Life on an Island: the Effects of Insularity on the Ecology and Home Range of the Aegean Wall Lizard (*Podarcis erhardii*)

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Abstract.—The study of island taxa can help reveal the mechanisms of natural selection when it acts on small, isolated populations. To elucidate how small populations evolve in high-competition, low-predation environments, we examined differences in morphological characteristics, tail autotomy rates, and home range sizes in several populations of Aegean Wall Lizards (*Podarcis erhardii*; Lacertidae) living on one large-island site and three small-islet sites. While there was relatively little consistent morphological divergence between the study populations, we did observe significantly higher rates of shed and regenerated tails on predator-free, small-island sites, a counter-intuitive pattern for a known antipredator defense. Rather than a sign of failed predation events, this pattern is best explained by the fact that tail-shedding can be precipitated by intraspecific aggression and tail cannibalism, which are known to be particularly frequent on small islands. We also found that small-island female lizards, but not males, maintained significantly smaller home ranges than large-island females. Our results indicate that differences in prevailing ecological conditions (most likely reduced food availability and relaxed predation pressure) drive distinct changes in tail shedding rates and home range size in these island lizards.

Key Words.—Aegean islands; antipredator defense; Greece; intraspecific competition; island syndrome; population density

Introduction

Island species have long been a focus of landmark studies in ecology and evolution (MacArthur and Wilson 1967; Losos 2011). Islands, because of their isolation and simplified ecologies, present an ideal system to illuminate evolutionary drivers of life-history traits both within and between populations (Case 1978). Insular ecosystems can differ dramatically from continental ecosystems, and often present unique environmental challenges for vertebrate survival. Variable food resources, less available space, and altered thermal conditions relative to the mainland are added challenges for island populations, though these populations may concurrently experience the benefits of release from both predation and interspecific competition pressures (Adler et al. 1994; Lomolino 2005). In island populations, reduced predation pressure can bring about significant changes in antipredator behavior (Cooper et al. 2012) and increases in population density relative to mainland populations (Pafilis et al. 2009; Raia et al. 2010), which can result in increased intraspecific competition over resources (Donihue et al. 2016). Thus, life on an island can have widespread effects on animal morphologies, ecological interactions, and social behaviors.

To contend with variable ecological conditions and increased intraspecific competition, island vertebrates often develop dramatically different morphologies as compared to mainland populations of the same species (Case 1978; Lomolino 2005). In lizards, morphological and performance differences between mainland and insular populations have been assessed and studied extensively. As a consequence of the increased population densities and elevated intraspecific competition characteristic of island environments, insular lizard populations can develop larger body sizes, different head shapes, and higher bite forces compared to their mainland counterparts (Case et al. 1993; Meiri 2007; Raia et al. 2010; Sagonas et al. 2014; Donihue et al. 2016). Lizard body size has a direct bearing on the outcome of social interactions contesting limited food and space resources (Perry et al. 2004; Donihue et al. 2016), and bite force, which is shown to be positively related to skull height in several species of lizards (Herrel et al. 2001; Huyghe et al. 2009). Bite force is an important factor for predicting the outcome of aggressive interactions (Lailvaux et al. 2004; McLean et al. 2015). As such, it is expected that lizard populations in small-island settings should be relatively larger in terms of both body size and in head dimensions compared to those in a mainland context.

Species on islands may also have fewer predators than on the mainland (MacArthur and Wilson 1967; Blumstein et al. 2005; Foufopoulos et al. 2011; Cooper et al. 2012; Brock et al. 2015). Because antipredator defenses are evolutionarily costly to maintain, in the absence of predators, these defenses for island species may be diminished or be selected against (Blumstein et al. 2005). Autotomy, or the ability to shed an organ if attacked by a predator, is an antipredator defense that has evolved independently across animal groups (Fleming et al. 2007). Many species of lizards have autotomous tails, employing specialized fracture planes in their caudal vertebrae to shed their tails as a final means of defense against predatory attacks (Bellairs and Bryant 1985; Chapple et al. 2002). Tail autotomy is documented in at least 13 of the approximately 20 lizard families, including lacertids (Arnold 1984; Downes et al. 2001; Bateman et al. 2009). Conventionally, tail autotomy is considered an antipredator mechanism (Bateman et al. 2011); however, recent studies suggest that intraspecific aggressive interactions drive tail loss as well, especially in insular settings (Bateman et al. 2009; Itescu et al. 2017). In island lizard populations, a higher population density than on the mainland and a subsequent increase in intraspecific competition may result in elevated tail injuries and autotomy (Pafilis et al. 2009; Brock et al. 2014) and even cannibalism (Matuschka et al. 1987; Cooper et al. 2014; Deem et al. 2014; Madden et al. 2018**)**. Although aggressive interspecific behavior is observed among individuals of the same sex and between sexes, male lizards generally are more aggressive towards their conspecifics than females (Matuschka et al. 1987; Raia et al. 2010; Cooper et al. 2014). Therefore, it might be expected that behavioral differences in aggression leads to disparities in autotomy frequencies between sexes. Several studies report higher incidence of tail loss in males than females for various lizard families including Scincidae (Vitt 1981) and Gekkonidae (Itescu et al. 2017); however, the majority of research to date has yet to demonstrate a significant sex difference in lizard tail loss frequency (Bateman et al. 2009 and references therein; Itescu et al. 2017).

Island life is strongly influenced by resource availability, which is usually more limited compared to the mainland (Case 1978; Lomolino 2005). The establishment and size of a home range (HR) are important space-use strategies used by free-ranging vertebrates to secure the necessary resources for survival and reproduction and are therefore essential components of the overall fitness of an individual. Home range is defined as the area in which an animal performs its normal activities (i.e., food gathering, mating), and may overlap with the ranges of other individuals in neutral zones that are not actively defended (Burt 1943). Both broad ecological factors and species-specific factors can influence aspects of space use ecology; for instance, species-specific factors such as population density, reproductive strategy, and competitive ability impact the behaviors a male employs to obtain resources such as mates and food (Kwiatkowski et al. 2002; Healey et al. 2008; Molnár et al. 2016).

