pattern observed in communities (Underwood and Chapman, 1996) with variable intensity (Moody et al., 1997). However, distribution patterns may also shift in time. For instance, some species shift from regular to clustered distribution as population density increases (Gorton et al., 1979).

Many potential factors may drive the spatial structure of a multispecies community, including the distribution of energy or matter sources (light, water, soil nutrients, food), availability of shelters and resting places, presence of other species (predators, competitors, parasites), mates and other conspecifics. In animals, few studies describe how populations are locally distributed (Frost and Bergmann, 2012; Sillero and Gonçalves-Seco, 2014) and even less considered as well species interactions (Underwood and Chapman, 1996). Therefore, the factors driving the distribution pattern of a community are still poorly understood. In this context, the spatial ecology of parthenogenetic (all-female) species can be particularly elucidative as it may provide insights on the contribution of sexual reproduction to species' spatial patterns. Are parthenogenetic species using the space in a similar way as their sexual relatives? How are both types of species spatially organized when they coincide? In particular, parthenogenetic lizards can provide an excellent model system for testing the effects of sexual and interspecific interactions on spatial patterns.

Some studies analysed the home ranges of single parthenogenetic lizards (Eifler and Eifler, 1998; Galoyan, 2013), but only Sillero et al. (2016) considered several species in sympatry and none analysed the community spatial distributions. According to the lizard literature, adult males and females often are randomly distributed, while juveniles have a regular distribution, as they are excluded to less suitable habitats (Frost and Bergmann, 2012; Sillero and Gonçalves-Seco, 2014). In principle, a population of a parthenogenetic species may have a more clustered distribution. In fact, our non-systematic observations reported groups of many females basking together in the same spot, as expected from the lack of mate competition and aggregation for resources. However, following Sillero et al., (2016), if a mixed community composed of asexual and sexual species behaves like a population composed by a single sexual species, we should expect a similar spatial pattern: both sexes distributed randomly (Frost and Bergmann, 2012). Therefore, if there is no competition for limited resources but only interferences among individuals (Žagar et al., 2015) of asexual and sexual species, we should expect their distributions to be mutually independent (depending only on conspecifics and resources). On the contrary, if they compete for space we should expect larger distance between heterospecifics than between conspecifics.

The main aim of this work is, hence, to analyse the instantaneous spatial structure of a lizard mixed community in order to determine whether different species segregate spatially or not. Here, we studied a community of lizards in true sympatry composed of several *Darevskia* species (*Darevskia armeniaca*, *D. valentini*, *D. unisexualis*) and their hybrids at Kuchak, Armenia (Danielyan et al., 2008). The genus *Darevskia* (Arribas, 1999), the first vertebrate group where parthenogenesis was described (Darevsky, 1967), occurs across all Caucasus, adjacent regions of Asia Minor, northern Iran and Balkans. A total of 25 sexual species and seven parthenogenetic forms have been described (Darevsky, 1967; Fu et al., 1995; Murphy et al., 1996; Arnold et al., 2007; Freitas et al., 2016b) although their phylogenetic relationships and taxonomy are still under discussion. In Armenia, up to nine *Darevskia* species occur along a relatively small area and frequently overlap locally (Arakelyan et al., 2011). Specifically, the aims of this study are:

(1) To determine whether the short-term spatial structure of a community of lizards displays a clustered, random, or regular distribution. We predict that the species will not be distributed randomly or regularly along

the study area, but in clusters, largely determined by the spatial structure of the area.

(2) To identify the community clusters and their specific composition. We hypothesize that lizards will form clusters of several species, since parthenogenetic female lizards are supposed to be less aggressive than sexual females (Tarkhnishvili et al., 2010), and asexual populations have been reported to attain higher densities than sexual ones in similar habitats (Darevsky, 1967). As we do not expect much behavioural interference between species, parthenogens will be present in almost all clusters due to their low intraspecific aggressiveness and high population density (Tarkhnishvili et al., 2010).

(3) To determine if habitat is a segregating factor among species, given differential habitat selection among species has been reported for Armenia (Arakelyan et al., 2011) with *D. valentini* tending to occupy meadows and grassland scattered with rocks, *D. unisexualis* steep rocky exposures, and *D. armeniaca* being intermediate in habitat use.

