Infection of parthenogenetic lizards by blood parasites does not support the “Red Queen hypothesis” but reveals the costs of sex

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ABSTRACT
Sexual organisms should be better suited than asexual ones in a context of continuous evolution in response to opposite organisms in changing environments (“Red Queen” hypothesis of sex). However, sex also carries costs associated with the maintenance of males and mating (sex cost hypothesis). Here, both non-mutually excluding hypotheses are tested by analysing the infestation by haemogregarines of mixed communities of Darevskia rock lizards composed of parthenogens generated by hybridisation and their bisexual relatives. Prevalence and intensity were recorded from 339 adult lizards belonging to six species from five syntopic localities and analysed using Generalized Mixed-Models (GLMM). Both infestation parameters depended on host-size (like due to longer exposure with age), sex and, for intensity, species. Once accounting for locality and species, males were more parasitized than conspecific females with bisexual species, but no signal of reproductive mode itself on parasitization was recovered. Essentially, male–male interactions increased haemogregarine intensity while females either sexual or asexual had similar reproductive costs when in the same conditions. These findings deviate from the predictions from “Red Queen” dynamics while asymmetric gender costs are here confirmed. Thus, increased parasitization pressure on males adds to other costs, such as higher social interactions and lower fecundity, to explain why parthenogenetic lizards apparently prevail in the short-term evolutionary scale. How this is translated in the long-term requires further phylogenetic analysis.

1. Introduction
In evolutionary terms, unisexuality among the Metazoans is polyphyletic, infrequent, derived and ephemeral when compared to sexual reproduction involving males and females (Otto, 2009). Indeed, the benefits of sexuality, promoting recombination either to join beneficial alleles or to separate them from deleterious mutations, are well-recognised (Maynard-Smith, 1978). However, sex also carries substantial costs associated with both the maintenance of males (~50% individuals which do not produce progeny) and mating (behavioural stress and predation risks for both sexes), and the eventual genome dilution (Lehtonen et al., 2012). This paradox of sex is often explained by the greater adaptive potential of sexual species when abiotic or biotic pressures change along time (McDonald et al., 2016; Luijckx et al., 2017).

Van Valen (1973) initially formulated the concept of “Red Queen” applied to an evolutionary race where organisms continuously evolve to survive against antagonistically interacting organisms in changing environments. Although originally applied to simple host-parasite coevolution, the hypothesis has been later diversified to encompass more complex patterns involving different abiotic scenarios, multispecies interactions, intraspecific competition and sexual conflict (Brockhurst et al., 2014; Rabajante et al., 2015; Muraille, 2018). When purely focused on the issue of biparental sex, Red Queen hypothesis predicts that sexual organisms should be better suited than unisexual ones when interacting with parasites in variable environments.

In this context, parthenogenetic species naturally generated by hybridisation and overlapping with their bisexual relatives may become excellent models to investigate the role of sex at different time scales (Avise, 2008). Some studies suggest that, due to their low genetic variability, obligate parthenogens become less responsive in an arms-race between hosts and parasites in accordance with version of the “Red Queen” hypothesis (Moritz et al., 1991; Darevsky, 1995; Kearney et al., 2009). However, the generalisation of those findings remains...
The Caucasian rock lizards of the genus *Darevskia* Arribas, 1997 (Family Lacertidae) provide a promising study group which contains multiple biparental and parthenogenetic representatives (currently 24 and seven, respectively, Uetz and Hošek, 2019), which frequently overlap at geographic and local scale (Darevsky, 1967; Arakelyan et al., 2011). According to several phylogenetic evidences (Moritz et al., 1992; Murphy et al., 1997, 2000; Fu et al., 2000; Freitas et al., 2016), all current parthenogens have recently arisen from independent directional hybridizations between bisexual members of two distant clades within the genus. This was interpreted as the result of reticulate evolution dynamics in which parthenogens originate repeatedly but, eventually, become extinct, being unable to withstand long-term competition with their bisexual relatives (Darevsky, 1995).

Some lines of evidence, however, might challenge this simplistic view. Certainly, all parthenogenetic *Darevskia* populations are apparently composed only of females which reproduce clonally (Darevsky, 1967) and some occupy very restricted ranges. However, others are widespread and even dominate local lizard communities, suggesting competitive exclusion of their bisexual relatives (Tarkhnishvili et al., 2010). They may also coexist in sympoty with bisexual species, particularly in Armenia (Arakelyan et al., 2011), although parthenogens tend to be more abundant. In some of these mixed communities, behavioural interactions between bisexual and parthenogenetic *Darevskia* and even occasional reproduction producing polyplid individuals have been reported based on field observations, overall morphology, karyology (Danielyan et al., 2008), copulation marks (Carretero et al., 2018) and population genetics (Freitas et al., 2019).

