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Unisexual rock lizard might be outcompeting its bisexual progenitors in the Caucasus

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We compared the distributions, abundances and ecological requirements of parthenogenetic lizard *Darevskia 'dahli'* and its bisexual progenitors, *D. portschinskii* and *D. mixta*, in Georgia. We developed a regression model relating the species abundances with the distribution of climates. *Darevskia portschinskii* lives in warmer and drier climates than *D. mixta*; *D. 'dahli'* has the intermediate requirements. Temperature is more important than humidity for *D. portschinskii*, humidity is more important for *D. mixta* and both temperature and humidity are important for *D. 'dahli'*. Suitable habitats of all three species overlap broadly; however, the observed ranges partly overlap only for *D. 'dahli'* and *D. portschinskii*. The observed abundance of each species, related to its predicted abundance, is lower at the sites with potential competitors. *Darevskia 'dahli'* occupies a higher proportion of the suitable habitats and has higher abundances than the progenitor species. Competition with *D. 'dahli'* is an important factor determining current distribution pattern of *D. portschinskii* and *D. mixta*. The parthenogen is a stronger competitor than the bisexual breeders and potential advantages of the bisexual reproduction remain unrealized in the given temporal and spatial scale. To explain domination of bisexually breeding lizards on the global scale, considering climate changes in geological timescale is necessary. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **101**, 447–460.

ADDITIONAL KEYWORDS: climatic niche – competition – lizards – niche displacement – parthenogenesis – suitable habitat analysis.

INTRODUCTION

Unisexually reproducing populations breed more rapidly than bisexual breeders with similar ecology. This has an important short-term advantage (Maynard Smith, 1978; Bell, 2005). Yet, aggregation of deleterious mutations in unisexuals and their failure to adapt to changing environments explain the domination of bisexual forms (Ghiselin, 1974; Maynard Smith, 1978; Kondrashov, 1988; Stearns, 1988). Many plants and invertebrates occasionally switch to clonal reproduction; in changing conditions, they return to bisexual breeding. This strategy accelerates population growth until the resources become limited (Green & Noakes, 1995).

Unisexual reproduction in amniotes is rare. Occasional or artificial parthenogenesis is recorded for reptiles and birds (Olsen, 1975; Dawley & Bogart, 1989; Groot, Bruins & Breeuwer, 2003; Watts *et al*., 2006). Yet, some geckos, tejids, lacertids and blind snakes have long-lasting unisexual forms (Darevsky, 1958, Darevskii, 1967; Nussbaum, 1980; Darevsky, Kupriyanova & Uzzell, 1985). Parthenogenetic lizards have hybrid origin (Parker & Selander, 1976; Dawley, 1989; Moritz *et al*., 1989; Darevsky, 1992). There is no evidence of switching to bisexual reproduction, although diploid unisexual tejids (*Cnemidophorus*) backcross with the parental species, producing nonsterile triploids (Reeder, Cole & Dessauer, 2002). In summary, parthenogenesis can hardly be viewed as an adaptive strategy in amniotes. Yet, it may have an impact on the niche structure and, potentially, a deleterious effect on the progenitor species that may endure competitive pressure from the daughter clones.

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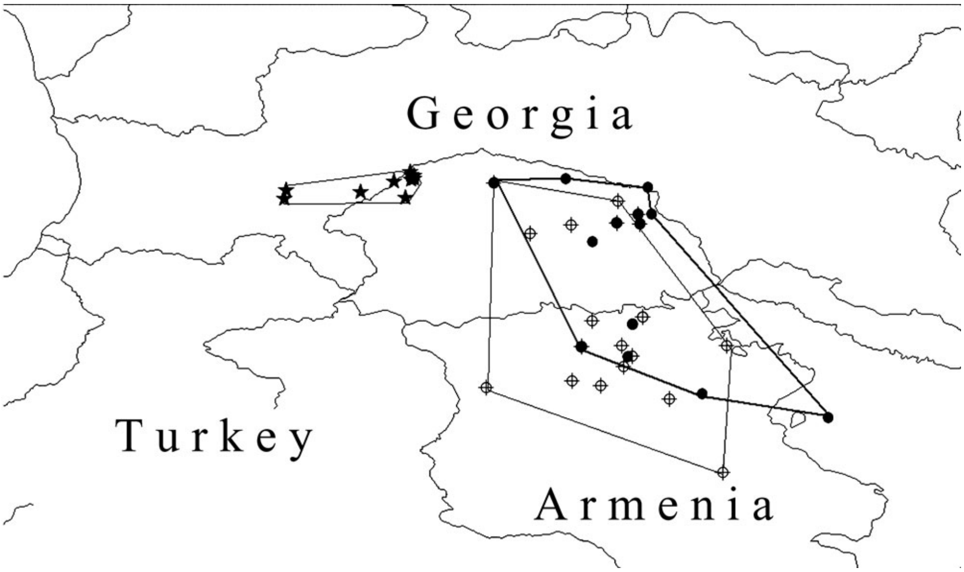

Figure 1. Geographic extents of distributions of *Darevskia portschinskii* (black circles), *Darevskia mixta* (stars) and *Darevskia dahli* (crossed circles), according to Darevskii (1967), modified.

Unisexual forms occasionally have wide ecological niches beyond the tolerance limits of their bisexual ancestors, the pattern called geographic parthenogenesis (Glesener & Tilman, 1978; Kearney, Wahl & Autumn, 2004; Vrijenhoek & Parker, 2009). Prevalence of clones in habitats that are marginal for their progenitors is explained by competitive superiority of bisexuals in central environments (Glesener & Tilman, 1978). Multiple clones may drive the progenitor species out of their habitats (Weeks, 1993), but it remains unclear whether a single robust clone may overcompete the related bisexual forms. Inhibitory effect is expected to be small, because of a broader overall ecological niche of bisexuals (Gaggiotti, 1994; Vrijenhoek & Parker, 2009).

