SHORT COMMUNICATION

Intraspecific competition and high food availability are associated with insular gigantism in a lizard

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Abstract Resource availability, competition, and predation commonly drive body size evolution. We assess the impact of high food availability and the consequent increased intraspecific competition, as expressed by tail injuries and cannibalism, on body size in Skyros wall lizards (*Podarcis gaigeae*). Lizard populations on islets surrounding Skyros (Aegean Sea) all have fewer predators and competitors than on Skyros but differ in the numbers of nesting seabirds. We predicted the following: (1) the presence of breeding seabirds (providing nutrients) will increase lizard population densities; (2) dense lizard populations will experience stronger intraspecific competition; and (3) such aggression, will be associated with larger average body size. We found a positive correlation between seabird and lizard densities. Cannibalism and tail injuries were considerably higher in dense populations. Increases in cannibalism and tail loss were associated with large body sizes. Adult cannibalism on juveniles may select for rapid growth, fuelled by high food abundance, setting thus the stage for the evolution of gigantism.

Keywords *Podarcis gaigeae* · Insularity · Cannibalism · Seabird subsidy · Population density

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Introduction

Interpopulation variations in body size have been reported for numerous taxa (Meiri et al. 2005; Wu et al. 2006), especially on islands (Sondaar 1977; Lomolino 2005). Evolution of both dwarfism and gigantism has been attributed to the particularities of island environments such as relaxed predation regime, low food availability, and strong competition (Meiri et al. 2004; Dayan and Simberloff 2005; Meiri 2008).

Density-dependent intraspecific competition is thought to strongly impact population dynamics, as well as multiple aspects of an organism's life history (Lack 1954; Sinervo et al. 2000). On islands, low predation pressure often results in higher densities and thus increased intraspecific competition. Juvenile mortality, through potential infanticide, is also related to higher levels of intraspecific competition (Jenssen et al. 1989; Elgar and Crespi 1992). Population densities and body sizes of many island vertebrates are correlated to the presence of seabirds (Sanchez-Piñero and Polis 2000; Bonnet et al. 2002) that, through accumulation

of fecal material, food scraps, and carcasses boost nutrient availability in islands (Polis and Hurd 1996).

In this study, we assessed the impact of such "seabird subsidies," population density, and intraspecific competition on body size of an endemic Mediterranean lizard showing extreme interpopulation body size variation (Valakos et al. 2008). The study populations all live under the same climatic conditions but differ considerably in population density, levels of intraspecific competition, and the size of yellow-legged gull (*Larus michahellis*) colonies on the islands they inhabit. We tested three predictions: (1) lizard population density is positively correlated to seabird presence; (2) higher population density is associated with elevated levels of intraspecific competition (measured as tail autotomy and cannibalism rates); and (3) higher levels of intraspecific competition and greater gull abundance select for larger body size.

Materials and methods

Study organism and site

The Skyros wall lizard (*Podarcis gaigeae*, Sauria: Lacertidae) is a small [snout-vent length (SVL) ~60 mm; mass, 6.6 g] insectivorous lacertid endemic to the Skyros Archipelago (38º51′ N, 24º33′ E; central Aegean Sea, Greece). We compare lizard populations living on Skyros Island and four of its satellite islets. Lizards were collected in mid-July of three consecutive years (2005, 2006, and 2007). To avoid pseudoreplication and monitor population dynamics, we toe-clipped every lizard we caught and measured lizards only in the first year they were caught. Because the islands vary widely in levels of predation, competition, and presence of seabird colonies while experiencing the same climate, they provide a unique opportunity to test the effects of the former three factors on lizard body size (Table 1).

Intraspecific competition

Intensity of intraspecific competition was assessed by measuring rates of caudal autotomy and cannibalism. Cannibalism was quantified by dissecting museum specimens and examining the digestive track for lizard body parts. Lizards shed their tail primarily to avoid predation and also to escape attacks by conspecifics (Arnold 1988). We quantified ease of autotomy by simulating predation in the laboratory (Pérez-Mellado et al. 1997). Lizards were placed in a terrarium with cork substrate to provide traction. To reduce pressure variation and standardize the experimental conditions, we used digital callipers to apply comparable pressure (by comparing callipers' indications)

to lizard tails, 20 mm from the cloaca, for 15 s and recorded whether this resulted in autotomy.

