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ORIGINAL PAPER

Effects of insularity on digestion: living on islands induces shifts in physiological and morphological traits in island reptiles

Kostas Sagonas[1] · Panayiotis Pafilis[2] · Efstratios D. Valakos[1]

Abstract Living on islands entails numerous challenges for animals, among which resource scarcity stands out. In order to survive, animals have to optimize energy acquisition. We examined the impact of insularity on digestion comparing a series of physiological and morphological traits of adult males between insular and mainland populations of the Balkan green lizard. Island lizards had longer gastrointestinal tracts and gut passage times and higher digestive efficiencies. The dissection of the hindgut revealed an unexpected finding, the presence of cecal valves that were more frequent in island lizards. Thanks to all above islanders retain food for longer periods and thus maximize energy income and increase the amount of the extracted nutrients. That way, they secure energy income from the limited, in time and quantity, food resources of the islands.

Introduction

Island life is enabled by an impressive constellation of adaptations (Losos and Ricklefs 2009). The simplicity of insular

✉ Kostas Sagonas
ksagonas@biol.uoa.gr

[1] Department of Human and Animal Physiology, Faculty of Biology, University of Athens, Panepistimioupoli Zografou, 15784 Athens, Greece

[2] Department of Zoology and Marine Biology, Faculty of Biology, University of Athens, Panepistimioupoli Zografou, 15784 Athens, Greece

biocommunities and the restricted resources induce shifts in body size, life history, and behavior, but also erect challenges in terms of energy flow (Adler and Levins 1994; McNab 1994; Clegg and Owens 2002; Cooper et al. 2014). To overcome dietary limitations, island populations can expand their feeding preferences and/or maximize energy acquisition (Brown and Pérez-Mellado 1994; Van Damme 1999; Pafilis et al. 2007).

Digestion is the main physiological procedure determining energy balance. In general, the effective digestion of food, through nutrient absorption, regulates energy input to support bodily functions. It is a dynamic process that responds to changes in energy supply and demand (Karasov and Martinez Del Rio 2007). During low food abundance, appropriate shifts in digestive performance may enable survival (Bennett and Dawson 1976). Digestive efficiency and the structure and size of the gastrointestinal (GI) tract demonstrate high plasticity (Barton and Houston 1993; Naya et al. 2011). Reptiles in particular have been reported to adjust their digestive system following external or internal changes (Skoczylas 1978). They are apt to gut remodeling in response to food intake (Starck and Beese 2002), increase or decrease digestive efficiency depending on food quality and temperature (McKinon and Alexander 1999; Pafilis et al. 2007), and elongate or shorten the period food remains in the body according to temperature (Van Damme et al. 1991; Vervust et al. 2010). In some extreme cases, dietary shifts may even lead to new microstructures that improve digestive performance (Herrel et al. 2008).

Mediterranean islands are notorious for being arid, sparsely vegetated, and low in food availability (Fuentes 1984; Brown and Pérez-Mellado 1994). In response to this food scarcity, even lizards, known for their low metabolic rates, supplement their insectivorous diet with increasing portions of plant material (Pérez-Mellado and Corti 1993; Van Damme 1999; Carretero 2004). Previous

research demonstrated that this high consumption of plant material induced several physiological and morphological shifts in the digestive system so as to process and digest plant fibers (Pafilis et al. 2007; Herrel et al. 2008; Vervust et al. 2010). Hence, island lizards increase the GI tract length to retard food passage (Sokol 1967; Schluter 1984; but see Van Damme 1999), change structural and functional elements of the GI tract to increase the per se digestive performance (Sokol 1967; Pafilis et al. 2007; Vervust et al. 2010), and modify their feeding apparatus to generate powerful bites that improve the mechanical reduction of food (Herrel et al. 2008). Though these studies yielded valuable data, they suffered from innate problems: they either deal exclusively with insular population (thus lacking the comparison with mainland) or with different species (and hence, results might be altered by phylogeny).

