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Parthenogenesis through the ice ages: A biogeographic analysis of Caucasian rock lizards (genus *Darevskia*)



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ABSTRACT

Darevskia rock lizards include both sexual and parthenogenetic species, mostly distributed in the heterogeneous and ecologically diverse Caucasus. The parthenogenetic species originated via directional hybridogenesis, with only some of the sexual species known to serve as parentals. However, it remains unclear when and where these events happened and how many parental lineages were involved. A multilocus phylogeographic analysis was performed on the parthenogens *D. unisexualis*, *D. bendimahiensis* and *D. uzzeli*, and their putative maternal species *D. raddei*. Results show the parthenogenetic species all have relatively recent origins, approximately 200–70 kyr ago, and at least three hybridization events were involved in their formation. Ecological niche models identify the region where hybridization events leading to the formation of *D. unisexualis* took place, namely in the northeast of the current distribution. Models also suggest that the sexual *D. raddei* might have undergone a habitat shift between the Last Interglacial and the Last Glacial Maximum.

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1. Introduction

The study of parthenogenetic organisms, which reproduce in the absence of sex, provides an opportunity to understand the significance of sexual reproduction and the evolution of sex. In particular, taxa that present both sexual and parthenogenetic reproduction within the same clade, provide an opportunity to compare both reproductive forms and analyse their eventual ecological interactions (Gilbert et al., 2014; Otto and Nuismer, 2004). Reptiles are good model organisms for such studies due to the wide variety of reproductive modes and life history strategies, and lizards in particular are recurrent models used in studies of

speciation, phylogeography and adaptation (Camargo et al., 2010). Several lizard families include parthenogenetic and sexual species, making them especially interesting for studying the evolution and function of sexual reproduction (Avisé, 2008). Indeed, parthenogenesis was first described in vertebrates in the lizard genus *Darevskia* (Darevsky, 1967). Since then, at least 43 other cases of parthenogenetic reproduction have been described in the Squamata (Kearney, 2003; Vrijenhoek, 1989). It is estimated that 0.6% of squamates (which comprise around 7000 species) can reproduce parthenogenetically, either obligatorily or facultatively (Kearney et al., 2009). Parthenogenesis is found across the squamate phylogeny and through a wide geographical range and ecological conditions. Most, but not all, parthenogenetic forms arose after hybridization between two related species, but the scenario for the origin of the parthenogenesis varies with the group and it is highly complex (Avisé, 2008). Given this widespread distribution and the fact that parthenogenetic reproduction is frequently considered an “evolutionary dead-end” (Bell, 1982), it is still not fully

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understood whether new parthenogenetic lineages regularly appear and how they compete with sexual forms.

In this study we focus on lizards of the genus *Darevskia* Arribas, 1997 of the family Lacertidae. This is a group of small lizards found across the Caucasus and adjacent regions, including Turkey, Iran and the Balkans (Arnold et al., 2007). Currently 32 species are recognised (Ahmadzadeh et al., 2013b; Uetz and Hošek, 2015) which occupy a wide diversity of habitats, from forest and meadows to rocky habitat. Initial estimates of phylogenetic relationships based on partial Cytochrome-*b* (Cyt-*b*) mitochondrial DNA sequences and protein electrophoretic data suggest parthenogenetic lineages result from successful directional hybridization events between sexual *Darevskia* species. Only four parent species are thought to have been involved, *D. raddei* (Boettger, 1892) and *D. mixta* (Méhely, 1909) as the maternal donors and *D. valentini* (Boettger, 1892) and *D. portschinskii* (Kessler, 1878) as the paternal donors (Fu et al., 1997; Murphy et al., 2000). The sexual *Darevskia* species that most commonly contributes as a parental for the parthenogenetic lineages is *D. raddei*, being the proposed maternal species for at least five of them: *D. unisexualis* (Darevsky, 1966) (Armenia, northeastern Turkey and southern Georgia), *D. uzzelli* (Darevsky & Danielyan, 1977) (northeastern Turkey), *D. bendimahiensis* (Schmidtler, Eiselt & Darevsky, 1994) (northeast of Lake Van), *D. sapphirina* (Schmidtler, Eiselt & Darevsky, 1994) (north of Lake Van in the vicinity of Erçiş) and *D. rostombekowi* (Darevsky, 1957) (northern Armenia and western Azerbaijan) (Fu et al., 1997; Baran et al., 2012). Nevertheless, *D. raddei* itself has been suggested to be a species-complex containing the forms “*raddei*”, “*nairensis*” and “*vanensis*” whose status and phylogenetic relationships are still a matter of debate (Grechko et al., 2007). As a consequence, it remains unclear if different *D. raddei* lineages may have been involved in the hybridization events that led to the parthenogenetic lineages. The form “*raddei*” is distributed throughout the south and northeast of Armenia and Nagorno-Karabakh (Arakelyan et al., 2011), Azerbaijan and the northern part of the east Azerbaijan and Ardabil provinces of Iran (Anderson, 1999). The form “*vanensis*” is found in easternmost Anatolia, east of Lake Van and the west Azerbaijan Province of Iran (Baran et al., 2012). The differences between them are based on quantitative morphological traits that are not fully diagnostic (Anderson, 1999). The third form “*nairensis*” is restricted to the northeastern part of Armenia, along the western margin of the Sevan Lake. It is noteworthy that sympatry of *D. raddei* “*nairensis*” with one of the parthenogenetic forms (*D. unisexualis*) has been described for a single locality: Lchap (Gegharkunik province), on the west margin of the Sevan Lake in Armenia (Arakelyan et al., 2011; M. Arakelyan and F. Danielyan, unpubl. com.). Examining the diversity of Cyt-*b* sequences within the *D. raddei* complex (except “*vanensis*”), MacCulloch et al. (2000) concluded that the forms “*raddei*” and “*nairensis*” were conspecific due to the paraphyletic relationships found. A fourth form, *D. raddei* “*chaldoranensis*” has been recently described based on scalation and coloration characters, from a single locality of northern Zagros, western Azerbaijan Province of Iran (Rastegar-Pouyani et al., 2011, 2012), falling within the putative range of the form “*vanensis*”.

