

Anatomical and Physiological Changes Associated with a Recent Dietary Shift in the Lizard *Podarcis sicula*

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ABSTRACT

Dietary shifts have played a major role in the evolution of many vertebrates. The idea that the evolution of herbivory is physiologically constrained in squamates is challenged by a number of observations that suggest that at least some lizards can overcome the putative physiological difficulties of herbivory on evolutionary and even ecological timescales. We compared a number of morphological and physiological traits purportedly associated with plant consumption between two island populations of the lacertid lizard *Podarcis sicula*. Previous studies revealed considerable differences in the amount of plant material consumed between those populations. We continued the investigation of this study system and explored the degree of divergence in morphology (dentition, gut morphology), digestive performance (gut passage time, digestive efficiency), and ecology (endosymbiont density). In addition, we also performed a preliminary analysis of the plasticity of some of these modifications. Our results confirm and expand earlier findings concerning divergence in the morphology of feeding structures between two island populations of *P. sicula* lizards. In addition to the differences in skull dimensions and the prevalence of cecal valves previously reported, these two recently diverged populations also differ in aspects of their dentition (teeth width) and the lengths of the stomach and small intestine. The plasticity experiment suggests that at least

some of the changes associated with a dietary shift toward a higher proportion of plant material may be plastic. Our results also show that these morphological changes effectively translate into differences in digestive performance: the population with the longer digestive tract exhibits longer gut passage time and improved digestive efficiency.

Introduction

Dietary shifts have played a major role in the evolution of many vertebrates (e.g., Grant 1986; Hunter and Jernvall 1995; Albertson et al. 1999; Kaplan et al. 2000; Vitt et al. 2003). However, the rate at which such shifts have appeared seems to vary considerably among taxa. For example, while herbivory has evolved repeatedly in many vertebrate groups, it is rare among squamate reptiles, where less than 2% of all species habitually consume plant material (King 1996; Cooper and Vitt 2002; Espinoza et al. 2004). The paucity of herbivorous reptiles has traditionally been explained by the demands imposed by herbivory. Adaptations associated with plant consumption mostly relate to the problem of having to break down the cellulose, hemicellulose, and lignin in the plant cell wall. These adaptations include modifications of the craniocervical apparatus that improve the mechanical reduction of food, such as the development of powerful jaw muscles and dental grinding systems (Herrel et al. 1998, 1999, 2008), and changes in the digestive system that increase processing efficiency, such as lengthening and compartmentalization of the hind gut and the presence of symbiotic microorganisms. Until fairly recently, many researchers believed that the requirements of large bodies (to support voluminous guts) and high body temperatures (necessary for microbial fermentation) precluded many squamate lineages from evolving a herbivorous life style (e.g., Pough 1973; Zimmerman and Tracy 1989; King 1996).

The idea that the evolution of herbivory is physiologically constrained in squamates is, however, challenged by a number of observations. First, in some lizard lineages, herbivory did evolve, sometimes repeatedly, despite small body sizes and low body temperatures (Van Damme 1999; Espinoza et al. 2004; Evans and Manabe 2008; Takahashi 2008). Second, there is evidence that evolutionary changes in diet and trophic morphology can occur rapidly (Espinoza et al. 2004), even within ecological timescales (Herrel et al. 2008). Finally, although strict herbivory (where plants constitute more than 90% of the dietary volume) is rare among lizards, omnivory (diet consisting of 10%–90% plant material) is much more widespread than previously thought; half of the lizard species for which volumetric data are

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available eat plants (Cooper and Vitt 2002). Several species show ontogenetic changes in diet, with adults typically consuming larger quantities of plant material than hatchlings (e.g., Nagy and Shoemaker 1984; Duffield and Bull 1998; Rocha 1998; Durtsche 2000). Omnivorous lizards have also been reported to change diets according to seasonal variation in food availability (Durtsche 1995; Duffield and Bull 1998; Greeff and Whiting 2000). These observations suggest that at least some lizards can overcome the putative physiological difficulties of herbivory on evolutionary and even ecological timescales. Clearly, we must learn more about the phenotypic modifications permitting plant consumption and the amount of time required to develop them.

