



Original article

The relevance of morphology for habitat use and locomotion in two species of wall lizards



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ARTICLE INFO

Article history:

Received 4 August 2015

Received in revised form

1 December 2015

Accepted 2 December 2015

Available online 28 December 2015

Keywords:

Morphology

Habitat

Performance

Lizards

ABSTRACT

Understanding if morphological differences between organisms that occupy different environments are associated to differences in functional performance can suggest a functional link between environmental and morphological variation. In this study we examined three components of the ecomorphological paradigm – morphology, locomotor performance and habitat use – using two syntopic wall lizards endemic to the Iberian Peninsula as a case study to establish whether morphological variation is associated with habitat use and determine the potential relevance of locomotor performance for such an association. Differences in habitat use between both lizards matched patterns of morphological variation. Indeed, individuals of *Podarcis guadarramae lusitanicus*, which are more flattened, used more rocky environments, whereas *Podarcis bocagei*, which have higher heads, used more vegetation than rocks. These patterns translated into a significant association between morphology and habitat use. Nevertheless, the two species were only differentiated in some of the functional traits quantified, and locomotor performance did not exhibit an association with morphological traits. Our results suggest that the link between morphology and habitat use is mediated by refuge use, rather than locomotor performance, in this system, and advise caution when extrapolating morphology-performance-environment associations across organisms.

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1. Introduction

Whether or not, and how, organisms adapt to their environment are two central questions in ecology, evolution and conservation biology (Aerts et al., 2000; Arnold, 1998; Collar et al., 2010; Elstrott and Irschick, 2004; Kaliontzopoulou et al., 2010a). Different climatic, structural and biotic characteristics of the environment may impose ecological pressures on organisms, and mould phenotypic evolution and morphological diversification (Irschick and Garland, 2001; Ricklefs et al., 1981; Vitt et al., 1997). To start understanding the potential evolutionary meaning of morphological variation, we need to evaluate whether specific traits increase the functional capability of an organism (Arnold, 1983; Garland and Losos, 1994). This is usually done in the framework of the ecomorphological

paradigm, where differences in morphology are expected to be associated with different ecological performance capacities (e.g. maximum sprint speed), which in turn translate into variation in fitness among individuals in a given environment (Arnold, 1983). Here, selection acts on whole-organism performance to maximise the ability of the individuals to perform certain ecological and social tasks, guarantee their survivorship, and enhance their reproductive success, with correlated effects on morphological characters of biomechanical relevance for these functions (Irschick et al., 2008). Because the functional challenges that organisms face vary across environments, this type of microevolutionary process eventually leads to an association between morphological and environmental variation. As such, establishing whether morphological differences among organisms that occupy different environments are reflected into differences in functional performance can help us to disentangle the complex relationship between traits that culminate in differences in fitness and enhance our understanding of the underlying evolutionary mechanisms (Irschick and Garland, 2001; Irschick et al., 2005a; Miles, 2004; Vanhooydonck and Van Damme, 2001).

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Lizards have been extensively used as model organisms for ecomorphological studies because they are present in a great variety of habitats, and they exhibit a wide range of morphologies and locomotor modes (Arnold, 1998; Garland and Losos, 1994; Irschick and Garland, 2001; Irschick, 2002). Numerous studies indicate that different aspects of locomotor performance are ecologically relevant in different structural habitats, as lizards need to move to capture prey, escape from predators, thermoregulate, find mates and defend territories (Garland and Losos, 1994). As such, those lizard species that live in open areas and use sprinting as their main antipredatory strategy are considered as runners, and they are expected to have long hind limbs to enable longer strides; relatively short forelimbs, to avoid interference with the cycling of the hind limbs; and laterally flattened bodies, to enhance lateral flexibility and maximise stride length (Da Silva et al., 2014; Kaliontzopoulou et al., 2010a; Losos and Sinervo, 1989; Melville and Swain, 2000; Vanhooydonck and Van Damme, 2001). In contrast, lizards living mostly in rocks are considered as climbers, and they are expected to have shorter limbs and dorsally flattened bodies, to lower the centre of gravity closer to the substrate (Da Silva et al., 2014; Kaliontzopoulou et al., 2010a; Melville and Swain, 2000; Sinervo and Losos, 1991; Van Damme et al., 1997; Vanhooydonck and Van Damme, 2001). Therefore, traits that are favoured in one microhabitat preference may conflict with those that are beneficial in another (Clemente et al., 2013).

