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The castaway: characteristic islet features affect the ecology of the most isolated European lizard

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Abstract. The ecological importance of islet endemics are in the front line of conservation efforts and thus the good knowledge of their biology is required. *Podarcis levendis* is a lacertid lizard, endemic to two rocky islets in the Cretan Sea, Greece, that was raised to specific level in 2008 and since then no data on its biology are available. Here we present the first ecological information on the species, focusing on population density, tail autotomy and feeding preferences. We recorded regenerated and damaged tails in the field and estimated population density with the transect method. We also dissected museum specimens and analyzed their stomach content. Regenerated tails were common and reached a considerable 71%. The latter finding could be attributed to the intense intraspecific competition due to high population density but also to the seasonal predation pressure by migratory birds. The diet of *P. levendis* coincides with that of other insular congenerics, including high percentages of plant material.

Keywords. Islands, population density, intraspecific competition, feeding ecology, Lacertidae, *Podarcis levendis*.

INTRODUCTION

Deviations of island life from mainland norms have been repeatedly underlined (Van Valen, 1973; Adler and Levins, 1994). Studying the constellation of these departures, island biology attracted scientific interest and became a hot spot in ecological and evolutionary studies during the last 30 years (Carlquist, 1974; Losos and Ricklefs, 2009). Herpetological research is in the frontline of this general trend. Insular giants (Harlow et al., 2010) and dwarfs (Hedges and Thomas, 2001) and the impressive adaptations of island herpetofaunas (Herrel et al., 2008; Stuart et al., 2014) stimulate a growing body of literature. In this framework, Mediterranean islands lend themselves to understanding the particularities of insularity. Among the numerous endemic reptiles and amphibians that live on the Mediterranean islands, *Podarcis* wall lizards (family Lacertidae) stand out.

Podarcis is the largest genus of European lizards comprising 23 species that occur in Europe and North Africa (Uetz and Hošek, 2016). Though most *Podarcis* species have both mainland an insular populations, 10 of them are strictly endemic to Mediterranean islands. The overall biology of these species depart in many aspects from their mainland peers, including thermal biology (Grbac and Bauwens, 2001; Adamopoulou and Valakos, 2005), feeding ecology (Salvador, 1986; Capula and Luiselli, 1994), life history (Adamopoulou and Valakos, 2000; Castilla and Bauwens, 2000), digestive performance (Pafilis et al., 2007, in press), defensive tactics (Pafilis et al., 2009a; Li et al., 2014), and behavior (Pérez-Mellado et al., 2000; Traveset and Riera, 2005; Cooper et al., 2009;

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Brock et al., 2014a). *Podarcis* islanders differ in the limits of their range. Three of them live on very large islands (*P. tiliguerta* in Corsica and Sardinia, *P. waglerianus* in Sicily and *P. cretensis* in Crete), six on medium-sized islands (e.g., *P. filfolensis* in Malta, *P. gaigeae* in Skyros), while three are exclusively restricted on small islets: *P. lilfordi* lives on rocky islets off Menorca and Mallorca and the Cabrera Archipelago in Spain, *P. raffonei* inhabits three rocky islets and few isolated places on Vulcano Island at the Aeolian Islands in Italy, and *P. levendis* occurs only on two islets in the west Cretan Sea in Greece.

Podarcis levendis was recognized as distinct species and separated from *P. erhardii*, which dominates the south and central Aegean islands, only recently (Lymberakis et al., 2008). The species is found on the islets Pori and Lagouvardos, north of Antikythira Island, between Crete and the Peloponnese (Fig. 1). This very restricted and remote range had two main consequences: the complete lack of knowledge on the biology of the species since its first description, and its categorization by IUCN as 'vulnerable'. To the best of our knowledge, the only other paper referring to the Pori population is the first record of lizards (under the former name, *P. erhardii*) on the islet (Valakos et al., 1999).