In the present study, we seek to clarify how insularity affects digestion. To this end, we compared an array of crucial digestion parameters between mainland and island populations of a single lizard species (*Lacerta trilineata*) to minimize the effects of phylogenetic signal. A previous study revealed that the insular populations of *L. trilineata* have broadened their dietary spectrum and also consumed significantly more plant material (Sagonas et al. 2015). This dietary shift led to increased head dimensions and higher bite force (Sagonas et al. 2014), a common trend in omnivorous lacertid lizards to better exploit plant material (Herrel et al. 2004; but see Lopez-Darias et al. 2015). We expected that these changes in prey/food selection would affect digestion as well. In particular, we predicted that (i) island lizards would have longer GI tracts to retain the plant material food for longer periods and thus facilitate enzymatic hydrolysis and (ii) digestive efficiency for a given meal composition would be higher in the islands due to the (presumably) longer tracts of the islanders.

Material and methods

Study sites and species

The focal species was the Balkan green lizard (*L. trilineata*), a robust, terrestrial, mainly insectivorous lacertid lizard that occurs in the majority of habitats in the Balkans, including most Greek islands (Valakos et al. 2008). The study was conducted on two insular and two mainland populations: the islands of Andros (37° 51′ N, 24° 51′ E; Cyclades group) and Skyros (38° 54′ N, 24° 31′ E; Sporades group) in the Aegean Archipelago and Stymphalia Lake (37° 52′ N, 22° 28′ E; north Peloponnese) and Karditsa plateau (39° 22′ N, 21° 55′ E; Thessaly) in mainland Greece. The four biotopes share the

same vegetation type that comprises maquis and phrygana with many meadows (Sagonas et al. 2013). Seventy-four adult males were captured and transported to the animal facilities of the University of Athens (sample size, body size, and mass in Table 1) and were individually housed in glass terraria (80 cm×30 cm×40 cm) with sandy substrate and artificial shelters. The animals held at 30 °C (temperature that animals achieve in the field; Sagonas et al. 2013) under a controlled photoperiod provided by fluorescent bulbs (12 light/12 dark), while additional incandescent lamps (60 W) upon each terrarium allowed animals to thermoregulate behaviorally for 8 h/day. Lizards had access to water ad libitum and were fed every other day with mealworms (*Tenebrio molitor*). All lizards were collected in accordance with the Greek National Legislation (Presidential Decree 67/81). Prior to the experiment, lizards remained in the terraria for a 2-week period to acclimatize.

Gut passage time and gut morphology

Before the gut passage time (GPT, the rate with which food passes through the body), food was withheld from the animals for 4–5 days, until no feces were found in the terrarium. GPT was measured by estimating the time between consumption and defecation of a marked mealworm (Van Damme et al. 1991). Once a lizard consumed the marked mealworm, it was returned in its terrarium. Terraria were inspected every hour throughout day and night. The feces were collected and searched for the presence of the plastic marker.

A total of 28 lizards (7 from each population) were dissected upon chilled surface to investigate gut morphology. The length of the stomach, small intestine (sum of duodenum, jejunum, and ileum), and hindgut (sum of cecum and colon) were measured with a digital caliper (Vervust et al. 2010). The structure of the hindgut was examined under a dissecting microscope for the presence of cecal valves.

Apparent digestive efficiency

With the completion of GPT estimation, lizards returned to the normal feeding schedule for a 2-week period. After that, we evaluated apparent digestive efficiency (ADE, the relative percentage of ingested energy absorbed through the gut) (McConnachie and Alexander 2004). To estimate ADE, for proteins, lipids, and sugars, we employed the methodology proposed by Pafilis et al. (2007) and Vervust et al. (2010). Briefly, each lizard was fed with five mealworms every day during the experiment. Five identical mealworms (same size and mass of those that were fed to lizards) were stored at −80 °C for further analyses. Fecal material collected was frozen immediately in liquid nitrogen and stored as well at −80 °C. Before freezing, urate material from fecal samples was removed.