We estimated autotomy rates by determining the fraction of animals with regenerated tails in the field and among museum specimens. Whereas simulated predation trials represent the intrinsic ability for tail shedding, field autotomy rates reflect the combined influence of intrinsic tendencies and the external stimuli to do so. The relative difference between these two variables, expressed as the percent to which laboratory autotomy rates differ from field rates,

$$RD_{FLAR} = [(Laboratory\ rates - Field\ rates)/Field\ rates] \times 100$$

reflects the intensity of environmental opportunities (predation and social interactions) to cause autotomy (Pafilis et al. 2009).

Measurements

We examined 218 preserved specimens at the Alexander Koenig Zoological Museum (Bonn) and 471 live field-caught animals. SVLs were measured using digital callipers. No statistical difference was found between SVLs of specimens measured in museums and in the field (three-way analysis of variance with sex, museum/field, and island as factors: sex, $F_{1,616}=468.1$, $P<0.05$; museum/field, $F_{1,616}=0.27$, $P>0.05$, island: $F_{4,616}=378.0$, $P<0.05$). That was also the case for autotomy rates (χ^2 test with Yate's correction, $df=1$, all $\chi^2 \leq 2.5$, $P>0.05$). We therefore pooled museum and field measurements (Table 1).

We used mean population SVL as a measure of size rather than maximum SVL, which can mask intraspecific variation and may underestimate true potential size (Meiri 2007). That said, population mean and maximum SVLs were highly correlated with each other (juveniles, $r=0.983$; females, $r=0.974$; males, $r=0.969$; $n=5$ in all cases), and we thus believe that different indices of size distributions will yield similar results.

Population densities (lizards/hectare) were calculated by the same observer (PP) using a single (some islands are too small for multiple transects), randomly placed, line transect of 4-m width and 100–200-m length in each island (see Jaeger 1994).

Statistical analysis

We used χ^2 tests to compare the frequencies of tail autotomy and simple linear regression to estimate the relationships between the ecological conditions on different islands and lizard density, cannibalism, autotomy frequency, and body size.

Table 1 Geographic origin, snout vent length (in mm), autotomy, cannibalism percentages, and population density (individuals ha^{-1}) of the animals used in this study

Location Traits	Skyros	Valaxa	Mesa Diavates	Lakonissi	Exo Diavates
SVL males (museum and field pooled)	61.36 (185)	64.55 (33)	66.12 (46)	71.95 (64)	85.28 (69)
SVL females (museum and field pooled)	55.65 (101)	57.07 (19)	57.98 (25)	62.27 (25)	70.34 (43)
SVL juveniles (Field)	28.14 (37)	28.77 (7)	28.97 (7)	30.82 (10)	32.52 (18)
Autotomy (museum and field pooled)	32.16% (92/286)	32.7% (17/52)	29.6% (21/71)	70.78% (63/89)	88.4% (99/112)
Autotomy (Lab)	35.13% (39/111)	35% (7/20)	31.25% (10/32)	33.33% (6/18)	40% (4/10)
RD$_{FLAR}$	9.19	7.03	5.57	−52.95	−54.75
Cannibalism	1.20% (1/83)	0% (0/12)	0% (0/11)	4.54% (1/22)	21.42% (3/14)
Densities	185	95	110	350	850
Species richness	4 (1, 2, 3, 4)	4 (1, 2, 3, 4)	2 (2, 4)	2 (2, 4)	2 (2, 4)
Snake predators	3 (1, 2, 3)	1 (3)	0	0	0
Bird predators	6 (1, 2, 3, 4, 5, 6)	1 (3)	1 (3)	0	1 (3)
Gull presence	0	5	8	10	50
Area (km^2)	207	4.33	0.0384	0.016	0.019
Distance from Skyros (m)	0	140	306	666	1.400