MATERIALS AND METHODS

Study area

The study area was located near the village of Kuchak (Armenia; 44.385 N, 40.532 W, ca. 1940 m a.s.l.; Fig. 1) at the foothills of Mount Aragats. The study area includes several longitudinal rocky outcrops alternating with grasslands and bushes (for a general view of the landscape see Figure 151 in Arakelyan et al., 2011). These outcrops are composed by accumulations of big rock boulders, reaching an approximate altitude of 1955 m a.s.l. in the highest point. Sampling was performed around the highest outcrops (0.34 ha; Fig. 1). Previous surveys had identified high density of lizards in the study area.

Species community composition

The lizard community was composed of three species: one sexual (*Darevskia valentini*) and two asexual (*D. armeniaca*, *D. unisexualis*), as well as two hybrid forms (*D. valentini*/*D. armeniaca*, *D. valentini*/*D. unisexualis*). In this locality hybridisation between sexual and asexual species is frequent, producing both diploid and polyploid hybrids (Danielyan et al., 2008). Individuals were first determined at species level using external characteristics according to Darevsky (1967), Danielyan et al. (2008), and Arakelyan et al. (2011) and then corroborated by microsatellite analysis (Freitas et al., 2016a).

Surveys

We performed intensive surveys across the study area during three consecutive days (1-3 June 2011), coinciding with the reproductive period (Arakelyan et al., 2011). We concentrated sampling effort within a short time period to prevent pooling spatial locations shifted in time as expected from dispersal mediated by social interactions or with seasonal changes on home ranges (Boudjemadi et al., 1999; Galoyan, 2013). Each survey took around 8 hours covering the whole study area (Fig. 1). We surveyed all outcrops inside the study area. Therefore, each zone of the study area was visited only once. Lizards were also captured once to prevent pseudo-replication, we used tail-removal for parallel genetic analyses (see below) as individual mark. We recorded the position of each lizard with a professional GPS unit (Trimble GeoExplorer, 2008 HX), with a precision of 50 cm after post-processing.

Data collection and lizard capturing

We created a GPS data dictionary with Trimble GPS Pathfinder office software v 5.0, transferring it posteriorly to the GPS unit. For all the observed lizards we recorded species, size class, sex; plant cover (0-25, 25-50, 50-75, 75-100%); and plant height (top, middle, down). Two team members (NS and EGM) walked randomly through the study area capturing lizards with a noose (García-Muñoz and Sillero, 2010). MAC measured SVL with a calliper to the nearest 0.01 mm and took pictures of each individual for confirmation of species identifications. Finally, EA recorded the exact location of the individual with the GPS unit as well as introduced all the data inside the GPS dictionary. In the end, we released each lizard in the exact capture site. The tail tip of each lizard was collected and kept for later genetic analyses, in order to confirm species determinations (Freitas et al., 2016a).

Global clustering analysis

We applied several tests of spatial statistics to describe the distribution pattern of the lizards. First, we analysed the distance threshold of clustering for all the species together. Subsequently, we grouped species by reproductive mode (parthenogens: *Darevskia armeniaca* and *D. unisexualis*; and sexual individuals: *D. valentini* and hybrids). For this, we used the Ripley's K distance function (Bivand et al., 2008; Ripley, 1976; Rogerson, 2001), which measures the distribution of pairwise distances among events. The Ripley's K function was calculated using the envelope function of the package "spatstat" (Baddeley and Turner, 2005) of the R software (R Team, 2014). In addition, a complete spatial randomness (CSR) point process with the same estimated intensity in the study area was simulated (999 replicates) and compared with the empirical values of Ripley's K, to check whether the empirical function is contained inside.

Determination of topological clusters

Many methods have been proposed to determine clusters in a cloud of points (Bivand et al., 2008; Rogerson, 2001). What is considered a cluster, depends on the size of the study