Table 1 Values of body size and digestive performance parameters examined (SVL, body weight, GPT, and ADE): means±standard deviation; sample size in parenthesis

Traits	Skyros Isl. (Sk)	Andros Isl. (A)	Karditsa (K)	Stymphalia (St)
SVL (cm)	13.75±2.13; (14)	12.73±1.54; (14)	12.73±1.51; (22)	12.15±1.88; (24)
Weight (g)	77.93±17.04; (14)	61.09±23.12; (14)	63.09±28.90; (22)	56.02±18.95; (24)
GPT (h)	85.71±6.43; (14)	82.36±7.00; (14)	70.55±5.42; (22)	68.12±4.62; (24)
ADE proteins (%)	80.50±6.06; (14)	82.57±8.72; (14)	69.33±6.28; (22)	70.66±6.02; (24)
ADE lipids (%)	77.74±4.62; (14)	79.48±4.18; (14)	66.25±10.89; (22)	69.64±8.30; (24)
ADE sugars (%)	76.52±7.58; (14)	75.59±6.89; (14)	65.40±7.01; (22)	63.08±6.16; (24)

Total lipids were determined in tissue samples (30–40 mg) that were homogenized with 1.5 ml of a 2:1 mixture of chloroform and absolute methanol. The homogenate was centrifuged at 3000 rpm for 10 min in 4 °C, the pellet formed was discarded, and the supernatant was used for the determination of lipid levels using a dilution of phosphovaniline against an olive oil and corn oil standard (2:1 v/v) (Alexis et al. 1985). Absorbance was read at 530 nm using a spectrophotometer (Novaspec II, Pharmacia Biotech).

Total proteins were estimated using the classical Biuret method (Layne 1957) compared to a standard of bovine serum albumin (0.5–10 mg/ml). The pellet obtained from the lipid analysis was dissolved with 0.5 ml of 0.1 N NaOH and incubated at 37 °C for 30 min, vortexed occasionally. We then took 50 μl and diluted them with 950 ml H_2O. This dilution was added to a volume of 4 ml of biuret reagent. The mixture was incubated for 30 min at room temperature, and then, the absorbance was read at 550 nm.

Total sugars were determined according to Dubois et al. (1956). Tissue samples (150 mg) were homogenized with H_2O at a 1:10 w/v ratio and then boiled for 30 min. We diluted 20 μl of this sample in H_2O (1:500 v/v) and incubated them with 1 ml phenol (5 % w/v) and 5 ml of 95 % H_2SO_4 for 10 min at room temperature and then for 40 min at 30 °C. The absorbance was read at 490 nm, and glucose content was estimated against a known glucose standard.

ADEs for lipids, proteins, and sugars were calculated according to the following equation:

$$ADE_x = \frac{100(I_x - E_x)}{I_x},$$

where I_x is the amount of the nutrient (x=proteins, lipids, or sugars) ingested and E_x is the amount of the nutrient (x=proteins, lipids, or sugars) remained in the fecal material after the enteric absorption was completed.

Statistical analyses

One-way analysis of variance (ANOVA) was used to compare snout-vent lenght (SVL), gut dimensions, ADE, and GPT among populations. This analysis was repeated taking into account the SVL of each individual. A multivariate analysis of covariance (MANCOVA) was also performed to investigate the effects of GPT on ADE. We performed an analysis of covariance (ANCOVA) in order to reduce the within-group error in GPT caused by SVL and the length of the GI tract. Variation in GI tract morphology was assessed through regression analysis with SVL on one side and GI tract length on the other. In all cases, Tukey honest significant difference (HSD) post hoc test was applied. We used principal component analysis (PCA) to investigate the interrelationships between ADE and GPT values.

Results

Body size and gut morphology

There were no differences in SVL and mass among the four populations (ANOVA; $F_{3,70}=2.39$, $P=0.076$) with the exception of the larger body mass of lizards from Skyros compared to Stymphalia (ANOVA; $F_{3,70}=2.77$, $P=0.048$; Table 1).

Island lizards had a longer small intestine and hindgut compared to their mainland counterparts (ANOVA; intestine: $F_{3,24}=8.74$, $P<0.001$; hindgut: $F_{3,24}=18.81$, $P<0.001$). The length of the stomach was longer only in the case of Skyros lizards (ANOVA; $F_{3,24}=6.51$, $P=0.002$). Due to the positive effect of body length on GI length ($r=0.38$, $F_{1,26}=4.46$, $P=0.044$), we repeated the aforementioned analysis using SVL as a covariate. When SVL was used as covariate, both insular populations showed significantly longer lengths for all three parts of the GI tract (ANCOVA; stomach: $F_{3,23}=6.95$, $P=0.002$; small intestine: $F_{3,23}=16.77$, $P<0.001$; hindgut: $F_{3,23}=17.33$, $P<0.001$; Fig. 1a).