Caucasian rock lizards (*Darevskia*) have several unisexual forms (Darevskii, 1967; Moritz *et al*., 1992; Murphy *et al*., 2000). One of those, *Darevskia 'dahli'*, is common in Georgia. The maternal progenitor of *D. 'dahli'* is *Darevskia mixta*; its paternal progenitor is *Darevskia portschinskii* (Darevskii, 1967; Uzzell & Darevsky, 1975; Fu, Murphy & Darevsky, 1999; Murphy *et al*., 2000). Minute genetic diversity of *D. 'dahli'* suggests that the majority of the individuals descend from a single hybridization event (Murphy *et al*., 1997; Kan *et al*., 1998; Fu *et al*., 1999; Davoyan *et al*., 2007). The range of *D. 'dahli'* overlaps with that of *D. portschinskii* (Fig. 1), but the upper altitudinal limit of the unisexual form is higher (Darevskii, 1967).

We conducted field and laboratory studies in order to specify ecological requirements of the *D. 'dahli'*, *D. portschinskii* and *D. mixta* (hereafter 'species'), to detect possible negative interactions and to rule out reproductive relationships between the unisexual and bisexual populations. The paramount question is whether the dispersal of *D. 'dahli'* to the upland habitats can be attributed to the competitive pressure from its progenitors. Not less important is to demonstrate whether *D. 'dahli'* can have an inhibitory effect on the progenitor forms and, if yes, why the species continue to coexist.

MATERIAL AND METHODS

FIELD SURVEY AND SPECIES IDENTIFICATION

In April–July, 2008–2009, we extensively surveyed the extent of occurrence of the target species in Georgia. A total of 239 potential sites (rocky outcrops) were studied. The sites with elevation, annual rainfall level and annual mean temperature beyond the limits where either of the species was recorded were excluded from the analyses, reducing the number of the sites to 160. At each site, the research team conducted a survey lasting up to 1 h in order to either confirm or reject the presence of the lizards. After the first lizard was recorded, the first author (D.T.) counted the number of adults of each species for 20 min from a single watching point at a distance of *c*. 5 m from the scanned rock. All the counts were carried out in sunny windless hours, therefore reducing weather impact on lizard activity. The counts were completed within 1 month after mass appearance of the lizards on the surface, starting in April at locations that lay below 1000 m. a.s.l. and finished in

Figure 2. Temporal and anal areas of the bisexually breeding female *Darevskia portschinskii* (left), unisexual female of *Darevskia 'dahli'* (middle) from the same location in Georgia and bisexually breeding female of *Darevskia mixta* (right).

July at locations from above 1800 m. a.s.l. The count results were interpreted as an abundance index (AI). Altogether, 512 *D. 'dahli'*, 249 *D. portschinskii* and 41 *D. mixta* were identified in the field. For each site, geographic coordinates and elevation were scored using Garmin Etrex 12-channel GPS unit (Garmin Corp., Olathe, KS, USA). The extent of the rock, vegetation, landscape setting and weather conditions were recorded. One to 12 lizards from each site were caught and their affiliation to one or another species was additionally tested using scalation traits (Darevskii, 1967; Fig. 2). Pileus, dorsum, temporal and anal areas of each individual were photographed for controlling species identification afield. Tail tips of the caught lizards were stored in 96% ethanol solution for genetic study.

In order to control the identification, DNA haplotypes in 40 *D. 'dahli'* and in 44 *D. portschinskii* were analysed. DNA was extracted from the samples; the fragments of the mitochondrial cytochrome-b gene were amplified with the protocol and primers described by Fu *et al*. (1999) and sequenced on the 4-capillary ABI gene analyser 3310. The sequences were aligned with the reference sequence of *D. portschinskii* (GenBank accession no. AF206176) and *D. 'dahli'* (accession no. AF147800.1) using BIOEDIT ver. 7.09.0 (Hall, 1999). The obtained sequences were attributed to either of the species, dependent on the state of the diagnostic positions.

QUANTIFYING ENVIRONMENTAL VARIABLES

A complex of environmental variables was recorded for each studied site during the field survey (see above) and using a remote sensing approach. For scoring climatic characteristics, elevation and terrain ruggedness of each site, free online data were downloaded and managed using ArcView ver. 3.3 GIS software. Those were: (1) bioclimatic data from WorldClim ver. 1.4 (http://www.worldclim.org/bioclim), a set of 19 global climate layers (climate grids) with a spatial resolution of 1 km^2, which describe temperature and rainfall over the globe (Hijmans *et al*., 2005); (2) terrain data measured from the Shuttle Radar Topography Mission (SRTM) elevation data in the UTM projection (dataset from the Global Land Cover Facility, http://www.landcover.org) at a resolution of 90 m.

MODELLING SUITABLE HABITATS

Spatial distribution of the suitable habitats was modelled separately for three studied species, based on the AI estimates. In the analysis, 19 bioclimatic variables were included along with the terrain ruggedness, elevation and rock size (23 variables in total). Prior to the modelling, we exponentieted each predictor variable, so that it followed the normal probability density function:

$$x = e^{-1/2[(Y-\mu)/\sigma]^{\wedge}2}$$

where Y was the original value of the variable at a geographic point and μ and σ were species-specific average and standard deviation, respectively. The transformation was applied in order to infer monotonic dependence of the AI on the studied variables. Stepwise linear regression (SLR) (significance level 0.025 for entry and 0.05 for removal) of the AI of each species on the transformed 23 environmental variables was calculated. Species-specific predicted abundance (PAI) values and residual values (ResAI = AI-PAI) were scored for each presence location for inferring spatial models of habitat suitability and estimating deviations between the predicted and observed abundances.