Supporting references: Handrinos and Akriotis 1997; Valakos et al. 2008. Numbers in parentheses are sample sizes unless the identity of species is given. Snakes: 1, *Zamenis situlus*; 2, *Elaphe quatuorlineata*, 3 *Telescopus fallax*. Birds: 1, *Buteo buteo*; 2, *Falco tinnunculus*; 3, *Falco eleonorae*; 4, *Athene noctua*; 5, *Lanius senator*; 6, *Corvus* sp. Lizards: 1, *Lacerta trilineata*; 2, *Cyrtopodion kotschyi*; 3, *Hemidactylus turcicus*; 4, *Podarcis gaigeae*

While a multiple regression would have enabled us to distinguish between different hypotheses regarding the ecological drivers of these four factors, we feel that, with only five islands, a multiple regression model will be grossly over-parameterized. While an analysis of residuals seems to overcome this problem, there are multiple problems with the use of residual analysis, ranging from false parameter estimates, issues of co-linearity between predictor variables, inflated rates of both type 1 and type 2 errors, and error rates in the residuals themselves. Moreover, the retention of the degrees of freedom is also false (see discussion in Smith 1999; Darlington and Smulders 2001; Garcia-Berthou 2001; Freckleton 2002). We therefore feel that, until data from more populations is gathered, we cannot readily tease apart the influence of the different ecological variables.

Results

We recovered body parts (tails and feet) or even entire juveniles from the stomach of adult lizards. Because we found only males cannibalizing juveniles, percentages reported in this study (Table 1) reflect male cannibalism only.

No statistically significant differences in lab autotomy rates were found between the examined populations ($\chi^2 = 0.316$, $df = 4$, $P = 0.98$). In contrast, field rates were different from those in the lab ($\chi^2 = 135.0$, $df = 4$, $P = 0.002$), but this difference disappeared when Lakonissi and Exo Diavates were removed ($\chi^2 = 0.199$, $df = 2$, $P = 0.91$). Similarly, there were no differences between field and laboratory autotomy rates for most populations (all $\chi^2 \leq 0.01$, $P > 0.05$) with the exception of Lakonissi and Exo Diavates ($\chi^2 = 14.8$ and $\chi^2 = 12.9$, respectively, $P < 0.05$) reflecting the presence of extremely strong drivers causing autotomy (Fig. 1).

Fig. 1 Male lizards from Exo Diavates (*left*), Lakonissi (*middle*), and Skyros (*right*)

Field autotomy rates were strongly correlated with cannibalism ($r=0.89$, $F_{1,3}=10.82$, $P<0.05$) and population density ($r=0.92$, $F_{1,3}=18.3$, $P<0.05$). Seabird presence was strongly correlated with cannibalism ($r=0.98$, $F_{1,3}=67.99$, $P<0.05$) and population density ($r=0.95$, $F_{1,3}=30.18$, $P<0.05$). Lastly, density and cannibalism were also highly correlated ($r=0.99$, $F_{1,3}=190.00$, $P<0.05$).

Across the five islands and for all groups (female, male, and juvenile *P. gaigeae*), there were no significant correlations between SVL (log-transformed in all analyses) and the (non-transformed) number of lizard, bird of prey, and snake species. Neither was SVL correlated with snake presence or absence. Cannibalism frequency, lizard density, and seabird density (log-transformed), however, were all significantly and positively correlated with SVL of females, males, and juveniles (Table 2). The small number of islands for which we have ecological data precludes the use of more complex models.

Discussion

Seabird presence was closely related to population densities, with Exo Diavates and Lakonissi having both the largest seabird colonies and highest lizard densities, supporting our first hypothesis. Gulls do, in general, not prey on lizards (Cooper et al. 2004); instead, lizards appear to profit from gull presence (Gruber 1986). First,

gull aggression discourages lizard predators from hunting near island colonies (Vervust et al. 2007). More importantly, gulls subsidize island ecosystems by importing nutrients in the form of guano, fish scraps, and carcasses (Sobey and Kenworthy 1979; Anderson and Polis 1998), therefore supporting dense lizard populations (Markwell and Daugherty 2002; Barrett et al. 2005). We found study islands with nesting seabirds to have more luxurious and more nitrophilous vegetation and higher arthropod densities (Pafilis, unpublished data). Food abundance is positively correlated with body size of insular carnivorous animals (Raia and Meiri 2006). High seabird density has been associated with gigantism in reptiles especially if these happen to feed on seabird eggs, regurgitates, carcasses, and chicks (Case and Schwaner 1993; Boback 2003). We hypothesize that indirect effect of seabird colonies, in the form of high nutrient input, support the increased body size in our study system.