The morphological analysis of the hindgut revealed an unusual microstructure, cecal valves (Fig. 2), never reported before for the genus *Lacerta*. Cecal valves were present in both mainland and island lizards though they were much more common in insular populations (19 vs 62 %; $\chi^2=38.36$, $P<0.001$).

Fig. 1 **a** MANCOVA results for digestive biometric traits (stomach, intestine, and hindgut lengths) log$_{10}$-transformed with SVL as covariate, **b** GPT variation with SVL as covariate, **c** GPT variation with GI tract length as covariate. *Points* represent the means and *bars* the standard error. **d** Relationships between GI tract length and SVL log$_{10}$-transformed. *Open triangle and dashed black*, Skyros ($y=0.63+0.56x$); *filled black circles and black line*, Andros ($y=0.64+0.57x$); *open gray squares and gray line*, Karditsa ($y=0.75+0.28x$); *filled gray diamonds and dashed gray line*, Stymphalia ($y=1.06+0.11x$)
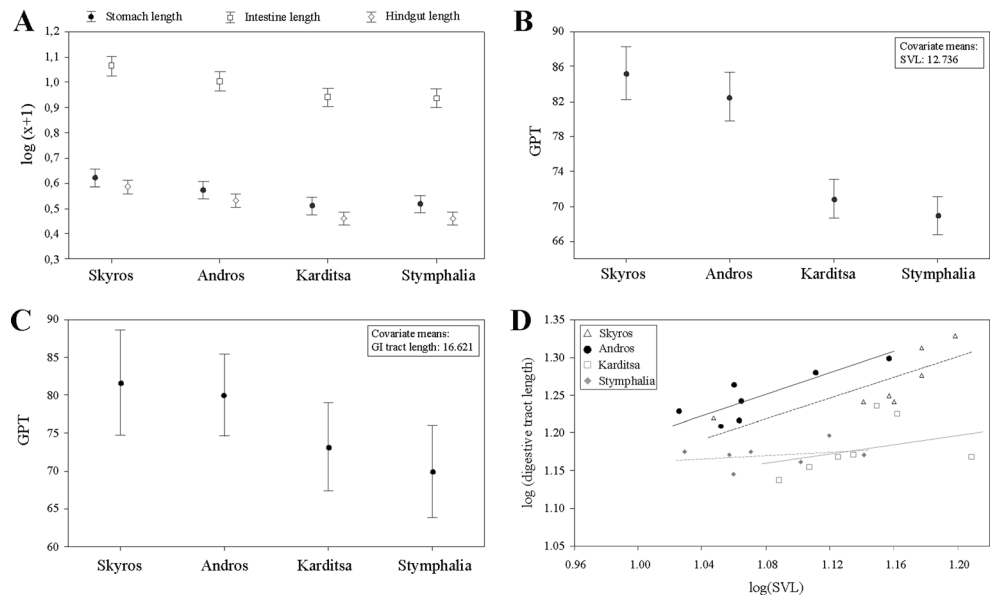
Gut passage time

GPTs differed considerably among the four populations (ANOVA; $F_{3,70}=40.23$, $P<0.001$). The post hoc Tukey HSD test formed two groups: one comprising the islanders that have higher GPT and one with the mainland lizards (84 vs 69 h, respectively; Table 1, Fig. 1b). When SVL and GI tract length were taken into account, the differences remained (ANCOVA; SVL: $F_{3,69}=35.84$, $P<0.001$; GI: $F_{3,23}=1.68$, $P=0.198$; Fig. 1b, c, respectively).