In order to effectively protect species that may face the threat of extinction we need to know their biology as best we can. In this study we provide the first ecological data for *P. levendis*. We assessed population density, body size (estimating also body condition, a proxy for fitness), frequencies of autotomized tails and feeding preferences of the Pori population. We made three hypotheses. First, we predicted that the population should be dense. Due to their small area, islets usually host very few (or even no) predators and, as a result, lizard densities are usually high (Pérez-Mellado et al., 2008). Alternatively high densities could be attributed to high food abundance through 'marine subsidies' (Polis and Hurd, 1996). Second, we expected high frequencies of broken tails. Intraspecific competition on islets could be intense due to high population density and these antagonistic interactions may induce caudal autotomy (Pafilis et al., 2008; Cooper et al., 2015). Furthermore Pori serves as a refueling station of migratory birds that increase predation pressure during their stay on the islet. Third, we hypothesized that plant material would constitute a significant part of stomach content as many microinsular lacertids demonstrate a clear shift towards herbivory (Van Damme, 1999).

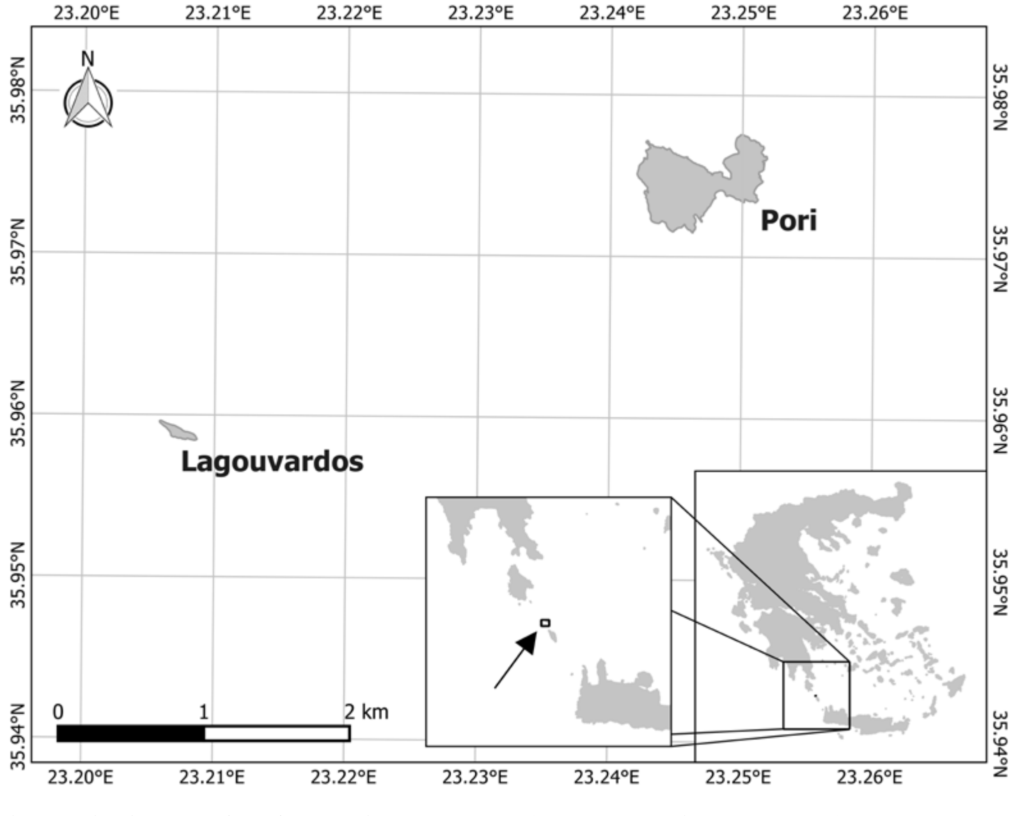

Fig. 1. Map of the two islets hosting *P. levendis* in northwest Cretan Sea (Greece, NE Mediterranean Basin).

MATERIALS AND METHODS

Study system

Levendis wall lizard (*Podarcis levendis*) is a well-built, medium sized lacertid lizard (snout vent length, SVL, 72.25 ± 3.44 mm). The vegetation on the islets Pori (0.317 km^2, max altitude: 129 m) and Lagouvardos (0.0127 km^2, max altitude: 19.3 m) consists of sparse phrygana shrubs among which *Sarcopoterium spinosum* and *Euphorbia dendroides* are the most common while several *Olea europaea* and *Pistacea lentiscus* are also present. The only other terrestrial reptile living on the two islets is the Kotschy's gecko (*Mediodactylus kotschyi*).