The region where these forms occur, the Caucasus, includes a remarkable habitat and topographical heterogeneity likely to have promoted the formation of important biological barriers, and harboured multiple glacial refugia for sedentary species, including reptiles, during the last cold period (Ahmadzadeh et al., 2013a,b; Tarkhnishvili et al., 2000, 2013). Nevertheless, evolutionary studies reveal heterogeneous biogeographic patterns for the biota in this region. While the Caucasus may have acted as a complex secondary contact zone for some species (Seddon et al., 2002), for others it appears to have acted as a barrier to expansion (Tarkhnishvili et al., 2000).

Here, we aim to infer the biogeographic patterns of parthenogenetic and bisexual rock lizards by addressing three questions: (1) Where and when did the parthenogenetic *Darevskia* species appear and could this be related to known biogeographic events? (2) How many parental lineages contributed for the parthenogenetic species under study? and (3) Have parthenogenetic species undergone identifiable periods of range expansion or contraction since their origin? We focus on the *Darevskia raddei* sensu lato sexual species and the hybrid parthenogenetic daughter lineages, *D. unisexualis*, *D. uzzelli* and *D. bendimahiensis*.

To answer the first and second questions, a phylogenetic dating approach was employed. The molecular markers were used to determine the specific maternal lineage for each of the parthenogenetic forms analysed and, specifically, whether the parthenogenetic lineages come from single or multiple hybridization events. To try to infer the location of those events ecological niche modelling was performed based on the current environment and on projections to two different paleoscenarios, the Last Interglacial (LIG – 130 to 115 kyr ago) and the Last Glacial Maximum (LGM – 22 kyr ago), taking into account the age estimates for each species. If the origin of the parthenogenetic species occurred after the LIG, then comparisons of the potential distributions during the paleoscenarios analysed (LIG and LGM) with the present distribution model would allow inference regarding where these lineages could have been during the hybridization events. Regarding the last question, tests on population expansion/contraction were performed.

Furthermore, the current distribution ranges of the sexual species and of the parthenogen *D. unisexualis* were compared to the present habitat suitability model and to the projections for the estimated paleoscenarios as inferred by ecological niche modelling. With this we intend to infer how competition may influence the distribution of both parthenogenetic species and the sexual parentals. Due to their extremely restricted distribution, insufficient to infer ecological models, the other two parthenogenetic species, *D. uzzelli* and *D. bendimahiensis*, could not be included in this analysis.

2. Material and methods

2.1. Study area and datasets

A total of 235 samples collected across the whole species ranges were used for the molecular analyses (Supplementary Table 1). *D. raddei* sensu lato individuals were selected from 90 localities covering the whole distribution range of the complex, *D. unisexualis* from 15 localities (N=32), and *D. uzzelli* (N=5) and *D. bendimahiensis* (N=3) from one locality each, due to their locally restricted distribution (Fig. 1, Supplementary Table 1). Presence records for 165 individuals (see Supplementary Table 1) were used to construct the ecological niche models (ENMs). In all cases, only records confirmed by molecular data were used. Geographic coordinates of sampling localities were geo-referenced with a Global Positioning System (GPS) receptor on the WGS84 datum. The study area is a polygon which includes the global distribution of both species (*D. raddei* and *D. unisexualis*) as provided by IUCN, defined by the coordinates xMin,yMin 37.8275,34.8814:xMax,yMax 53.12645,1208. This area was chosen in order to detect suitable habitats outside the distribution ranges of both species and to analyse the overlap between both ENMs, but taking into account their limited dispersal rate. Outgroup species used were sampled (*D. portschinskii*, *D. rudis* Bedriaga, 1886, and *D. valentini*) or their sequences downloaded from Genbank (*Iranolacerta*). From all individuals sampled in the field, tail tips, photographs and basic mea-

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