In this article, we compare a number of morphological and physiological traits purportedly associated with plant consumption between two island populations of the lacertid lizard *Podarcis sicula*. One population consists of the descendants of a small founder population experimentally introduced onto the island Pod Mrčaru in 1971 (Nevo et al. 1972). The other population holds the progeny of the source population for this transplantation and lives on the nearby island Pod Kopište. Herrel et al. (2008) compared the diet, head size, bite force, gut morphology, and prevalence of nematodes in the hindgut between the two populations. Stomachs of lizards on Pod Mrčaru contained a considerably greater proportion of plant material (spring: 34% dietary volume; summer: 60%) than those of lizards on Pod Kopište (spring: 7%; summer: 4%). Head dimensions and bite forces were significantly higher in the Pod Mrčaru lizards, which probably helps them to tear up tough plant material. In all individuals examined from Pod Mrčaru, cecal valves were present in the hindgut. Cecal valves are thought to slow down food passage and to provide fermenting chambers, allowing commensal microorganisms to convert cellulose to volatile fatty acids (McBee 1971; Troyer 1984). In accordance, nematodes were present in the guts of Pod Mrčaru lizards but absent in those of Pod Kopište lizards (Herrel et al. 2008).

Here, we continue the investigation of this study system and explore the degree of divergence in morphology (dentition, gut morphology), digestive performance (gut passage time, digestive efficiency), and ecology (endosymbiont density). We predicted that plant-eating lizards from Pod Mrčaru would have teeth that are more typical of herbivorous lizards (three-cusp or polycuspid teeth; Mateo and Lopez-Jurado 1992; Valido and Nogales 2003; Herrel et al. 2004, 2008), longer and heavier intestinal tracts with cecal valves, larger populations of endosymbionts, longer gut passage times, and higher apparent digestion efficiencies than Pod Kopište lizards. In addition, we also performed a preliminary analysis of the plasticity of some of these modifications. By examining individuals from Pod Mrčaru after they had been fed an exclusively arthropod diet, we sought to test whether the changes in gut morphology are reversible (and hence, plastic).

Material and Methods

Study System and Laboratory Conditions

The Italian wall lizard *Podarcis sicula* is a robust, ground-dwelling, heliothermic, actively foraging lacertid lizard (adult snout-

to-vent length [SVL], 55–70 mm) that occupies a variety of semiopen habitats in the Mediterranean. While most populations of *P. sicula* feed predominantly on arthropod prey (review in Henle and Klaver 1986), others (most notably, island populations) also consume considerable amounts of plant material (Radovanovic 1959; Ouboter 1981; Henle 1984; Herrel et al. 2008). Detailed information on the general biology of this species can be found in Henle and Klaver (1986).

The islets of Pod Mrčaru (surface area, 0.3 km²; 42°46'N, 16°46'E) and Pod Kopište (surface area, 0.9 km²; 42°45'N, 16°43'E), which are home to our study populations, are situated 4.5 km apart in the Adriatic Sea, northwest of the larger island of Lastovo. The islands resemble each other in general aspects but differ in the abundance and diversity of their vegetation (see Vervust et al. 2007, 2009 for more details on the islets and the history of their populations). Lizards on Pod Mrčaru eat substantially more plant material than do those on Pod Kopište (see above and Herrel et al. 2008).

Initial comparisons between the two populations were conducted in April 2008, immediately following capture, in a field laboratory on the nearby island of Lastovo. A subset of individuals from Pod Mrčaru was transported to our laboratory in Antwerp. There they were housed in terraria (150 cm × 50 cm × 50 cm) with a sandy substrate and a number of small rocks under which the lizards could hide. A 100-W lightbulb suspended above one end of the terrarium provided light (12L : 12D) and heat so that lizards could maintain a body temperature within their preferred range. The lizards were fed vitamin-dusted arthropods (mealworms *Tenebrio molitor* and crickets *Acheta domestica*) ad lib. and had access to freshwater at all times. After being fed for 15 wk on this exclusively insect diet, we examined the gut morphology of 20 individuals.

Gut Passage Time

Gut passage time was estimated using animals imported from the islands (export permit UP/I-612-07/08-33/0049 issued by the Croatian Ministry of Culture). Gut passage time was estimated by force-feeding lizards with mealworms labeled with a small (3 mm × 2 mm × 0.1 mm) plastic tag (Van Damme et al. 1991; Pafilis et al. 2007). Once the mealworm was swallowed, lizards were kept individually in plastic containers (30 cm × 23 cm × 22 cm) and provided with a hiding place. Before the experiment, lizards received crickets and mealworms daily. During the experiment, lizards were fed mealworms only. Freshwater was continuously available. A few individuals that refused to eat were force-fed one mealworm per day to assure that all experienced the same pressure of incoming food on the material present in the gastrointestinal system (Harlow et al. 1976; Harwood 1979). The containers were kept in a room with 12L : 12D regime and an air temperature that ranged between 28° and 32°C. Containers with lizards from the two populations were randomized with respect to their relative positioning in the room. The containers were inspected for feces every 2 h. All excrements were collected and examined for the presence of the plastic tags. The time

elapsed between the swallowing of the tag and its appearance in the feces was taken as the gut passage time.