For validation of the derived models, we used 21 presence test locations of *D. 'dahli'* and 15 presence test locations of *D. portschinskii* (Fig. 1) from the papers of Darevskii (1967) and Tarkhnishvili, Kandaurov & Bukhnikashvili (2002). Validation of the model inferred for *D. mixta* was omitted because of coincidence between the bibliographic and the studied locations. Instead of true absence test locations, 100 random points generated within the extent of the polygon outlining the distribution of the species were used for the model validation (pseudoabsence locations). This was performed because the animals, especially in the patchy habitats typical for the rock lizards, may be absent from a location as a result of random extinctions (Levins, 1968; Hanski, 1999), which can bias spatial outcome of the model based on the environmental predictors. Species-specific PAI values were scored for each of the test-locations. ROC (Receiver Operated Character) curve analysis was applied to define the strength of agreement between the observed and predicted data (Hanley & McNeil, 1982; Zweig & Campbell, 1993). For the calculations, the package SPSS ver. 11 for Windows (SPSS Inc., Chicago, IL, USA) was applied. Visualization of the model was conducted using ArcView GIS 3.3.

COMPARATIVE ANALYSIS OF ECOLOGICAL NICHES

Extremes, mean and standard deviation of annual temperature, annual rainfall, rock dimensions and elevation were scored for each species. Each variable was weighted by the AI, in order to describe resource utilization curves more precisely. In order to identify the variables affecting the abundances, correlation coefficients between the AI and the normal-transformed 19 bioclimatic variables, elevation, slope and rock dimensions were computed. The correlations were assumed to be 'significant' for the variables with $P < 0.05$ after sequential Bonferroni correction (Rice, 1989).

A covariance matrix between the 19 bioclimatic variables was inferred from the 160 analysed sites. Mahalanobis distances (MD; Manly, 1994) from the species-specific centroid vectors were calculated from each individual site, using the same set of the variables. The average MD between the species-specific centroids and individual sites, weighted by the AI, was interpreted as multivariate standard deviation of suitable ecological conditions (hereafter 'niche breadth').

INTERACTION BETWEEN THE SPECIES AND EFFICIENCY OF THE SUITABLE HABITAT USE

The association between the ResAI of each species and the AI of the potential competitor was calculated using both parametric correlation coefficients and non-parametric association indexes (Kendall's tau and Spearman's rho) for the locations where either of the studied species was presented. The proportion of the occupied habitats and the species AI was calculated for the areas where PAI for *D. 'dahli'* and either of its progenitor species exceeded unity, in order to compare how effectively suitable locations were used by different studied species.

RESULTS

We recorded *D. portschinskii* at 63 sites and *D. 'dahli'* at 82 sites. At 28 sites, both species were recorded. *Darevskia mixta* was present at 11 sites, whereas both *D. mixta* and *D. 'dahli'* occurred at one site only (Fig. 3, Appendix). *Darevskia 'dahli'* were more abundant at the presence sites than the two progenitor species (Table 1).

Mitochondrial sequences of all 44 individuals visually identified as *D. portschinskii* (GenBank accession nos LP200801–LP200818) clustered together with the published sequences of the same species. The sequences of all 40 *D. 'dahli'* (GU216632–GU216649) clustered together with the published conspecific sequence. Therefore, identification based on the visual observation did not cause any confusion between the species.

IMPORTANT LIMITING FACTORS

All three species live in the mountain forest belt (elevation between 700–800 and 1500–1900 m); *D. mixta* and *D. 'dahli'*, unlike *D. portschinskii*, are also found above the timberline. Only *D. portschinskii* occurs in scrubland landscape below the forest belt. Interspecific differences in the altitudinal distribution, annual temperature, rainfall and rock dimensions are shown in Table 1. *Darevskia mixta* lives at higher elevations, in colder climates with a higher rainfall level than *D. portschinskii* and it is more commonly found at smaller rocks. *Darevskia 'dahli'* has habitat requirements intermediate between the two progenitors. The differences between the species are significant for most of the variables (Table 1).

The abundances significantly correlated with the elevation and some bioclimatic variables. Nine variables associated with the temperature and one associated with the rainfall significantly correlated with the AI of *D. portschinskii* (Table 2). The AI of *D. mixta* significantly correlated with four variables associated with the rainfall and one associated with the temperature. The AI of *D. 'dahli'* correlated with

