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Competition with wall lizards does not explain the alpine confinement of Iberian rock lizards: an experimental approach

Camila Monasterio[a,b,*], Alfredo Salvador[a,b], José A. Díaz[b]

[a] Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, E-28006 Madrid, Spain
[b] Departamento de Zoología y Antropología Física (Vertebrados), Facultad de Biología, Universidad Complutense, José Antonio Novais, E-28040 Madrid, Spain

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ABSTRACT

Interspecific competition can limit the distribution of species along altitudinal gradients. It has been suggested that Western European rock lizards (genus *Iberolacerta*) are restricted to mountains due to the expansion of wall lizards (*Podarcis*), but there is no experimental evidence to corroborate this hypothesis. This study examines if interference competition with *Podarcis muralis* is a plausible explanation for the alpine confinement of Iberian rock lizards *Iberolacerta cyreni*. In a first experiment, we used an enclosure with four types of microhabitats to investigate whether adult rock and/or wall lizards shifted microhabitat or refuge preferences in the presence of the other species, and to detect aggressive interactions between them. In a second experiment, we staged heterospecific encounters between naïve, laboratory-born juveniles to identify behavioural differences and agonistic interactions. In the enclosure, neither rock nor wall lizards changed their microhabitat preferences in the presence of the other species. Nevertheless, rock lizards increased the diversity of microhabitats and nocturnal refuges used in the single species trials, which had twice the number of conspecifics. Aggressive interactions involved mainly large rock lizard males. Juveniles did not show any interspecific agonistic behaviour, but rock lizards spent more time basking and less time moving. Thus, we found no evidence of competition between both species in terms of habitat shifts or agonistic interactions, although intraspecific interactions seemed to explain the behaviour of adult rock lizards. We conclude that other factors are currently determining the alpine confinement of rock lizards.

1. Introduction

Interspecific competition, combined with other biotic and abiotic factors, can limit the distribution of species in potentially suitable habitats (Brown et al., 1996; Pulliam, 2000). While dominant species successfully exploit the shared habitat, subordinate ones can be relegated to suboptimal areas either by their reduced exploitative ability or by direct behavioural interference (Schoener, 1983; Petren et al., 1993). In evolutionary time, competitive exclusion can lead to phenotypic divergence of sympatric species, which diversify their use of resources (Schluter, 2000; Pfennig et al., 2007; Moen and Wiens, 2009). Also, in an effort to minimise overlapping, species can segregate in space by selecting different habitats, a behavioural mechanism which can contribute to generate allopatric distributions (Hess and Losos, 1991; Taniguchi and Nakano, 2000).

Lizards, for their dynamic distribution ranges and moderate dispersal ability, are good models to investigate the role of interspecific competition in community structure. Several studies have demonstrated the crucial role of interspecific competition in the evolution, distribution, and abundance of island lizards (see Case and Bolger, 1991 for a review). For example, success in island colonisation by anoles is seemingly shaped by interspecific competition (Losos et al., 1993; Losos and Spiller, 1999), and the evolutionary radiation and community structure of Caribbean anoles and *Phelsuma* geckos in the Indian Ocean were likely driven by competitive interactions (Losos, 1994; Leal et al., 1998; Harmon et al., 2007).

Although much of the relevant literature concerns island species, elevation has also drawn the attention of biogeographers and evolutionary ecologists seeking to explore the role of interspecific competition in the vertical zonation of organisms (Tannerfeldt et al., 2002; Cadena, 2007; Twomey et al., 2008). For reptiles, the possible effect of competitive interactions on the distribution of species along altitudinal gradients is unclear. While in some cases interspecific competition appears to modify population responses to elevation (Buckley and Roughgarden, 2005, 2006), the altitudinal distribution of other communities seems unrelated to interactions among species (Hofer et al., 1999; Carothers et al., 2001). Nevertheless, studies are still scarce, and further research is needed to

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[*] Corresponding author.
E-mail address: camila@mncn.csic.es (C. Monasterio).

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improve our understanding of how biotic interactions shape lizard assemblages along altitudinal gradients.

West European rock lizards within the genus *Iberolacerta* have small, widely separated ranges in highland areas of the western Mediterranean. They form a monophyletic group with four main units: *I. horvathi* of North-west Croatia and neighbouring regions, the Pyrenean species (*I. bonnali*, *I. aranica* and *I. aurelioi*), the *I. monticola* group from Central Portugal and North-west Spain, and *I. cyreni* of the Iberian Sistema Central, with distinctive populations in Béjar, Gredos and Guadarrama mountain ranges (Carranza et al., 2004). Molecular analyses suggest that *Iberolacerta* has produced few external branches since its initial fragmentation, at approximately the same time when wall lizards (*Podarcis*) diversified into a series of widespread lineages that have persisted until present time (Carranza et al., 2004). Thus, *Iberolacerta* rock lizards may have been restricted to mountains by competition with *Podarcis* (Carranza et al., 2004; Crochet et al., 2004).

This study aims to clarify whether competitive exclusion by wall lizards *P. muralis* is a plausible explanation for the alpine confinement of Iberian rock lizards *I. cyreni*. To detect competition, which among lacertids is mainly manifested as direct behavioural interference rather than indirect exploitation of resources (Downes and Bauwens, 2002), we conducted two experiments. In the first one, we used adult lizards to investigate whether *I. cyreni* and/or *P. muralis* shifted microhabitat or refuge preferences in the presence of the other species, and to detect aggressive interactions. In the second one, we staged heterospecific encounters between pairs of naïve, laboratory-born juveniles of both species to identify behavioural differences which might lead to a competitive advantage of one species over the other.