Apparent Digestive Efficiency

Apparent digestive efficiency was measured in freshly caught adult individuals that had been held in the field lab on Lastovo for 1 wk before the start of the experiment. Methodology used to estimate digestive efficiency follows Pafilis et al. (2007). Adult lizards were kept in groups of five in large (150 cm × 50 cm × 50 cm) containers provided with shelters and dishes with drinking water. Only lizards of the same sex and from the same population were put together. The containers were placed randomly in a room with the same L : D and temperature regimes as described above. To ensure daily feeding, each lizard was force-fed a mealworm every day of the experiment. This precaution was taken to assure that food pressure was similar in all individuals, because gastric residence time is known to affect digestive efficiency (Harlow et al. 1976). After a period of 4 d (which would allow the evacuation of any material present in the gut before the experiment), all excrements were removed. From then on, the containers were inspected every 2 h, and all fecal material was collected and stored immediately at -80°C in a container cooled by liquid nitrogen.

The frozen feces were transported to the lab in Athens for examination. Before the biochemical content analysis was performed, urate material was removed from each feces sample. The total amounts of lipids, carbohydrates, and proteins in the excrements were determined using protocols described in Pafilis et al. (2007) and compared with the amounts present in mealworms. Apparent digestive efficiency (ADE) for lipids, carbohydrates, and proteins were computed according to the following equation:

$$\text{ADE}_x = \frac{100(I_x - E_x)}{I_x},$$

where I_x is the amount (x = lipids, carbohydrates, or proteins) ingested and E_x is the amount (lipids, carbohydrates, or proteins) remaining in the fecal material after enteric absorption was completed. This measure is denoted “apparent” digestive efficiency (sensu Throckmorton 1973) because feces may contain gastrointestinal secretions, tissue abraded from the gut lining, and other material that is not undigested food. The analyses were performed on 10 samples (five from males, five from females) from Pod Kopašte and 30 samples (10 from males, 20 from females) from Pod Mrčaru.

Gut Morphology

A total of 38 museum-curated lizards (14 from Pod Mrčaru and 24 from Pod Kopašte) were dissected, and their intestinal tracts were removed, from the posterior point of the esophagus to the most posterior end of the rectum. Lengths of the stomach, small intestine (sum of duodenum, jejunum, and ileum), and hindgut (sum of cecum and colon) were measured using

electronic calipers (Mitutoyo, CD-15CPX, precision = 0.01 mm), taking care that all elements were uncoiled but not stretched. Each segment was measured three times consecutively, and the average of the three measurements was used in the statistical analyses. The segments were emptied, separated from mesenteries, and weighed on an electronic balance (Mettler Toledo, MT5, precision = 1 g). The hindguts were opened, and the presence and number of cecal valves was recorded.

The same measurements and observations on gut morphology were carried out on eight males and 12 females of the Pod Mrčaru population after they had been fed an exclusively arthropod diet for 15 wk. These 20 lizards had died of oxygen deficiency following a power cut in the animal house at Antwerp University. None of the animals were killed for the purpose of this study.

Dentition

We examined tooth characteristics in a subset of 12 specimens (six males and six females). The skulls were cleaned following procedures outlined by Panakakoski and Hanski (1989). The heads were skinned, detached from the bodies, and boiled for 5 min in water. They were then put in containers with a papain solution (60 mg papain in 100 mL of 0.9% NaCl solution) and kept there for 3 d at a temperature of 38°C . The containers were shaken gently once per day. The cleaned skulls were washed in water and allowed to dry on blotting paper. Digital photographs of the lateral and dorsal aspects of the teeth were taken using a Nikon D70 camera fitted with a 50-mm micro Nikkor lens. The numbers of teeth were counted from the left dentary bone only. Tooth shape was quantified for the three most posterior teeth, starting above the most posterior of the multiple fenestra on the beginning of the dentary bone, using the tspDig software (ver. 1.40; James F. Rohlf, <http://life.bio.sunysb.edu/morph/>). For each tooth, the following variables were measured: tooth height perpendicular to the jaw, tooth width halfway down the tooth, and the number of cusps (see Herrel et al. 2004). The values for the three measured teeth per individual were averaged, and these averages were used as input for statistical analyses.