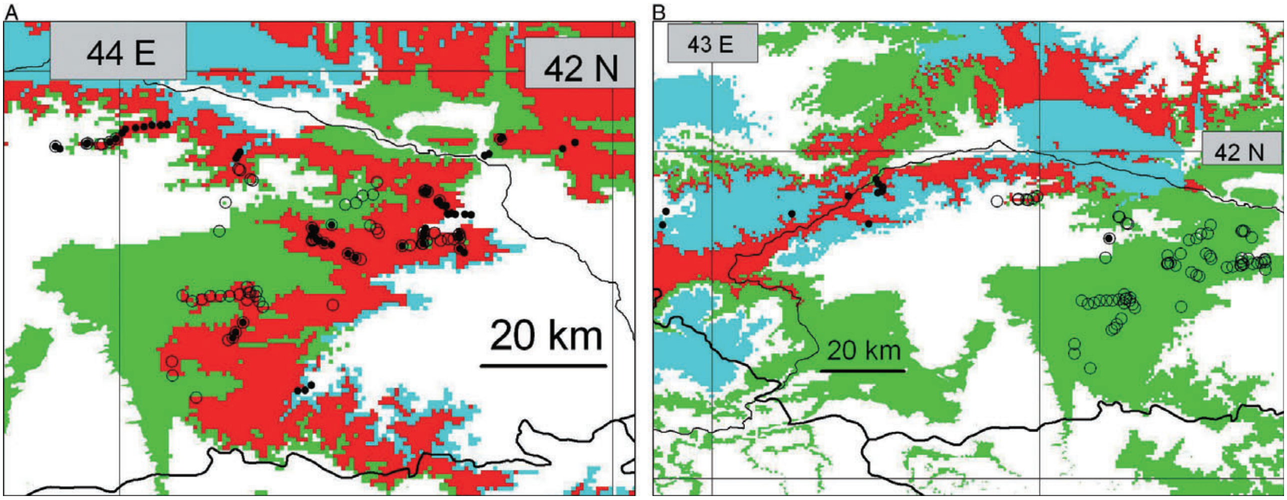

Figure 3. Predicted range (PAI > 1) of the studied species inferred from the stepwise multiple linear regression. Upper panel: predicted range of *Darevskia 'dahli'* (green), *Darevskia portschinskii* (blue) and both *D. 'dahli'* and *D. portschinskii* (red). Recorded locations of *D. portschinskii* (solid black dots) and *D. 'dahli'* (open circles). Lower panel: predicted range of *D. 'dahli'* (green), *Darevskia mixta* (blue) and both *D. 'dahli'* and *D. mixta* (red). Recorded locations of *D. mixta* (solid black dots) and *D. 'dahli'* (open circles).

Table 1. Statistics of environmental and abundance parameters at presence locations of rock lizards

	Species	*N*	Minimum	Maximum	Mean	SD	*P**
AI	*D. dahli*	80	0	40	6.53	7.34	0.017†
	D. portschinskii	64	1	15	3.89	3.17	
	D. mixta	12	1.00	6.00	2.42	2.02	
Elevation (m)	*D. dahli*	524	830	1960	1204	204	< 0.001†
	D. portschinskii	249	539	1399	1038	197	
	D. mixta	41	778	2109	1266	418	
Rainfall (mm)	*D. dahli*	524	554	860	715	68	< 0.001
	D. portschinskii	249	507	798	694	63	
	D. mixta	41	710	951	771	99	
Temperature (°C)	*D. dahli*	524	3.6	10.1	7.71	1.10	< 0.001
	D. portschinskii	249	6.0	12.1	8.73	1.23	
	D. mixta	41	2.3	8.3	5.91	2.16	
Rock‡ height (m)	*D. dahli*	524	< 1	> 10	5–6		0.12†
	D. portschinskii	249	2–3	> 10	5–6		
	D. mixta	41	< 1	> 10	3–4		
Rock length (m)	*D. dahli*	524	< 10	> 200	100–120		< 0.001†
	D. portschinskii	249	< 10	> 200	60–80		
	D. mixta	41	20	> 200	80–100		
AI of the competitor§	*D. dahli*	524	0	15	2.20	3.755	< 0.001
	D. portschinskii	249	0	40	4.62	8.597	
	D. mixta	41	0	1	0.02	0.156	

*Significance of interspecific differences; univariate ANOVA.

†Differences significant only between *Darevskia 'dahli'* and *Darevskia portschinskii*.

‡Rock dimensions were organized as ordinal variables for the analyses, but in the table the output is presented as original dimensions in metres.

§*Darevskia 'dahli'* for *D. portschinskii* and *Darevskia mixta*, *D. portschinskii* for *D. 'dahli'*.

AI, abundance index.

Rainfall: annual rainfall in mm; temperature: annual mean temperature.

Mean, SD, skewness and kurtosis estimated from the values at individual locations weighted by the species AI.

Table 2. Climatic variables significantly correlating with the abundance of *Darevskia 'dahli', Darevskia portschinskii* and *Darevskia mixta**

	D. 'dahli'		*D. portschinskii*		*D. mixta*	
	160		160		160	
N	Rxy	*P*	Rxy	*P*	Rxy	*P*
Annual mean temperature	0.280	0.000	0.278	0.000	0.158	0.046
Isothermality (BIO2/BIO7) (×100)	0.167	0.035	0.239	0.002	0.055	0.487
Temperature seasonality	0.174	0.028	0.221	0.005	0.085	0.283
Maximum temperature of warmest month	0.268	0.001	0.278	0.000	0.166	0.036
Minimum temperature of coldest month	0.257	0.001	0.270	0.001	0.178	0.024
Temperature annual range (BIO5–BIO6)	–0.053	0.505	0.211	0.007	0.150	0.058
Mean temperature of wettest quarter	0.124	0.119	0.053	0.508	0.257	0.001
Mean temperature of driest quarter	0.288	0.000	0.241	0.002	0.046	0.561
Mean temperature of warmest quarter	0.274	0.000	0.278	0.000	0.157	0.047
Mean temperature of coldest quarter	0.270	0.001	0.278	0.000	0.173	0.028
Annual precipitation	0.055	0.488	0.212	0.007	0.119	0.134
Precipitation of driest month	0.364	0.000	0.040	0.615	0.435	0.000
Precipitation seasonality	0.247	0.002	0.065	0.416	0.422	0.000
Precipitation of wettest quarter	0.146	0.065	0.155	0.050	0.204	0.010
Precipitation of driest quarter	0.329	0.000	0.076	0.342	0.374	0.000
Precipitation of warmest quarter	0.117	0.139	0.187	0.018	0.193	0.014
Precipitation of coldest quarter	0.329	0.000	0.078	0.328	0.417	0.000

*Correlation coefficient that remained significant after sequential Bonferroni corrections are shadowed.
The variables significant for more than one species are shaded.

Table 3. Stepwise linear regression models describing the dependence of the abundance index (AI) of individual species on the important environmental variables

Species AI	Variables	B	SE	*t*	*P*	R^2	AUC
Darevskia 'dahli'	Precipitation of driest month	4.228	1.050	4.027	0.000	0.348	0.727
	Annual mean temperature	2.456	1.076	2.282	0.024		
Darevskia portschinskii	Maximum temperature of warmest month	2.652	0.323	8.218	0.000	0.298	0.857
Darevskia mixta	Precipitation seasonality	1.747	0.270	6.461	0.000	0.208	–

AUC, area under rock curve.

ten variables, having six variables in common with *D. portschinskii* and four with *D. mixta* (Table 2).