Regression analyses between the GI tract length and SVL revealed a positive correlation in all populations ($P<0.05$; Fig. 1d). No differences were obtained between mainland or between island populations (islands: $t=1.35$, $df=10$, $P=0.207$ and mainland: $t=1.71$, $df=10$, $P=0.118$). The comparison of the four regression coefficients across populations yielded significant differences, with islanders having higher coefficient than mainland lizards (all

pairwise comparisons between island and mainland populations, $P<0.05$; Fig. 1d).

Apparent digestive efficiency

Island lizards achieved higher ADEs than the mainland ones (MANOVA; Wilks lambda$=0.308$, $F_{9,165.64}=11.46$, $P<0.001$; Table 1) for all three types of nutrients (ANOVA; proteins: $F_{3,70}=17.57$, $P=0.001$; carbohydrates: $F_{3,70}=17.96$, $P<0.001$; lipids: $F_{3,70}=10.73$, $P<0.001$). When GPT was used as covariate, the differences persisted (ANCOVA; proteins: $F_{3,69}=12.16$, $P<0.001$; carbohydrates: $F_{3,69}=3.41$, $P=0.022$; lipids: $F_{3,69}=4.49$, $P=0.006$).

Principal component analysis

PCA, taking into account ADEs and GPT, yielded two main axes that together can explain 75.89 % of the variation in the dataset (Table 2a). GPT loaded strongly on the first principal

Fig. 2 Digestive tract and the cecal valves in the hindgut of *L. trilineata*

cecal valve
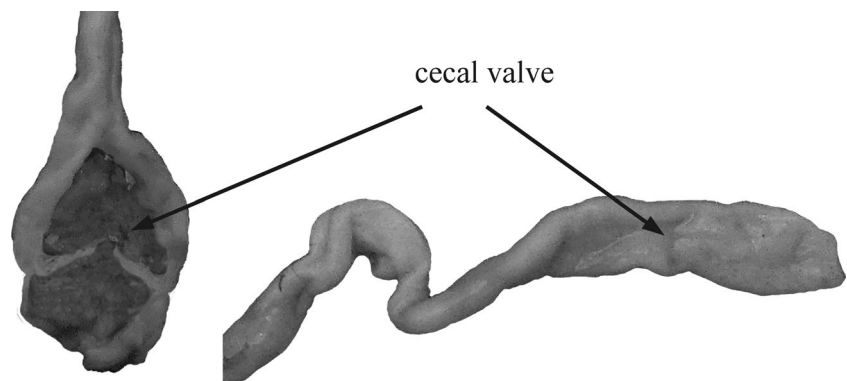
component (PC1), while ADE_LIPIDS comprised the second component (Table 2b). In the corresponding plot (Fig. 3), islanders separated from their mainland counterparts along PC1, while insular and mainland populations got isolated along the PC2.

Discussion

Insularity is a powerful driver of evolution, inducing changes in behavior, physiology, and morphology (Raia and Meiri 2006; Raia et al. 2010; Monti et al. 2013; Li et al. 2014). Digestion represents no exception: the omnivorous islanders had longer GI tracts, demonstrated slower food passage time, and achieved higher ADEs compared to their mainland conspecifics.

Though no differences in body size arose between island and mainland lizards, the GI tract of the islanders was longer (approximately 23 %). Apparently, island lizards increased the ratio between the GI tract length and SVL (Fig. 1d) and thus delayed food and kept it for longer periods inside their body. In that way, they provide longer exposure of ingesta to digestive enzymes, a common strategy among plant-eating lizards that elongate their intestine to prolong food passage (Dearing 1993; Herrel et al. 2004).

The examination of the hindgut revealed an unexpected finding: the presence of cecal valves, a structure previously unknown from green lizards (genus *Lacerta*). Such morphological structures are found in herbivorous lizards and serve as fermenting chambers that host commensal microorganisms, which break down cellulose (Iverson 1982). However, they have been only rarely reported from insectivorous species and even then they refer to populations that shift to omnivory (Herrel et al. 2008). Cecal valves were present in mainland populations as well, though in significant fewer individuals. The higher consumption of plant material by island lizards (30 vs 10 % for mainland) is reflected to the higher frequency of cecal valves in insular populations (62 vs 19 %).

