

# The intestinal helminth community of the spiny-tailed lizard *Darevskia rudis* (Squamata, Lacertidae) from northern Turkey

V. Roca<sup>1\*</sup>, F. Jorge<sup>2,3</sup>, Ç. Ilgaz<sup>4,5</sup>, Y. Kumlutaş<sup>4,5</sup>, S.H. Durmuş<sup>6</sup> and M.A. Carretero<sup>2</sup>

<sup>1</sup>Departament de Zoologia, Facultat de Ciències Biològiques, Universitat de València. Dr. Moliner, 50, 46100 Burjassot, Spain: <sup>2</sup>CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 7. 4485-661 Vairão Vila do Conde, Portugal: <sup>3</sup>Departamento de Biología, Faculdade de Ciências da Universidade do Porto, R. Campo Alegre, s/n, 4169-007 Porto, Portugal: <sup>4</sup>Dokuz Eylül University, Faculty of Science, Department of Biology, 35160, Buca-İzmir, Turkey: <sup>5</sup>Dokuz Eylül University, Fauna and Flora Research and Application Center, 35160, Buca-İzmir, Turkey: <sup>6</sup>Dokuz Eylül University, Faculty of Education, Department of Biology, 35160, Buca-İzmir, Turkey

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## Abstract

Populations of the lizard *Darevskia rudis* (Bedriaga, 1886) from northern Anatolia were examined for intestinal parasites in adult specimens. One cestode, *Nematotaenia tarentolae* López-Neyra, 1944 and four nematode species, *Spauligodon saxicolae* Sharpilo, 1962, *Skrjabinelazia hoffmanni* Li, 1934, *Oswaldo-cruzia filiformis* (Goeze, 1782) and *Strongyloides darevskyi* Sharpilo, 1976, were found. Three of these nematodes, *S. saxicolae*, *S. hoffmanni* and *S. darevskyi* are suggested to be part of a module in the network of *Darevskia* spp. and their parasites. Only one, *S. darevskyi*, was identified as a *Darevskia* spp. specialist. The very low infection and diversity parameters are indicative of the depauperate helminth communities found in this lacertid lizard, falling among the lowest within the Palaearctic saurians. Nevertheless these values are higher than those found in parthenogenetic *Darevskia* spp. Interpopulation variation in the intensity of *S. saxicolae* and *N. tarentolae* is attributable to local changes in ecological conditions. On the other hand, parasite abundance and richness increased in the warmer localities, while the effect of lizard sex and size on infection was negligible. The structure of these helminth communities in *D. rudis* are compared with those observed in other European lacertid lizards.

## Introduction

Caucasian rock lizards (*Darevskia* spp.) are small lacertids from western Asia and south-eastern Europe. Although they are ecologically similar to European rock lizards they include not only bisexual species but also

\*Fax: +34 963543049  
E-mail: vicente.roca@uv.es

parthenogenetic forms (Darevsky, 1967; Ananjeva *et al.*, 2006; Arnold *et al.*, 2007; Tarkhvishnili, 2012). Among the former, *D. rufus* (Bedriaga, 1886) is a common species that occurs in northern coastal Turkey, Georgia, Russia and Azerbaijan (Eiselt & Darevsky, 1991). This species ranges from sea level to 2400 m above sea level (asl), inhabiting rocky areas in temperate forests, but also montane steppes, and walls and other human structures (Akarsu *et al.*, 2009; Kaska *et al.*, 2009).

Little attention has been paid to the parasites of *Darevskia* lizards, and thus no helminthological data are available for most species. Published studies are restricted to taxonomic and faunistic aspects (Schad *et al.*, 1960; Markov & Bodganov, 1962; Sharpilo, 1962, 1976; Saygi, 1993; Roca *et al.*, 2014). Preliminary helminth community data are available for parthenogenetic forms of *Darevskia* and their bisexual relatives (Sargsyan & Vardanyan, 2011; Sargsyan & Harutyunyan, 2012; Sargsyan *et al.*, 2014).

Only a recent study by Sargsyan (2013) has suggested the influence of abiotic factors on the parasite infection in *Darevskia raddei* (Boettger, 1892). However, evidence from other small lacertids certainly indicates that helminth communities are sensitive to local climatic conditions, the presence of alternative hosts and the degree of isolation (Roca & Hornero, 1994; Roca *et al.*, 2009; Carretero *et al.*, 2014). Moreover, helminth infracommunities in lacertids are also known to vary according to host traits, such as body size, sex and diet (Sanchis *et al.*, 2000; Martin & Roca, 2004; Martin *et al.*, 2005; Roca *et al.*, 2005).

Thus, in this study, we quantitatively analyse the infection of several populations of *D. rufus* by helminths,

specifically addressing the following issues: (1) basic characterization of the helminth community in terms of species richness and diversity patterns; (2) characterization of the helminths parasitizing the host as either specialists or generalists; (3) characterization of the helminths as core, secondary or satellite species; (4) assessment of the influence of host sex, size and environmental (climatic) factors (varying across host populations) on parasitism; and (5) characterization of the pattern of parasite infection of *D. rufus*, comparing the helminth community with that of European and other Caucasian rock lizards.