Multiple SLR showed that different variables were significantly associated with the AI of the studied species. The maximum temperature of the warmest month is the only significant variable for *D. portschinskii*, precipitation seasonality for *D. mixta* and precipitation of the driest month and mean annual temperature for *D. 'dahli'* (Table 3).

SUITABLE HABITATS AND PREDICTED RANGES

The PAI inferred from the SLR models significantly correlated with the observed AI: Rxy = 0.404 for *D. 'dahli',* 0.278 for *D. portschinskii*, 0.422 for *D. mixta* ($P < 0.001$ for all cases). The spatial outcome of the models is shown in Figure 3. The area with PAI of *D. 'dahli'* exceeding unity within the extent of the polygon outlining the research area is 4748 km^2, larger than the area for PAI of *D. portschinskii* and *D. mixta*, exceeding unity (2639 and 2115 km^2, respectively). The spatial overlap of the suitable areas (PAI > 1) is strongly asymmetrical for *D. portschinskii* and *D. 'dahli'*. The area suitable for both species simultaneously is 94% of the total suitable area of *D. portschinskii*, but only 52% of the total suitable area of *D. 'dahli'*. The area suitable simultaneously for *D. 'dahli'* and *D. mixta* covers 35% of the suitable area of *D. mixta*, but only 15% of the suitable area of *D. 'dahli'* (Fig. 3).

Table 4. Association between residual AI (PAI-AI) of individual lizard species with the observed AI (abundance) and presence (1 vs. 0) of the potential competitor

N	Residual AI		Kendall's tau_b		Spearman's rho		Competitor
			Abundance	Presence	Abundance	Presence	
117	*Darevskia portschinskii*	Corr	***–0.247***	***–0.351***	***–0.338***	***–0.427***	*D. dahli*
		P	0.001	0.001	0.001	0.001	
76		Corr	***–0.380***	***–0.390***	***–0.472***	***–0.473***	*D. mixta*
		P	0.001	0.001	0.001	0.001	
91	*Darevskia mixta*	Corr	0.047	***–0.325***	0.030	***–0.380***	*D. dahli*
		P	0.547	0.001	0.778	0.001	
76		Corr	–0.191	***–0.379***	–0.249	***–0.444***	*D. portschinskii*
		P	0.027	0.001	0.030	0.001	
117	*Darevskia dahli*	Corr	–0.149	***–0.198***	–0.189	***–0.242***	*D. portschinskii*
		P	0.030	0.009	0.041	0.009	
91		Corr	–0.166	–0.164	–0.204	–0.200	*D. mixta*
		P	0.050	0.058	0.053	0.057	

Coefficients significant after sequential Bonferroni correction are shown in bold italics.
Corr, coefficients of association; *P*, two-tailed significance.
AI, abundance index; PAI, predicted abundance values.

Testing the models showed reasonable correspondence between the predicted and actual distribution of *D. portschinskii* and *D. dahli*, taking into account that randomly generated points were used in the test instead of the true absence points (Table 3).

NICHE BREADTH, OVERLAP AND PROPORTION OF THE OCCUPIED SITES

MD between the centroids of multivariate niches, defined by the 19 bioclimatic variables, reaches 1.29 for *D. 'dahli'* and *D. portschinskii*, 17.11 for *D. 'dahli'* and *D. mixta* and 16.85 for *D. portschinskii* and *D. mixta*. Niche breadth (species-specific average MD) of individual species reaches 12.72 for *D. 'dahli'*, 15.07 for *D. portschinskii* and 62.01 for *D. mixta*.

Within the area with the predicted AI of *D. portschinskii* and *D. 'dahli'*, simultaneously exceeding unity, *D. 'dahli'* were recorded at 60 sites (57% of the inspected locations) and *D. portschinskii* at 46 sites (44% of the inspected locations). For this area, the mean observed AI was 3.95 for *D. 'dahli'* and 1.92 for *D. portschinskii.* Within the area with the predicted AI exceeding unity for *D. 'dahli'* and *D. mixta,* the former species was recorded at 32% of the inspected sites, with mean density 0.53, and the latter at 26%, with mean density 0.89.

ASSOCIATION BETWEEN THE SPECIES

In Table 4, the non-parametric association coefficients between the ResAI of each individual species and the observed AI of each of the other species or presence of the potential competitor, coded as 1 vs. 0, are shown. There were no significant parametric correlations between the variables, but for most of the cases Kendall's tau and Spearman's rho showed negative association between the ResAI of a species and both presence and abundance of its competitor.

DISCUSSION

Our results suggest that *D. 'dahli'* and *D. portschinskii* are genetically isolated taxa, competing for resources in their natural habitats. *Darevskia 'dahli'* occupies a wide range of the habitats beyond the range of its progenitor species, yet the inhibitory effect of the progenitors cannot fully explain this pattern. Conversely, *D. 'dahli'* has an inhibitory effect on *D. portschinskii* and *D. mixta*. Currently, an observed range overlap between *D. 'dahli'* and *D. portschinskii* reflects an unstable equilibrium caused by patchy habitats and excess of the resources at some locations.

WAYS OF INTERACTION BETWEEN THE SPECIES

There is no haplotype introgression between *D. 'dahli'* and *D. portschinskii.* Possible hybridizations between them do not produce expanding bisexual individuals. This supports the suggestion that *D. 'dahli'* descends from a single or a few hybridization events that happened within a short period of time (Fu *et al*., 1999). Ongoing sexual interactions are unlikely. *Darevskia 'dahli'*, at sites where it coexists with *D.*

portschinskii, often have mating bites on their belly; otherwise, the parthenogens do not show the mating bites and obviously reproduce without contact with males. Negative behavioural interactions are unlikely. During the fieldwork, we occasionally observed aggressive behaviour (driving another lizard from an area) between the males, but not between the females of different species, or between the males and females. In conclusion, the interactions between the species are restricted to competition for food or cover, which do not show any remarkable differences between the rock lizard species (Darevskii, 1967).

