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Partitioning thermal habitat on a vertical rock, a herculean task

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ABSTRACT

Species occurring in sympatry have to effectively segregate their niche in order to co-exist. In the case of ectotherms in particular, the very important parameter of thermal biology has to be taken into account. Here we investigated the thermoregulatory effectiveness (*E*) of two endemic Greek lizards (*Hellenolacerta graeca* and *Podarcis peloponnesiacus*) that live syntopically on a rocky cliff in the Peloponnese. We presumed that the two species would select different microhabitats, to avoid interspecific competition, and follow a similar thermoregulation pattern as they experience the same conditions. We also expected that *E* values for both species would differ depending on the season. Overall, we found that the two species had similar *E* values for each season but differentiated partial thermoregulatory attributes. Though they both occurred in the same types of microhabitat, *H. graeca* selected higher sites (average 99 cm above ground) than *P. peloponnesiacus* (average 44 cm). Also, the latter achieved higher preferred temperatures during summer and winter. Finally, the effectiveness of thermoregulation for both species varied interseasonally and received its highest values during summer, in response to the lowest thermal quality that was observed then. Similar studies stress the importance of thermal shifts for ectotherm co-existence.

1. Introduction

The dominant role of temperature in reptilian biology is reflected in the large, ever-growing body of thermal biology literature. Pioneer researchers clarified the relationship between the environment and lizard thermoregulation (Weese, 1917; Cowles and Bogert, 1944), while subsequent generations added an impressive amount of information on the thermal biology of numerous species living in different types of habitat. There soon arose a need to take the next step in thermal studies: not the mere assessment of thermoregulation in a single species, but the evaluation of thermal resource partitioning in sympatric species (Schall, 1977; Dial, 1978). During the early 1990s many studies focused on this topic and paved the way for future research (Adolph, 1990; Van Damme et al., 1990; Hertz, 1992; Bergallo and Rocha, 1993). Indeed, since 2000 lots of research has been done on thermal habitat partitioning (e.g. Angert et al., 2002; Leal and Fleishman, 2002; Scheers and Van Damme, 2002).

Lizards that live in sympatry have to partition their habitat effectively, in order to ensure access to resources (e.g. food, shelter, mates) with the minimum possible interspecific competition (Carretero et al., 2006; Murray et al., 2016). They are also quite effective at thermal microhabitat partitioning. Lizards choose more open sites to bask in when air and/or substrate temperatures are low, and they retreat to more shady places when they are high (Avery, 1978; Monasterio et al., 2009; Žagar et al., 2015). Lizard species may prefer particular microhabitats with special thermal characteristics and variable thermal quality (Díaz et al., 2005; Scheers and Van Damme, 2002). Shuttling between different microhabitats can influence thermoregulatory behavior and, eventually, affect thermoregulation effectiveness (Smith and Ballinger, 2001). Furthermore, lizards may shift their activity or space use (Corbalán et al., 2013; Osojnik et al., 2013).

Coexisting in the same area becomes much more demanding in the case of syntopic species, when the available space is much more limited (Sagonas et al., 2017; Žagar et al., 2015). Cases of syntopy are interesting as they allow us to study how species may coexist in the very same habitat without outcompeting each other. Several studies on syntopic lizards shed light on various aspects of lizard biology (Colli et al., 1992; Cooper and Avalos, 2010; Van Sluys et al., 2004), but only a few have focused on thermal biology (Gómez Alés et al., 2017; Ibargüengoytía, 2005; Sagonas et al., 2017).