Ecological theory suggests an inverse relationship between HR size and population density (Schoener et al. 1980; Kwiatkowski et al. 2002; Haenel et al. 2003), and which factors determine HR size may also vary according to sex. Across species of lizards, males tend to maintain larger HRs than females, and this relationship is positively correlated with body size (Schoener et al. 1982; Haenel et al. 2003). While males prioritize access to mates over actual resource availability when selecting their HR, females generally tend to prioritize the energetic means or food resources necessary to produce a successful clutch (Schoener et al. 1980; Alberts 1993; Kwiatkowski et al. 2002; Perry et al. 2002). In environments of reduced predation or interspecific competition pressure, species may experience niche expansion or ecological release, which is characterized by density compensation, morphological trait variation, and importantly, broadened resource use (Lister 1976; Martin et al. 2010; Des Roches et al. 2011). Because island environments support fewer species in total than mainland areas of similar latitude and topography, the paucity of potential competitors can open a broader spectrum of resources than would be typical for a given species (Lister 1976). In other words, although fewer total food resources are available, a wider range of resource options are viable for consumption on islands. Thus, it is not immediately clear as to how island vertebrate HR sizes might compare to those of mainland conspecifics, considering the differences in population densities, traditional food resource availability, and sex differences for space use priorities.

In this study, we investigated whether living in a small-island environment affected relative lizard population abundance and body size, as well as two key life-history aspects, tail autotomy rates and HR sizes. To do this we compared several populations of Aegean Wall Lizards (*Podarcis erhardii*) living in two types of island environments: a large, resource- and predator-rich island (mainland analog) and offshore small-scale rocky islets that were resource- and predator-poor. Our study sites varied considerably in area (spanning five orders of magnitude), as well as in resource abundance, species richness, and faunal composition (Valakos et al. 2008). Previously published work demonstrated that our small-island study sites lacked the predator diversity of our large-island site (Brock et al. 2015); as such, we hypothesized that the differential abundance of predators between island environments would affect *P.*

FIGURE 1. An adult male (white-throated morph) Aegean Wall Lizard (*Podarcis erhardii*) basking on a stone wall in the Tragea Valley region of Naxos, Greece. (Photographed by Johannes Foufopoulos).
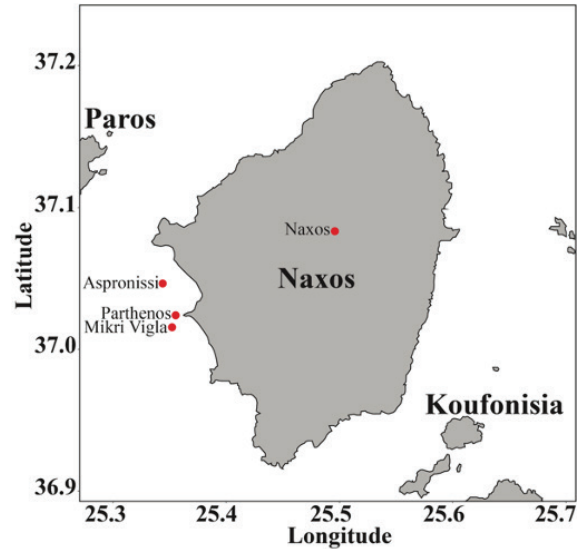

FIGURE 2. A map of the Cycladic island of Naxos, Greece, and neighboring islands. We conducted field work on the island of Naxos (Site L1) and on three offshore rocky islets situated near the western peninsula of Mikri Vigla on Naxos: Parthenos (Site S1), Mikri Vigla (Site S2), and Aspronissi (Site S3).

erhardii population densities. Specifically, we predict that *P. erhardii* relative population abundances will be higher on the small islands than on the large island, and in turn, small island lizards will have larger skull and body sizes in both males and females. We also predict that smaller, densely populated islet populations of lizards will exhibit reduced HR size, and increased tail autotomy rates due to increased competition for more limited resources.

MATERIALS AND METHODS

Focal species.—*Podarcis erhardii* (Fig. 1) is a lacertid lizard widely distributed throughout the southern Balkan Peninsula, including many Aegean islands. A substantial amount of differentiation is documented among the fragmented populations of the Aegean islands, with over 25 recorded subspecies (Gruber 1986). *Podarcis erhardii* ranges from 49–78 mm in snout-vent length (SVL; Valakos et al. 2008). The species is largely insectivorous, feeding on a broad diversity of arthropods (Valakos 1986) and occasionally plant matter in certain island settings (Brock et al. 2014; Donihue et al. 2016). In the Cycladic Island region, *P. erhardii naxensis* is typically found near rocky or stone wall refugia (Vanhooydonck et al. 1999); although on smaller uninhabited islets, it will use all available habitats so long as they provide some cover. The species is an active thermoregulator (Belasen et al. 2017) with early summer activity peaks in the morning (0800 to 1200) and later afternoon (1600 to 1900).

Study sites.—We conducted the study on four islands located in the Cyclades archipelago, an island cluster in the central Aegean Sea, Greece (Fig. 2). The island of Naxos served as a large-island baseline (446 km², 37°04'49"N, 25°29'31"E; Site L1), which we compared to three nearby small-island sites: the islets of Parthenos

(0.0044 km², 37°01'43"N, 25°21'38"E; Site S1), Mikri Vigla (0.002 km², 37°01'24"N, 25°21'27"E; Site S2), and Aspronissi (0.0102 km², 37°02'48"N, 25°21'02"E; Site S3). All sites are land-bridge islands that were once part of a common ancestral landmass known as the Protocycladic Block, and have become fragmented by rising sea levels since the end of the last ice age (Foufopoulos et al. 1999; Poulos et al. 2009). Parthenos, Mikri Vigla, and Aspronissi all separated relatively recently from neighboring Naxos (approximately 5,500, 6,000 and 6,100 y ago, respectively) and harbor relict populations of *P. erhardii*. Climatic conditions in the Cyclades region are broadly similar across islands. The climate in the region is typical Mediterranean and is characterized by long, warm, and dry summer seasons and a mild rainy winter season (Giannikopoulou et al. 2014).