## Materials and methods

### Collection and examination of lizards

A total of 308 adult lizards (148 males and 160 females) of *D. rufus*, from the herpetological collection of the Fauna and Flora Research and Application Centre, Dokuz Eylül University (İzmir, Turkey), was examined. This sample was taken from 23 lizard populations and collected across the range of species in North Anatolia in spring (table 1). In a previous study by Arribas *et al.* (2013), specimens from northern Anatolia and the Middle Taurus Mountains in Anatolia were examined for external morphology and osteology, and *Darevskia bithynica* was raised to species rank, with two subspecies: *D. b. bithynica* and *D. b. tristis* in the western and Black Sea Region of Anatolia. Following this taxonomic arrangement, some populations, such as those from Kirazlı Plateau-Uludağ to Kapsiyu-Kurucaşile (see table 1), examined for parasites would be ascribed

Table 1. The localities of host populations of *Darevskia rufus* and corresponding environmental traits. Temperature seasonality: standard deviation (SD) of the weekly mean temperatures expressed as a percentage of the mean of those temperatures. Precipitation seasonality: coefficient of variation (CV) as the standard deviation of the weekly precipitation estimates expressed as a percentage of the annual mean.

Locality, province	Coordinates, latitude (°N), longitude (°W)	Altitude (m)	Annual mean temperature (°C)	Temperature seasonality (SD × 100)	Annual precipitation (mm)	Precipitation seasonality (CV)
Ardahan-Şavşat, Ardahan	42.45, 42.45	1913	3.6	799.8	73.0	2.6
Kutur Plateau-Ardanuç, Artvin	42.21, 42.21	2137	5.2	674.1	117.2	1.9
Barcilar-Borçka, Artvin	41.84, 41.84	1297	10.2	705.1	87.3	1.8
Borçka-Hopası, Artvin	41.56, 41.56	471	11.5	626.9	130.3	2.4
Arhavi-Güneşli, Artvin	41.33, 41.33	237	14.0	546.9	194.9	3.2
Çamlısemşin-Ayder Plateau, Rize	41.03, 41.03	370	11.9	650.7	124.5	2.4
Hemşin, Rize	40.9, 40.9	346	12.6	618.1	146.9	2.8
İkizdere-Ispırı, Rize	40.69, 40.69	1650	6.6	794.9	54.9	3.3
Surmene-Köprübaşı, Trabzon	40.11, 40.11	114	13.6	600.2	113.2	2.9
Maçka, Trabzon	39.62, 39.62	328	12.5	624.5	75.7	2.6
Akçaabat-Düzköy, Trabzon	39.49, 39.49	257	13.0	593.0	78.7	2.7
Kirazlı Plateau-Uludağ, Bursa	29.18, 29.18	1720	14.0	639.0	61.8	3.6
Güzeldere, Düzce	42.45, 42.45	554	11.4	634.0	69.9	2.5
Samandere waterfall, Düzce	42.21, 42.21	1174	8.8	658.5	66.8	3.2
Yedigöller, Bolu	41.84, 41.84	1260	8.5	648.1	71.4	3.4
Yığılca, Bolu	41.56, 41.56	821	10.1	639.0	62.8	2.8
Yığılca-Alaplı, Bolu	41.33, 41.33	295	12.6	608.4	83.6	2.6
Zonguldak-Gökçebey, Zonguldak	41.03, 41.03	345	11.9	596.8	82.5	2.7
Yenice, Karabük	40.9, 40.9	145	6.3	651.7	96.5	3.5
Ulus, Bartın	40.69, 40.69	490	11.5	648.7	74.6	2.2
Safranbolu, Bartın	40.11, 40.11	980	9.5	667.1	79.3	3.0
Amasra, Bartın	39.62, 39.62	295	12.2	596.7	90.5	2.8
Kapsiyu-Kurucaşile, Bartın	39.49, 39.49	1	13.5	596.1	84.2	2.8

to *D. bithynica*. However, in the absence of molecular evidence supporting such specific separation, this study follows a conservative approach, retaining all the populations within *D. rufa* sensu lato.

Populations were sampled along a 1000-km range in North Anatolia, with altitude levels ranging from sea level to 2137 m asl. In this region climate gradually changes from Mediterranean in the west to Oceanic in the east, with a more abrupt transition between the temperate humidity of the Black Sea coast to the arid continental climate of the slopes facing the Anatolian Plateau (Şensoy *et al.*, 2008). Such conditions provide a good representative spectrum of the bioclimatic range where this species occurs. To quantify these environmental characteristics, four bioclimatic variables for all localities were downloaded from the Worldclim database (<http://www.worldclim.org/bioclim>; Hijmans *et al.*, 2005), namely, annual mean temperature, temperature seasonality, annual precipitation and precipitation seasonality, which were introduced in subsequent analyses (table 1).

To assess host size, the snout vent length (SVL) of each lizard was measured with a digital calliper to the nearest 0.01 mm (see table 2). Gender and sexual maturity of the host were assessed from body size and gonad inspection (Carretero & Llorente, 1993; Arribas *et al.*, 2013; Gür *et al.*, 2014). Populations from Hemsin and Surmene-Köprübaşı were removed from analyses because their host samples lacked representatives of both sexes.

#### Helminthological procedures

Lizards were dissected for parasitological examination. This method ensures better detection and quantification of intestinal parasites with a few specimens than some non-invasive techniques (Jorge *et al.*, 2013). Helminths were processed following Hornero (1991). The parasite vouchers were deposited in the parasitological collection of the Department of Zoology of the University of Valencia, Spain.

