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Parthenogenetic *Darevskia* lizards mate frequently if they have the chance: a quantitative analysis of copulation marks in a sympatric zone

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Several Caucasian rock lizards of the genus *Darevskia* of hybrid origin are known to reproduce parthenogenetically. Local communities can be composed exclusively of parthenogens, though syntopy with bisexual members of the genus may occur. In some localities, reproduction between bisexual and parthenogenetic *Darevskia* has been previously reported based on lizard intermediate morphology and karyology (3n, 4n). However, the frequency of such heterospecific matings remains unknown. We indirectly quantified the reproductive interactions through the inspection of copulation marks in females in a mixed *Darevskia* community from Kuchak (Armenia) composed of two hybrid parthenogens (*D. armeniaca* and *D. unisexualis*), one bisexual species (*D. valentini*) and their putative backcrosses. A total of 139 adults were randomly collected and photographed. Females were later measured (SVL), inspected for inguinal marks and ranked from 0 (no scars) to 3 (≥ 3 scars). The lizard species and ploidy determination was ensured by a parallel microsatellite analysis. Sex-ratio in the community was extremely biased due to the high abundance of parthenogenetic females. All female types displayed copulation marks with frequencies varying from 80% in *D. valentini* to 64% in *D. armeniaca*. Remarkably, 7 out of 11 (64%) backcross females also showed marks. In the most abundant *D. armeniaca*, the prevalence and intensity of copulation marks increased with body size, just as predicted for polygynous female lacertids. These results indicate that copulation between parthenogenetic and bisexual species in *Darevskia* mixed communities is common and driven by sexual selection, thus reinforcing previous suggestions of reproductive interaction in syntopy. Evolutionary implications of these findings are discussed.

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Introduction

Asexual lineages are infrequent, polyphyletic and generally short-lived along the evolutionary tree of Eukaryote (Vrijenhoek 1998). Nonetheless, reports of animals displaying obligate or facultative parthenogenesis increase day by day. Some of them, but not all, are of hybrid origin (Avise 2008). Although the benefits of sexual reproduction are obvious in terms of recombination, joining beneficial alleles or separating them from harmful mutations (Maynard-Smith 1978), several groups have apparently conserved this reproductive strategy for long periods of time (Judson and Normark 1996) while others may alternate it with sexual reproduction (Avise 2008). This is gradually shifting the scientific view of parthenogenetic species as natural rarities or evolutionary dead-ends towards useful models organisms in animal evolution, namely, to investigate the role of sex and the contribution of genetic exchange between distant lineages to produce evolutionary novelties (Arnold 2006).

The Caucasian rock lizards of the genus *Darevskia* (Family Lacertidae) were the first group of terrestrial vertebrates for which parthenogenesis was demonstrated (Darevsky 1967). In fact, as many as seven members of the genus are known to be composed only of females which reproduce clonally (Arnold et al. 2007). Phylogenetic evidence indicates that such parthenogens result from directional hybridizations between two distant clades within the genus (Murphy et al. 2000) and that such events were rare, recent and geographically localized (Freitas et al. 2016). One or more of these all-female parthenogens may monopolize local lizard communities in the Caucasus, suggesting competitive exclusion (Tarkhnishvilli et al. 2010). However, they also occur in syntopy with bisexual members of the genus, particularly in Armenia (Arakelyan et al. 2011). In some of these localities, reproduction between bisexual and parthenogenetic *Darevskia* has been reported based on lizard intermediate morphology (Danielyan et al. 2008). Moreover, karyological analyses have demonstrated that some intermediate, large-sized specimens are triploid and even tetraploid (Danielyan et al. 2008). Nevertheless, the frequency and directionality of the suspected heterospecific matings is still unknown.

Quantifying reproductive interactions by direct observation in the field for large numbers of individuals can only provide limited results. However, other sources of evidence are available here. Namely, copulation represents a crucial step in vertebrate reproduction involving multiple features, all under sexual selection (Andersson 1994). Courtship behaviour in lizards may induce reproductive isolation and carry substantial phylogenetic inertia. In particular, male lacertids repeatedly bite females during mating (In den Bosch and Zandee 2001) but the position of the bite varies across large phylogenetic groups (Arnold et al. 2007). Interestingly, there is also variation within *Darevskia* with the *D. saxicola* and *D. rudis* (including *D. valentini*) clades displaying a flank or inguinal bite commonly found in other Lacertinae, while the *D. caucasica* clade (including *D. raddei*) displays a peculiar thigh bite (Darevsky 1967; Murphy et al. 2000). Thus, the analysis of copulation marks on females may allow identification of the species of the male involved, and the intensity of reproductive interactions to be inferred.