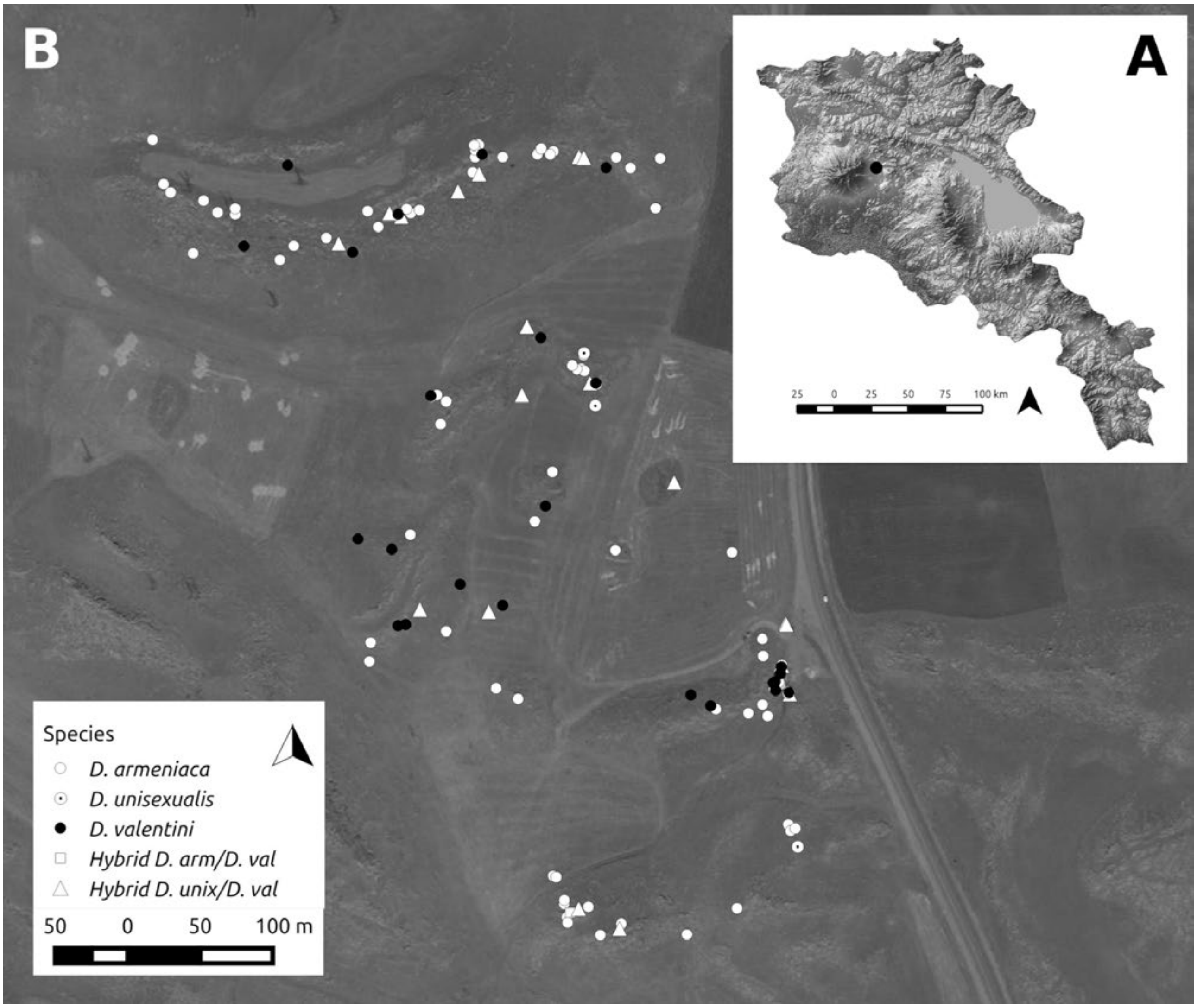

Fig. 1. Study area and records distribution. A: The study area was located near the village of Kuchak (Armenia) at the foothills of Mount Aragats. B: The lizard community is composed by one sexual species *Darevskia valentini*, two parthenogens (*D. armeniaca* and *D. unisexualis*) and the hybrids between the sexual and the asexual species.

area and a threshold distance (Sillero and Gonçalves-Seco, 2014). Multiple solutions are possible to define clusters inside a cloud of points, depending on the distance threshold selected, i.e. the distance where any cluster point is farther from any point outside the cluster. In order to avoid subjective solutions, this threshold distance must be determined statistically. Reliable solutions are distance functions like the K function (Ripley, 1976) or the Nearest Neighbor Index (NNI; Clark and Evans, 1954). Every pair of points separated by a distance below the threshold distance is supposed to belong to the same cluster. In our study case, we used the Delaunay's triangulation to identify spatially the clusters of lizards' locations using the expected mean distance between neighbours provided by the NNI as statistical threshold. The Delaunay's triangulation is a very well-known mathematical method, where for a given set P of discrete points in a plane, a triangulation is defined that no point in P is inside the circumcircle of any triangle in the plane. The expected distance provided by the NNI determines a cluster when the mean nearest neighbour distance is lower than the expected nearest neighbour distance. We selected the Delaunay triangles with lines shorter than the expected nearest neighbour distance (Clark and Evans, 1954). The points inside the selected Delaunay triangles were considered clustered. This analysis was performed in QGIS 2.0.