A longer digestive tract and the presence of cecal valves slow down the pace of food passage (van Marken Lichtenbelt 1992; Herrel et al. 2004). Indeed, island lizards exhibited approximately 17–26 % longer GPTs (Table 1). Slow food passage rates offer extra time to digestive enzymes to process digestion and maximize energy absorption (McConnachie and Alexander 2004). In plant-eating lizards, long GPTs compromise for the low-quality food and guarantee the effective digestion of plant material (Zimmerman and Tracy 1989; Bjorndal 1997). The same pattern was observed in the lacertid *Podarcis siculus* from the islet Pod Mrčaru (Croatia) where a dramatic shift to herbivory (61 % during summer) triggered the development of cecal valves that subsequently led to prolonged GPTs (Herrel et al. 2008; Vervust et al. 2010). Hence, island green lizards (that eat more plant material) benefit from their longer GI tract. A complementary advantage for this GI tract elongation could be the potential to digest more efficiently feeding resources that are also common in mainland.

Digestive efficiency depends largely on GPT (Skoczylas 1978; Beaupre et al. 1993). Indeed, in our study, the higher GPTs of the insular populations had a favorable effect on ADE values that were higher for all nutrients compared to those of their mainland conspecifics (Table 1). The prolonged period that digesta remained in the GI tract fostered the ability of islanders to extract nutrients from their food. Furthermore, symbiotic microorganisms, which are hosted in the cecal valves, use the extra time to break down plant material and convert it to volatile fat acids (Herrel et al. 2008).

Several morphological traits may be evolved in particular environments and are functionally adapted to those environments (Herrel 2007; da Silva et al. 2014). Food scarcity, typical of Mediterranean islands, promotes evolutionary shifts
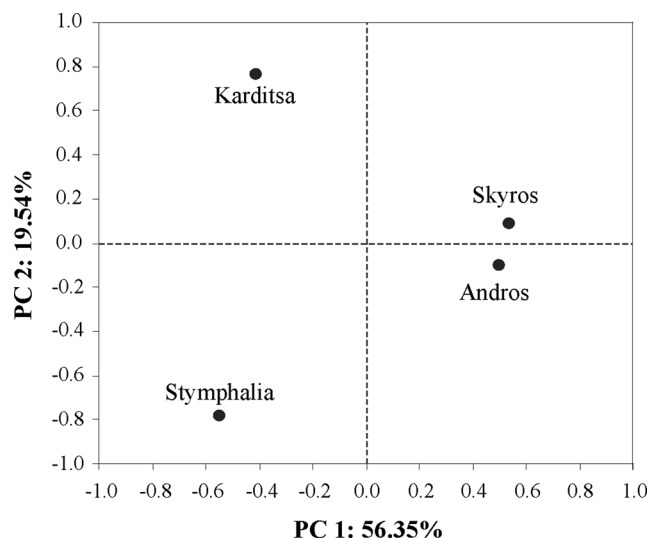
Table 2 PCA of GPT and ADE values

A.	Component	Eigenvalues	% Variance	Cumulative %
	1	2.254	56.354	56.354
	2	0.781	19.535	75.889
	3	0.622	15.561	91.450
	4	0.341	8.549	100.000
B.		PC1	PC2	PC3
	GPT	**−0.836**	−0.201	0.307
	ADE_PROTEINS	−0.723	0.166	**−0.665**
	ADE_LIPIDS	−0.655	**0.675**	0.289
	ADE_SUGARS	−0.777	0.508	0.045

Variables loading strongly on each principal component are given in bold

Fig. 3 Scatter plot illustrating the results of PCA taking into account ADEs and GPTs

and anatomical changes in the digestive system of insular lizards (Carretero 1997; Pafilis et al. 2007; Herrel et al. 2008; Vervust et al. 2010). Island male *L. trilineata* populations did extend their GPTs by elongating the GI tract and developing cecal valves. Thereby, they processed food significantly slower and achieved higher ADEs. Such adaptations allow insular populations to take advantage of the limited (in quantity and time) food resources of the islands and, eventually, overcome food dearth. Energy flow in insular environments, the digestive performance of insular populations, and the connections within them are key elements to understand the ability of animals to colonize islands and maintain viable populations.