Nematode Populations

The feces of 279 (160 from Pod Kopašte, 119 from Pod Mrčaru) wild-caught individuals were crushed. They were then visually examined for the prevalence of nematodes.

Statistical Analyses

All metric variables were \log_{10} transformed, and apparent digestive efficiencies (%) were arcsine transformed before testing. The transformed variables fulfilled the assumptions of (multivariate) normality and heteroscedascity. We used ANOVA to compare means among populations and sexes. SVL (\log_{10} transformed) was entered as a covariate in all analyses examining variation in gut dimensions; length of the dentary bone was used as a covariate when comparing tooth dimensions. In all analyses, we

started with a full factorial model and then progressively removed nonsignificant (interaction) effects. The F values reported refer to the simplest model containing the factor in question. Where more than one variable was measured in the same individual, we first conducted a multivariate analysis examining overall differences between populations or sexes. Subsequently, we performed “protected” univariate tests on the individual variables to locate the origins of any differences. The effects of population, sex, and season on endosymbiont prevalence were estimated using a generalized linear model with a binomial distribution.

Results

Gut Passage Time

The indigestible markers remained considerably (ca. 30%) longer in the digestive tracts of Pod Mrčaru lizards than in those of Pod Kopašte lizards (Table 1; population effect: $F_{1,83} = 11.4$, $P = 0.001$). Pod Mrčaru males had lower gut passage times than did females from the same population, while on Pod Kopašte the reverse was the case (Table 1). This resulted in a significant sex \times population effect ($F_{1,83} = 6.68$, $P = 0.011$).

ADE

ADEs were significantly higher in Pod Mrčaru lizards than in Pod Kopašte lizards (MANOVA; population effect: $F_{3,34} = 123.33$, $P < 0.001$). This proved to be the case for all three types of nutrients investigated (ANOVA; carbohydrates: $F_{1,36} = 197.17$, $P < 0.0001$; proteins: $F_{1,36} = 81.73$, $P < 0.0001$; lipids: $F_{1,36} = 4.82$, $P = 0.035$). Pod Mrčaru lizards had considerably higher digestion efficiencies (Table 1; Fig. 1). The difference in efficiency was highest between the females of both populations; whereas males from Pod Kopašte performed better, the reverse was the case on Pod Mrčaru. This produced a significant sex \times population effect for all three efficiency indexes (Fig. 1; carbohydrates: $F_{1,36} = 16.92$, $P < 0.001$; proteins: $F_{1,36} = 4.87$, $P = 0.034$; lipids: $F_{1,36} = 4.82$, $P = 0.035$).

Gut Morphology

MANCOVA on the gut dimensions detected no island \times sex interaction effect ($F_{6,26} = 1.88$, $P = 0.14$) or sexual dimorphism ($F_{6,27} = 1.47$, $P = 0.22$), but the difference between the two island populations was significant ($F_{6,28} = 3.11$, $P = 0.018$). The results of subsequent univariate tests are shown in Table 1. Lizards from Pod Mrčaru tended to have longer stomachs and longer small intestines than lizards from Pod Kopašte, even when the difference in SVL was taken into account. In 12 of the 16 individuals (75%) examined from Pod Mrčaru, the hindgut contained cecal valves. In sharp contrast, we found no such valves in any of the 27 individuals from Pod Kopašte (Pearson χ^2 ; $\chi^2_{1,43} = 28.089$, $P < 0.0001$). We found no difference in the occurrence of cecal valves between the sexes within the Pod Mrčaru population (Pearson χ^2 ; $\chi^2_{1,16} = 0.085$, $P = 0.77$).

To test the effect of an “artificial” arthropod diet on gut morphology, we compared the digestive tracts of freshly caught,

preserved Pod Mrčaru lizards with those of preserved lizards of the same provenance that had been fed an exclusively arthropod diet for 15 wk. MANCOVA found no sex \times diet interaction effect ($F_{1,21} = 0.51$, $P = 0.79$) and no difference between the sexes ($F_{6,22} = 0.97$, $P = 0.47$), but the diet effect was highly significant ($F_{6,23} = 7.55$, $P < 0.001$). Results of univariate ANCOVA can be found in Table 2. Lizards maintained on an arthropod diet showed a reduction in the weight of the small intestine and the hindgut. In addition, we found no evidence of cecal valves in any of the twenty specimens that had been fed arthropods. This was in sharp contrast to the high proportion (12/16) of individuals with valves among the freshly caught individuals (Pearson χ^2 ; $\chi^2_{1,36} = 22.5$, $P < 0.0001$).