In line with our second hypothesis, intraspecific competition, as quantified through rates of cannibalism and field autotomy, appeared to be stronger in denser lizard populations. Field autotomy rates have traditionally been interpreted as an index of predation pressure (Pianka, 1970; Turner et al. 1982); on the study islets, which support few predators (predation is relaxed in the whole Skyros Archipelago, Pafilis et al. 2005), autotomy rates reflect likely high intraspecific aggression. Lizards can attack conspecifics causing tail shedding (Jennings and

Table 2 Correlations between ecological variables and female, male, and juvenile *P. gaigeae* snout vent lengths (SVL) across the five islands in Table 1

| Response variable	Explanatory variable	t	P value	R^2
Female SVL	Cannibalism	5.449	0.012*	0.908
	Density	3.802	0.032*	0.828
	Gulls	4.148	0.026*	0.852
	Lizard richness	−1.597	0.208	0.460
	Raptor richness	−0.979	0.400	0.242
	Snake presence	−1.597	0.208	0.460
	Snake richness	−1.377	0.262	0.387
Male SVL	Cannibalism	5.159	0.014*	0.899
	Density	3.334	0.045*	0.788
	Gulls	4.761	0.018*	0.883
	Lizard richness	−1.636	0.200	0.472
	Raptor richness	−1.074	0.362	0.278
	Snake presence	−1.636	0.200	0.472
	Snake richness	−1.481	0.235	0.422
Juvenile SVL	Cannibalism	3.727	0.034*	0.822
	Density	3.690	0.035*	0.820
	Gulls	4.021	0.028*	0.844
	Lizard richness	−1.747	0.179	0.504
	Raptor richness	−1.094	0.354	0.285
	Snake presence	−1.747	0.179	0.504
	Snake richness	−1.541	0.221	0.442

Thompson 1999; Langkilde and Shine 2007), and this tendency is further exacerbated in crowded conditions (Salvador 1986; Pafilis et al. 2008). Despite the minimal presence of predators, autotomy field rates were highest on the dense Exo Diavates and Lakonissi populations, suggesting that the causative factor of autotomy is intense intraspecific competition. This is further underscored by the strikingly low values of RD_{FLAR} values in these two islets (Table 1), which indicate that tremendous pressures act on the lizards to shed their tail. Although forced laboratory rates are usually higher than field rates (Pafilis et al. 2009), the latter were by far higher on these two islets. Our results suggest that lizards on Exo Diavates and Lakonissi shed their tail because of strong intraspecific competition (Fig. 2).

Cannibalism is common in lacertids (Sadek 1981; Castilla and Van Damme 1996), including *P. gaigeae* (Adamopoulou et al. 1999). We show that, in our system, it is particularly pronounced in dense, snake-free islets. Cannibalism can be an important cause of juvenile mortality (Wagner and Wise 1996) and an important

selection force on morphology, as well as possibly earlier sexual maturation (Polis and Myers 1985). Large size at birth can considerably enhance juvenile survival because of better physiological performance (Olsson et al. 2002; Le Galliard et al. 2005). Larger juveniles are often fitter, (Sinervo 1993) and large size confers advantages in intraspecific competition and predator avoidance (Case 1978; Melton 1982). Hence, cannibalism, whether associated with territoriality or not, may exert a strong selective pressure for larger offspring in dense populations. Even though cannibalism appears to be relatively rare on most islands, we found high population density and cannibalism to be associated with gigantism.