References

Adler GH, Levins R (1994) The island syndrome in rodent populations. Q Rev Biol 69:473–490

Alexis MN, Papaparaskeva-Papoutsoglou E, Theochari V (1985) Formulation of practical diets for rainbow trout (*Salmo gairdneri*) made by partial or complete substitution of fish meal by poultry by-products and certain plant by-products. Aquaculture 50:61–73

Barton NWH, Houston DC (1993) A comparison of digestive efficiency in birds of prey. Ibis 135(4):363–371

Beaupre SJ, Dunham AE, Overall KL (1993) The effects of consumption rate and temperature on apparent digestibility coefficient, urate production, metabolizable energy coefficient and passage time in canyon lizards (*Sceleporus merriami*) from two populations. Funct Ecol 7:273–280

Bennett AF, Dawson WR (1976) Metabolism. In: Gans C, Dawson WR (eds) Biology of the Reptilia. Academic, London and New York, pp 127–223

Bjorndal K (1997) Fermentation in reptiles and amphibians. In: Mackie R, White B (eds) Gastrointestinal microbiology. (Chapman & Hall Microbiology Series) Chapman & Hall, New York, pp 199–230

Brown RP, Pérez-Mellado V (1994) Ecological energetics and food acquisition in dense menorcan islet population of the lizard *Podarcis lilfordi*. Funct Ecol 8(4):427–434

Carretero MA (1997) Digestive size and diet in Lacertidae: a preliminary analysis. In: Böhme W, Bischoff W, Zeigler T (eds) Herpetologia Bonnensis. S.E.H, Bonn, pp 43–49

Carretero MA (2004) From set menu to à la carte. Linking issues in trophic ecology of Mediterranean lacertids. Ital J Zool 2:121–133

Clegg SM, Owens IPF (2002) The 'island rule' in birds: medium body size and its ecological explanation. Proc R Soc Lond B 269(1498):1359–1365

Cooper WE, Pyron RA, Garland T (2014) Island tameness: living on islands reduces flight initiation distance. Proc R Soc Lond B 281(1777):20133019

da Silva JM, Herrel A, Measey GJ, Vanhooydonck B, Tolley KA (2014) Linking microhabitat structure, morphology and locomotor performance traits in a recent radiation of dwarf chameleons. Funct Ecol 28(3):702–713

Dearing MD (1993) An alimentary specialization for herbivory in the tropical whiptail lizard *Cnemidophorus murinus*. J Herpetol 27(1):111–114

Dubois M, Gilles KA, Hamilton JK, Rebers BA, Smith F (1956) Colorimetric method for determination of sugars and related substances. Anal Chem 28:350–356

Fuentes JA (1984) Evolution of lizard niches in Mediterranean habitats. In: Di Castri F, Goodall DW, Specht R (eds) Mediterranean type shrublands: ecosystems of the world, vol 11. Elsevier Science Publishing Co, Amsterdam, pp 417–444

Herrel A (2007) Herbivory and foraging mode in lizards. In: Reilly SM, McBrayer LD, Miles DB (eds) Lizard ecology: the evolutionary consequences of foraging mode. Cambridge University Press, Cambridge, pp 209–236

Herrel A, Huyghe K, Vanhooydonck B, Backeljau T, Breugelmans K, Grbac I, Van Damme R, Irschick DJ (2008) Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. Proc Natl Acad Sci 105(12):4792–4795

Herrel A, Vanhooydonck B, Van Damme R (2004) Omnivory in lacertid lizards: adaptive evolution or constraint? J Evol Biol 17(5):974–984

Iverson JB (1982) Adaptations to herbivory in iguanine lizards. In: Burghardt GM, Rand AS (eds) Iguanas of the world: their behavior, ecology and conservation. Noyes, Park Ridge, pp 60–76

Karasov WH, Martinez Del Rio C (2007) Physiological ecology: how animals process energy, nutrients, and toxins. Princeton University Press, New Jersey

Layne E (1957) Spectrophotometric and turbidimetric methods for measuring proteins. Methods Enzymol 10:447–455

Li B, Belasen A, Pafilis P, Bednekoff P, Foufopoulos J (2014) Effects of feral cats on the evolution of anti-predator behaviours in island reptiles: insights from an ancient introduction. Proc R Soc Lond B 281(1788)