LIMITING ENVIRONMENTAL VARIABLES

Interspecific differences in the suitable landscapes and rock dimensions are minor and secondary in respect to the differences in the preferred climates. This is in line with the studies, which show differential climatic limitations in bisexual lizards and their daughter clones (Kearney *et al.*, 2004). *Darevskia portschinskii* can survive in drier and warmer habitats than the two other species and the most important physical factor limiting its distribution is temperature. *Darevskia mixta* survives in colder and more humid habitats than the other species and a suitable level of humidity delimits its range. *Darevskia 'dahli'* lives in the intermediate climates and its distribution depends on both temperature and humidity. The intermediate requirements of *D. 'dahli'* are not surprising, taking into account its hybrid origin (see Moore, Miller & Schultz, 1970 for comparison).

NICHE BREADTH AND DIMENSIONS

Do the species differ in their ability to broaden the ecological niche and suitable range? Genetic recombination may help bisexuals to adapt to extreme and changing environments (Maynard Smith, 1978). *Darevskia 'dahli'* has a narrower climatic niche than both parental species. However, in respect to elevation, annual rainfall and annual mean temperature, the differences in the variance of the resource utilization curves are insignificant. Given the spatial distribution of the climates in the studied region, the predicted range of *D. 'dahli'* exceeds that of the either of its progenitors (Fig. 3). High adaptability of unisexuals to the severe climates, related with their progenitors, is not surprising: a similar pattern was earlier shown for parthenogenetic geckos of genus *Heteronotia* (Kearney *et al.*, 2004; but see Cullum, 1997).

An important advantage of the unisexuals is rapid reproduction and dispersal (Peck, Yearsley & Waxman, 1998). For *D. 'dahli'*, this advantage is reflected in a higher abundance, higher proportion of occupied sites and a broader geographic range, related to the progenitors. This pattern is not year-specific and is in line with observations of Darevskii (1967), who recorded usually higher abundances of *D. 'dahli'*, relative to *D. portschinskii*.

In spite of the intermediate ecological requirements, the range of *D. 'dahli'* does not keep an intermediate position between the ranges of *D. portschinskii* and *D. mixta*. *Darevskia 'dahli'* survives in the cold but reasonably dry uplands of Georgia and Armenia, conditions suitable for neither of its progenitors. Different important variables limiting the distribution of the progenitor species explain this. The temperature and rainfall produce a complex landscape mosaic and the areas with intermediate climates do not keep the intermediate geographic position.

NEGATIVE INTERACTIONS: *DAREVSKIA 'DAHLI'* VS. *DAREVSKIA PORTSCHINSKII*

Although competition is thought to be a major force shaping biological communities (Pianka, 1986), its universal role is disputed (Connell, 1980). Many authors interpret resource partitioning between related species as an outcome of the competition (Hutchinson, 1957; MacArthur, 1958; Schoener, 1971; Pianka, 1973, 1986; Losos & De Queiroz, 1997; Wahungu, Mumia & Nzau, 2004 Attum, Eason & Cobbs, 2007), but others require evidence that is more direct, such as detection of inhibitory effects (Putman, 1996; Daly, Dickman & Crowther, 2008). Obviously, competition is an important force often, but not always. One could hardly recognize its effect if the resources are not limited or habitats are unstable and populations do not reach the equilibrium size (Andrewartha & Birch, 1984; Rohde, 2005).

Could competition with *D. portschinskii* explain the higher altitudinal limit of *D. 'dahli'*? Niche breadths of *D. portschinskii* and *D. 'dahli'* exceed the distance between the niche centroids; consequently, they cannot avoid competition only by habitat segregation (Begon, Townsend & Harper, 2005). Hence, competition is an expected outcome of their coexistence.

Abundance of both species depends on the climatic variables both within and outside of the predicted overlap area. However, for equally suitable habitats, the average observed density of a species is lower if a potential competitor is present. The negative associations between the difference in predicted and observed abundances of a species and presence of the competitor reflects the mutual inhibitory effect of *D. 'dahli'* and *D. portschinskii*, yet the absence of significant parametric correlations indicates that the presence of a competitor is important irrespective of its abundance.

One can conclude that, when the resources become depleted, one of the competitors is rapidly driven out of a location and only the remaining one is usually recorded. As the resources are not limited, both species successfully coexist.

The overlap of the potential ranges is asymmetrical. *Darevskia 'dahli'* has a greater 'shelter' area unavailable for its competitor than *D. portschinskii*. Within the area suitable (PAI > 1) and highly suitable (PAI > 2) for both, the proportion of the sites occupied by *D. 'dahli'* is higher than that of *D. portschinskii*. This pattern suggests that local extinction events for *D. portschinskii* are commoner than local extinction events for *D. 'dahli'*.

The assumption about the higher competitive ability of bisexuals, related to parthenogens (Gaggiotti, 1994), does not apply to the studied assemblage. Conversely, a general-purpose parthenogenetic genotype has a universal advantage on the given temporal and spatial scale and the presence of the overlap area is the outcome of the complex metapopulation structure rather than the consequence of the niche shift or competitive resistance of the bisexual breeder. In this respect, the important role of spatial structure in the coexistence between parthenogens and bisexual breeders, implied by Haag & Ebert (2004), is a more realistic pattern than other anticipated explanations (see Vrijenhoek & Parker, 2009 for review).

NEGATIVE INTERACTIONS: *DAREVSKIA 'DAHLI'* VS. *DAREVSKIA MIXTA*

Negative association between *D. 'dahli'* and *D. mixta* is even stronger than between *D. 'dahli'* and *D. portschinskii*. From 19 survey locations with predicted probability of both species exceeding unity, we recorded *D. 'dahli'* at six locations and *D. mixta* at five locations, but none of these locations had both species. Are the inhibitory interactions asymmetrical, similar to those between *D. 'dahli'* and *D. portschinskii*? An isolated location of *D. mixta* 50 km west of its 'main' range (Fig. 3) and outside its predicted range suggests that the predicted suitable area for this species is biased and narrower than the actual fundamental niche. Most likely, competition with *D. 'dahli'* was the major factor driving the distribution edge of *D. mixta* westwards from its ancient range.