On the other hand, haemogregarines (Apicomplexa, Coccidia, Adeleorina) are intraerythrocytic parasites extremely common among reptiles including *Darevskia* sp. (Beyer, 1968), with an inditterd life cycle with lizards as definitive hosts and ticks and mites as common vectors (Telford, 2008). Their host specificity across congeneric reptile hosts is low (Tomé et al., 2014) and infections often become chronic (Sorci, 1995). Effects reported for lacertid lizards include anaemia, reduced tail regeneration (Oppliger and Colbert, 1997), decreased locomotion performance (Sorci, 1995), lower body condition (*Lazi et al., 2017*) and lower survival (Oppliger et al., 1996) which suggest impact on fitness. In contrast, other studies find no detectable effects (e.g. Ekner-Gryzb et al., 2013). This, together with the high prevalence frequently found in many lacertid populations (Mega-Palma et al., under revision; see results), suggests that fitness costs may depend more on host immune state and haemogregarine density than on infection per se.

Consequently, here we test the “Red Queen” and the sex costs hypotheses in *Darevskia* by analysing the infection patterns by blood haemogregarines on representative communities composed of both parthenogenetic and bisexual species living in sympatry. In a “Red Queen” scenario, parthenogens are expected to be more susceptible to parasite infestation than bisexual species when in the same environmental conditions. On the other hand, if sex costs are relevant, then bisexual species are those predicted to be more parasitized, while both sexes may diverge in parasitization due to their different reproductive roles. Importantly, both hypotheses may be not mutually exclusive (Lively, 1992). Results are expected not only to elucidate the selective pressures acting on bisexual and unisexual but also to shed light on the ecology and evolution of this complex lizard group including the putative role of host-parasite interactions in this system.

### 2. Materials and methods

#### 2.1. Sampling

To exclude environmental factors (climate, disturbance, host and vector density) that may contribute to local variation in parasitaemia (*Lazi et al., 2017; Carbayo et al., 2019; Mega-Palma et al., under revision*), *Darevskia* species (three parthenogenetic and two bisexual) were sampled in different combinations from five localities from Armenia where they occur in strict syntopy (Table 1) and, hence, were expected to have similar parasite exposure within each locality. Lizard densities were always high and no evidence of spatial segregation between species or sexes was observed (Sillero et al., 2016, 2018).

Lizard hosts were collected with nooses (García-Muñoz and Sillero, 2010) from 2001 to 2010 during the breeding period in spring-early summer (Danielyan et al., 2008; Abrahamyan et al., 2014). The snout-vent length of each lizard was measured with a calliper to the nearest 0.01 mm (Roitberg et al., 2011). Lizards were photographed and, after removing tail tips (no behavioural disturbance expected, García-Muñoz et al., 2011) for blood parasite examination, were released in the sites of collection. Species and sex identification and adult state assessment were based on general morphology, colouration, scalation and size according to Darevsky (1967), Danielyan et al. (2008) and Arakelyan et al. (2011).

#### 2.2. Parasitological analysis

Thin smears were prepared from blood obtained from each lizard’s tail tip and prepared and examined following standard protocols. Namely, blood slides were air-dried, fixed in methanol, and stained with Giemsa stain. Presence or absence of haemogregarines was determined by searching of the blood smear under light microscope at ×650 magnification (Svahn, 1974; Van As et al., 2015). Parasite load was quantified in terms of prevalence (the proportion of infected hosts within a given sample) and intensity of infection (the number of infected cells within 2000 erythrocytes for each lizard host, Tomé et al., 2018). The general reliability and comparativeness of these parameters have been corroborated by quantitative molecular methods (Maia et al., 2014). The few slides that attained poor quality were not considered and the individual hosts removed from the analyses.

#### 2.3. Statistical analysis

Because both parasite prevalence and intensity deviate from normality in lacertid hosts the analysis of the factors acting on infestation was based on Generalized Mixed-Models (GLMM). Goodness-of-fit tests indicated no deviation of the data (Chi-square test p > 0.05) from a binomial and negative binomial distribution for prevalence and intensity, respectively (see a similar result in *Lazi et al., 2017*). As such, a binomial error distribution was considered for prevalence and a negative binomial error distribution was considered for intensity, both with a logit link function in both cases containing the following categorical predictors: locality, reproductive mode, species and sex. Year was not entered as factor to prevent overparameterization but the longevity