Here we analyse bite marks to assess the direction and to quantify the reproductive interactions between the components of a *Darevskia* mixed community constituted by one bisexual species, two parthenogens and their putative backcrosses. This source of evidence is expected to shed light on the behaviour and evolution of this complex lizard group. Namely, we focus on the relationships between sexual and asexual reproductive strategies.

Materials and methods

The sampling was conducted in an area dominated by rocky outcrops, grasslands and bushes near Kuchak, Armenia (44.385 N, 40.532 W, 1940 m asl) at the foothills of Mount Aragats (for a detailed description see Arakelyan et al. 2011; Sillero et al. 2016). In this locality, the presence of three *Darevskia* species, one bisexual (*D. valentini*) and two parthenogens (*D. armeniaca, D. unisexualis*), as well as their putative backcrosses *D. valentini* × *D. armeniaca* and *D. valentini* × *D. unisexualis*, was previously reported based on their morphology and karyology (Danielyan et al. 2008). It is noteworthy that phylogenetic evidence indicates that *D. armeniaca* resulted from the hybridization between male *D. valentini* and female *D. mixta*, and *D. unisexualis* from the hybridization between male *D. valentini* and female *D. raddei*, although such hybridization events did not take place in this locality (Murphy et al. 2000; Freitas et al. 2016).

Sampling was conducted during three consecutive days (1–3 June 2011) in the middle of the reproductive period (Danielyan et al. 2008; Abrahamyan et al. 2014) to ensure no major differences in the temporal accumulation of scars between individuals. For 8 h/day, random unidirectional surveys in search of adult lizards sampled non-redundant parts of the study area (Sillero et al. submitted). Lizards were collected by noosing (García-Muñoz and Sillero 2010) by two researchers, their SVL measured with a calliper to the nearest 0.01 mm (Roitberg et al. 2011) and dorsal and ventral pictures were taken. After recording some environmental variables (GPS coordinates, habitat and temperature) and removing 1 cm of tail tip (no behavioural disturbance expected, García-Muñoz et al. 2011) stored in ethanol for genetic analyses (Freitas et al. in press), each lizard was released in the exact capture site. Even if collected transects were unidirectional (ensured by GPS locations), this tail removal also prevented recapturing the same individual.

Digital pictures of each individual were first examined for preliminary species identification based on general morphology and coloration according to Darevsky (1967), Danielyan et al. (2008) and Arakelyan et al. (2011). Such identification, including hybrid status and ploidy level, was later confirmed by genotypic individuals using a battery of 12 polymorphic microsatellites (Freitas et al. in press). In those cases of identification discordance between morphological and genetic evidence (<10%), priority was given to the second.

Pictures of the ventral area of each individual were then carefully inspected double blind for bite marks (either inguinal or on the thighs) suggesting an attempt of copulation (Darevsky 1967). Marks were ranked from 0 (no scars) to 3 (≥ 3 scars). There were only two cases of discordance between both readings. In these cases, we ascribed rank to the lowest of the two discordant values.

Deviations of sex ratio from 1:1 were tested using a Yates-corrected chi-square. Comparisons of SVL between individuals with and without scars and across individuals with different scar ranks were performed using ANOVA after ensuring normality (Shapiro–Wilk's test, $p > 0.05$) and homoscedasticity (univariate Levene's test or multivariate Box M, $p > 0.05$) of the data.

Results

A total of 139 adult lizards were collected during the sampling; 116 were females and only 23 were males. The parthenogen *D. armeniaca* was the most abundant in the sample ($N = 96$) followed by the bisexual *D. valentini* ($N = 23$), but the parthenogen *D.*

Table 1. Number of male and female lizards examined and presence of copulation scars among female lizards from Kuchak (Armenia) according to species and reproduction type. The quality of picture did not allowed recognition of scars in one female *D. valentini* and one *D. armeniaca*.

Group	Ploidy	Reproduction type	N males	N females	No scars	Scars
D. valentini	2n	Bisexual	17	6	1 (20%)	4 (80%)
D. armeniaca	2n	Parthenogen	–	96	34 (36%)	61 (64%)
D. unisexualis	2n	Parthenogen	–	3	1 (33%)	2 (67%)
D. valentini × *D. armeniaca*	3n	Backcross	0	2	1 (50%)	1 (50%)
D. valentini × *D. unisexualis*	3n	Backcross	6	9	3 (33%)	6 (67%)

unisexualis and the backcrosses of *D. valentini* with both parthenogens were found in lower numbers (Table 1). For the whole sample, the deviation from a balanced sex ratio towards females was significant ($\chi^2 = 37.49$, df = 1, $p < 0.0001$) but, when calculated for *D. valentini* alone, it was not (Yates corrected $\chi^2 = 2.74$, df = 1, $p = 0.10$).