Spatial segregation

We measured the spatial segregation among species in two different ways. First, we calculated the degree of overlap between species pairs. We calculated buffers with a radius equal to the expected nearest neighbour distance (Clark and Evans, 1954). We expect that species sharing space will have a high degree of overlap, while those spatially segregated will have a low degree of overlap. The overlaps were calculated with the Intersect function of QGIS 2.8. And second, we tested if males and females used differently habitats by means of log-linear models of the frequencies of both sexes and reproduction modes (asexual and sexual) in plant cover and height.

RESULTS

In the surveys we found a total of 149 lizards (Table 1 and Fig. 1): 101 *Darevskia armeniaca*, three *D. unisexualis*, 24 *D. valentini*, and 21 triploid hybrids (two *D. armeniaca* – *D. valentini*, and 19 *D. unisexualis* – *D. valentini*). There were fewer females of *D. valentini* (six) in comparison with hybrid females (13; Table 1 and Fig. 1). However, we found 18 males of *D. valentini* and only eight hybrid males (Table 1 and Fig. 1).

Ripley's K indicated that all species presented a clustered distribution, either together or grouped by reproduction mode (parthenogenetic and sexual individuals; Fig. 2).

We identified 11 clusters located in the north and in the south of the study area, with two clusters in the middle (Fig. 3). *D. armeniaca* was the main species inside the clusters (Table 2). The clusters were composed of one to three species, with at least one parthenogen or hybrid participating (Table 2). Nevertheless, *D. unisexualis* never participated in a cluster (Table 2).

The species pairs with the lowest overlap always included *D. unisexualis*. In fact, there was not overlap between *D. unisexualis* and hybrids of *D. armeniaca/D. valentini*. The pair of species overlapping the most was *D. armeniaca* and *D. valentini* (Table 3). Females and males used similar plant heights ($\chi^2 = 0.411$, P = 0.873; Table 4); both used areas with intermediate plant cover more often than expected by chance ($\chi^2 = 8.451$, P = 0.014; Table 4). Lizards with both types of reproduction were more frequent at middle height and in areas with intermediate plant cover (respectively: $\chi^2 = 1.946$, P = 0.378; $\chi^2 = 6.197$, P = 0.045; Table 4). When considering sex and reproduction mode, all individuals were associated to middle plant heights ($\chi^2 = 2.485$, P = 0.672; Table 4), and used intermediate plant cover more often than expected by chance ($\chi^2 = 9.543$, P = 0.044; Table 4).

DISCUSSION

As predicted, species were not distributed randomly or regularly in the space but presented a clustered distribution, either together or separately, as expected if resources within the study area were not randomly distributed (Kwiatkowski and Sullivan, 2002). Indeed, since Kuchak area is composed by longitudinal rock outcrops alternating with grasslands and bushes, refuges and basking sites can be considered the main constraints for lizards. In fact, other studies on lizards' communities showed similar results (Sillero and Gonçalves-Seco, 2014; Sillero and Gomes, 2016).

Local clusters were composed of one to three species. As predicted, parthenogens (except *Darevskia unisexualis*) or their hybrids were present in all clusters probably due to their lower intraspecific aggressiveness (Galoyan, 2013) and high abundance (Tarkhnishvili et al., 2010). Particularly, *D. armeniaca*, the most abundant species in Kuchak, entered in all clusters. Conversely, *D. unisexualis* did not enter in any cluster, likely because of its low presence in Kuchak (only three individuals recorded). Asexual females are supposed to be less aggressive than sexual females (Tarkhnishvili et al., 2010; Galoyan, 2013) and asexual populations have been reported to attain higher densities than sexual ones in similar habitats (Darevsky, 1967). It is important to highlight here that *D. valentini*

Table 1. List of species detected and number of records per species, sex, and age.

Species	Female			Male		
	Adult	Subadult	Juvenile	Adult	Subadult	Juvenile
D. armeniaca	96	2	3			
D. unisexualis	3					
D. valentini	6			17	1	
Hybrid *D. arm -D. val*	2					
Hybrid *D. uni- D. val*	9	1	1	6	1	1
Total Result	**116**	**3**	**4**	**23**	**2**	**1**