<table>
<thead>
<tr>
<th>Table 1</th>
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<tbody>
<tr>
<td>Localities and sympatric species of the rock lizards (<em>Darevskia</em> sp.) examined for host and blood parasites.</td>
</tr>
<tr>
<td>Latitude</td>
</tr>
<tr>
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</tr>
<tr>
<td>Kuchak</td>
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<tr>
<td>Lchapol</td>
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<td>Lchashen</td>
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<tr>
<td>Soke</td>
</tr>
<tr>
<td>Stepanavan</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Localities</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Altitude (metres)</th>
<th>Sexual species</th>
<th>Parthenogenetic species</th>
</tr>
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<td>44.373</td>
<td>1940</td>
<td>D. valentini</td>
<td>D. armeniaca, D. unisexualis</td>
</tr>
<tr>
<td>Lchapol</td>
<td>40.462</td>
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<td>1920</td>
<td>D. raddei</td>
<td>D. unisexualis</td>
</tr>
<tr>
<td>Lchashen</td>
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<td>44.936</td>
<td>1920</td>
<td>D. valentini. D. raddei</td>
<td>D. armeniaca</td>
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<td>Stepanavan</td>
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<td>1440</td>
<td>D. aranchinskii</td>
<td>D. dahil</td>
</tr>
</tbody>
</table>

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*M. Arakelyan, et al.*  
*Zoology 136 (2019) 125709*
Fig. 1. Relationships of blood parasite prevalence (above) and intensity (below) with host snout-vent length (SVL) in the sympatric populations of parthenogenetic and bisexual rock lizards (*Darevskia* sp.) considering species and sex. Parthenogens are in bold.
range reported for these species (3–9 years, Danielyan et al., 2008; Arakelyan et al., 2013; Kurnaz et al., 2017) suggests a considerable cohort overlap and hence stability of parasitization parameters. To focus on the comparison between parthenogenetic and bisexual lizards, a hierarchical nested design with reproductive mode nested within locality, species nested within reproductive mode and sex nested within species was implemented (see Table 3). Since both prevalence and intensity tend to increase with size (Lazić et al., 2017; Fig. 1), but size varies between species and sexes (see results), SVL was entered nested within species as continuous predictor in the analyses. Due to the multiple factors involved, the risks of overparametrization were extremely high. As such, we adopted a model building approach following Zuur et al. (2009). The models with the lowest Akaike Information Criterion (AIC) score, lower variable complexity and most explanatory significant results were selected. According to Burnham and Anderson (2003) only models with ΔAIC < 2 were considered to provide substantial evidence. To test for model significance, a Chi-square test was applied. The significance level was set at p = 0.05 in all cases. All analyses were performed in Statistica 13.4 (TIBCO, 2018).

3. Results

Overall, 339 adult rock lizards belonging to five species of genus Darevskia from five localities of sympatry were analysed (Table 2). Darevskia valentini and D. portschinskii, but not D. raddei, displayed sexual size dimorphism (males > females), while no significant size variation between localities for the same species and sex was recovered (ANOVA, species $F_{1,151} = 2.13$, p = 0.15; locality $F_{3,151} = 1.82$, p = 0.15; sex (species) $F_{1,151} = 4.10$, p = 0.008).

Parasitological examination resulted in 233 positive cases of infection by haemogregarines (67.85% overall prevalence), widely distributed across localities, species and, in the bisexual species, sexes (Table 2). Plots indicated a weak but evident increase of prevalence with S VL in most of the groups analysed (Fig. 2). The intensities of infestation displayed a wide variation, between 0 and 287/2000 erythrocytes, also affecting all localities, species and sexes (Table 2). Again, S VL clearly increased the probability of being highly infected but not in a deterministic fashion since some large individuals remained carrying low or null intensities (Fig. 2).

Of the GLMM evaluated for prevalence, only a model including species (nested within reproductive mode) and sex interacting with S VL was selected (Table 3). All other models, including those entering locality as factor, were poorly supported. Essentially, for the same locality and lizard size, males were more frequently parasitized than conspecific females (sex*S VL Wald $\chi^2 = 32.38$, p < 10$^{-6}$) and some species (e.g. D. portschinskii) attained higher prevalence (species (reproductive mode) Wald $\chi^2 = 26.01$, p = 0.00009) but intrinsic differences between bisexual and parthenogenetic females were not supported (Fig. 2).