We conducted our field sampling from June-July 2017. The dry conditions favor shrubby, slow-growing, summer-deciduous vegetation communities that contain many aromatic or spinose taxa. On Naxos, dwarf bush ecosystems occupy a significant portion of the island, with Spiny Broom (*Genista acanthoclada*) and Conehead Thyme (*Coridothymus capitatus*) the dominant plants of the scrubland, which occur on flysch and limestone substrates, respectively. Two tree species, Phoenician Juniper (*Juniperus phoenicea*) and Olive (*Olea europaea*), can also be found throughout the island. Site L1 is an ancient agricultural terrace (0.0012 km²) located on the large island of Naxos and is situated among other shaded dry-stone terraces near

FIGURE 3. (A) The large-island on Naxos, Greece, which we believe is effectively a mainland field site (Site L1). The site is characterized by Olive Tree (*Olea europaea*) groves and stone terraces. (B) The islet of Aspronissi (Site S3) consists of large granodiorite boulders surrounding flat protected areas covered by a shallow layer of soil. Dense vegetation cover, which is also characteristic of Mikri Vigla (Site S2), did not permit the collection of home range data. (C) The small-island site of Parthenos (Site S1), with Naxos in the background. Dense vegetation mats located on a granodiorite substrate cover part of the island. (Photographed by Johannes Foufopoulos).

the village of Moni, where *O. europaea* groves are the prominent element in the landscape (Fig. 3). Site L1 has a diverse predator community comprised of five snakes, three mammals, and two bird species of consequence described in Brock et al. (2015). Sites S1–S3 are rocky granodiorite islets off the western coast of Naxos near the cove of Mikri Vigla and are dominated by a species-rich plant community of dense, tough, summer-deciduous coastal heath (Fig. 3; Fielding and Turland 2008). For Sites S1–S3, we considered the entire islets as sites, and surveyed all of their accessible area. No known lizard predators inhabit Sites S1–S3.

Sampling and measurement.—We captured *P. erhardii* using extendable fishing poles with a thread noose. We assigned each captured lizard a unique identifying number, recorded both the time and date of capture, and input the location of capture into Google Earth Pro Version 7.3.2.5576 (Google LLC, Mountain View, California, USA). To ensure identification in the field, we used two complementary types of lizard-marking techniques. As a means of permanent identification, we toe-clipped each animal using a unique three-digit clipped toe code. For readily visible short-term field identification, we also painted an identifying number on the back using a white-out marker (Jones et al. 1980; Molnár et al. 2016). This method permitted visual field identification that allowed us to gather additional location, time, and date information while avoiding unnecessary lizard recaptures, but was useful only temporarily until skin shedding rendered the markings illegible.

We obtained population relative abundance data for each island by walking one transect (100 m length and 4 m width) through homogenous environments representative of each island. The only exception was a 50 m transect (4 m width) on the islet of Mikri Vigla (Site S2), which was too small for a 100 m-length transect. Each transect was walked three times. We conducted transect sampling prior to capturing any lizards at each site, and on separate days from the collection of HR data to avoid influencing lizard behavior. For each transect, we walked slowly through the low vegetation and recorded all lizards we saw or heard within the area of the transect (Brock et al. 2015). Across our field sites, the short burst of noise produced by these lizards when crawling through brush is distinct from any other animal (pers. obs.), and as such an erroneous tally of a lizard is unlikely. We collected all field data on days when conditions were most conducive for lizard activity (i.e., sunny with ambient temperatures 21°–25° C and wind speeds ≤ 3 Beaufort).

To test for morphological differences of lizards among island populations, we recorded sex and mass (in g) using a digital balance, and collected morphological information including SVL, skull height, skull width, and skull length, as well as tail length (all in millimeters) for each lizard using Mitutoyo 500-196-30 Digimatic digital calipers (Mitutoyo America Corporation, Aurora, Illinois, USA) and following procedures detailed by Donihue et al. (2016). We performed the morphological comparisons between island populations together for

both sexes, but examined sex as a fixed factor. We excluded two individuals from SVL comparisons between island populations (Cases #3 and #18 from S3) because they were outliers whose standardized residuals (3.855 and 3.976, respectively) exceeded three standard deviations. Additionally, we recorded condition of the tail (intact or autotomized and regrown) based on morphological differences (e.g., scarring) between intact and regrown tails. After measurements, we promptly returned all lizards to their original site of capture.

Home range size.—We measured lizard HR size for Site L1 and Site S1, for which brush cover was open enough to allow for reliable repeat observations. We did not collect HR data on sites S2 and S3 as vegetation cover was too dense. We conducted sampling on Site S1 when weather permitted access to the small islet site via sea kayak. For repeat observations, we typically revisited Site L1 every other day and Site S1 every fourth day over the course of the field sampling effort. We first obtained precise coordinates for all observations by registering them in Google Earth Pro, and then exported those locations to ArcGIS 10.5.1 (Esri, Redlands, California, USA); however, for most lizards we collected too few locations (1–4) to calculate HR. For those individual lizards with five or more observations (Site L1 = four females, six males; Site S1 = six females, 11 males), we constructed subject HRs using the aggregate point polygon tool to build minimum convex polygons in ArcGIS (Molnár et al. 2016; Brazeau et al. 2018) and then calculated HR area (in m^2) using the ArcGIS field calculator function. We compared average HR size between populations from the predator-rich mainland site and one predator-free islet (Site L1 and Site S1). Because it is known that sex influences HR size in lizards (Perry et al. 2002), we analyzed data separately for males and females. Additionally, we excluded one animal (Case #9 from L1) from the analyses because it was an outlier (standardized residual of 4.468 > 3 standard deviations).

Statistical analyses.—We assessed data for normality using the Shapiro-Wilk test and checked for homogeneity of variance using Levene's test. If necessary, data were log-transformed to achieve normality. We used a Two-factor ANOVA to test for differences in SVL between lizard populations while considering the effect of sex on SVL. Because SVL has a direct effect on body mass and we were interested in differences in body mass beyond corresponding changes in underlying frame size, we used an Analysis of Covariance (ANCOVA) for mass with SVL as a covariate to compare the lizard populations between each island site. Similarly, we used an ANCOVA with SVL as a covariate to compare skull widths, heights, and lengths between island populations.