2. Materials and methods

2.1. Study system

The lacertid lizards *I. cyreni* and *P. muralis* provide an excellent system to investigate the possible restricting role of competitive exclusion in shaping species distributions. Both are heliothermic, actively foraging, and saxicolous lizards, but they present some morphological differences, *I. cyreni* being slightly larger than *P. muralis* (adult snout–vent length of 73–80 mm and 48–70 mm, respectively). While rock lizards are endemic to the mountains of the Sistema Central in the Iberian Peninsula, wall lizards present a widespread distribution in Central Europe that reaches its south-western limit at the Sierra de Guadarrama (Central Spain), where both species are present. In this mountain range, rock lizards are only found above 1600 m, preferably in rocky outcrops and mixed-shrub formations (Martín and Salvador, 1997; Monasterio et al., 2010), whereas wall lizards occupy lower altitudes (from 1230 m to 2100 m a.s.l.) and a wider range of habitats, including rocky outcrops, oak and pine forests, forest track banks, walls, and other human constructions (Martín-Vallejo et al., 1995; Amo et al., 2007a). The Sierra de Guadarrama presents contrasting seasonal conditions, with cold wet winters and short dry summers. Its mountain bases (1200–1700 m a.s.l.) are covered with deciduous Pyrenean oak (*Quercus pyrenaica)* forests, which are progressively substituted by Scots pine (*Pinus sylvestris*) forests at higher altitudes. These forested areas, which can spread from 1500 m to 2100 m a.s.l., gradually become less dense until vegetation is dominated by a mosaic of dense mixed-shrub formations (of perennial *Juniperus communis* and *Cytisus oromediterraneus*) interspersed with small meadows of *Festuca* and other grasses. These alpine areas above the tree line (1700–2300 m a.s.l.) are also characterised by extensive patches of large granite rocks and scree interspersed among shrub formations (Costa et al., 2005).

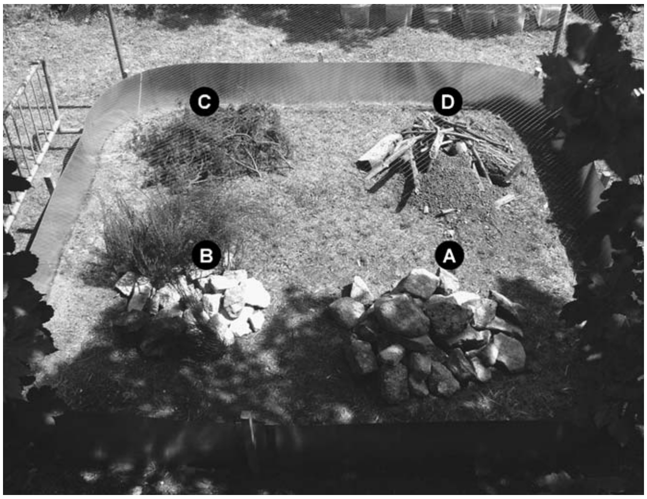

Fig. 1. General view of the experimental enclosure used to study microhabitat preferences of adult rock and wall lizards. A = rocks, B = rock–shrub, C = shrub, and D = logs.

2.2. Experimental procedure

2.2.1. Adults

For this experiment, we captured 15 adult rock lizards (9 males and 6 females) and 15 wall lizards (5 males and 10 females) in the Sierra de Guadarrama and transported them to 'El Ventorrillo' field station (1500 m), where we weighed and measured (snout–vent length, SVL) them to the nearest 0.1 g and 0.5 mm, respectively. We housed lizards separately in outdoor terraria with a sand substrate, rocks and vegetation. Lizards were fed live crickets every day and they had water available *ad libitum*. Capture methods, housing conditions and release procedures were appropriate for these species, and we observed no adverse effect of either the experiment or the housing methods on lizards' health. All individuals were in good condition, both during the experiment and when released at the site of capture.

We carried out an experiment during June and July 2007 to ascertain the microhabitat preferences of both species, either alone or together, when different microhabitats were offered. For that purpose, we used an outdoor enclosure (4 m × 4 m) with four types of distinct, representative microhabitats (Fig. 1): bare rocks (hereafter rocks), rocks with *C. oromediterraneus* shrubs (hereafter rock–shrub), *J. communis* shrub (hereafter shrub), and logs with gravel (hereafter logs). Sun was available from 09:00 h until 17:30 h (Greenwich Mean Time), allowing lizards to thermoregulate normally. To characterise the thermal environment, we placed four electronic temperature recording devices (tidbits; Onset Computer Corp., Pocasset, MA, USA) on the top of and inside each type of microhabitat. We programmed data loggers to register temperature hourly during 8 days (for tidbits on top of microhabitats) or 10 days (for tidbits inside refuges). Insect prey was naturally available in the enclosure, and we observed lizards feeding on several occasions.

Our experimental design compared the behaviour of lizards when each species was alone in the enclosure and when both species were together. In the first treatment (each species alone), we introduced different combinations of 10 individuals of either rock or wall lizards in the enclosure. In the second treatment, we placed simultaneously different combinations of 5 individuals of each species in the enclosure. To decide which individuals were to be used in each combination, we used the following criteria: (1) we tried to keep constant the proportion of males and females in all cases; (2) we maintained the same proportion of large (72–75 mm