The quality of the digital pictures was good enough to grant reliable inspection of copulation scars for 114 females (all but one *D. valentini* and one *D. armeniaca*). Females from all groups, either bisexual or parthenogens, displayed copulation marks (Figure 1) with a frequency ranging from 80% in *D. valentini* to 64% in *D. armeniaca*. Remarkably, 7 out of 11 (64%) backcross females also displayed marks (Table 1). Males showed no evidence of marks while marks from all females analysed were exclusively found in the flank, inguinal region.

In the most abundant parthenogen *D. armeniaca*, the variation patterns of prevalence and intensity of copulation marks with body size could be examined in detail. In particular, *D. armeniaca* with copulation marks attained larger SVL than without them ($F_{1,88} = 13.05$, $p = 0.0005$). Furthermore, SVL also increased gradually with the increasing rank of copulation marks ($F_{3,86} = 4.80$, $p = 0.004$, Figure 2).

Discussion

Copulation between bisexual and parthenogenetic *Darevskia* had already been reported indirectly based on the finding of lizards with intermediate morphology and on karyological data (Danielyan et al. 2008). However, the scarce number of triploid individuals found in mixed communities suggested that this might be a rare event. Here, the quantitative analysis of bite marks proved that this was not the case at least in the study area. It may be argued that some bites may have not resulted in effective copulations. Moreover, it is true that some parthenogenetic species, such as whiptail lizards, *Aspidoscelis* sp. (Crews and Fitzgerald 1980; Crews et al. 1986; Crews and Young 1991; Crews and Moore 1993; among others) and *Lepidodactylus* geckos (McCoid and Hensley 1991) exhibit pseudocopulation between females of the same clonal lineage. However, pseudocopulatory behaviour is not reported for other parthenogenetic reptiles (Avise 2008) and in the case of parthenogenetic *Darevskia*, apparently these female–female reproductive interactions do not occur (Darevsky 1967). In fact, isolated females successfully reproduce in captivity for generations (A. van der Meijden unpubl.) and marks were completely absent in other Armenian populations of the parthenogens *D. armeniaca* and *D. unisexualis* where no bisexual species (no males) were present (authors' unpublished field data). This evidence suggests (1) that bisexual males were