To estimate the extent of the regression of the digestive tracts following an arthropod regime, we also compared gut dimensions between the laboratory population of Pod Mrčaru lizards and the wild-caught specimens of Pod Kopašte. We found no multivariate sex \times island interaction ($F_{6,31} = 0.81$, $P = 0.57$) or sexual dimorphism ($F_{6,32} = 1.48$, $P = 0.21$), but the difference between the two populations remained significant ($F_{6,33} = 6.88$, $P < 0.001$). The results of the univariate analyses can be found in Table 3.

Nematode Populations

Analysis indicated a significant difference between islands (island effect; $\chi^2_{1,279} = 6.318$, $P < 0.0001$). Occurrence in individuals from Pod Mrčaru (16.94%, 21 present vs. 98 absent) was higher than in individuals from Pod Kopašte (2.50%, four present vs. 156 absent). We found more nematodes in feces during the spring compared with the fall (season effect; $\chi^2_{1,279} = 16.762$, $P < 0.0001$). Females (9.52%) had a tendency to contain more nematodes than males (2.59%; $\chi^2_{1,279} = 4.931$, $P = 0.085$).

Dentition

In both populations, all specimens examined exhibited a dentition with cylindrical teeth and a single cusp attached to the inside of the jaw (typical pleurodont dentition). We found no differences in the number of teeth between populations ($F_{1,39} = 3.59$, $P = 0.065$) or between sexes ($F_{1,39} = 2.65$, $P = 0.112$). The island \times sex interaction effect was also not significant ($F_{1,39} = 3.95$, $P = 0.054$).

ANCOVA on tooth width with island, sex, and tooth number (1–4) entered as factors and dentary bone length entered as a covariate revealed no significant interaction effects (all $P > 0.10$). Relative tooth width differed between islands ($F_{1,156} = 10.29$, $P = 0.002$), sexes ($F_{1,156} = 8.34$, $P = 0.004$), and number ($F_{3,156} = 3.27$, $P = 0.023$). Inspection of marginal means determined that Pod Mrčaru lizards had relatively wider teeth than Pod Kopašte lizards, and that males had wider teeth than females. Posterior teeth were wider than anterior teeth (Table 4). A similar analysis on relative teeth height revealed a significant island \times sex effect ($F_{1,155} = 5.75$, $P = 0.019$). On Pod Mrčaru, males had longer teeth than females ($F_{1,80} = 17.75$, $P < 0.001$); on Pod Kopašte, the difference was reversed

Table 1: Gut morphometric and digestive performance data for wild *Podarcis sicula* individuals from Pod Mrčaru and Pod Kopašte