We applied a Bonferroni post-hoc correction for SVL, mass, and skull dimensions, correcting for multiple testing among the individual small-island sites and the large-island site with a critical *P*-value of 0.008. We analyzed population densities and tail autotomy rates between sites with Chi-square tests. We analyzed HR size differences between Sites L1 and S1 for males and females separately using Two-sample *t*-tests. We carried out all statistical analyses in IBM SPSS Statistics Version 24.0 (IBM Corp., Armonk, New York, USA), and set all alpha levels *a priori* to 0.05.

RESULTS

Among small island populations, lizard population abundances tended to be higher (Site S1, 11 individuals/100 m; Site S2, 8/50 m; Site S3, 19/100 m) than the large island population (Site L1, 6/100 m); however, these abundances were not significantly different ($\chi^2 = 4.00$, df = 3, $P = 0.261$). SVL differed significantly between all island populations ($F_{3,195} = 20.46$, $P < 0.001$), and sex had a significant effect ($F_{1,195} = 41.04$, $P < 0.001$) on SVL (Table 1). Site S1 lizards (males and females together) had significantly larger SVLs than Site L1 ($P < 0.001$), Site S2 ($P < 0.001$), and Site S3 ($P = 0.018$) animals, and Site S3 lizards had significantly larger SVLs than those at Site L1 ($P = 0.021$). SVL-corrected body mass differed significantly between islands ($F_{3,199} = 6.74$, $P < 0.001$), and sex exhibited a significant effect on mass ($F_{1,199} = 172.9$, $P < 0.001$), where males had significantly greater masses than females (Table 1). Site S2 lizards (males and females together) weighed significantly less than Site L1 ($P = 0.006$) and Site S1 ($P < 0.001$) lizards (Table 1). There were no significant size-corrected mass differences in the lizards from the other islands.

Size-corrected skull width ($F_{1,199} = 151.2$, $P < 0.001$), skull height ($F_{1,199} = 130.6$, $P < 0.001$), and skull length ($F_{1,199} = 265.0$, $P < 0.001$) differed significantly between individual island populations. Site S2 lizards had significantly narrower skulls than the other two small-island sites, Site S1 ($P = 0.014$) and Site S3 ($P = 0.002$), but not the large-island site, Site L1 ($P = 0.311$). Site S2 lizards had significantly shallower skulls relative to those of Site L1 ($P < 0.001$), Site S1 ($P < 0.001$), and Site S3 ($P = 0.001$). Site S1 lizards had significantly taller skulls than Site L1 lizards ($P = 0.027$). Site S2 lizards had significantly shorter skulls than Site S1 ($P = 0.14$) and Site S3 ($P = 0.002$), but not Site L1 ($P = 1.000$). Site S3 lizards had significantly longer skulls than those of Site L1 ($P = 0.010$).

The tail-autotomy rate of lizards on Site L1 was 7.25% (n = 69) whereas the small-island populations on Sites S1, S2, and S3 had tail-autotomy rates of 24.69% (n = 81), 34.78% (n = 23), and 31.25% (n = 32), respectively.

Table 1. Descriptive statistics of the four study populations for lizard mass (g), SVL (mm), skull dimensions (mm) including height, width, and length, tail length (mm), and log-transformed home range (HR) area (m^2). For each site (L1 = Naxos, S1 = Parthenos, S2 = Mikri Vigla, S3 = Aspronissi) morphological parameters are presented with the mean ± standard error. HR data were only collected at sites L1 and S1, for which sample sizes of lizards with five or more observations were four females (F) and six males (M) at Site L1, and six F and 11 M at Site S1.

Site	Sex	n	Mass (g)	SVL (mm)	Skull Height (mm)	Skull Width (mm)	Skull Length (mm)	Tail Length (mm)	Area (m^2 log-transformed)
L1	F	37	4.31 ± 0.15	58.21 ± 0.67	6.10 ± 0.06	7.72 ± 0.08	12.73 ± 0.12	81.62 ± 1.98	1.22 ± 0.12
	M	32	6.56 ± 0.25	62.17 ± 0.77	7.67 ± 0.11	9.62 ± 0.13	15.25 ± 0.17	100.82 ± 3.24	1.17 ± 0.24
	T	69	5.35 ± 0.20	60.04 ± 0.56	6.83 ± 0.11	8.60 ± 0.14	13.90 ± 0.18	90.53 ± 2.26	1.19 ± 0.14
S1	F	40	5.37 ± 0.15	63.72 ± 0.53	6.65 ± 0.06	8.28 ± 0.07	13.55 ± 0.10	73.15 ± 3.11	0.66 ± 0.15
	M	41	7.75 ± 0.20	66.59 ± 0.56	8.15 ± 0.07	10.16 ± 0.10	16.39 ± 0.14	93.07 ± 2.81	1.03 ± 0.14
	T	81	6.58 ± 0.18	65.17 ± 0.42	7.41 ± 0.09	9.23 ± 0.12	14.99 ± 0.18	83.51 ± 2.35	0.90 ± 0.11
S2	F	11	3.92 ± 0.35	58.57 ± 1.24	5.90 ± 0.10	7.68 ± 0.15	12.73 ± 0.17	74.68 ± 3.85	
	M	12	6.15 ± 0.26	63.89 ± 1.35	7.30 ± 0.17	9.43 ± 0.34	15.25 ± 0.27	84.22 ± 3.46	
	T	23	5.08 ± 0.32	61.35 ± 1.06	6.63 ± 0.17	8.60 ± 0.22	14.05 ± 0.31	79.45 ± 4.80	
S3	F	20	4.34 ± 0.28	58.84 ± 1.71	6.08 ± 0.12	7.96 ± 0.13	12.99 ± 0.22	78.82 ± 4.52	
	M	12	6.68 ± 0.31	65.27 ± 1.02	8.05 ± 0.16	10.16 ± 0.18	16.39 ± 0.28	91.39 ± 6.90	
	T	32	5.22 ± 0.29	61.25 ± 1.06	6.82 ± 0.20	8.79 ± 0.22	14.26 ± 0.34	80.79 ± 3.87	