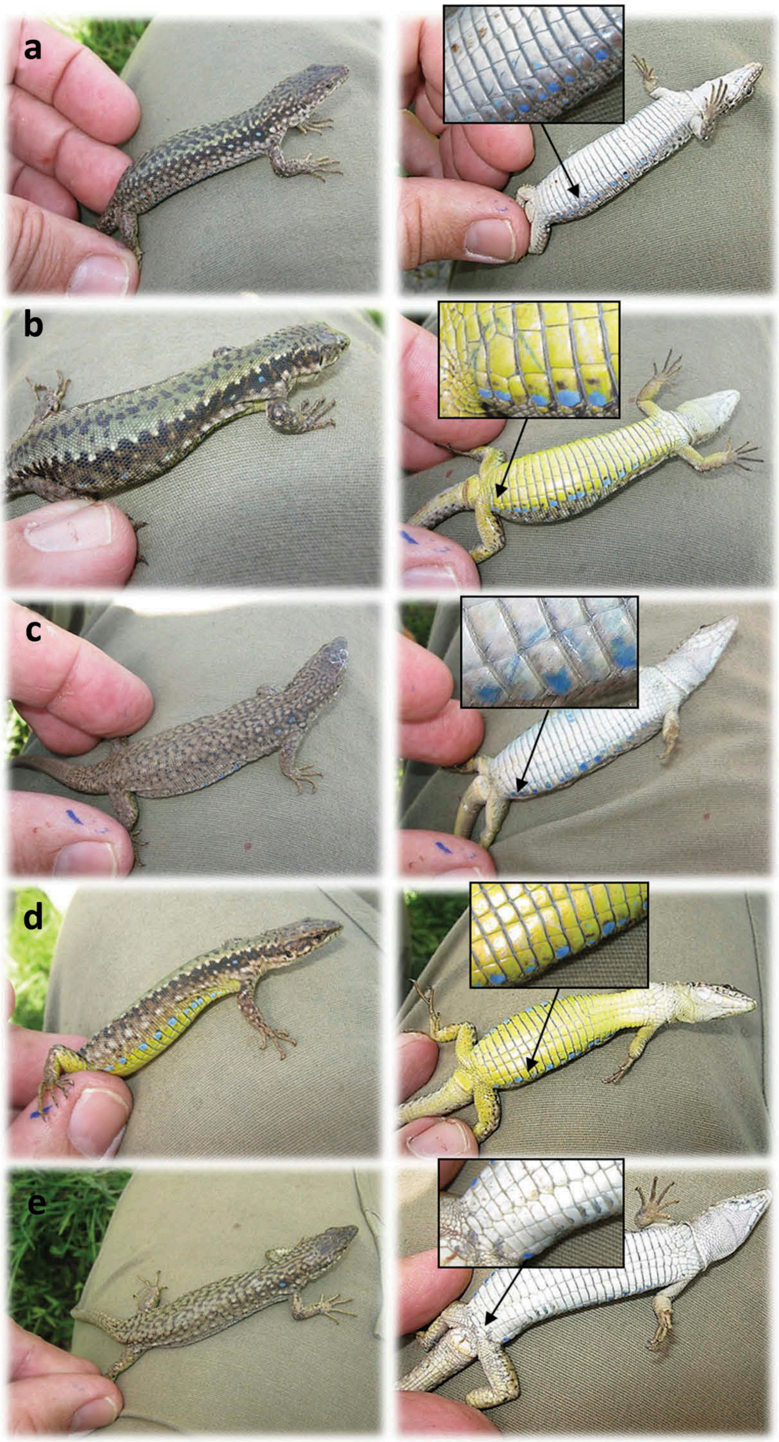

Figure 1. Representative images of females of *Darevskia* sp. from Kuchak (Armenia). Left: dorsal view; right: ventral view and scar detail. (a) *D. valentini* (2n, bisexual); (b) *D. armeniaca* (2n, parthenogenetic); (c) *D. unisexualis* (2n, parthenogenetic); (d) *D. valentini* × *D. armeniaca* (3n, backcross); (e) *D. valentini* × *D. unisexualis* (3n, backcross). Identifications are all supported by genetic data (Freitas et al. in press)

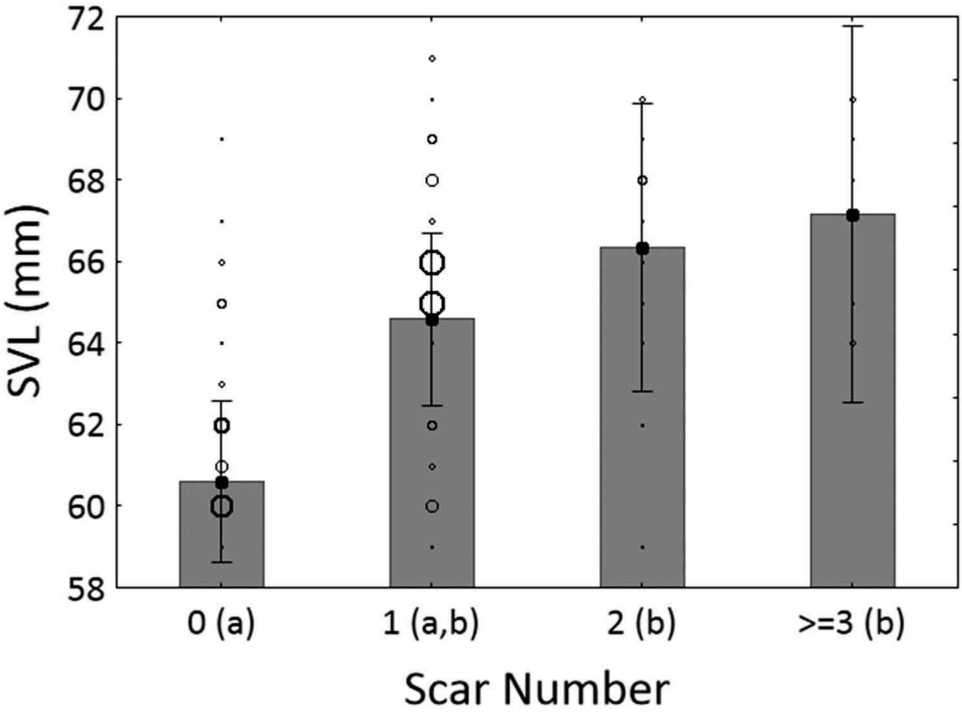

Figure 2. Variation of snout–vent length (SVL, in mm) according to the number of copulation marks in parthenogenetic females of *D. armeniaca* from Kuchak (Armenia). Mean values and 0.95 confidence intervals are displayed as well as the raw data with symbols proportional to the number of individuals. Letters between parenthesis on the x-axis indicate the groups according to Duncan post-host tests ($p < 0.05$) after significant ANOVA (see results).