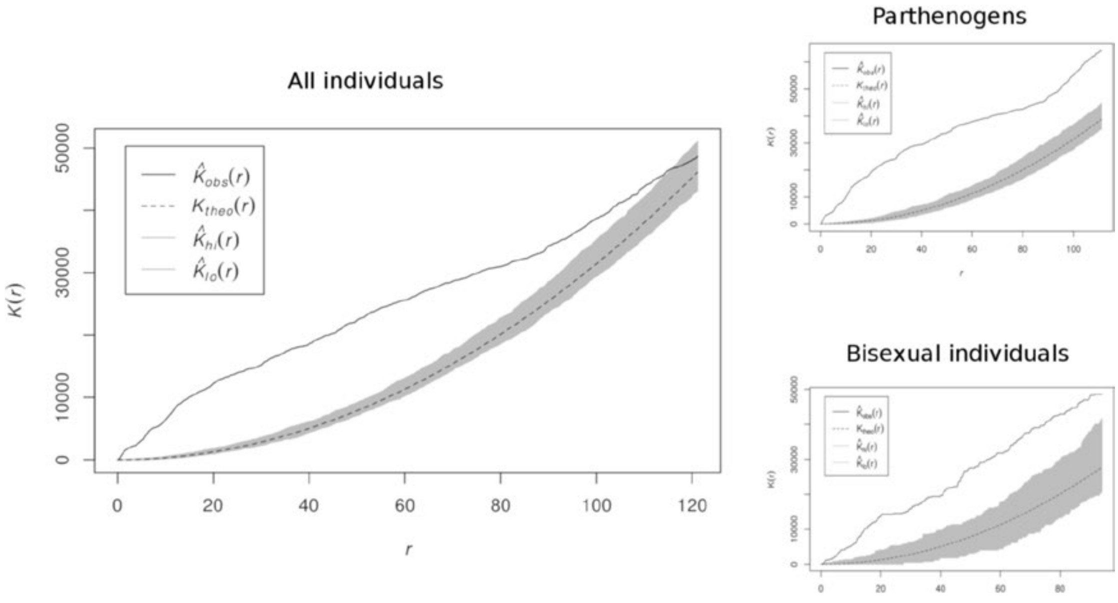

Fig. 2. Ripley's K plots of all records together and grouped by reproduction modes (parthenogens: *Darevskia armeniaca* and *D. unisexualis*; and sexual individuals: *D. valentini* and hybrids). The continuous line is the observed function of the species records; the dashed line is the theoretical function of a complete spatial randomness (CSR) point process; and the grey shadow is the lower and higher limits of the CSR point process after 999 replications. If the observed function is above the CSR limits, the point process is considered as clustered; if it is below the limits, as regular; if it is between the limits, as random.

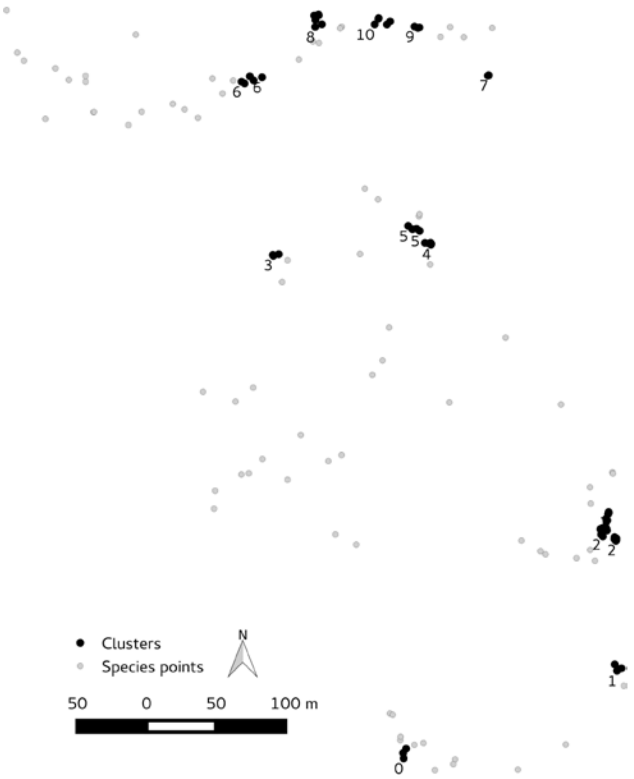

Fig. 3. Distribution of clusters identified with Delaunay triangulation and the expected nearest neighbour distance (see methods for more details). Numbers refer to cluster numbers in Table 2.

Table 2. Number of species records per cluster. A cluster is a set of points where the distance to any point inside the cluster is farther from any other point outside the cluster. Cluster distance was determined using the expected nearest neighbour distance (20 m). See methods for more details. Column numbers refer to cluster numbers in Figure 3.