Among the four populations, rates of tail autotomy differed significantly ($\chi^2 = 13.20$, df = 3, $P = 0.004$; Fig. 4). Tail autotomy rates in the small island sites S1–S3 did not differ significantly from each other ($\chi^2 = 1.13$, df = 2, $P = 0.567$); however, tail autotomy rates did differ significantly between the grouped small island sites and the large island Site L1 ($\chi^2 = 10.61$, df = 1, $P = 0.001$). Within each population, rates of tail autotomy between males and females did not significantly differ from each other, both at the large-island Site L1 ($P = 1.000$) and the small-island sites S1 ($P = 0.846$), S2 (P
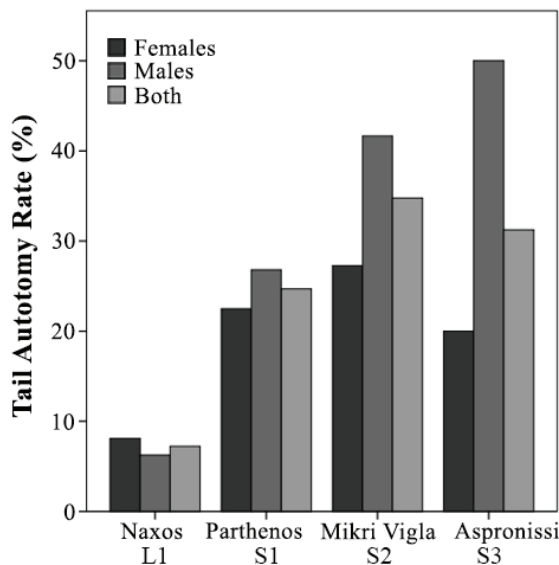
= 0.775), and S3 ($P = 0.168$). For male lizards among the four populations, rates of tail autotomy differed significantly ($\chi^2 = 11.93$, df = 3, $P = 0.008$), whereas for female lizards among all four populations, rates of tail autotomy did not differ significantly ($\chi^2 = 3.75$, df = 3, $P = 0.290$). HR sizes differed significantly for females between Site S1 and Site L1, with small-island females from Site S1 maintaining significantly smaller HRs than
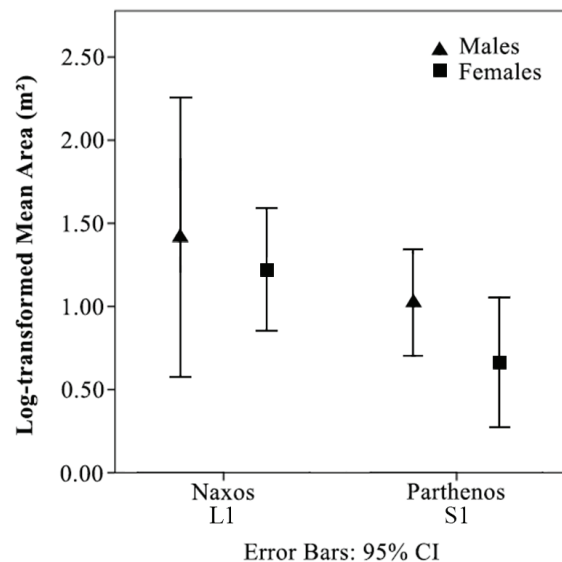

Figure 4. Rates of tail loss at each site, grouped by females, males, and both sexes for Aegean Wall Lizards (*Podarcis erhardii*) on islands of Greece.

Figure 5. Mean log-transformed home range area (m^2) of Aegean Wall Lizards (*Podarcis erhardii*) on two islands of Greece. For male lizards, we found no significant difference in home range size between small- and large-island lizards. Small-island (Site S1) female lizards had significantly smaller home ranges than large-island (Site L1) females.

large-island females from Site L1 ($t = 2.92$, df = 8, $P = 0.019$; Fig. 5). Male HR sizes among sites did not differ significantly ($t = 1.09$, df = 7, $P = 0.310$).

Discussion

Island environments can have profound effects on the evolution and ecology of resident wildlife. In this study, we compared several morphological and ecological traits of an island endemic lizard between a large, resource- and predator-rich area (Site L1; mainland analog) and three small nearby islets that are resource- and predator-poor (Sites S1-S3). External ecological factors such as predation pressure often differ dramatically between these two types of environments, which we expected to impact lizard population densities, and in turn, HR use and the frequency of tail autotomy as a result of aggressive interspecific interactions.

We found lizard abundances on the small-island sites to be two to three times higher than those on the large-island site, but these differences were not significant. Relative to mainland environments, islands tend to have lower species diversity due to limited space and food resources, meaning small-island populations may experience release from interspecific competition and predation pressures (Case et al. 1993; Adler et al. 1994) and a subsequent increase in population density (Pérez-Mellado et al. 2008; Pafilis et al. 2009; Raia et al. 2010). Previous research conducted in the Cyclades archipelago provides a general index of predation pressure for each of our study islands and demonstrates a lower predator diversity on the small islets sites as compared to our large island site (Brock et al. 2015); however, due to the elusive nature of potential predator species (i.e., nocturnal, semi-fossorial, and aerial hunters), we lack comprehensive predator density estimates and demographic sampling data for our specific study sites.

For our particular study islands, the effects of relaxed predation on lizard density are further enhanced by substantial marine subsidies derived from the resident seabird colonies (Pafilis et al. 2009, 2011). All three islets harbor Yellow-Legged Gull (*Larus michahellis*) and European Shag (*Phalacrocorax aristotelis*) colonies, and *P. erhardii* have been observed feeding on food scraps, bird carcasses, or on seabird-associated arthropods (Dinos Protopappas, pers. comm.). By importing nutrients in the form of guano, fish scraps, and carcasses, seabirds are demonstrated to support higher densities of insular lizards (Markwell et al. 2002; Barrett et al. 2005; Pafilis et al. 2009). Our field surveys suggest that these differences could shape lizard population densities on our study islands, although the relative contributions of predation release compared to marine subsidies remain to be determined.

We investigated morphological differences between the four island sites. Although we did not find significant differences in population abundances between island sites, abundances were higher on small island sites. It is possible that our small sample sizes contributed to a lack of significance. We predicted that lizards from the small islet sites would have larger SVLs and skull sizes than those from the large island population. We found that lizards from one of the small-island sites (Site S1) had significantly larger SVLs than the large-island population (Site L1); however, this relationship did not hold for the other two small-island populations. Parthenos (S1) lizards were significantly larger than all three other island sites, which may reflect local differences in the social landscape. More detailed work investigating the interacting effects of diet and differences in lizard growth rates may elucidate local causes of small islet differences in SVL.