Four possible, non-mutually exclusive processes underlie our results: (1) The largest juveniles, which presumably grow into the largest adults, are most likely to escape cannibalism and survive into adulthood; (2) in adults, large size allows more effective feeding on both juveniles and on tails; and (3) in crowded conditions, the largest males will be able to control access to females (Jenssen and Nunez 1998). Thus, we hypothesized that cannibalism results in

Fig. 2 Map of Skyros Archipelago in the Aegean Sea. Islands sampled are labeled with their name and an *arrow* if very small
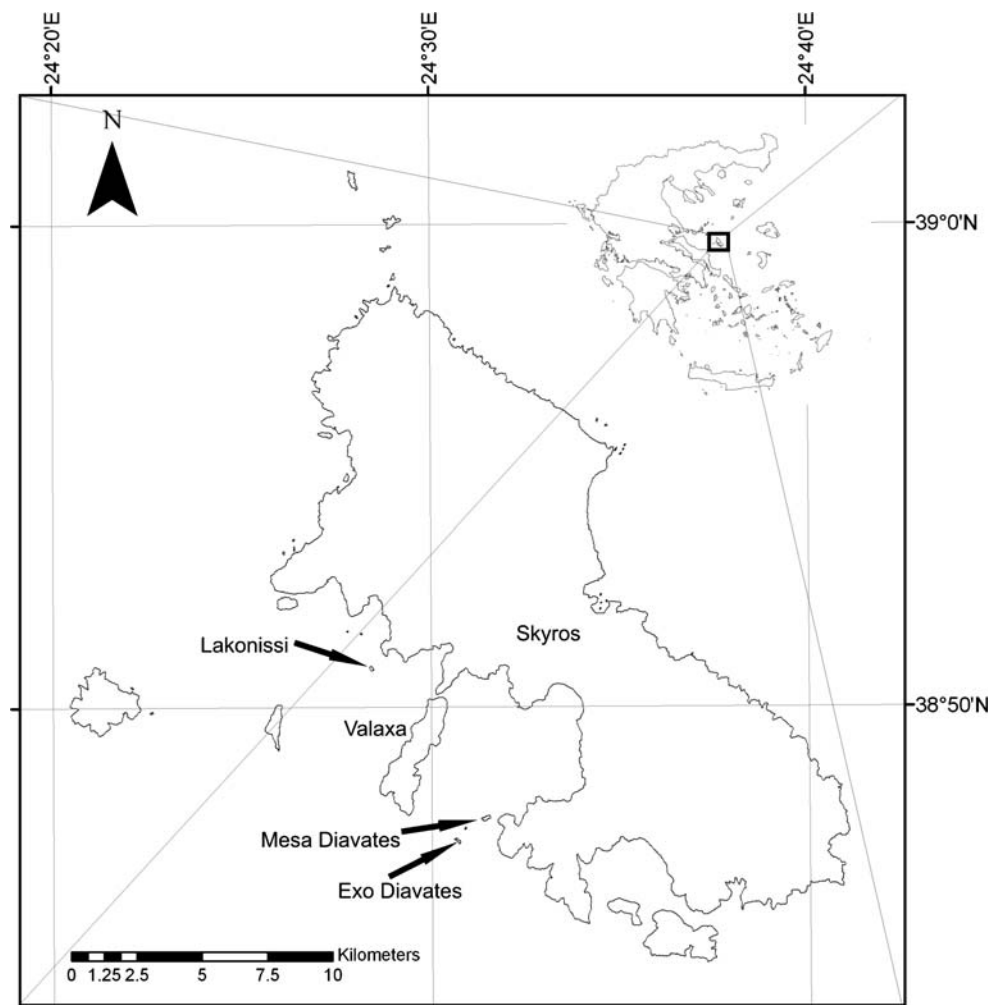
selection for increased body size, although (4) large size and cannibalism may be independently related to a third factor, e.g., increased seabird density and, hence, high food abundance. High resource availability, even in the absence of cannibalism, has also been shown to promote gigantism (Goltsman et al. 2005, Raia and Meiri 2006). While our results lend support to the importance of cannibalism and intraspecific competition, we cannot discount at this point the importance of direct effects of food abundance. A more detailed selection experiment conducted under controlled environmental conditions would be needed to further elucidate these relationships.

In predator-free islands, lizards occur in higher densities and tend to evolve large size to escape predation and intraspecific competition (Case 1978, Meiri 2008). We suggest that, in the Skyros Archipelago, seabird presence (and the respective increased food availability), population density, and cannibalism drive the evolution of larger body sizes. Thus, gull colonies allow the persistence of dense lizard populations in which intraspecific competition is strong. Juveniles evolve large body size to escape predation, but extra food is required (Stamps and Tanaka 1981). Some islands have resources unavailable on the mainland (Meiri 2007), and in Skyros, seabirds appear to provide the necessary energy.