Podarcis wall lizards from the Iberian Peninsula and North Africa form a monophyletic clade and they are considered a cryptic species complex (i.e. *Podarcis hispanica* species complex; Kaliontzopoulou et al., 2011; Kaliontzopoulou et al. 2012a). In NW Iberia, we encounter two endemic forms – *Podarcis bocagei* and *P. guadarramae lusitanicus* (Geniez et al., 2014; previously treated as *P. hispanica* type 1A, see Kaliontzopoulou et al., 2011). These two sister forms are particularly interesting from an ecomorphological perspective because, unlike most other members of the group, their distributions overlap widely, both at a wide and local geographic scale (Carretero, 2008; Kaliontzopoulou et al., 2011). Further, despite being sister taxa, both forms markedly differ in body shape, whereby *P. bocagei* has relatively longer limbs, and a higher and more rounded head compared to *P. g. lusitanicus* (Galán, 1986; Kaliontzopoulou et al., 2012b; Pérez-Mellado, 1980). It has been suggested that these differences in body shape reflect different habitat preferences, where *P. g. lusitanicus* is highly saxicolous (Galán, 1986; Gosá et al., 1986; Pérez-Mellado, 1980; Sá-Sousa et al., 2002), whereas *P. bocagei* is mostly ground-dwelling (Domínguez and Salvador, 1989; Galán, 1986, 1994; Kaliontzopoulou et al., 2012b; Pérez-Mellado, 1980). However, differences in habitat use between the two species have never been formally quantified and the relevance of their potential ecological segregation for their morphological differentiation has never been examined.

In this study, we investigate the three components of the ecomorphological paradigm – morphology, locomotor performance and habitat use – using a community with *P. bocagei* and *P. g. lusitanicus* as a case study to examine whether morphological variation is associated with habitat use and determine the potential relevance of locomotor performance for such an association. For this purpose, we first examine if there are differences in habitat use between both forms, which would suggest that they exploit different ecological resources in terms of structural niche. Further, we test whether both forms differ in locomotor performance, as we would expect under predictions of the ecomorphological paradigm. Finally, we test if individual variation in morphology translates into variation in habitat use and locomotor performance, as suggested by studies in other lizard groups. Based on previous observations on the morphology and ecology of the two species, and considering ecomorphological patterns in other lizards, we hypothesize that *P. g.*

lusitanicus, which has been generally considered as saxicolous, will mainly use rocky environments. In addition, if morphological variation bears a functional meaning, we expect *P. g. lusitanicus*, which has a flattened head and shorter limbs, to perform better when climbing. On the other hand, *P. bocagei*, which is generally ground-dwelling, with a much higher and rounded head and longer limbs, is expected to be more flexible in terms of habitat use. Because this species uses different types of habitat including vegetation (Kaliontzopoulou et al., 2012b; Sá-Sousa, 2001), we predict that it might perform equally well under different locomotor conditions.

2. Material and methods

Lizards for this study were captured in the coastal zone near the beach of Moledo (N Portugal coast – 41°50'N, 8°52'W), where *P. bocagei* and *P. g. lusitanicus* are found in syntopy across a sandy area with rocks, sparse vegetation, and agricultural fields delimited by human constructed stone walls. The total area sampled was about 6500 m². We collected a total of 121 adult individuals by noosing (García-Muñoz and Sillero, 2010), including 65 animals for studying habitat use and 56 for locomotor performance experiments (see also below).

2.1. Morphological variables

In all individuals captured (i.e., 47 males and 32 females of *P. bocagei*, and 20 males and 22 females of *P. g. lusitanicus*), we measured the following linear biometric traits: trunk length (TRL), head length (HL), head width (HW), head height (HH), fore limb length (FLL) and hind limb length (HLL), using electronic callipers (precision 0.01 mm; see Kaliontzopoulou et al., 2007 for a detailed description of variables). In order to separate size and shape, we calculated the isometric size (SIZE) of each individual by projecting all log-transformed linear measurements on an isometric vector (Kaliontzopoulou et al., 2010a) and used it as a multivariate estimate of total body size. To obtain size-corrected variables representing shape variation, we regressed each linear trait on SIZE and retained the regression residuals (hereafter prjTRL, prjHL, prjHW, prjHH, prjFLL and prjHLL) (Kaliontzopoulou et al., 2010a). Animals used to quantify locomotor performance were also weighted using a digital balance (precision 0.0001 g).

2.2. Habitat use variables

In May 2011, when the activity of lizards is at its maximum, we captured a first set of 48 *P. bocagei* (30 males and 18 females) and 15 *P. g. lusitanicus* (five males and 10 females) in order to perform habitat and microhabitat use observations in the field. For each individual captured, we recorded the exact location of capture, using a high-precision GPS (Trimble GPS GeoExplorer 2008 HX). Each individual was measured to record morphological traits and marked with a unique colour code using non-toxic marker paint, so we could distinguish individuals in the field without capturing them. All the animals were released in the same location of capture.

To record microhabitat and habitat use, we performed normalised transects during seven days and 10 h/day with favourable weather conditions. To ensure that all lizards were observed at different times of the day, and therefore capture the individual variability in habitat use, transects were performed in a random order and allowing at least 1 h and a half between repetitions of the same transect. During these transects, we collected a total of 197 observations for *P. bocagei* (114 for males and 83 for females) and 60 observations for *P. g. lusitanicus* (20 for males and 40 for females) and recorded their associated microhabitat variables. To quantify microhabitat use we recorded the type of substrate where the

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