The cranial morphology of a lizard can confer a suite of fitness advantages, including access to a wider breadth of prey items (Verwaijen et al. 2002; Herrel et al. 2008; Sagonas et al. 2014) and greater advantage in intraspecific contests for resources (Lailvaux et al. 2004; McLean et al. 2015). We predicted that skull sizes from the small-island sites would be larger than those from the large-island site, and although we observed a few significant differences in various skull dimensions among the four populations of lizards, the trends were not consistent enough between the large- and small-island sites to confirm our prediction. Compared to the large-island Site L1, lizards from the small-island Site S1 had taller skulls, and those from S3 had longer skulls. In a recently conducted inter-island study on *P. erhardii* bite force, social interactions, and diet, the gut contents of lizards from the small, predator-free islet of Parthenos (S1) contained conspecific body parts, suggesting cannibalistic tendencies (Donihue et al. 2016). Indeed, cannibalistic interactions in *P. erhardii* have been observed on S1 (pers. obs.), as well other islands with high population densities (Madden et al. 2018). Skull height in lizards is associated with having a larger gape and harder bite force (Herrel et al. 2001; Verwaijen et al. 2002; Huyghe et al. 2009; Donihue et al. 2016) and observed differences in skull height between small island populations could reflect local islet natural selection for larger head size, which in turn could be advantageous for obtaining resources and avoiding cannibalism. Conversely, we observed on our smallest islet site S2 (0.002 km²) that lizards had significantly shorter skulls in terms of height than all other sites respective to SVL. Despite some seabird nutritional subsidies, this is most likely due to the extremely low availability of food on this rocky islet.

We tested whether rates of tail autotomy differed between different island settings. The proportion of tails autotomized to those intact differed significantly

between the four lizard populations. We found that all small-island populations (Sites S1-S3) had significantly higher proportions of shed and regenerated tails relative to the large-island (Site L1) population. This is noteworthy given that these small islands are, apart from the presence of occasional raptors, likely free of any lizard predators, whereas Naxos lizards are subject to mammalian, snake, and avian predation (Brock et al. 2015). Thus, our results support the hypothesis that lizard tail loss is affected more so by rates of intraspecific competition than predation, at least on islands. Previous studies show that high levels of intraspecific aggression amid the denser populations of small-island environments exist, both in *P. erhardii* (Brock et al. 2015; Donihue et al. 2016) and in related species (Pafilis et al. 2009; Cooper et al. 2014). These reports discuss intense male-male fighting bouts that result in both tail loss (Deem et al. 2014; Itescu et al. 2017), toe loss (Vervust et al. 2007; Donihue et al. 2016), and even cannibalism (Matuschka et al. 1987; Deem et al. 2014; Madden et al. 2018). We found on our small islet sites regular fights between lizards as animals regularly probed the HR of neighbors. It is possible that the magnitude of aggression is higher in dense, small island populations.

We investigated whether HR sizes in small-island lizard populations differed from those in a large-island population. Specifically, for male lizards, we found that while islet HRs tended to be smaller on average, these differences were not significant. This was in part attributable to the large variation in HR size in large-island males, which in turn could be driven by divergent reproductive and foraging strategies among individual lizards (Kwiatkowski et al. 2002; Healey et al. 2008; Molnár et al. 2016). We also did not collect as many locations as probably needed to characterize the HR of lizards well, and this may be the overriding reason for our results. In contrast, we demonstrated significant differences in the HR sizes of female lizards. On the islet Parthenos (Site S1), females had HRs that were only 54% as big as the corresponding HRs on Naxos (Site L1), although HR sizes of females were based on small sample sizes of locations and number of animals. Future work on these populations should collect upwards of 30–50 locations per animal.

Podarcis erhardii is color polymorphic, and male color morphs from Naxos vary in their head and body sizes whereas female color morphs do not (Brock et al. 2020). Male color morphs from other color polymorphic lizard species employ different reproductive strategies that include differences in mate guarding and territoriality behaviors (Sinervo et al. 1996; Molnár et al. 2016), and in the related polymorphic Madeira Wall Lizard (*Podarcis dugesii*), an island-scale geographic analysis suggests that morphs even respond differently to variation in the thermal environment (Báez et al. 1997). Color morph diversity varies from island to island in *P. erhardii* (pers. obs.), and nothing is yet known about how male morph differences in body size, head size, or chemical signaling contribute to differences in reproductive strategies. Future research on HR size in this species also should focus on sex differences that incorporate color morph identity.

Although our results indicate ecological and morphological differences between several nearby populations of *P. erhardii,* these changes observed across islands could be attributed to phenotypic plasticity rather than solely to evolutionary processes. At the individual level, lizards are shown to exhibit plastic seasonal changes in head morphology and bite performance (Irschick et al. 2007), territorial behavior (Knapp et al. 2003), and reproductive tactics (Moore 1991), and it is thought that plasticity accounts for differences in escape behavior as well (Cooper et al. 2012). In summary, we demonstrated differences in tail autotomy rates and HR sizes of female lizards between small- and large-island populations of *Podarcis erhardii*. These differences are most likely explained by localized ecological differences in resource and predator abundance and the resulting differences in population density. These results broadly corroborate previous research relating to patterns of intraspecific competition and ecological release in island and mainland populations of lizards (Lister 1976; Des Roches et al. 2011). Thus, our findings indicate that different ecological conditions among island and mainland environments can drive important departures in the morphologies and behaviors of individual species inhabiting them.

Literature Cited

Adler, G.H., and R. Levins. 1994. The island syndrome in rodent populations. Quarterly Review of Biology 69:473–490.

Alberts, A.C. 1993. Relationship of space use to population density in an herbivorous lizard. Herpetologica 49:469–479.

Arnold, E.N. 1984. Evolutionary aspects of tail shedding in lizards and their relatives. Journal of Natural History 18:127–169.

Báez, M., and R.P. Brown. 1997. Testing multivariate patterns of within-island differentiation in *Podarcis dugesii* from Madeira. Journal of Evolutionary Biology 10:575–587.