Traits	Descriptive Statistics														
	Pod Mrčaru			Pod Kopašte			Island Effect			Sex Effect			Island × Sex Effect		
	♂ ♂	♀ ♀	♀ ♀	♂ ♂	♀ ♀	♀ ♀	F	P	F	P	F	P	F	P	
Stomach length (mm)	25.29 ± 1.9 (7)	26.8 ± 2.07 (8)	18.12 ± 1.18 (8)	18.12 ± 1.18 (8)	16.55 ± .93 (17)	16.55 ± .93 (17)	12.04	.001	2.92	.096	.14	.706			
Stomach weight (mg)	135.95 ± 15 (7)	175.26 ± 29 (8)	79.16 ± 11.96 (8)	79.16 ± 11.96 (8)	54.18 ± 10.77 (17)	54.18 ± 10.77 (17)	1.38	.25	4.88	.034	1.86	.18			
Small intestine length (mm)	74.71 ± 6.8 (6)	67.7 ± 4.33 (8)	46.31 ± 3.6 (6)	46.31 ± 3.6 (6)	39.29 ± 2.83 (17)	39.29 ± 2.83 (17)	11.58	.002	.39	.54	.17	.68			
Small intestine weight (mg)	138.95 ± 29 (6)	144.54 ± 22 (8)	55.20 ± 11.68 (6)	55.20 ± 11.68 (6)	45.59 ± 12 (17)	45.59 ± 12 (17)	1.03	.32	6.21	.018	.05	.82			
Cecum length (mm)	19.04 ± 1.65 (6)	16.06 ± 1.1 (8)	12.08 ± .88 (6)	12.08 ± .88 (6)	9.57 ± .93 (17)	9.57 ± .93 (17)	.61	.44	3.91	.06	.64	.43			
Cecum weight (mg)	183.8 ± 19.3 (6)	155.9 ± 27.6 (8)	92.17 ± 21.72 (6)	92.17 ± 21.72 (6)	44.83 ± 13 (17)	44.83 ± 13 (17)	1.10	.30	.42	.52	.70	.41			
	♂ ♂ (N = 10)	♀ ♀ (N = 20)	♂ ♂ (N = 5)	♂ ♂ (N = 5)	♀ ♀ (N = 5)	♀ ♀ (N = 5)	$F_{1,39}$	P	$F_{1,39}$	P	$F_{1,39}$	P			
ADE lipids (%)	85.42 ± .147 (10)	85.71 ± .13 (20)	83.21 ± .015 (5)	83.21 ± .015 (5)	82.67 ± .039 (5)	82.67 ± .039 (5)	197.17	< .0001	.36	.55	4.82	.035			
ADE proteins (%)	60.022 ± .32 (10)	60.39 ± .16 (20)	58.47 ± .029 (5)	58.47 ± .029 (5)	57.72 ± .036 (5)	57.72 ± .036 (5)	57.67	< .0001	.69	.41	4.87	.034			
ADE carbohydrates (%)	81.036 ± .37 (10)	82.33 ± .11 (20)	79.75 ± .57 (5)	79.75 ± .57 (5)	78.88 ± .045 (5)	78.88 ± .045 (5)	81.73	< .0001	.78	.38	16.92	< .0001			
	♂ ♂ (N = 21)	♀ ♀ (N = 21)	♂ ♂ (N = 13)	♂ ♂ (N = 13)	♀ ♀ (N = 29)	♀ ♀ (N = 29)	$F_{1,83}$	P	$F_{1,83}$	P	$F_{1,83}$	P			
GPT (min)	3,093.47 ± 221.5	3,958.67 ± 223.6	2,906.38 ± 276.16	2,906.38 ± 276.16	2,548.41 ± 201.902	2,548.41 ± 201.902	11.403	.0011	1.149	.286	6.68	.0115			

Note. Data are nontransformed means ± SE, with sample sizes in parentheses. Animals from both populations were tested shortly after being captured in the field. ADE = apparent digestive efficiency, GPT = gut passage time. F statistics and P values are derived from one-way ANCOVA on \log_{10} -transformed data, with \log_{10} of snout-vent length entered as a covariate and with nonsignificant (interaction) terms removed from the model. Significant values ($P < 0.05$) are indicated in bold.

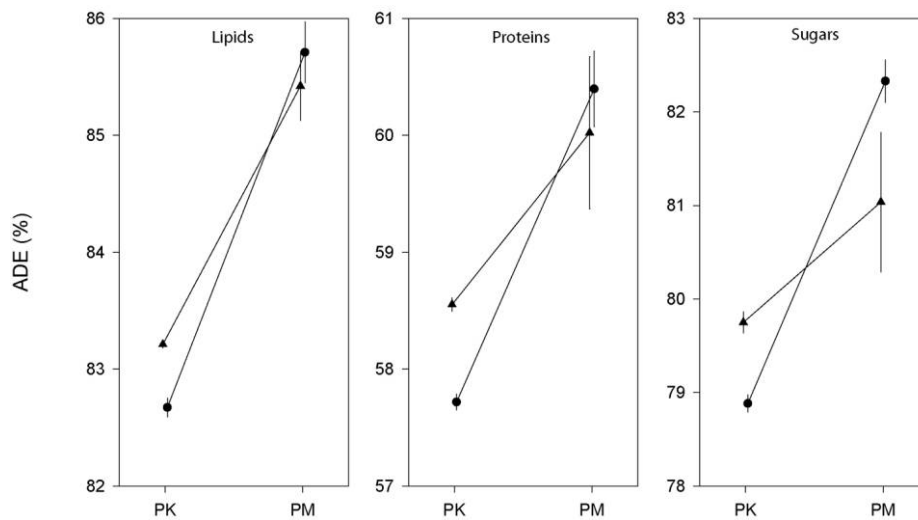


Figure 1. Apparent digestive efficiencies (ADE) for lipids, proteins, and carbohydrates. Triangles represent males, and circles represent females. The difference in efficiency was highest between the females of both populations; whereas males performed better on Pod Kopište (PK), the reverse was the case on Pod Mrčaru (PM).