#### Data analysis

The following descriptors were calculated for the helminth infracommunity of the pooled sample as well as separately for sex and locality: prevalence (%), percentage of infected hosts in the sampled population), abundance (A, percentage of the total number of parasites in a given host sample) and resource use index (IU; Jover, 1989). The latter index emphasizes the homogeneity (of parasitization across the host sample) as a criterion for evaluating the importance of different parasite species (Carretero, 2004; Martin *et al.*, 2005; Roca *et al.*, 2005; Carretero *et al.*, 2011, 2014). Mean intensity and mean abundance of infection were calculated following Bush *et al.* (1997). Prevalence of 10% was adopted as the lowest limit in identifying satellite species (Kennedy & Bakke, 1989). Species with values of prevalence between 10% and 30% were assigned as secondary species (Hanski, 1982; Roca, 1993). Species with prevalence of 30% or higher were considered as core species (Roca, 1993). The criteria of Edwards & Bush (1989) and Roca & Hornero (1994) were used in the consideration of the helminth species as specialists or generalists. Brillouin's indices were applied

Table 2. Descriptors of helminth species and communities in *Darevskia rufa*, relative to host size, based on snout vent length, and sex. N, number of hosts examined; N<sub>2</sub>, number of helminth infracommunities quantified; P, number of parasites; SE, standard error; A, prevalence; %, prevalence; IP, probabilistic index; IU, resource use index; Hp, host population density (following Jover, 1989).

Host sex	Host size (mm)	Parasite species				Parasite communities			
		<i>Ostivaldocruzia filiformis</i>	<i>Strongyloides darevskii</i>	<i>Spauligodon saxicola</i>	<i>Skrjabinielazia hoffmanni</i>	<i>Nematoxenia tarentolae</i>	N <sub>2</sub>	mean	SE
Males	N	148	P	1	169	11	2	1.24	0.20
	mean	64.75	%	1.72	87.93	5.17	148	0.38	0.00
	SE	0.62	A	0.55	92.35	6.01	148	0.00	2.00
	min.	40.26	IP	0.03	—	94.14	3.96	1.09	0.16
Females	N	87.32	IU	0.00	—	99.28	0.72	1.87	—
	mean	160	P	10	30	143	8	7	—
	SE	61.52	%	1.92	78.85	7.69	5.77	1.25	0.53
	min.	34.22	IP	2.42	15.15	72.22	4.04	3.535	0.30
Total	N	308	P	0.00	0.00	97.31	1.4166	1.2705	40.00
	mean	63.07	%	1.82	30	312	19	9	40.00
	SE	0.48	A	2.89	0.91	83.64	6.36	3.64	2.00
	min.	34.22	IP	1.07	7.87	81.89	4.99	2.36	0.00
	max.	87.32	IU	0.16	0.59	91.76	2.94	3.64	0.00
					97.26	1.76	0.83	1.18	0.00

for calculating diversity and evenness of parasite communities, according to Magurran (2004). Host population diversity of parasites (Hp) was also estimated by a jackknife resampling procedure (Jover, 1989; Carretero, 2004; Martin *et al.*, 2005; Roca *et al.*, 2005; Carretero *et al.*, 2011, 2014) and compared between sexes by *t*-tests (corrected for false discovery rate, FDR; Benjamini, & Hochberg, 1995) due to the non-additive nature of diversity (Carretero, 2004; Martin *et al.*, 2005; Roca *et al.*, 2005; Carretero *et al.*, 2006, 2011, 2014). All the remaining variables were calculated as mean individual values and compared through two-way analysis of variance (ANOVA) with sex and host population as factors. These analyses were performed in STATISTICA 12 (StatSoft Inc., 2013).

Relationships between abiotic factors and parasite species and helminth community traits (see above) were represented using canonical correlation analysis (CCorA; Legendre & Legendre, 1998); to test the significance of the observed correlation between canonical vectors, a permutation procedure with 1000 permutations was performed in XLSTAT 2014, evaluation version (<http://www.xlstat.com>; accessed 12 March 2014). Finally, similarities between helminth communities of the different host populations were estimated through the inverse of Pianka's overlap index (Pianka, 1973) applied on the IU values of each parasite species (Carretero *et al.*, 2006) using Ecosym 7.0 (Gotelli & Entsminger, 2001). The subsequent 1-overlap matrix obtained was then correlated with the matrix of geographic distances between localities, calculated in QGIS v. 2.2.0-Valmiera, using a Mantel test with 10,000 permutations performed in XLSTAT 2014.

## Results

### *Helminth composition*

Five helminth species, one cestode, *Nematotaenia tarentolae* López-Neyra, 1944 and four nematodes, *Spauligodon saxicola* Sharpilo, 1962, *Skrjabinellazia hoffmanni* Li, 1934, *Oswaldocruzia filiformis* (Goeze, 1782) and *Strongyloides darevskyi* Sharpilo, 1976, were found in *D. rufus*. All species occupied the small intestine, except *S. saxicola* which was found in the caecum. The descriptors of parasite species and communities for the pooled host sample and separately for male and female hosts are shown (table 2). The overall prevalence of infection was 32.1%. Mean intensity and mean abundance of infection were  $3.9 \pm 4.7$  (1–40) and  $1.2 \pm 3.2$  (0–40), respectively. *Spauligodon saxicola* constituted the main component of the helminth communities of *D. rufus*, whereas the other helminth species infected less than 3% of their host population (table 2). Five species of helminths were identified in the host populations of *D. rufus*, which exceeded both a mean of 0.34 and a maximum of 2 species per individual lizard. Values of helminth richness, abundance, diversity and evenness are indicated (table 2).