Barrett, K., W.B. Anderson, D.A. Wait, L.L. Grismer, G.A. Polis, and M.D. Rose. 2005. Marine subsidies alter the diet and abundance of insular and coastal lizard populations. Oikos 109:145–153.

Bateman, P.W., and P.A. Fleming. 2009. To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. Journal of Zoology 277:1–14.

Bateman, P.W., and P.A. Fleming. 2011. Frequency of tail loss reflects variation in predation levels, predator efficiency, and the behaviour of three populations of brown anoles. Biological Journal of the Linnean Society 103:648–656.

Belasen, A., K. Brock, B. Li, D. Chremou, E. Valakos, P. Pafilis, B. Sinervo, and J. Foufopoulos. 2017. Fine with heat, problems with water: microclimate alters water loss in a thermally adapted insular lizard. Oikos 126:447–457.

Bellairs, d'A.A., and S.V. Bryant. 1985. Autotomy and regeneration in reptiles. Pp. 301–410 *In* Biology of the Reptilia, Volume 15. Gans, C., and F. Billet (Eds.). John Wiley & Sons, New York, New York, USA.

Blumstein, D.T., and J.C. Daniel. 2005. The loss of anti-predator behaviour following isolation on islands. Proceedings of the Royal Society B: Biological Sciences 272:1663–1668.

Brazeau, D.J., and S.J. Hecnar. 2018. Summer movements of the Common Five-lined Skink (*Plestiodon fasciatus*) in the northern portion of its range. Herpetological Conservation and Biology 13:743–752.

Brock, K.M., S. Baeckens, C.M. Donihue, J. Martín, P. Pafilis, and D.L. Edwards. 2020. Trait differences among discrete morphs of a color polymorphic lizard, *Podarcis erhardii*. PeerJ 8:e10284. https://doi.org/10.7717/peerj.10284.

Brock, K.M., P.A. Bednekoff, P. Pafilis, and J. Foufopoulos. 2015. Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): the sum of all fears? Evolution 69:216–231.

Brock, K.M., C.M. Donihue, and P. Pafilis. 2014. New records of frugivory and ovophagy in *Podarcis* (Lacertidae) lizards from East Mediterranean Islands.

North-Western Journal of Zoology 10:223–225.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Case, T.J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. Ecology 59:1–18.

Case, T.J., and T.D. Schwaner. 1993. Island/mainland body size differences in Australian varanid lizards. Oecologia 94:102–109.

Chapple, D.G., and R. Swain. 2002. Distribution of energy reserves in a viviparous skink: does tail autotomy involve the loss of lipid stores? Austral Ecology 27:565–572.

Cooper, W.E., Jr., and V. Pérez-Mellado. 2012. Historical influence of predation pressure on escape by *Podarcis* lizards in the Balearic Islands. Biological Journal of the Linnean Society 107:254–268.

Cooper, W.E., Jr., I. Dimopoulos, and P. Pafilis. 2014. Sex, age, and population density affect aggressive behaviors in island lizards promoting cannibalism. Ethology 120:1–10.

Deem, V., and H. Hedman. 2014. Potential cannibalism and intraspecific tail autotomization in the Aegean Wall Lizard, *Podarcis erhardii*. Hyla: Herpetological Bulletin 2014:33–34.

Des Roches, S., J.M. Robertson, L.J. Harmon, and E.B. Rosenblum. 2011. Ecological release in White Sands lizards. Ecology and Evolution 1:571–578.

Donihue, C.M., K.M. Brock, J. Foufopoulos, and A. Herrel. 2016. Feed or fight: testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard. Functional Ecology 30:566–575.

Downes, S., and R. Shine. 2001. Why does tail loss increase a lizard's later vulnerability to snake predators? Ecology 82:1293–1303.

Fielding, J., and N. Turland. 2008. Flowers of Crete. 2nd Edition. Royal Botanic Gardens, Kew, Surrey, London, U.K.

Fleming, P.A., D. Muller, and P.W. Bateman. 2007. Leave it all behind: a taxonomic perspective of autotomy in invertebrates. Biological Reviews 82:481–510.

Foufopoulos, J., and A.R. Ives. 1999. Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. American Naturalist 153:1–25.

Foufopoulos, J., A.M. Kilpatrick, and A.R. Ives. 2011. Climate change and elevated extinction rates of reptiles from Mediterranean islands. American Naturalist 177:119–129.

Giannikopoulou, A.S., E. Kampragkou, F.K. Gad, A. Kartalidis, and D. Assimacopoulos. 2014. Drought characterisation in Cyclades complex, Greece.

European Water 47:31–43.

Gruber, U. 1986. *Podarcis erhardii* (Bedriaga, 1876) - Ägäische Mauereidechse. Pp. 25–49 *In* Handbuch der Reptilien und Amphibien Europas. Böhme, W. (Ed.). Aula-Verlag, Wiesbaden, Germany.

Haenel, G.J., L.C. Smith, and H.B. John-Alder. 2003. Home-range analysis in *Sceloporus undulatus* (Eastern Fence Lizard). I. Spacing patterns and the context of territorial behavior. Copeia 2003:99–112.

Healey, M., and M. Olsson. 2008. Territory acquisition in a polymorphic lizard: an experimental approach. Austral Ecology 33:1015–1021.

Herrel, A., E. De Grauw, and J.A. Lemos-Espinal. 2001. Head shape and bite performance in xenosaurid lizards. Journal of Experimental Zoology 290:101–107.

Herrel, A., K. Huyghe, B. Vanhooydonck, T. Backeljau, K. Breugelmans, I. Grbac, R. Van Damme, and D.I. Irschick. 2008. Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. Proceedings of the National Academy of Sciences of the United States of America 105:4792–4795.

Huyghe, K., A. Herrel, D. Adriaens, Z. Tadić, and R. Van Damme. 2009. It is all in the head: morphological basis for differences in bite force among colour morphs of the Dalmatian Wall Lizard. Biological Journal of the Linnean Society 96:13–22.

Irschick, D.J., and J.J. Meyers. 2007. An analysis of the relative roles of plasticity and natural selection in the morphology and performance of a lizard (*Urosaurus ornatus*). Oecologia 153:489–499.