Species	0	1	2	3	4	5	6	7	8	9	10	Total
D. armeniaca	2	3	23	2	3	4	3	3	5	1	5	54
D. unisexualis												0
D. valentini			6	1	1		1		1			10
Hybrid *D. arm – D. val*	1		1									2
Hybrid *D. uni – D. val*			2		1		1			2		6
Total	3	3	32	3	5	4	5	3	6	3	5	72

females seem to be in minority in Kuchak, while hybrid females are more abundant. This pattern was also found by Danielyan et al. (2008), Sillero et al. (2016) and Carretero et al. (2018) in the same site in different years.

Females and males were concentrated in areas with medium plant cover. We were not able to confirm that *D. valentini* occupies ground habitats, i.e. meadows and grassland as described in general for Armenia (Arakelyan et al., 2011). As reported previously, sexual species (as well as parthenogens) were located mainly in habitats of middle height, which do not correspond to ground habi-

Table 3. Spatial segregation by pairs of species. Values are ranked from lowest to the highest degree of overlap.

Species pairs	Overlap (m^2)
D. unix × H *D. arm*	0.00
D. uni × H *D. uni*	1034.96
D. uni × *D. val*	1143.84
D. val × H *D. arm*	1236.06
H *D. arm* × H *D. uni*	2158.25
D. arm × H *D. arm*	2472.13
D. arm × *D. uni*	2650.51
D. val × H *D. uni*	8852.00
D. arm × H *D. uni*	11716.96
D. arm × *D. val*	13852.21

D. arm: *Darevskia armeniaca*; *D. uni*: *D. unisexualis*; *D. val*: *D. valentini*; H *D. arm*: Hybrid *D. armeniaca-D. valentini*; H *D. uni*: Hybrid *D. unisexualis-D. valentini.*

tats (Arakelyan et al., 2011). Distance analyses showed *D. armeniaca* and *D. valentini* were the species with a higher degree of overlap. This was expected since the first species is present in all habitats across the area. In contrast, *D. unisexualis* was included only in the clusters with the lowest overlaps, probably because of its low presence in Kuchak. As we stated above, the low abundance of this species was mostly responsible for its absence in clusters. These results seem to confirm that the Kuchak community acts like a sexual population of a single species (Sillero et al., 2016), even if strongly biased in sex ratio (Carretero et al., 2018). This is corroborated by the indirect evidence from inguinal scars in females which indicate that copulation attempts between species are as frequent as within species in this community (Carretero et al., 2018). The low density of *D. valentini* females strongly supports this conclusion. *D valentini* females are scarce likely due to genetic incompatibilities (Haldane's rule) and parthenogens (and hybrid females) may be replacing them even for sexual interactions (Sillero et al., 2016). On the other hand, the species pair with the lowest overlap was constituted by both types of hybrids, likely because they are scarce and tend to behave like normal sexual species.

Local spatial segregation by habitat or competition has been also related to clustered distribution patterns (Underwood and Chapman, 1996), with different degrees of intensity (Moody et al., 1997). Habitat is the main segregating factor in several communities of reptiles (Jones and Droge, 1980; Mellado, 1980; Scali and Zuffi, 1994). Micro-habitat selection promotes spatial segregation in lizards (Ortega and Barbault, 1982): juveniles of *Anolis aeneus* occupy open habitats instead of forests to avoid predation by *A. richardi* (Stamps, 1983a, 1983b). Spatial segregation in birds can be caused by competition between species (Moody et al., 1997). Plants segregate due to competition (Phillips and MacMahon, 1981; Haase et al., 1996; Getzin et al., 2006; Gray and He, 2009) and habitat selection (Schenk et al., 2003).

Overall, spatial statistics offer new insights to interpret the spatial structure of species communities. By having a better statistical support, we were able to interpret how and why species segregate locally in space. This could be completed by a habitat segregation analysis as a continuous component of the environment once geographical information of habitats will be made available for Armenia. Although some spatial statistic methods require data with homogeneous intensity, the clustering and overlapping analyses applied here do not require this assumption as they are topographical distance-based

Table 4. Number of individuals per plant height (down, middle, top) and plant cover (0-25, 25-50, 50-75, 75-100%), grouped by sex as well as sex and reproduction mode.