### *Helminth variation with host traits*

Intraspecific variations between host sexes but, mainly, between host populations were examined for species- and

community-level comparisons (table 2). Once host populations from Hemşin and Surmene-Köprübaşı (which lacked males and females, respectively) were removed from the analysis, sexual size dimorphism (larger males) and geographic variation in size were detected, but the first remained invariant across sites (ANOVA, sex:  $F_{1,259} = 11.40$ ,  $P = 8 \times 10^{-5}$ ; population:  $F_{20,259} = 15.45$ ,  $P < 10^{-6}$ ; sex  $\times$  population:  $F_{20,259} = 0.89$ ,  $P = 0.59$ ). Regardless of their sex, lizards from localities Barcilar, Borçka to Çamlısemşin-Ayder Plateau were especially large. Infection by the most abundant helminth, *S. saxicola*, varied with population but not with sex (ANOVA, sex:  $F_{1,259} = 2.30$ ,  $P = 0.13$ ; population:  $F_{20,259} = 1.90$ ,  $P = 0.01$ ; sex  $\times$  population:  $F_{20,259} = 1.28$ ,  $P = 0.196$ ). *Oswaldocruzia filiformis* displayed variation mainly due to higher infection values in the females of the population from Kapisuyu-Kuruçışile (ANOVA, sex:  $F_{1,259} = 5.56$ ,  $P = 0.02$ ; population:  $F_{20,259} = 4.63$ ,  $P < 10^{-6}$ ; sex  $\times$  population:  $F_{20,259} = 4.66$ ,  $P < 10^{-6}$ ). The infection by *N. tarentolae* was higher in localities Kirazlı Plateau-Uludağ, Yedigölle and Yiğilca-Alaplı (ANOVA, sex:  $F_{1,259} = 3.55$ ,  $P = 0.06$ ; population:  $F_{20,259} = 3.32$ ,  $P = 5 \times 10^{-6}$ ; sex  $\times$  population:  $F_{20,259} = 3.49$ ,  $P = 2 \times 10^{-6}$ ; Scheffé post-hoc tests:  $P < 0.05$ ). By contrast, *S. hoffmanni* did not show any variation, either with population or with host sex (ANOVA  $P > 0.42$  in all cases).

### *Helminth communities*

Species richness also varied between host populations but not between host sexes (ANOVA, sex:  $F_{1,259} = 0.71$ ,  $P = 0.40$ ; population:  $F_{20,259} = 2.12$ ,  $P = 0.004$ ; sex  $\times$  population:  $F_{20,259} = 0.98$ ,  $P = 0.49$ ). No significant variation was detected for parasite abundance, infracommunity diversity or evenness (ANOVA  $P > 0.10$  in all cases). Host population diversity of parasites was moderately correlated with infracommunity diversity ( $r = 0.53$ ,  $r^2 = 0.28$ ,  $P = 0.009$ ) and also lacked significant variation across host sexes and populations (multiple *t*-tests FDR-corrected,  $P > 0.18$ ). Remarkably, values of host population diversity of parasites exceeded by 5–10 times those of infracommunity diversity (tables 2 and 3). No correlation between parasite species abundances or any of the community descriptors and host size (SVL) was detected, either considering values for individual host or for host population ( $r < 0.12$ ,  $P > 0.34$ ).

The canonical correlation analysis (CCorA) between parasitization and environmental variables for each lizard population produced divergent results whether applied to parasite species abundance or to the parameters of parasite community (fig. 1). The environmental signal on the infection by the different parasite species was weak: only *N. tarentolae* showed some trend to be more abundant at higher altitudes, *S. saxicola* in warmer environments and *S. darevskyi* in rainy areas. *Strongyloides darevskyi* was also associated with large host body sizes. However, a clearer scenario emerged from the analysis of communities, since lizard populations occurring in warmer areas harboured more abundant and richer parasite assemblages, while higher precipitation had an effect on host size but not on parasite communities. Finally, Mantel tests did not detect correlation between

Table 3. A comparison between Brillouin's diversity indices of helminth communities in Caucasian and European lacertid lizards.

Host species	Brillouin's index
Caucasian	
<i>Darevskia rufus</i>	0.009
<i>Darevskia ullaelli</i>	0
<i>Darevskia bendimahiensis</i>	0
European continental	
<i>Podarcis bocagei</i>	0
<i>Podarcis carbonelli</i>	0.001
<i>Zootoca vivipara</i>	0.002
European insular	
<i>Podarcis pityusensis</i>	0.242
<i>Podarcis lilfordi</i>	0.108
<i>Podarcis sicula</i>	0.141
<i>Podarcis tiliguerta</i>	0.034
<i>Podarcis erhardii</i> (Sporades)	0.048
<i>Podarcis erhardii</i> (Cyclades)	0.108

the community dissimilarities and geographic distances matrices ( $r = -0.025$ ,  $P = 0.69$ ).

## Discussion

All the helminths found in *D. rufus* are also common in reptiles from south-east Europe and the former USSR (Schad *et al.*, 1960; Markov & Bodganov, 1962; Sharpilo, 1976; Saygi, 1993; Sharpilo *et al.*, 2001; Yildirimhan *et al.*, 2011; Roca *et al.*, 2014).