Itescu, Y., R. Schwarz, S. Meiri, and P. Pafilis. 2017. Intraspecific competition, not predation, drives lizard tail loss on islands. Journal of Animal Ecology 86:66–74.

Jones, S.M., and G.W. Ferguson. 1980. The effect of paint marking on mortality in a Texas population of *Sceloporus undulatus*. Copeia 1980:850–854.

Knapp, R., D.K. Hews, C.W. Thompson, L.E. Ray, and M.C. Moore. 2003. Environmental and endocrine correlates of tactic switching by nonterritorial male Tree Lizards (*Urosaurus ornatus*). Hormones and Behavior 43:83–92.

Kwiatkowski, M.A., and B.K. Sullivan. 2002. Mating system structure and population density in a polygynous lizard, *Sauromalus obesus* (= *ater*). Behavioral Ecology 13:201–208.

Lailvaux, S.P., A. Herrel, B. Vanhooydonck, J.J. Meyers, and D.J. Irschick. 2004. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the Green Anole Lizard (*Anolis carolinensis*). Proceedings of the Royal Society B: Biological Sciences 271:2501–2508.

Lister, B.C. 1976. The nature of niche expansion in West Indian *Anolis* lizards I: ecological consequences of reduced competition. Evolution 30:659–676.

Lomolino, M.V. 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32:1683–1699.

Losos, J.B. 2011. Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. University of California Press, Berkeley, California, USA.

MacArthur, R.H. and E.O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey, USA.

Madden, I., and K.M. Brock. 2018. An extreme case of cannibalism in *Podarcis erhardii mykonensis* (Reptilia: Lacertidae) from Siros Island, Cyclades, Greece. Herpetology Notes 11:291–292.

Markwell, T.J., and C.H. Daugherty. 2002. Invertebrate and lizard abundance is greater on seabird-inhabited islands than on seabird-free islands in the Marlborough Sounds, New Zealand. Ecoscience 9:293–299.

Martin, R.A., and D.W. Pfennig. 2010. Field and experimental evidence that competition and ecological opportunity promote resource polymorphism. Biological Journal of the Linnean Society 100:73–88.

Matuschka, F.R., and B. Bannert. 1987. Cannibalism and autotomy as predator-prey relationship for monoxenous Sarcosporidia. Parasitology Research 74:88–93.

McLean, C.A., and D. Stuart-Fox. 2015. Rival assessment and comparison of morphological and performance-based predictors of fighting ability in Lake Eyre dragon lizards, *Ctenophorus maculosus*. Behavioral Ecology and Sociobiology 69:523–531.

Meiri, S. 2007. Size evolution in island lizards. Global Ecology and Biogeography 16:702–708.

Molnár, O., K. Bajer, G. Szövényi, J. Török, and G. Herczeg. 2016. Space use strategies and nuptial color in European Green Lizards. Herpetologica 72:40–46.

Moore, M.C. 1991. Application of organization-activation theory to alternative male reproductive strategies: a review. Hormones and Behavior 25:154–179.

Pafilis, P., J. Foufopoulos, K. Sagonas, A. Runemark, E. Svensson, and E.D. Valakos. 2011. Reproductive biology of insular reptiles: marine subsidies modulate expression of the "island syndrome." Copeia 2011:545–552.

Pafilis, P., S. Meiri, J. Foufopoulos, and E. Valakos. 2009. Intraspecific competition and high food availability are associated with insular gigantism in a lizard. Naturwissenschaften 96:1107–1113.

Pérez-Mellado, V., J.A. Hernández-Estévez, T. García-

Díez, B. Terrassa, M.M. Ramón, J. Castro, A. Picornell, J. Martín-Vallejo, and R. Brown. 2008. Population density in *Podarcis lilfordi* (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). Amphibia-Reptilia 29:49–60.

Perry, G., and T. Garland, Jr. 2002. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. Ecology 83:1870–1885.

Perry, G., K. LeVering, I. Girard, and T. Garland, Jr. 2004. Locomotor performance and social dominance in male *Anolis cristatellus*. Animal Behavior 67:37–47.

Poulos, S.E., G. Ghionis, and H. Maroukian. 2009. Sea-level rise trends in the Attico-Cycladic region (Aegean Sea) during the last 5000 years. Geomorphology 107:10–17.

Raia, P., F.M. Guarino, M. Turano, G. Polese, D. Rippa, F. Carotenuto, D.M. Monti, M. Cardi, and D. Fulgione. 2010. The blue lizard spandrel and the island syndrome. BMC Evolutionary Biology 10:289. doi:10.1186/1471-2148-10-289.

Sagonas, K., P. Pafilis, P. Lymberakis, C.M. Donihue, A. Herrel, and E.D. Valakos. 2014. Insularity affects head morphology, bite force and diet in a Mediterranean lizard. Biological Journal of the Linnean Society 112:469–484.

Schoener, T.W., and A. Schoener. 1980. Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. Journal of Animal Ecology 49:19–53.

Schoener, T.W., and A. Schoener. 1982. Intraspecific variation in home-range size in some *Anolis* lizards. Ecology 63:809–823.

Sinervo, B., and C.M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. Nature 380:240–243.

Valakos, E.D. 1986. The feeding ecology of *Podarcis erhardii* (Reptilia-Lacertidae) in a main insular ecosystem. Herpetological Journal 1:118–121.

Valakos, E.D., P. Pafilis, K. Sotiropoulos, P. Lymberakis, P. Maragou, and J. Foufopoulos. 2008. The Amphibians and Reptiles of Greece. Edition Chimaira, Frankfurt, Germany.

Vanhooydonck, B., and R. Van Damme. 1999. Evolutionary relationships between body shape and habitat use in lacertid lizards. Evolutionary Ecology Research 1:785–805.

Vervust, B., I. Grbac, and R. Van Damme. 2007. Differences in morphology, performance and behaviour between recently diverged populations of *Podarcis sicula* mirror differences in predation pressure. Oikos 116:1343–1352.

Verwaijen, D., R. Van Damme, and A. Herrel. 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. Functional Ecology 16:842–850.

Vitt, L.J. 1981. Tail autotomy and regeneration in the tropical skink, *Mabuya heathi*. Journal of Herpetology 15:451–454.

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