References

Adamopoulou C, Pafilis P, Valakos E (1999) Diet composition of *Podarcis milensis*, *Podarcis gaigeae* and *Podarcis erhardii* (*Sauria: Lacertidae*) during summer. Bonn Zool Beitr 48:275–282

Anderson WB, Polis GA (1998) Marine subsidies of island communities in the Gulf of California: evidence from stable carbon and nitrogen isotopes. Oikos 81:75–80

Arnold EN (1988) Caudal autotomy as a defense. In: Gans C, Huey RB (eds) Biology of the reptilia 16, ecology B: defense and life history. Liss, New York, pp 235–273

Barrett K, Anderson WB, Wait AD, Grismer LL, Polis GA, Rose MD (2005) Marine subsidies alter the diet and abundance of insular and coastal lizard populations. Oikos 109:145–153

Boback SM (2003) Body size evolution in snakes: evidence from island populations. Copeia 2003:81–94

Bonnet X, Pearson D, Ladyman M, Lourdais O, Bradshaw D (2002) Heaven' for serpents? A mark–recapture study of tiger snakes (*Notechis scutatus*) on Carnac Island, Western Australia. Austral Ecol 27:442–450

Case TJ (1978) A general explanation for insular body size trends in terrestrial vertebrates. Ecology 59:1–18

Case TJ, Schwaner TD (1993) Island mainland body size differences in Australian varanid lizards. Oecologia 94:102–109

Castilla AM, Van Damme R (1996) Cannibalistic propensities in the lizard *Podarcis hispanica atrata*. Copeia 4:991–994

Cooper WE, Pérez-Mellado V, Vitt LJ (2004) Ease and effectiveness of costly autotomy vary with predation intensity among lizard populations. J Zool 262:243–255

Darlington RB, Smulders TV (2001) Problems with residual analysis. Anim Behav 62:599–602

Dayan T, Simberloff D (2005) Ecological and community-wide character displacement: the next generation. Ecol Lett 8:875–894

Elgar MA, Crespi BJ (1992) Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, Oxford

Freckleton RP (2002) On the misuse of residuals in ecology: regression of residuals versus multiple regression. J Anim Ecol 71:542–545

Garcia-Berthou E (2001) On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. J Anim Ecol 70:708–711

Goltsman ME, Kruchenkova P, Sergeev S, Volodin I, Macdonald DW (2005) "Island syndrome" in a population of Arctic foxes (*Alopex lagopus*) from Mednyi Island. J Zool 267:405–418

Gruber U (1986) *Podarcis erhardii* (Bedriaga, 1876) Ägäische Mauereidechse. In: Böhme W (ed) Handbuch der Reptilien und Amphibian Europas, Echsen 3. Aula, Wiesbaden, pp 25–49

Handrinos G, Akriotis T (1997) Birds of Greece. Helm and Black, London

Jaeger RG (1994) Transect sampling. In: Heyer WR, Donnelly MA, McDiarmin RW, Hayek LC, Foster MC (eds) Measuring and monitoring biological diversity. Smithsonian Institution Press, Washington, pp 103–107

Jennings WB, Thompson GG (1999) Territorial behavior in the Australian scincid lizard *Ctenotus fallens*. Herpetologica 55:352–361

Jenssen TA, Nunez SC (1998) Spatial and breeding relationships of the lizard, *Anolis carolinensis*: evidence of intra-sexual selection. Behavior 135:981–1003

Jenssen TA, Marcellini DL, Buhlmann KA, Goforth PH (1989) Differential infanticide by adult curly-tailed lizards, *Leiocephalus schreibersi*. Anim Behav 38:1054–1061

Lack D (1954) The natural regulation of animal numbers. Clarendon, Oxford

Langkilde T, Shine R (2007) Interspecific conflict in lizards: social dominance depends upon an individual's species not its body size. Austral Ecol 32:869–877

Le Galliard JF, Ferrière R, Clobert J (2005) Juvenile growth and survival under dietary restriction: are males and females equal? Oikos 111:368–376