The most common helminth in the communities of *D. rufus* *sensu lato* is the pharyngodonid nematode *S. saxicola*, which should be considered as a rock lizard specialist (*sensu* Roca & Hornero, 1994), since it has been recorded from *Darevskia* and *Podarcis* species (Sharpilo,

1976; Roca *et al.*, 1986, 2009). *Strongyloides darevskyi* seems a true *Darevskia* specialist as it has been recorded only in *D. saxicola* and *D. rufus*. The remaining helminth species have been recorded from several other lizard genera, so they appear to be generalists (Roca *et al.*, 1990; Roca & Hornero, 1992; Yildirimhan *et al.*, 2011). No other species of Pharyngodonidae were found in *D. rufus*. This contrasts with the usual pattern found in different European lacertid lizards, in which other species of *Spauligodon* frequently share reptile hosts with species of the genera *Skribabinodon* (but see Jorge *et al.*, 2014) and *Parapharyngodon* (Roca *et al.*, 1986, 2009; García-Adell & Roca, 1988; Roca & Hornero, 1994; Yildirimhan *et al.*, 2011).

The total number of helminth species in the populations of *D. rufus* greatly exceeded both the average and the maximum number of species per individual lizard, with no single infracommunity presenting all species locally available. This marked variation in infracommunities is also supported by the low ratio between infracommunity and host population diversity of parasites obtained for all host populations. The upper limit of species richness is not usually attained (Poulin, 1998). This agrees with observations of *Gallotia* spp. (Martin & Roca, 2004) and seems also to be a typical pattern of many European lacertid lizards (Roca & Hornero, 1994; Sharpilo *et al.*, 2001; Martin & Roca, 2004; Yildirimhan *et al.*, 2011).

Most helminth species found in *D. rufus* occurred at low prevalence. Only *S. saxicola* can be considered as a core species, whereas the remainder are satellite species. This, again, differs from the typical pattern of helminth infection in many reptiles, i.e. few species occur frequently, few species occur with moderate prevalence and many species are rare (Aho, 1990; Roca & Hornero, 1994; Sharpilo *et al.*, 2001; Yildirimhan *et al.*, 2011). In the case of *D. rufus*, no secondary species were found in their helminth infracommunities.

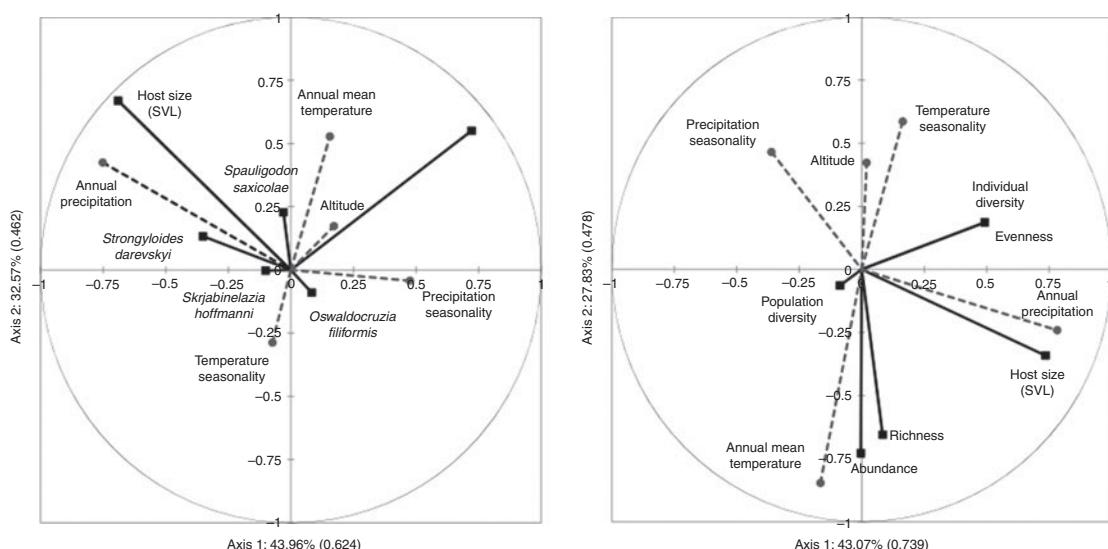


Fig. 1. Canonical correlation analysis (CCorA) between host/parasite traits (squares) and environmental variables (circles) for helminth species (left) and communities (right). Variance percentages are indicated after the axes and eigen values follow, in parentheses.

The observed low diversity of the intestinal helminth community of *D. rufus* points to a depauperate isolationist community, being in accordance with the general pattern observed in reptiles (Aho, 1990; Roca & Hornero, 1994). However, some differences have been observed among distinct European lacertid lizards (see Roca *et al.*, 2009). Insular lizards show higher values for both helminth diversity (table 3) and prevalence than continental ones, which is probably due to unusual insular conditions concerning hosts, such as lizard population densities, food strategies and prey availability, as well as ecological conditions concerning parasite recruitment opportunities (Martin & Roca, 2004; Roca *et al.*, 2009). On the other hand, continental European lacertid lizards have low values of Brillouin's index of diversity, with the parthenogenetic *Darevskia* spp. (and *Podarcis bocagei*) being those with extremely impoverished helminth communities. Several factors have been cited as possible causes of very low helminth diversity in continental lacertid lizards, i.e. small body size of the host, low number of interactions with other reptile or amphibian species, and low opportunities for parasite recruitment due to habitat conditions (Galdón *et al.*, 2006; Roca *et al.*, 2014). Although *D. rufus* shows low values of helminth diversity, they are still higher than those of other European lizards and also higher than those of parthenogenetic congeneric species (Roca *et al.*, 2014). This suggests more opportunities for parasite recruitment, which is in accordance with the widest geographical distribution of this species among the Caucasian rock lizards, and the high diversity of habitats occupied within this range.