mainly responsible for the marks; (2) that bite marks provide a reliable proxy of copulation attempt frequency; and (3) that copulation of parthenogens was at least as frequent as in the bisexual species (Darevsky 1967). Remarkably, all marks were found in an inguinal position, therefore pointing to *D. valentini* males as responsible and discarding eventual undiscovered males of *D. raddei*, which display leg copulation (Darevsky 1967). Backcross males *D. valentini* × *D. armeniaca* or *D. valentini* × *D. unisexualis*, whose copulatory behaviour is unknown, could also account for some copulation events, albeit they should be very few according to their low frequency in this community.

The most relevant demographic factor determining reproductive interactions in Kuchak must have been the scarcity of males and the high abundance of parthenogenetic females, in particular, *D. armeniaca*. As non-cryptic mate choice in lacertids seems to rely mostly on males (Olsson and Madsen 1995; While et al. 2015), female-biased composition should decrease male–male competition (Le Galliard et al. 2005; Fitze et al. 2006) while increasing male ‘choosiness’ towards females (Fitze et al. 2008). In this context, despite not being conspecific, the superabundant parthenogenetic females were far from neutral. First, *D. valentini* females were probably difficult to find by conspecific males according the frequencies found here and by Danielyan et al. (2008). Second, parthenogenetic *Darevskia* have been reported to be less aggressive and to tolerate higher densities than their bisexual relatives (Galoyan 2013). Third, the parthenogens *D. armeniaca* and *D. unisexualis* in fact share half of the genome with *D. valentini* due to their hybrid origin (Murphy et al. 2000, Freitas et al. 2016). All these factors have likely potentiated copulations between bisexual and parthenogenetic lizards in this community.

The sample of *D. armeniaca* allowed deeper analysis of intraspecific variation, evidencing a clear increase of the number of bite marks with female size (Figure 1). This is expected from the fertility assurance hypothesis in polygynous lizards such as lacertids (Uller and Olsson 2005). In other words, large females potentially able to lay bigger clutches attracted more matings and probably more male partners, as reported for other lacertid species (Fitze et al. 2006)..

The present results agree with previous studies on home ranges and spatial distribution, suggesting that *Darevkia* mixed communities composed of bisexual species and hybrid parthenogens are behaviourally more interactive between species than common multispecies communities (Sillero et al. 2016). This intense interaction is, nevertheless, contrasting with the low proportion of triploid backcrosses in the community (Danielyan et al. 2008; Freitas et al. in press). This can be interpreted as an evidence of postmating, rather than premating, reproductive isolation. Indeed, Darevsky et al. (1978) and Danielyan et al. (2008) report numerous instances of low embryo viability as well as adult sterility and intersexes in *Darevskia* backcross hybrids, suggesting postzygotic barriers.

Nonetheless, evidence from population genetics (Freitas et al. in press) suggests such postzygotic barriers are not absolute. The causes may be multiple. Parthenogenetic reproduction allows parthenogens to duplicate their reproductive output compared to bisexual species, saving behavioural costs associated with reproduction and bypassing the costs of hybridization with other species (Avise 2008). Thus, short-term dominance of parthenogens in demographic terms may lead them to outcompete bisexual species in syntopy (Tarkhnishvili et al. 2010) but, alternatively, may provide an enlarged window of opportunity for hybridization between sexual and parthenogenetic species as found here. Whether this finally results in reticulate evolution in *Darevskia* sp. should be analysed at the phylogenetic level. However, parthenogenetic reproduction of F1 hybrids (parthenogens) and the frequent reproductive interactions with bisexual species certainly increase the probabilities of introgression.

Overall, these results indicate that copulation between parthenogenetic and bisexual *Darevskia* in mixed communities is not just a curious and isolated event, but a common phenomenon with likely evolutionary repercussions which deserves to be investigated deeply. Last but not least they highlight the importance of copulation marks as a key natural history trait to infer reproductive interaction in lizards within and across species, particularly if combined with other sources of evidence coming from phylogeny, population genetics and biogeography.

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