Here we explored the thermal biology of two lacertid lizards that live in close syntopy in the north Peloponnese (Greece). Both species

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Fig. 1. a) Greek rock lizard (*Hellenolacerta graeca*), b) Peloponnese wall lizard (*Podarcis peloponnesiacus*).

occur on a single cliff at the study site and hence have to separate their ecological requirements clearly. The Greek rock lizard (*Hellenolacerta graeca*) (Fig. 1a) has a slender, dorso-ventrally flattened body with a snout to vent length (SVL) of up to 80 mm. In general it prefers humid areas, but in some extreme cases can be found even at sea level, a few meters from the shore (Gavriilidi et al., 2017). It is an excellent climber, feeds on arthropods, with a preference for spiders, beetles and flying insects and produces a single clutch per season comprising up to six eggs (mean clutch size: 3.44) (Maragou, 1997). *Hellenolacerta graeca* is strictly endemic to the Peloponnese (Valakos et al., 2008). The Peloponnese wall lizard (*Podarcis peloponnesiacus*) (Fig. 1b) is slightly larger (SVL up to 85 mm) with a much more robust body shape and a strong head. It can be found in a great variety of habitats (rocky areas, scrubland, drystone walls, ruins, olive groves, etc). It is not an exclusive ground dweller but climbs freely, though clumsily. *Podarcis peloponnesiacus* feeds on arthropods with insects and their larvae being the dominant prey groups (Valakos et al., 2008). It produces two clutches per season (mean clutch size: 3.52, 1–6 eggs) (Maragou, 1997). The species was believed to be endemic to the Peloponnese, but recently it was recorded for the first time outside the peninsula (Hedman et al., 2017).

We presumed that due to the limited area, the two lizards would have to partition their thermal habitat to avoid interspecific competition, as they should exploit different thermal resources. To assess the thermal biology of the two species under these demanding conditions in terms of space availability, we focused on the accuracy, precision and effectiveness of thermoregulation (E). To this end, we recorded body (T_b) and operative (T_e) temperatures that animals and non-thermoregulating models reached in the field, and preferred temperatures (T_{pref}) that animals achieved under laboratory conditions with no eco-physiological restrictions (Hertz et al., 1993). The preferred temperatures largely determine the thermal identity of lizards and are affected by sex, age, reproductive status and body size (Andrews et al., 1999; Carretero et al., 2005; Veríssimo and Carretero, 2009; Sagonas et al., 2013a). We made three hypotheses. First, we anticipated that each species would select different microhabitats in order to avoid (or minimize) competition. Second, we expected that the above-mentioned thermoregulatory parameters would differ during the year for both species in response to climatic conditions. Third, we hypothesized that the two species might achieve similar E values as they experience the same climate and are hence subject to similar environmental conditions that might affect their T_{pref} as well.

Fig. 2. A general view of the rocky cliff on the periphery of lake Stymphalia where the two species occur in sympatry.

2. Material and methods

2.1. Study area

Fieldwork was carried out on the western banks of Lake Stymphalia (north Peloponnese, 37°51′36″N, 22°27′08″E, 600 m a.s.l.). The lake is famous for being the setting of the Sixth Labor of Hercules, where he killed the man-eating Stymphalian birds (*Στυμφαλίδες ὄρνιθες*, Stymphalídes órnithes) that nested in the marsh. The focal habitat was created some 50 years ago by the construction of a peripheral road around the lake. It is a rocky slope of approximately 200 m in length, with a maximum height of 8 m, located 20 m away from the lake (Fig. 2). The rock has many crevices, small overhangs with low plants (thyme - *Thymus vulgaris*, heath - *Erica* sp., Jerusalem sage - *Phlomis fruticosa*) and projecting edges. The main plants at the base and top of the slope are kermes oak (*Quercus coccifera*), Strawberry tree (*Arbutus unedo*), and Spanish broom (*Spartium junceum*). The climate is typically temperate with regular rainfall (annual precipitation 718.3 mm), chilly and snowy winters (mean T_{air} 7.01 °C) and warm summers (mean T_{air} 32.8 °C) (National Meteorological Service of Greece, http://www.hnms.gr/hnms/greek/index_html).

2.2. Field surveys (T_b and T_e)

We captured 245 (136 males and 109 females) *P. peloponnesiacus* and 97 *H. graeca* (59 males and 38 females) adult lizards throughout the year (26–27 October 1999, 18–19 January 2000, 23–24 April 2000 and July 12–13 2000). Each field trip lasted two days and field work was carried out during the activity period of lizards (Maragou, 1997). Body temperatures were measured to the nearest 0.1 °C, with a quick-reading cloacal thermometer (T-4000, Miller & Weber, Inc., Queens, NY).