	Height				Plant Cover %			
	Down	Middle	Top	Total	0-25	25-50	50-75	Total
Sex								
Female	24	74	25	123	32	86	23	123
Male	6	16	4	26	1	22	3	26
Total	30	90	29	149	33	90	26	149
Sex/Rep Mode								
Sexual Female	6	10	3	19	5	12	2	19
Sexual Male	6	16	4	26	1	22	3	26
Asexual Female	18	64	22	104	27	56	21	104
Total	30	90	29	149	33	90	26	149

methods. As such, they are independent of the type of intensity distribution. Therefore, these methods perform better than standard ones when the sample size is low and the intensity is heterogeneous. Then, studies of spatial biology can be more frequent and we will have a better insight on questions such as species segregation and habitat use of species communities.

ACKNOWLEDGMENTS

NS was supported by a post-doctoral grant (SFRH/BPD/26666/2006) and research contract (IF2013) from Fundação para a Ciência e Tecnologia (FCT, Portugal) and MAC is supported by project This research was supported by the FCT projects FCOMP-01-0124-FEDER-007062, PTDC/BIA-BEC/102280/2008, FCOMP-01-0124-FEDER-008929, 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 ¨C O Novo Norte), under the National Strategic Reference Framework (NSRF), through the European Regional Development Fund (ERDF) and by the project "Preserving Armenian biodiversity: Joint Portuguese ¨C Armenian program for training in modern conservation biology." of Gulbenkian Foundation (Portugal). Research was approved by Yerevan State University with permit nº 0606-433.

REFERENCES

Arakelyan, M., Danielyan, F., Corti, C., Sindaco, R., Levinton, A. (2011): Herpetofauna of Armenia and Nagorno Karabakh. Society for the Study of Amphibians and Reptiles, San Francisco.

Arnold, E.N., Arribas, O., Carranza, S. (2007): Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. Zootaxa **1430**: 1-86.

Arribas, O. (1999): Phylogeny and Relationships of the Mountain Lizards of Europe and Near East (*Archaeolacerta* Mertens, 1921, sensu lato) and Their Relationships Among the Eurasian Lacertid Radiation. Russ. J. Herpetol. **1**: 1 –22.

Baddeley, A., Turner, R. (2005): spatstat: an R package for analyzing spatial point patterns. J. Stat. Softw. **12**: 1-42.

Bivand, R.S., Pebesma, E.J., Gómez-Rubio, V. (2008): Applied Spatial Data Analysis with R. Springer, New York.

Boudjemadi, K., Lecomte, J., Clobert, J. (1999): Influence of connetivity on demography and dispersal in two contrasting habitats: an experimental approach. J. Anim. Ecol. **68**: 1207-1224.

Carretero, M.A., García-Muñoz, E., Argaña, E., Freitas, S., Corti, C., Arakelyan, M., Sillero, N. (2018): Parthenogenetic *Darevskia* lizards mate frequently if they have the chance: a quantitative analysis of copulation marks in a sympatric zone. J. Nat. Hist. **52**: 403-415.

Clark, P.J., Evans, F.C. (1954): Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology **35**: 445-453.

Danielyan, F., Arakelyan, M., Stepanyan, I. (2008): Hybrids of *Darevskia valentini*, *D. armeniaca* and *D. unisexualis* from a sympatric population in Armenia. Amphibia-Reptilia **29**: 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*). Leningrad.

Eifler, D.A., Eifler, M.A. (1998): Foraging Behavior and Spacing Patterns of the Lizard *Cnemidophorus uniparens*. J. Herpetol. **32**: 24-33.

Freitas, S., Butlin, R.K., Harris, D.J., Carretero, M.A. (2016a): Hybridization patterns between sexual and asexual species. Evolutionary Genomics of Sex 2016. Tempe, Arizona (USA), 17-19 November 2016.

Freitas, S., Rocha, S., Campos, J., Ahmadzadeh, F., Corti, C., Sillero, N., Ilgaz, Ç., Kumlutaş, Y., Arakelyan, M., Harris, D., Carretero, M.A. (2016b): Parthenogenesis through the Ice Ages: a biogeographic analysis of Caucasian rock lizards (genus *Darevskia*). Mol. Phylogenet. Evol. **102**: 117-127.

Frost, C.L., Bergmann, P.J. (2012): Spatial distribution and habitat utilization of the zebra-tailed lizard (*Callisaurus draconoides*). J. Herpetol. **46**: 203-208.

Fu, J., Darevsky, I.S., MacCulloch, R.D., Kupriyanova, L.A., Roitberg, E.S., Sokolova, T.M., Murphy, R.W. (1995): Genetic and morphological differentiation among caucasian rock lizards of the *Lacerta caucasica* complex. Russ. J. Herpetol. **1**: 36-42.