($F_{1,71} = 8.85$, $P = 0.005$). We found no population differences in tooth length when comparing males ($F_{1,79} = 0.69$; $P = 0.41$) or females ($F_{1,72} = 0.8$, $P = 0.37$) between islands.

Discussion

Our results confirm and expand earlier findings concerning divergence in the morphology of feeding structures between two island populations of *Podarcis sicula* lizards. In addition to the differences in skull dimensions and the prevalence of cecal valves previously reported by Herrel et al. (2008), these two recently diverged populations also differ in aspects of their dentition (teeth width) and the length of the stomach and small intestine. Our results also show that some of these morphological changes effectively translate into differences in digestive performance: the population with the longer digestive tracts exhibit longer gut passage time and improved digestive efficiency.

It is tempting to connect this divergence in morphology and performance to the reported differences in diet between the two populations. Many of the morphological and physiological features of the population on Pod Mrčaru could be interpreted as adaptations to an herbivorous diet. Pod Mrčaru lizards are larger than Pod Kopište lizards; animals with larger bodies have lower mass-specific rates of energy expenditure (Pough 1973; Alexander 1999) and are therefore better suited to subsist on plant tissue, which is typically low in digestible energy (Espinoza et al. 2004). Larger bodies can also carry more robust heads and more voluminous digestive tracts (Espinoza et al. 2004; our results). Pod Mrčaru lizards have more massive heads, even when correcting for body size; larger heads allow higher bite forces and thus aid in tearing up rough plant material (Herrel et al. 1998, 1999; Stayton 2006). Pod Mrčaru lizards have wider teeth, even when correcting for jaw length; broader, stronger teeth may possibly facilitate the tearing of rough plant materials. Pod Mrčaru lizards have longer and more complex intestines; longer digestive tracts

and the presence of valves increase gut passage time and thus the time available for microbial breakdown and assimilation (Iverson 1982; Dearing 1993; Durtsche 2000). Pod Mrčaru lizards exhibit prolonged gut passage times; an increased retention time seems a prerequisite for effective digestion of plant material in reptiles (Zimmerman and Tracy 1989; Bjorndal 1997a). And finally, Pod Mrčaru lizards have higher digestive efficiencies, which helps to compensate for their relatively low-energy diet (Johnson and Lillywhite 1979; Ruppert 1980; King 1996). It should be noted, however, that our study suffers from the problems associated with two-species (or two-population) comparisons (Adolph and Garland 1994). Although the populations considered have much of their evolutionary history and physical environment in common, they do differ in aspects that are not directly related to diet, and these may influence some of the characteristics mentioned. For instance, higher densities on Pod Mrčaru may have selected for higher competitive abilities (Verwust et al. 2009) and hence for larger body sizes, more robust heads, and higher bite forces. Clearly, data from other populations, with varying proportions of plant material in their natural diet, are required to test the idea of a causal relationship between diet and the morphological and physiological variables reported here.

Many comparative studies have tacitly assumed that the distinctive features of plant-eating lizards (large body size, skull dimensions, special dentition, gut morphology) are a product of genetic adaptation to the special demands of a plant-based diet (e.g., Van Damme 1999; Cooper and Vitt 2002; Espinoza et al. 2004; Herrel et al. 2008). Our results suggest that in *P. sicula*, at least some of the changes associated with a dietary shift toward a higher proportion of plant material may be plastic. Specimens from the Pod Mrčaru population, which in nature eat substantial amounts of plant material (Herrel et al. 2008), exhibited a reduction in digestive tract length and a total

Table 2: Gut morphometric data for *Podarcsis sicula* individuals from Pod Mrčaru