EVOLUTIONARY CONSIDERATIONS

The inferred inhibitory effect of *D. 'dahli'* on both parental species explains the absence of multiple clones produced by hybridization between *D. portschinskii* and *D. mixta*. Potentially, both progenitors of *D. 'dahli'* can survive in the same habitat. The extant range of *D. mixta* overlaps with those of *Darevskia rudis*, a species closely related to *D. portschinskii*; these species often coexist. Current allopatry of *D. mixta* and *D. portschinskii* could have been shaped after the expansion of *D. 'dahli'*. The competition shifted the distribution of *D. mixta* westwards, excluding it from the habitats occupied by *D. 'dahli'*. In consequence, the contact between *D. mixta* and *D. portschinskii* was broken, which excluded the possibility of further hybridizations.

The outcome of this study appears to contradict the considerations about a higher competitive ability of bisexuals related to their daughter clones (Gaggiotti, 1994; Vrijenhoek & Parker, 2009). The relatively narrow fundamental niche of *D. 'dahli'* does not affect its superior competitive ability [see ecological study of parthenogenetic geckos by Kearney & Shine, (2004) for comparison]. Instead, the hybrid clone expands, occupying the habitats suitable for its progenitors. From the evolutionary perspective, producing hybrid clones is deleterious for bisexually breeding lizards. However, the competitive advantage of the clones might not apply to the geological timescale. Adaptability of the bisexuals to the changing climates may reverse the pattern and cause extinction of the clones. This explains the young age of *D. 'dahli'* and global domination of bisexual breeders. The habitat patchiness and restricted dispersal helps bisexuals to survive thousands of generations, despite the inhibitory effect of the daughter clones, until rapid environmental changes are in place.

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APPENDIX

Description of individual lizard sites.

Site	Elevation (m)	Abundance of *Darevskia 'dahli'*	Abundance of *Darevskia portschinskii* or *Darevskia mixta**	Latitude	Longitude	Height of a rock outcrop (m)	Extension of a rock outcrop (m)	Landscape
1	1396	15	0	44.15	41.35	5	150	Sub-Alps
2	816	0	2	44.35	41.36	> 10	> 200	Shrubland
3	726	0	5	44.37	41.36	> 10	> 200	Shrubland
4	702	0	3	44.38	41.37	> 10	> 200	Shrubland
5	1408	3	0	44.10	41.39	10	100	Sub-Alps
6	1327	2	0	44.10	41.42	> 10	> 200	Sub-Alps
7	1194	2	0	44.21	41.46	10	150	Meadow
8	1103	6	13	44.22	41.47	3	100	Meadow
9	984	3	3	44.23	41.48	> 10	> 200	Forest
10	830	2	2	44.24	41.50	> 10	> 200	Forest
11	1424	20	0	44.28	41.53	3	200	Forest
12	1121	3	0	44.43	41.53	> 10	50	Shrubland
13	1415	6	0	44.28	41.54	> 10	> 200	Forest
14	1065	30	0	44.14	41.54	> 10	> 200	Forest
15	906	5	0	44.25	41.54	> 10	> 200	Forest
16	1026	6	0	44.16	41.55	> 10	> 200	Forest
17	1924	0	0	43.89	41.55	> 10	> 200	Sub-Alps
18	1320	8	0	44.27	41.55	> 10	> 200	Forest
19	957	4	0	44.20	41.55	> 10	> 200	Forest
20	959	5	0	44.22	41.55	10	> 200	Forest
21	989	10	0	44.18	41.55	> 10	> 200	Forest
22	1119	15	0	44.12	41.55	> 10	> 200	Forest
23	915	10	0	44.24	41.56	10	> 200	Forest
24	961	30	0	44.25	41.56	10	> 200	Forest
25	1164	10	0	44.26	41.56	> 10	> 200	Forest
26	1237	3	0	44.27	41.56	> 10	> 200	Forest
27	1099	2	0	44.25	41.57	> 10	> 200	Forest
28	897	6	0	44.48	41.63	2	20	Forest
29	873	8	2	44.47	41.63	3	100	Forest
30	904	1	4	44.46	41.64	> 10	> 200	Meadow
31	1322	0	10	44.69	41.64	5	> 200	Meadow
32	1142	40	10	44.68	41.65	> 10	> 200	Forest
33	1355	15	5	44.57	41.66	5	50	Meadow
34	1377	3	0	44.58	41.66	5	50	Meadow
35	961	0	2	44.42	41.66	3	> 200	Meadow
36	1456	0	0	44.63	41.66	5	100	Meadow
37	1325	2	0	44.61	41.66	5	100	Meadow
38	1363	15	5	44.61	41.66	20	150	Meadow
39	1565	2	0	44.29	41.66	> 10	> 200	Sub-Alps
40	968	3	2	44.41	41.66	6	30	Forest
41	1559	2	0	44.30	41.66	5	100	Sub-Alps
42	1400	5	0	44.62	41.66	5	30	Forest
43	1185	2	0	44.38	41.67	3	100	Meadow
44	1331	3	0	44.64	41.67	10	100	Meadow
45	1407	4	0	44.62	41.67	3	200	Forest
46	985	0	5	44.40	41.67	3	30	Forest
47	1140	3	0	44.39	41.67	8	100	Forest
48	1204	3	0	44.38	41.67	> 10	> 200	Forest
49	1309	20	0	44.66	41.67	> 10	50	Meadow