Results of the GLMMs for intensity were slightly different but involved the same variables. Namely, a model including species (nested within reproductive mode) and sex*S VL was again first selected (Table 3). However, a second, simpler model including only sex*S VL was still within the acceptable range of ΔAIC < 2 (Table 3). Other more complex models and those including the locality achieved low support. Some species showed some trend to be more parasitized than others (e.g. D. valentini and D. raddei more than D. portschinskii) but this did not depend on the reproductive mode itself (species (reproductive mode) Wald $\chi^2 = 11.7$, p = 0.037; Fig. 3). Again, for the same size and locality, male lizards attained higher intensities than females of the same species (Sex*S VL Wald $\chi^2 = 13.1$, p = 0.001; Fig. 3). However, in this case ignoring species as relevant factor was almost as explanatory as considering it (Table 3).

4. Discussion

The proximal causes for the dominance of sexual (i.e. male and female) over unisexual (i.e. only female) mode of reproduction along the tree of life as well as the circumstances in which asexuality may secondarily arise and persist, remain one of the major outstanding problems in evolutionary biology (Moritz et al., 1991; Lively, 1992; Otto, 2009; Schön et al., 2011; Lehtonen et al., 2012). Indeed, in Darevskia sp., some parthenogenetic species have an apparent increased success under natural conditions and attain high population densities, wide distribution and even exclude their bisexual congeners (Arakelyan et al., 2011; Freitas et al. 2016; Tarkhishvili et al., 2017). In this and other reptile groups, parthenogenetic forms appear paradoxical because their short-term ecological success (in terms of present abundance and distribution) seems inconsistent with their long-term evolutionary failure in terms of phylogenetic restriction and limited genetic variability (Darevsky, 1995).

In this context, the quantitative analysis of infestation by haemogregarines in multiple mixed communities of rock lizards provided solid results for the evaluation of both evolutionary hypotheses tested.
Table 3
Model building of the factors involved in the blood parasite parameters of the sympatric populations of parthenogenetic and bisexual rock lizards (*Darevskia* sp.). First 10 models are displayed. Rep: reproductive mode (bisexual, parthenogenetic), Sp: species, SVL: snout-vent length, Loc: locality, d.f.: degrees of freedom, AIC: Akaike’s Information Criterion, ΔAIC: delta score computed as AIC, – min AIC. Selected models are in **bold**.

### Prevalence: binomial distribution, long link function.

<table>
<thead>
<tr>
<th>Model variables</th>
<th>d.f.</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>Likelihood Ratio Chi²</th>
<th>p</th>
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### Intensity: negative binomial distribution, long link function.

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</table>

Fig. 2. Variation of blood parasite prevalence (shaded area) in the sympatric populations of parthenogenetic and bisexual rock lizards (*Darevskia* sp.) considering species, sex and locality. Parthenogens are in **bold**.
Certainly, parasite load varied across localities, species and sexes but it was in consistent fashion. Parasitaemia certainly varied between species but, under similar conditions, sexual species were as infected as the parthenogens, then, not supporting the “Red Queen” hypothesis of sex. However, within bisexual species, males were more parasitized than conspecific females, while the latter did not differ from parthenogenetic females. As such, findings are in accordance with the sex cost hypothesis, suggesting that males are mainly paying cost of sex in this system. Nevertheless, these results must be considered with some detail.

First, in methodological terms, prevalence and intensity were found to be host-size dependent and lizard size entered in all the explanatory models selected. While the same relation has already been observed in lizard intestinal parasites and partly attributed to larger gut space in large hosts (Sanchis et al., 2000; Martin et al., 2005; Carretero et al., 2011, 2014), in blood parasites it likely reflects longer parasitization exposure with age (Oppliger et al., 1999; Damas-Moreira et al., 2014; Lazić et al., 2017). Nevertheless, since, with few exceptions (Clobert et al., 2000), host age is rarely assessed in parasitological studies but inferred from body size as proxy, comparisons between host groups (e.g. species, sexes) differing in size and/or demography or between size-biased samples may be problematic and must be evaluated with caution. Differences between the gradual increase of prevalence with size and the more erratic trend of intensity found here are attributable to host condition and immune response (see below).

Together with host size, sex and species influenced prevalence in the sample as revealed by the GLLM. Males were more likely to carry haemogregarines than females, which can be interpreted as a result of the larger mobility and dispersal (Sillero et al., 2018), eventually increasing the probability of infestation. Prevalence also varied across species, but this was not due to systematic differences between parthenogenetic and bisexual lizards but to the higher infestation rates of *D. portschinskii* compared to the other bisexual species. Since, this species appeared in a single locality in the current dataset, it is difficult to disentangle if this was due to lower resistance to haemogregarines or simply to higher exposure to microhabitat or climate conditions favourable to infestation. This would require comparison across multiple localities and experimental work (Megía-Palma et al., under revision).