Fieldwork was conducted on Pori islet in May 2010. Lizards were captured by noose and then transferred to the laboratory facilities of the Department of Biology at the University of Athens. Animals were housed individually in vitreous terraria (80×30×40 cm) with sand and artificial shelters and were held at 30°C under a controlled photoperiod with fluorescent tube lighting (12 h light: 12 h dark). Additional incandescent lamps (60 W) allowed animals to thermoregulate for 8 h/day. Lizards had access to water *ad libitum* and were fed every other day with mealworms (*Tenebrio molitor*), coated with a powder containing vitamins and minerals supplements (TerraVit Powder, JBL GmbH & Co. KG).

Morphological measurements

For each lizard we recorded SVL and body mass using a digital caliper (Silverline 380244, accurate to 0.01 mm) and a digital scale (Ohaus, Scout-TM, accurate to 0.01g), respectively. To define body condition (BC) we included only lizards with intact or fully regenerated tail and non-gravid females. We estimated BC using the classical body mass index (mass divided by SVL), a standard measure for reptiles (Goodman, 2008; Battles et al., 2013; Damas-Moreira et al., 2014), and tested for differences between sexes using a Mann-Whitney test.

Additionally, we examined the tail condition (intact or broken/regenerated) in the 22 adult lizards (16 males and 6 females) that were captured in the field and also in 44 museum specimens (18 males and 26 females) that are deposited to the Herpetological Collection of the Natural History Museum of Crete (collected in January 1992). Chi-square test was used to examine for differences between sexes.

Population density

We estimated population density using the line transect method (Lovich et al., 2012). Eight random line transects of 100 m were walked by the same observer (LP) and all lizards seen within 4-m wide belt (2 m on either side of the survey line; total area covered per trail 400 m^2) were recorded. Transect surveys were made during morning hours when *Podarcis* lizards are active and line transects were chosen to cover as many different microhabitats as possible.

Diet composition

To assess the feeding preferences of the *P. levendis* we dissected 36 preserved specimens (15 males and 21 females) that were deposited to the Herpetological Collection of the Natural History Museum of Crete and removed the digestive tract to examine the prey remnants. Prey items were analyzed under a binocular dissecting microscope and identified to order level.

We recorded the percentage of the total number of prey items found in the stomachs (%n) as well as the percentage of lizards that ate a given prey taxon (F). Spearman correlation was performed to test whether F is related to %n. We also recorded the consumption of plant material (estimated as frequency of presence). We used the Shannon-Wiener diversity index (Krebs, 1998):

$$H' = \Sigma p_i \ln p_i,$$

to calculate the niche breadth (H'), where p_i is the percentage of each prey item found in the stomachs. We conducted a t-test to search for differences between sexes regarding the diversity index. As a complementary approach to test for sexual differences in food composition and to control for the effects of the most abundant prey items, we used the Jaccard similarity coefficient (Jaccard, 1908) as implemented in PAST (Hammer et al., 2001):

$$J_{(A,B)} = \frac{|X \cap Y|}{|X \cup Y|},$$

where *X* and *Y* correspond to the sets of entities that occur at A and B groups, respectively. Finally, using the program EcoSim 7.0 (Gotelli and Entsminger, 2001), we employed the Pianka's overlap index (Q_{jk}) and estimated the food niche similarity between sexes (Pianka, 1975):

$$Q_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 p_{ik}^2}},$$

where j and k refer to the two groups under comparison and p_{ij} and p_{ik} to the proportion of the food component i in each group.

RESULTS

Morphological measurements and population density

Males had significant longer SVL than females (Mann-Whitney test; Z = 2.469, P = 0.013) (Table 1). In addition, males were heavier compared to females, but these differences were not statistically significant (Mann-Whitney test; Z = 1.769, P = 0.077). Finally, we found no significant differences in body condition between sexes (Mann-Whitney test; Z = 0.589, P = 0.55) (Table 1).

Table 1. Snout vent length (SVL; mm), body mass (BM; g) and body condition (BC) of males (n = 16) and females (n = 16) of *P. levendis* population at Pori islet. Table reports means ± SD values; ranges are also given (within brackets).

Sexes	SVL	BM	BC
males	75.25 ± 2.11 (71.0-79.0)	8.21 ± 0.78 (6.7-9.5)	0.11 ± 0.01 (0.09-0.13)
females	66.00 ± 9.48 (54.0-76.0)	7.07 ± 1.46 (5.0-8.8)	0.11 ± 0.01 (0.09-0.12)

Table 2. Diet composition of *P. levendis* for males and females during summer. %n refers to the percentage of prey items in the stomachs, F refers to the proportion of lizards having eaten a specific prey category while H' to the Shannon-Wiener diversity index.