APPENDIX *Continued*

Site	Elevation (m)	Abundance of *Darevskia 'dahli'*	Abundance of *Darevskia portschinskii* or *Darevskia mixta**	Latitude	Longitude	Height of a rock outcrop (m)	Extension of a rock outcrop (m)	Landscape
50	1007	1	10	44.39	41.67	10	100	Forest
51	1297	10	0	44.67	41.67	5	> 200	Meadow
52	1358	18	2	44.68	41.67	> 10	> 200	Forest
53	1297	4	2	44.61	41.67	5	> 200	Forest
54	1047	0	10	44.38	41.68	> 10	50	Meadow
55	1316	3	6	44.68	41.68	> 10	100	Forest
56	1200	10	10	44.68	41.68	> 10	150	Meadow
57	1140	5	0	44.63	41.68	10	30	Forest
58	1350	4	0	44.52	41.68	3	30	Meadow
59	1085	3	1	44.61	41.68	> 10	100	Forest
60	1709	2	0	44.19	41.69	10	200	Sub-Alps
61	1179	3	15	44.39	41.69	10	200	Forest
62	1303	1	0	44.51	41.69	10	100	Forest
63	775	0	5	44.61	41.69	> 10	200	Forest
64	1153	3	0	44.38	41.69	2	200	Forest
65	1403	3	0	44.50	41.70	3	100	Meadow
66	1399	13	2	44.42	41.70	3	150	Meadow
67	539	0	1	44.71	41.72	> 10	> 200	Shrubland
68	662	0	2	44.67	41.72	> 10	> 200	Shrubland
69	579	0	1	44.69	41.72	> 10	> 200	Shrubland
70	850	0	2	44.66	41.72	> 10	> 200	Forest
71	887	0	1	44.66	41.72	> 10	> 200	Forest
72	690	0	2	44.67	41.72	> 10	> 200	Shrubland
73	1052	0	1	44.65	41.73	2	100	Shrubland
74	1018	0	5	44.65	41.74	> 10	> 200	Forest
75	1130	0	2	44.65	41.74	> 10	> 200	Shrubland
76	1800	3	0	44.45	41.74	1	> 200	Sub-Alps
77	1770	4	0	44.47	41.74	4	100	Sub-Alps
78	1960	1	0	44.21	41.74	> 10	> 200	Sub-Alps
79	1151	0	1	44.64	41.74	> 10	> 200	Forest
80	1198	4	2	44.64	41.75	3	100	Forest
81	1727	3	0	44.49	41.76	4	100	Sub-Alps
82	1617	7	0	44.51	41.76	5	100	Forest
83	889	0	3	44.62	41.76	3	100	Forest
84	993	12	3	44.62	41.77	5	> 200	Forest
85	847	12	2	44.61	41.77	10	200	Forest
86	867	1	1	44.61	41.77	5	50	Forest
87	1413	15	0	44.51	41.78	3	200	Forest
88	1149	2	0	44.26	41.79	5	100	Forest
89	1119	1	0	44.26	41.79	5	100	Forest
90	957	3	0	44.24	41.81	3	10	Forest
91	869	0	3	45.14	41.81	10	20	Forest
92	925	1	0	44.23	41.81	3	10	Forest
93	846	0	2	45.14	41.82	10	100	Forest
94	850	0	2	44.23	41.83	> 10	> 200	Shrubland
95	616	0	2	44.73	41.84	20	50	Shrubland
96	853	0	2	44.23	41.84	> 10	> 200	Shrubland
97	596	0	2	44.74	41.84	> 10	> 200	Shrubland
98	818	0	3	44.24	41.84	> 10	> 200	Shrubland
99	807	0	3	44.89	41.85	5	100	Forest

APPENDIX *Continued*

Site	Elevation (m)	Abundance of *Darevskia 'dahli'*	Abundance of *Darevskia portschinskii* or *Darevskia mixta**	Latitude	Longitude	Height of a rock outcrop (m)	Extension of a rock outcrop (m)	Landscape
100	1271	0	4	43.87	41.85	> 10	> 200	Forest
101	1360	1	3	43.86	41.86	> 10	> 200	Meadow
102	1128	1	0	43.96	41.86	20	100	Forest
103	1143	3	0	43.95	41.86	10	100	Forest
104	1148	2	1	43.93	41.86	> 10	> 200	Meadow
105	1142	1	4	43.93	41.86	5	300	Forest
106	965	0	2	44.92	41.86	10	50	Forest
107	1050	2	6	43.97	41.87	2	10	Sub-Alps
108	1167	12	12	44.77	41.87	5	200	Forest
109	998	1	4	43.99	41.87	10	200	Forest
110	1075	0	4	44.77	41.88	20	50	Forest
111	967	0	4	44.00	41.88	10	100	Forest
112	951	0	5	44.01	41.89	10	100	Forest
113	883	0	2	44.03	41.89	10	30	Meadow
114	843	0	5	44.04	41.90	10	> 200	Shrubland
115	817	0	2	44.06	41.90	3	> 200	Shrubland
116	770	0	2	44.08	41.90	3	> 200	Shrubland
117	746	0	5	44.09	41.90	3	> 200	Shrubland
118	991	0	10	43.54	41.90	3	50	Forest
119	1109	0	9*	43.53	41.90	3	100	Forest
120	2010	0	5*	43.50	41.88	3	100	Sub-Alps
121	2072	0	1*	42.85	41.82	> 10	> 200	Sub-Alps
122	1395	0	1*	43.49	41.76	3	100	Forest
123	2109	0	1*	43.48	41.77	3	100	Sub-Alps
124	1454	0	7*	43.50	41.71	3	100	Forest
125	849	0	1*	43.50	41.71	10	30	Forest
126	778	0	2*	43.51	41.70	2	10	Forest
127	1006	0	1*	43.52	41.69	3	100	Forest
128	855	0	3*	43.51	41.72	5	200	Forest

*Abundance of *D. mixta*.