Parasite intensity was also affected by host size, sex and species but the patterns did not completely mirror those of prevalence suggesting dynamic relations between haemogregarines and their lizard hosts. Males tended to attain higher intensities than females. Evidence on other lacertid species indicates that testosterone promotes immunosuppression, increasing vulnerability to infection during the breeding season. This is likely related with the high rate of social interactions (e.g. agonistic, copulations) increase stress (Oppliger et al., 1996; Salvador et al., 1997; Clobert et al., 2000; Olsson et al., 2005). Populations of parthenogens, which are characterized by high home range overlaps and low levels of intraspecific aggression (Galoyan, 2013), apparently become released of this socially-induced stress. However, bisexual females attained similar intensities in the same conditions. Remarkably, limited hybridization between bisexual males and parthenogens has been reported for Kuchak and Sotk localities analysed here (Carretero et al., 2018; Spangenberg et al., 2017; Freitas et al., 2019). All this evidence suggests that females, either parthenogenetic or bisexual, are under lower reproductive stress than males and that male-male aggression may increase haemogregarine intensity although this should be tested with behavioural data. Furthermore, *D. portschinskii* attained the highest prevalence but the lowest intensity among the bisexual species, reinforcing the idea that host resistance is as important as parasite exposure in this system.

Fig. 3. Variation of blood parasite intensity in the sympatric populations of parthenogenetic and bisexual rock lizards (*Darevskia* sp.) considering species, sex and locality. Parthenogens are in *bold*.
Overall, common parthenogenetic Darevskia lizards were not over- 
load with blood parasites when compared to its bisexual relatives in 
sympathy. These findings deviate from the predictions of the para-
sitological version of “Red Queen” hypothesis (Moritz et al., 1991). 
Expectations that parthenogenetic species should prevail in sparse host 
populations with low parasitization risks (Lively et al., 1990) were 
clearly not met. This was, however, not completely unexpected in the 
light of the recent parasitological literature. For instance, Pakosta et al. 
(2018) found similar prevalence of monogeneans in sexual and asexual 
Carassius gutbi fishes and even opposite temporal variations in ecto-
parasites and nematodes excluding Red Queen dynamics. On the other 
hand, Menezes et al. (2017) also report low richness of the nematode 
faua associated with unisexual Ameivula nati teid lizards versus 
their bisexual congers, although in that case it seems to be associated 
with narrower geographic distribution and low diversity of habitats 
occupied, which can be discarded here. Finally, similar patterns have 
already been found for other parasites of Darevskia sp. Thus, the hel-
mith fauna of D. armeniaca and other three parthenogens with re-
stricted range (D. uzzeli, D. bendimahiansis, D. sapphirina) showed re-
latively low infection rates by cestodes an nematodes and shared 
parasite species when compared to bisexual species in Western Ana-
tolia (Jorge et al., 2011; Roca et al., 2015; Roca et al., 2016a). This has 
to be taken with caution since males and females of bisexuals species 
were pooled together in these studies and that substantial geographic 
and climatic variation in helmith fauna within Darevskia species has 
also been described (Roca et al., 2016b). Nevertheless, higher sus-
ceptibility of males has already been reported in lizards (Menezes et al., 
2004).

Instead, the expectations from the sex cost hypothesis were almost 
fully met. Males were more frequently and more intensively parasitized 
than females of the same species regardless the site and even the spe-
cies. Differences in movement patterns, such as larger home ranges 
(Siller et al., 2016), are expected to promote higher male parasitiza-
tion (Kearney et al., 2009). On the other hand, Galoyan (2013) in-
dicated that home ranges, core areas, and even activity centres and 
basking sites of parthenogenetic females overlapped more extensively 
than in the females non-parthenogenic species. This would find support 
in spatial models of coevolution in metapopulations predicting that a 
large difference between host and parasite dispersal rates favours an 
obligatory asexuall host reproductive strategy over an obligatory sexual 
one (Ladle et al., 1993). However, this needs further evaluation since 
those home range comparisons between sexual and unisexual species 
were conducted in different sites and habitats (Galoyan, 2013). In the 
sympatric populations analysed here, bisexual and unisexual females 
were similarly parasitized.

It could also be argued that the hybrid nature of the parthenogens 
(Brown et al., 1995; Freitas et al., 2016; Ryskov et al., 2017) might have 
conferred them extra resistance to the parasites originally specialized 
in asexual hosts (Lacerta armeniaca). A comparison in the Red Queen 
https://doi.org/10.1098/rspb.2014.1382.

Brown, S.G., Kwan, S., Shero, S., 1995. The parasitic theory of sexual reproduction: 


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