Lopez-Darias M, Vanhooydonck B, Cornette R, Herrel A (2015) Sex-specific differences in ecomorphological relationships in lizards of the genus *Gallotia*. Funct Ecol 29(4):506–514

Losos JB, Ricklefs RE (2009) Adaptation and diversification on islands. Nature 457(7231):830–836

McConnachie S, Alexander GJ (2004) The effect of temperature on digestive and assimilation efficiency, gut passage time and appetite in an ambush foraging lizard, *Cordylus melanotus melanotus*. J Comp Physiol B 174(2):99–105

McKinon W, Alexander GJ (1999) Is temperature independence of digestive efficiency an experimental artefact in lizards? A test using the common flat lizard (*Platysuarus intermedius*). Copeia 1999:299–303

McNab BK (1994) Energy conservation and the evolution of flightlessness in birds. Am Nat 144(4):628–642

Monti DM, Raia P, Vroonen J, Maselli V, Van Damme R, Fulgione D (2013) Physiological change in an insular lizard population confirms the reversed island syndrome. Biol J Linn Soc 108(1):144–150

Naya DE, Veloso C, Sabat P, Božinović F (2011) Physiological flexibility and climate change: the case of digestive function regulation in lizards. Comp Biochem Physiol A Mol Integr Physiol 159(1):100–104

Pafilis P, Foufopoulos J, Poulakakis N, Lymberakis P, Valakos E (2007) Digestive performance in five Mediterranean lizard species: effects of temperature and insularity. J Comp Physiol B 177(1):49–60

Pérez-Mellado V, Corti C (1993) Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). Bonn Zool Bull 44(3/4):193–220

Raia P, Guarino F, Turano M, Polese G, Rippa D, Carotenuto F, Monti D, Cardi M, Fulgione D (2010) The blue lizard spandrel and the island syndrome. BMC Evol Biol 10(1):289

Raia P, Meiri S (2006) The island rule in large mammals: paleontology meets ecology. Evolution 60(8):1731–1742

Sagonas K, Pafilis P, Lymberakis P, Donihue CM, Herrel A, Valakos ED (2014) Insularity affects head morphology, bite force and diet in a Mediterranean lizard. Biol J Linn Soc 112:469–484

Sagonas K, Pafilis P, Lymberakis P, Valakos ED (2015) Trends and patterns in the feeding ecology of the widespread Balkan lizard *Lacerta*

trilineata (Squamata: Lacertidae) in insular and continental Greece. North-West J Zool 11(1):117–126

Sagonas K, Valakos ED, Pafilis P (2013) The impact of insularity on the thermoregulation of a Mediterranean lizard. J Therm Biol 38(8): 480–486

Schluter D (1984) Body size, prey size and herbivory in the Galápagos lava lizard *Tropidurus*. Oikos 43:291–300

Skoczylas R (1978) Physiology of the digestive tract. In: Gans C, Tinkle DW (eds) Biology of the Reptilia. Academic, London, pp 589–717

Sokol OM (1967) Herbivory in lizards. Evolution 21:192–194

Starck JM, Beese K (2002) Structural flexibility of the small intestine and liver of garter snakes in response to feeding and fasting. J Exp Biol 205(10):1377–1388

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

Van Damme R (1999) Evolution of herbivory in lacertid lizards: effects of insularity and body size. J Herpetol 33:663–674

Van Damme R, Bauwens D, Verheyen RF (1991) The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. Funct Ecol 5(4): 507–517

van Marken Lichtenbelt WD (1992) Digestion in an ectothermic herbivore, the green Iguana (*Iguana iguana*): effect of food composition and body temperature. Physiol Zool 65(3):649–673

Vervust B, Pafilis P, Valakos ED, Van Damme R (2010) Anatomical and physiological changes associated with a recent dietary shift in the lizard *Podarcis sicula*. Physiol Biochem Zool 83(4):632–642

Zimmerman LC, Tracy RC (1989) Interactions between the environment and ectothermy and herbivory in reptiles. Physiol Zool 62(2):374–409