Since phylogeny is a determinant factor for a modular structure in networks between parasites and hosts, and the formation of modules consisting of groups of hosts and parasites that are intimately related (Krasnov *et al.*, 2012), we expected that certain lineages of parasites were more likely to exploit *Darevskia* spp. as a particular lineage host. The most probable lineages of parasites involved in this situation are the nematode species belonging to the genera *Spauligodon*, *Strongyloides* and *Skrjabinelazia*, since species of each genus have been recorded parasitizing other *Darevskia* species (Sharpilo, 1976; Roca *et al.*, 2014; Roca *et al.*, unpublished data).

Notwithstanding the low complexity and heterogeneity of the parasitization between individual lizards (see above), host intraspecific variation was detected. This was mostly due to differences between lizard populations, while the effect of host sex was negligible. Interpopulation host variation affected not only the most abundant species, *S. saxicola*, but also *N. tarentolae*. Since canonical correlation analysis (CCorA) detected little climate signal in the infection by individual parasite species, such variation could be due to local changes in infection opportunities for each parasite, due to variations in microhabitat, and intermediate, paratenic and alternative definitive hosts (Roca & Hornero, 1994; Martin & Roca, 2004; Roca *et al.*, 2009). Similarly, Sargsyan (2013) did not observe a clear association with either temperature or precipitation when analysing the infection of five populations of *D. raddei* by *S. saxicola* in Armenia. In contrast, CCorA showed evidence of an increase in the parasite abundance and richness at community level in warmer localities. Precipitation also had a positive

influence on host size, presumably due to high prey availability (Pianka, 1986). However, such an effect did not have repercussions on parasite communities since no correlation between infection variables and lizard size was found, although it has been reported for other lacertids (Sanchis *et al.*, 2000; Martin *et al.*, 2005; Roca *et al.*, 2005; Carretero *et al.*, 2006, 2011, 2014). Such an effect is generally due to the low parasitization of juvenile lizards, which were not analysed in our study. Finally, the lack of significance in the Mantel tests allows us to discard biogeographical trends, at least at the scale of the study region.

In summary, the lacertid *D. rufus* harbours a depauperate helminth community, composed of both specialist and generalist species whose variation between host populations is more dependent on local ecological conditions and climate than on biogeographic units. This contrasts with the results of the analysis of insular and continental populations of the Mediterranean lacertid *Podarcis erhardii* (Roca *et al.*, 2009) which displays a strong biogeographic signal of insularity on parasitization. Further studies on multipopulation and multispecies host datasets are crucial to elucidate the relative contributions of ecological and historical factors to the formation of reptile helminth communities.

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## Conflict of interest

None.

## References

- Aho, J.M. (1990) Helminth communities of amphibians and reptiles: Comparative approaches to understanding patterns and processes. pp. 157–195 in Esch, G.,