Lomolino MV (2005) Body size evolution in insular vertebrates: generality of the island rule. J Biogeogr 32:1683–1699

Markwell TJ, Daugherty CH (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

Meiri S (2007) Size evolution in island lizards. Glob Ecol Biogeogr 16:702–708

Meiri S (2008) Evolution and ecology of lizard body sizes. Glob Ecol Biogeogr 17:724–724

Meiri S, Dayan T, Simberloff D (2004) Body size of insular carnivore: little support for the island rule. Am Nat 163:469–479

Meiri S, Dayan T, Simberloff D (2005) Area, isolation and body size evolution in insular carnivores. Ecol Lett 8:1211–1217

Melton RH (1982) Body size and island *Peromyscus*: a pattern and a hypothesis. Evol Theor 6:113–126

Olsson M, Wapstra E, Olofsson C (2002) Offspring size–number strategies: experimental manipulation of offspring size in a viviparous lizard (*Lacerta vivipara*). Funct Ecol 16:135–140

Pafilis P, Valakos ED, Foufopoulos J (2005) Comparative postautotomy tail activity in six Mediterranean lacertid species. Physiol Biochem Zool 78:828–838

Pafilis P, Pérez-Mellado V, Valakos ED (2008) Post autotomy tail activity in Balearic wall lizard, *Podarcis lilfordi*. Naturwissenschaften 95:217–221

Pafilis P, Foufopoulos J, Poulakakis N, Lymberakis P, Valakos ED (2009) Tail shedding in island lizards [Lacertidae, Reptilia]: Decline of antipredator defenses in relaxed predation environments. Evolution 63:1262–1278

Pérez-Mellado V, Corti C, LoCascio P (1997) Tail autotomy and extinction in Mediterranean lizards. A preliminary study of continental and insular populations. J Zool 243:553–541

Pianka ER (1970) Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. Ecology 51:703–720

Polis GA, Myers CA (1985) A survey of intraspecific predation among reptiles and amphibians. J Herpetol 19:99–107

Polis GA, Hurd SD (1996) Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am Nat 147:396–423

Raia P, Meiri S (2006) The island rule in large mammals: paleontology meets ecology. Evolution 60:1731–1742

Sadek RA (1981) The diet of the Madeiran lizard *Lacerta dugesii*. Zool J Linn Soc 73:313–341

Salvador A (1986) *Podarcis lilfordi* (Gunther, 1874)- Balearen-Eidechse. In: Boehme W (ed) Handbuch der Reptilien und Amphibien Europas 2, Echsen 3. Aula, Wiesbaden, pp 83–110

Sanchez-Piñero F, Polis GA (2000) Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. Ecology 81:3117–3132

Sinervo B (1993) The effect of offspring size on physiology and life history: Manipulation of size using allometric engineering. Bioscience 43:210–218

Sinervo B, Svensson E, Comendant T (2000) Density cycles and an offspring quantity and quality game driven by natural selection. Nature 406:985–988

Smith RJ (1999) Statistics of sexual size dimorphism. J Hum Evol 36:423–459

Sobey DG, Kenworthy JB (1979) The relationship between herring gulls and the vegetation of their breeding colonies. J Ecol 67:469–496

Sondaar PY (1977) Insularity and its effects on mammal evolution. In: Hecht MK, Goody PC, Hecht BM (eds) Major patterns of vertebrate evolution. Plenum, New York, pp 671–707

Stamps JA, Tanaka S (1981) The influence of food and water on growth rates in a tropical lizard (*Anolis aeneus*). Ecology 62:33–40

Turner FB, Medica PA, Jennrich RI, Maza BG (1982) Frequencies of broken tails among *Uta stansburiana* in southern Nevada and a test of the predation hypothesis. Copeia 1982:835–840

Valakos ED, Pafilis P, Sotiropoulos K, Lymberakis P, Maragou P, Foufopoulos J (2008) The amphibians and reptiles of Greece. Edition Chimaira, Frankfurt am Main

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

Wagner JD, Wise DH (1996) Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. Ecology 77:639–652

Wu Z, Li Y, Murray BR (2006) Insular shifts in body size of rice frogs in the Zhoushan Archipelago, China. J Anim Ecol 75:1071–1080