Sexes	Males		Females	
	F	%n	F	%n
Araneae	0.40	23.08	0.29	18.18
Opilionidia	0.00	0.00	0.14	4.55
Orthoptera	0.07	1.92	0.05	1.52
Gastropoda	0.20	7.69	0.24	9.09
Homoptera	0.00	0.00	0.14	4.55
Diptera	0.07	1.92	0.00	0.00
Isopoda	0.13	3.85	0.14	10.61
Lepidoptera	0.13	3.85	0.10	3.03
Coleoptera	0.67	28.85	0.48	24.24
Hymenoptera	0.07	3.85	0.00	0.00
Formicidae	0.20	7.69	0.43	16.67
Insect larvae	0.33	17.31	0.19	7.58
Plant material	0.13		0.14	
Total Preys	52		66	
Specimens	15		21	
Prey/stomach	3.47		3.14	
H'	1.923		2.054	

We examined tail condition in 66 adult lizards overall. 47 of them (71%) had regenerated or broken tails. We found no differences in the percentage of autotomized tails between males and females, either for lizards that we captured in the field (males: 75% and females: 67%; χ^2 = 0.008, P = 0.275), or for museum specimens (males: 66% and females: 73%; χ^2 = 0.006, P = 0.357).

Pori islet hosts a rather dense population of approximately 262 lizards per hectare. Taking into account the area of the islet (31.74 ha) our finding regarding population density provides the first (though rough) estimation of the total population of the species on the islet, which should be less than 7,000 individuals (given that the peripheral parts of the islands close to the sea are not available to lizards).

Diet composition

We found a significant correlation between the proportion of the number of prey taxa in the stomachs (%n) and the proportion of lizards that ate that given taxa (F) (Spearman test, r = 0.99, P < 0.05) (Table 2). The predominant prey groups in the diet of *P. levendis* were Coleoptera, Araneae and Formicidae (Table 2). We also found a considerable consumption of plant material, mostly leaves (five out of 36 lizards; 14%).

Food niche breath was high for both males (H' = 1.923) and females (H' = 2.054) and the comparison between them revealed no differences (t-test; t = 1.042, P = 0.30). We found no statistically significant differences between males and females regarding the total number of prey items found in the stomachs (Mann-Whitney test; Z = 0.513, P = 0.608). It is worth noting that almost 20% of the specimens examined had empty stomachs. Finally, our results revealed a high food niche overlap between males and females (Q_{jk} = 0.91), despite the relative low Jaccard similarity index (0.67).

DISCUSSION

Our results suggest that the particular conditions on Pori islet shaped the ecological profile of *P. levendis*. Our initial hypotheses were verified: Levendis wall lizard enhances its diet with plant material and autotomizes its tail frequently. Population density was high, though not as high as in other islet *Podarcis*. Body condition of lizards was remarkably high, suggesting a sufficient energy flow.

Population density was estimated at 262 individuals per hectare. This is a rather high value for eastern Mediterranean standards where insular lizards do not form very dense populations. Valakos (1990) reported 76 lizards/ha (*P. erhardii*, Naxos Island), Pafilis et al. (2009b) 95-185 lizards/ha (*P. gaigeae*, Skyros Island), Adamopoulou (1999) 395 lizards/ha (*P. milensis*, Milos Island) and Chondropoulos and Lykakis (1983) found densities that varied across islands from 118 to 247 lizards/ha (*P. tauricus*, numerous Ionian islands). A striking deviation comes from Diavates islet (off Skyros) that harbors 875 lizards/ha, the denser population on east Mediterranean islands (Pafilis et al., 2013). Lizard densities from western Mediterranean islands are much higher (Delaugerre and Cheylan, 1992; Scalerà et al., 2004), reaching even 8,000 lizards/ha (Pérez-Mellado et al., 2008).