Galoyan, E. (2013): Joint space use in a parthenogenetic Armenian rock lizard (*Darevskia armeniaca*) suggests weak competition among monoclonal females. J. Herpetol. **47**: 97-104.

García-Muñoz, E., Sillero, N. (2010): Two new types of noose for capturing herps. Acta Herpetol. **5**: 259-263.

Getzin, S., Dean, C., He, F., Trofymow, J.A., Wiegand, K., Wiegand, T. (2006): Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. Ecography **29**: 671-682.

Gorton, R.E., Fulmer, J., Bell, W.J. (1979): Spacing patterns and pominance in the cockroach, *Eublaberus* *posticus* (Dictyoptera: Blaberidae). J. Kansas. Entomol. Soc. **52**: 334-343.

Gray, L., He, F. (2009): Spatial point-pattern analysis for detecting density-dependent competition in a boreal chronosequence of Alberta. Forest. Ecol. Manag. **259**: 98-106.

Haase, P., Pugnaire, F.I., Clark, S.C., Incoll, L.D. (1996): Spatial patterns in a two-tiered semi-arid shrubland in southeastern Spain. J. Veg. Sci. **7**: 527-534.

Jones, S.M., Droge, D.L. (1980): Home range size and spatial distributions of two sympatric lizard species (*Sceloporus undulatus*, *Holbrookia maculata*) in the sand hills of Nebraska. Herpetologica **36**: 127-132.

Kwiatkowski, M.A., Sullivan, B.K. (2002): Mating system structure and population density in a polygynous lizard, *Sauromalus obesus* (= *ater*). Beh. Ecol. **13**: 201-208.

Mellado, J. (1980): Utilización del espacio en una comunidad de lacértidos del matorral mediterráneo en la Reserva Biológica de Doñana. Doñana, Acta Vertebrata **7**: 41-59.

Moody, A.L., Thompson, W.A., De Bruijin, B., Houston, A.I., Goss-Custard, J.D. (1997): The analysis of the spacing of animals, with an example based on oystercatchers during the tidal cycle. J. Anim. Ecol. **66**: 615-628.

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. Russ. J. Herpetol. **3**: 18-31.

Ortega, A., Barbault, R. (1982): Spatial organization and habitat partitioning in a mountain lizard community of Mexico. Acta Oecol. **3**: 323-330.

Phillips, D.L., MacMahon, J.A. (1981): Competition and spacing patterns in desert shrubs. J. Ecol. **69**: 97-115.

R Development Core Team. (2014): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Ripley, B.D. (1976): The second-order analysis of stationary point processes. J. Appl. Prob. **13**: 255-266.

Rogerson, P. (2001): Statistical methods for Geography. Sage Publications, London.

Scali, S., Zuffi, M. (1994): Preliminary report on a reptile community ecology in a suburban habitat of northern Italy. Bolletino di Zoologia **61**: 73-76.

Schenk, H.J., Holzapfel, C., Hamilton, J.G., Mahall, B.E. (2003): Spatial ecology of a small desert shrub on adjacent geological substrates. J. Ecol. **91**: 383-395.

Sillero, N., Corti, C., Carretero, M.A. (2016): Home ranges of parthenogenetic and bisexual species in a community of *Darevskia* lizards. Zool. Mid. East **62**: 306-318.

Sillero, N., Gomes, V. (2016): Living in clusters: the local spatial segregation of a lizard community. Basic Appl. Herp. **30**: 61-75.

Sillero, N., Gonçalves-Seco, L. (2014): Spatial structure analysis of a reptile community with airborne LiDAR data. Int. J. Geogr. Inf. Sci. **28**: 1709-1722.

Stamps, J.A. (1983a): The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (A*nolis aeneus*). Behav. Ecol. Sociobiol. **12**: 19-33.

Stamps, J.A. (1983b): Territoriality and the defence of predator-refuges in juvenile lizards. Anim. Behav. **31**: 857-870.

Tarkhnishvili, D., Gavashelishvili, A., Avaliani, A., Murtskhvaladze, M., Mumladze, L. (2010): Unisexual rock lizard might be outcompeting its bisexual progenitors in the Caucasus. Biol. J. Linn. Soc. **101**: 447-460.

Underwood, A.J., Chapman, M.G. (1996): Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia **107**: 212-224.

Žagar, A., Carretero, M.A., Osojnik, N., Sillero, N., Vrezec, A. (2015): A place in the sun: does interspecific interference affect thermoregulation in coexisting lizards? Behav. Ecol. Sociobiol. **69**: 1127-1137.