- Bush, A. & Aho, J. (Eds) *Parasite communities: patterns and processes*. London, Chapman and Hall.
- Akarsu, F., Tuniyev, B., Anajeva, N., Agasyan, N., Orlov, N. & Tuniyev, S. (2009) *Darevskia uzelli*. IUCN Red List of Threatened Species. Version 2013.1. Available at [www.iucnredlist.org](http://www.iucnredlist.org) (accessed November 2014).
- Ananjeva, N.B., Orlov, N.L., Khalikov, R.G., Darevsky, I.S., Ryabov, S.A. & Barabanov, A. (2006) The reptiles of northern Eurasia: taxonomic diversity, distribution, conservation status. *Pensoft Series Faunistica* **47**, 1–250.
- Arnold, E.N., Arribas, O. & Carranza, S. (2007) Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with description of eight new genera. *Zootaxa* **1430**, 1–86.
- Arribas, O.J., Ilgaz, Ç., Kumlutaş, Y., Durmus, S.H., Avci, A. & Üzüm, N. (2013) External morphology and osteology of *Darevskia rufus* (Bedriaga, 1886), with taxonomic revision of the Pontic and Small-Caucasus populations (Squamata: Lacertidae). *Zootaxa* **3626**, 401–428.
- Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistics Society B* **57**, 289–300.
- Bush, A.O., Lafferty, K.D., Loft, J.M. & Shostak, A.W. (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.
- Carretero, M.A. (2004) From set menu to à la carte. Linking issues in trophic ecology of Mediterranean lacertids. *Italian Journal of Zoology* **74**, 121–133.
- Carretero, M.A. & Llorente, G.A. (1993) Morfometría en una comunidad de lacértidos mediterráneos, y su relación con la ecología. *Historia Animalium* **2**, 77–79.
- Carretero, M.A., Perera, A., Harris, D.J., Batista, V. & Pinho, C. (2006) Spring diet and resource partitioning in an alpine lizard community from Morocco. *African Zoology* **41**, 113–122.
- Carretero, M.A., Roca, V., Larbes, S., Ferrero, A. & Jorge, F. (2011) Intestinal helminth parasites of wall lizards, *Podarcis vaucheri* complex (Sauria: Lacertidae) from Algeria. *Journal of Herpetology* **45**, 385–388.
- Carretero, M.A., Jorge, F., Llorente, G.A. & Roca, V. (2014) Relationships between helminth communities and diet in Canarian lizards: the evidence from *Gallotia atlantica* (Squamata: Lacertidae). *Journal of Natural History* **48**, 1199–1216.
- Darevsky, I.S. (1967) *Rock lizards of the Caucasus: Systematics, ecology and phylogeny of the polymorphic groups of Caucasian rock lizards of the subgenus Archaeolacerta*. Leningrad, Nauka (English translation 1978, New Delhi, Indian Natural Science Documental Centre).
- Edwards, D.D. & Bush, A.O. (1989) Helminth communities in avocets: importance of compound community. *Journal of Parasitology* **98**, 439–445.
- Eiselt, J. & Darevsky, I.S. (1991) *Lacerta rufus chechenica* ssp. n. aus dem Kaukasus (Reptilia: Lacertidae). *Annales Naturhistoriae Museum Wien* **92**, 15–29.
- Galdón, M.A., Roca, V., Barbosa, D. & Carretero, M.A. (2006) Intestinal helminth communities of *Podarcis bocagei* and *Podarcis carbonelli* (Sauria: Lacertidae) in NW Portugal. *Helminthologia* **43**, 37–41.
- García-Adell, G. & Roca, V. (1988) Helmintofauna de Lacértidos de los Pirineos centrales ibéricos. *Revista Ibérica de Parasitología* **48**, 257–267.
- Gotelli, N.J. & Entsminger, G.L. (2001) EcoSim: Null models software for ecology. Version 7.0. Available at <http://homepages.together.net/~gentsmin/ecosim.htm> (accessed November 2014).
- Gül, S., Ozdemir, N., Kumlutaş, Y. & Ilgaz, Ç. (2014) Age structure and body size in three populations of *Darevskia rufus* (Bedriaga, 1886) from different altitudes. *Herpetozoa* **26**, 151–158.
- Hanski, I. (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* **38**, 210–221.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965–1978.
- Hornero, M.J. (1991) Helmintofauna de los lacértidos endémicos de las Islas Baleares (Mediterráneo occidental). PhD thesis, Department of Zoology, University of Valencia, Valencia.
- Jorge, F., Carretero, M.A., Roca, V., Poulin, R. & Perera, A. (2013) What you get is what they have? Detectability of intestinal parasites in reptiles using faeces. *Parasitology Research* **112**, 4001–4007.
- Jorge, F., Roca, V., Carretero, M.A., Perera, A., Harris, D.J. & Poulin, R. (2014) Evolution of alternative male morphotypes in oxyurid nematodes: a case of convergence? *Journal of Evolutionary Biology* **27**, 1631–1643.
- Jover, L. (1989) Nuevas aportaciones a la tipificación trófica poblacional: El Caso de *Rana perezi* en el Delta del Ebro. PhD Thesis, Department of Animal Biology, University of Barcelona, Barcelona.
- Kaska, Y., Kumlutaş, Y., Avci, A., Üzüm, N., Yeniyurt, C. & Akarsu, F. (2009) *Darevskia rufus*. IUCN Red List of Threatened Species. Version 2013.1. Available at [www.iucnredlist.org](http://www.iucnredlist.org) (accessed November 2014).
- Kennedy, C.R. & Bakke, T.A. (1989) Diversity patterns in helminth communities in common gulls, *Larus canus*. *Parasitology* **98**, 431–445.
- Krasnov, B.R., Fortuna, M.A., Mouillot, D., Khokhlova, I.S., Shenbrot, G.I. & Poulin, R. (2012) Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks. *American Naturalist* **179**, 501–511.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*. 2nd English edn. Amsterdam, Elsevier.
- Magurran, A.E. (2004) *Measuring biological diversity*. Malden, Blackwell Publishing.
- Markov, G.S. & Bodganov, O.P. (1962) New nematodes for the fauna of the USSR. *Izvestia Akademii Nauk Turk. SSR* **1**, 73–77.
- Martin, J.E. & Roca, V. (2004) Helminth infracommunities of *Gallotia caesaris caesaris* and *Gallotia caesaris gomerae* (Sauria: Lacertidae) from the Canary Islands (Eastern Atlantic). *Journal of Parasitology* **90**, 266–270.
- Martin, J.E., Llorente, G.A., Roca, V., Carretero, M.A., Montori, A., Santos, X. & Romeu, R. (2005) Relationships between diet and helminths in *Gallotia caesaris* (Sauria: Lacertidae). *Zoology* **108**, 121–130.