Insular populations are much denser than the mainland ones (Rodda et al., 2001; Buckley and Roughgarden, 2006) as a result of the relaxed predation and interspecific competition on the islands (Buckley and Jetz, 2007; Novosolov et al., 2016). This is the case for Pori islet where there is not a single terrestrial predator while the only other reptile is Kotshyi's gecko (*Mediodactylus kotschyi*), which does not compete with *Podarcis* lizards for food or space (Valakos and Vlachopanos, 1989). Certain birds nest on the islet, such as falcons (*Falco eleonorae*), European shags (*Phalacrocorax aristotelis*) and yellow-legged gulls (*Larus michahellis*). These birds do not prey on *Podarcis* lizards (Walter, 1967; Pérez-Mellado et al., 2014). To the contrary, lizards seem to have developed a particular mutualism, at least with falcons, and benefit from their presence (Walter, 1967; Delaugerre et al., 2012). In addition, sea birds enhance islet ecosystems through 'marine subsidies' (Polis and Hurd, 1996) that fuel dense lizard populations (Barrett et al., 2005). Some Mediterranean islets also receive this sea-derived energy and thus may support high lizard abundances (Vidal et al., 2001; Pafilis et al., 2011).

The frequencies of autotomized tails are typically considered to reflect predation pressure (Arnold, 1988). However, intraspecific competition through aggressive encounters may also end up to caudal autotomy (Pafilis et al., 2008; Pafilis et al., 2009b). The high lizard densities on Mediterranean islets have been proven to be the major factor inducing tail shedding (Cooper et al., 2015; Donihue et al., 2015). Predation pressure is minimal at Pori, so the high population density should account for the high percentages of regenerated and broken tails in the field. The observed 71% lies within the top percentile for other islet *Podarcis* (Pérez-Mellado et al., 1997; Pafilis et al., 2008; Pafilis et al., 2009a; Brock et al., 2014a). Nevertheless, we may not exclude the possibility of predation pressure resulting from bird predators during migration as the islets are on an important migratory route (Hellenic Ornithological Society, 2016).

Food abundance on Mediterranean islands is quite restricted (Brown and Pérez-Mellado, 1994; Blondel et al., 2010). As a result insular lacertids widen their feeding preferences and thus adopt a wider food niche breadth (Pérez-Mellado and Corti, 1993; Sagonas et al., 2015a). Food scarcity is even more exacerbated on small islets (Pérez-Mellado and Corti, 1993; Castilla et al., 2008) where lizards adopt extreme feeding behaviors in order to survive (Castilla and Herrel, 2009; Brock et al., 2014b).

Though our sample size was rather small, our data implied that *P. levendis* followed the general trophic profile of the genus feeding mainly on terrestrial invertebrates with a clear preference on insects (Arnold, 1987). The predominant food groups were Coleoptera, Araneae and Formicidae (Table 2). Araneae and, much more, Coleoptera are the commonest prey groups in *Podarcis* lizards (Maragou et al., 1997; Carretero, 2004; Zuffi and Giannelli, 2013). Myrmecophagy, on the other hand, is a typical feeding strategy of island *Podarcis*, especially during late spring and summer when other food resources come in short supplies (Valakos, 1986; Pérez-Mellado and Corti, 1993; Valakos et al., 1997; Adamopoulou et al., 1999; Lo Cascio and Capula, 2011). Ants may be less rich in terms of nutrients and energy compared to beetles, but they compensate this disadvantage with their high numbers.

Previous studies reported an important shift towards herbivory in most island lacertid populations (Pérez-Mellado and Corti, 1993; Van Damme, 1999; Sagonas et al., 2015b). The percentage of plant material in the stomachs of *P. levendis* was not very high, though it seems to conform to this trend (14%). Islet populations follow the aforementioned pattern, demonstrating a clear preference for plant consumption (Lo Cascio and Pasta, 2006; Lo Cascio et al., 2006; Carretero et al., 2010; Pérez-Cembranos et al., 2016) that in some cases may be extreme and even induce morphological changes (Herrel et al., 2008; Vervust et al., 2010).

Mediterranean islets are demanding habitats with limited food resources (Ouboter, 1981; Brown et al., 1992). *Podarcis* lizards living on islets share many common characteristics imposed by the particular conditions of these habitats: low predation pressure (Tsasi et al., 2009; Durand et al., 2012), high population densities (Pérez-Mellado et al., 2008) and strong intraspecific competition (Cooper et al., 2015), while they usually have high body condition (Van den Berg et al., 2015). *Podarcis levendis* conforms to this general pattern. The importance of such isolated populations, some of which have developped unique adaptations (Pérez-Mellado et al., 2000; Herrel et al., 2008; Raia et al., 2010), is of top priority in conservation biology (Capula et al., 2002).

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