- Pianka, E.R.** (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics* **4**, 53–74.
- Pianka, E.R.** (1986) *Ecology and natural history of desert lizards*. New Jersey, Princeton University Press.
- Poulin, R.** (1998) *Evolutionary ecology of parasites*. London, Chapman and Hall.
- Roca, V.** (1993) Helmintofauna dels reptils. *Mono- grafies de la Societat d'Història Natural de les Balears* **2**, 273–292.
- Roca, V. & Hornero, M.J.** (1992) *Strongyloides ophiurusensis* sp. n. (Nematoda: Strongylidae), parasite of an insular lizard, *Podarcis pityusensis* (Sauria: Lacertidae). *Folia Parasitologica* **39**, 369–373.
- Roca, V. & Hornero, M.J.** (1994) Helminth infracommunities of *Podarcis pityusensis* and *Podarcis lilfordi* (Sauria: Lacertidae) from the Balearic Islands (western Mediterranean Basin). *Canadian Journal of Zoology* **72**, 658–664.
- Roca, V., Lluch, J. & Navarro, P.** (1986) Contribución al conocimiento de la helmintofauna de los herpetos ibéricos. I. Parásitos de Lacertidae: *Lacerta lepida* Daudin, 1802 y *Podarcis hispanica* Steindachner, 1870. *Revista Ibérica de Parasitología* **46**, 129–136.
- Roca, V., López-Balaguer, E., Hornero, M.J. & Ferragut, M.V.** (1990) *Skrjabinelazia hoffmanni* Li, 1934 (Nematoda: Seuratidae), parásito de reptiles lacértidos de la Península Ibérica. *Boletín de la Real Sociedad Española de Historia Natural (Sección Biología)* **86**, 125–132.
- Roca, V., Carretero, M.A., Llorente, G.A., Montori, A. & Martin, J.E.** (2005) Helminth communities of two lizard populations (Lacertidae) from Canary Islands (Spain): host diet–parasite relationships. *Amphibia-Reptilia* **26**, 535–542.
- Roca, V., Foufopoulos, J., Valakos, E. & Pafilis, P.** (2009) Parasitic infracommunities of the Aegean wall lizard *Podarcis erhardii* (Lacertidae, Sauria): isolation and impoverishment in small island populations. *Amphibia-Reptilia* **30**, 493–503.
- Roca, V., Jorge, F., Ilgaz, Ç., Kumlutaş, Y., Durmus, S.H. & Carretero, M.A.** (2014) Parasites of unisexual lizards (*Darevskia* spp., Lacertidae) in Turkey: extreme impoverishment of gastrointestinal helminth community. *Acta Zoologica Academiae Scientiarum Hungaricae*, in press.
- Sanchis, P.V., Roig, J.M., Carretero, M.A., Roca, V. & Llorente, G.A.** (2000) Host–parasite relationships of *Zootoca vivipara* Jacquin, 1787 in the Pyrenees (N. Spain). *Folia Parasitologica* **47**, 118–122.
- Sargsyan, N.H.** (2013) Influence of abiotic factors on infection of rock lizards *Darevskia raddei* by geohelminth *Spauligodon saxicolae*. *Proceedings of the Yerevan State University* **2**, 44–47 (in Armenian).
- Sargsyan, N.H. & Harutyunyan, T.K.** (2012) Comparative analysis of the blood and helminth parasites of rock lizards. *Biological Journal of Armenia* **3**, 6–9 (in Armenian).
- Sargsyan, N.H. & Vardanyan, L.K.** (2011) Helminthofauna in some reptiles. *Biological Journal of Armenia* **2**, 75–77 (in Armenian).
- Sargsyan, N.H., Arakelyan, M., Danielyan, F.D. & Vartanyan, L.** (2014) Helminthes of some species of reptiles from republic of Armenia. *Electronic Journal of Natural Sciences* **22**, 50–54 (in Armenian).
- Saygi, G.** (1993) The genus *Spauligodon* (Nematoda: Oxyuroidea) in *Lacerta parva* collected in Sivas, Turkey. *Türk Parazitoloji Dergisi* **17**, 40–45.
- Schad, G.A., Kuntz, R.E. & Wells, W.H.** (1960) Nematode parasites from Turkish vertebrates. An annotated list. *Canadian Journal of Zoology* **38**, 949–962.
- Şensoy, S., Demircan, M., Ulupınar, U. & Balt, İ.** (2008) *Türkiye İklimi*. Available at <http://www.dmi.gov.tr/iklim/iklim.aspx> (accessed December 2014).
- Sharpilo, V.P.** (1962) New nematode *Spauligodon saxicolae* nov. sp. parasite of the scaly lizard, *Lacerta saxicola*. *Trudy Ukraine Republic Nauchno Obshchestva Parazitologii* **1**, 241–244.
- Sharpilo, V.P.** (1976) *Parasitic worms of the reptilian fauna of the USSR. Systematics, chorology, biology*. Moscow, Naukova Dumka.
- Sharpilo, V.P., Biserkov, V.V., Kostadinova, A., Behnke, J.M. & Kuzumin, Y.I.** (2001) Helminths of the sand lizard, *Lacerta agilis* (Reptilia, Lacertidae), in the Palaearctic: faunal diversity and spatial patterns of variation in the composition and structure of component communities. *Parasitology* **123**, 389–400.
- StatSoft Inc** (2013) *Statistica (data analysis software system)*, version 12. Available from <http://www.statsoft.com> (accessed December 2014).
- Tarkhvishnili, D.** (2012) Evolutionary history, habitats, diversification, and speciation in Caucasian rock lizards. pp. 79–120 in Jenkins, O.P. (Ed.) *Advances in zoology research*. Vol. 2. New York, Hauppauge Science Publishers.
- Yıldırımhan, H.S., Bursey, C.R. & Altunel, F.N.** (2011) Helminth parasites of the Balkan green lizard, *Lacerta trilineata* Bedriaga, 1886, from Bursa, Turkey. *Turkish Journal of Zoology* **35**, 519–535.