Traits	Descriptive Statistics of Pod Mrčaru Individuals											
	Wild Population		Laboratory Population				Diet Effect		Sex Effect		Diet × Sex Effect	
	♂♂	♀♀	♂♂	♀♀	♀♀	F	P	F	P	F	P	
Stomach length (mm)	25.29 ± 1.9 (7)	26.80 ± 2.07 (8)	22.23 ± 1.36 (9)	22.65 ± 1.39 (11)		3.77	.06	.84	.37	.06	.81	
Stomach weight (mg)	135.95 ± 15 (7)	175.26 ± 29 (8)	88.18 ± 6.39 (9)	100.74 ± 20 (11)		3.38	.07	10.88	.002	.24	.63	
Small intestine length (mm)	74.717 ± 6.8 (6)	67.70 ± 4.33 (8)	73.42 ± 4.13 (9)	67.97 ± 3.33 (11)		1.74	.20	2.42	.13	.47	.50	
Small intestine weight (mg)	138.95 ± 29 (6)	62.23 ± 22 (8)	94.144 ± 10.83 (9)	73.53 ± 12.31 (11)		5.48	.03	.56	.45	.87	.36	
Colon length (mm)	19.04 ± 1.66 (6)	16.06 ± 1.1 (8)	12.71 ± .64 (8)	11.468 ± .56 (10)		16.30	<.0001	.24	.63	.43	.52	
Colon weight (mg)	183.75 ± 19.3 (6)	155.91 ± 27.58 (8)	64.11 ± 10.45 (8)	44.56 ± 8.08 (10)		31.83	<.0001	.004	.95	.37	.55	

Note. Data are nontransformed means ± SE, with sample sizes in parentheses. Wild-caught individuals (whose diet includes plant material) are compared with individuals that were fed an exclusively arthropod diet for 6 mo. *F* statistics and *P* values are derived from one-way ANCOVA performed on log₁₀-transformed data, with log₁₀ of snout-vent length entered as a covariate and with nonsignificant (interaction) terms removed from the model. Significant values (*P* < 0.05) are indicated in bold.

Table 3: Comparison of gut morphometric data between Pod Mrčaru lizards fed an arthropod diet for 6 mo in the laboratory and wild-caught Pod Kopašte lizards

Traits	Descriptive statistics										Diet Effect		Sex Effect		Diet × Sex Effect	
	Pod Mrčaru-Laboratory					Pod Kopašte-Wild					$F_{1,44}$		$F_{1,44}$		$F_{1,44}$	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	♂ ♂	♀ ♀	$F_{1,44}$	P	$F_{1,44}$	P	$F_{1,44}$	P		
Stomach length (mm)	22.23 ± 1.36 (9)	22.65 ± 1.39 (11)	18.12 ± 1.18 (8)	16.55 ± .93 (17)	6.13	.02	2.27	.14	.85							
Stomach weight (mg)	88.18 ± 6.39 (9)	100.74 ± 20 (11)	79.16 ± 11.96 (8)	54.18 ± 10.77 (17)	.001	.97	3.29	.08	.42							
Small intestine length (mm)	73.42 ± 4.13 (9)	67.97 ± 3.33 (11)	46.31 ± 3.6 (6)	39.29 ± 2.83 (17)	33.88	<.001	1.76	.19	.95							
Small intestine weight (mg)	94.144 ± 10.83 (9)	73.53 ± 12.31 (11)	55.20 ± 11.68 (6)	45.59 ± 12 (17)	.001	.98	4.55	.39	.30							
Colon length (mm)	12.71 ± .64 (8)	11.468 ± .56 (10)	12.08 ± .88 (6)	9.57 ± .93 (17)	1.89	.17	3.33	.08	.88							
Colon weight (mg)	64.11 ± 10.45 (8)	44.56 ± 8.08 (10)	92.17 ± 21.72 (6)	44.83 ± 13 (17)	15.40	<.0001	.50	.49	.83							

Note. Data are nontransformed means ± SE, with sample sizes in parentheses. F statistics and P values are derived from one-way ANCOVA performed on \log_{10} -transformed data, with \log_{10} of snout-vent length entered as a covariate and with nonsignificant (interaction) terms removed from the model. Significant values ($P < 0.05$) are indicated in bold.

Table 4: Tooth numbers and dimensions (nontransformed means \pm SE, with sample sizes in parentheses) for male and female lizards from Pod Mrčaru and Pod Kopište

Traits	Pod Mrčaru		Pod Kopište	
	♂ ♂	♀ ♀	♂ ♂	♀ ♀
Tooth number	17.8 \pm .066 (10)	18.82 \pm .042 (12)	19 \pm .035 (12)	18.89 \pm .043 (9)
Dentary bone length (mm)	8.86 \pm .05 (10)	7.73 \pm .23 (12)	8.05 \pm .11 (12)	6.90 \pm .15 (8)
Width tooth 1 (mm)	.30 \pm .01 (10)	.24 \pm .01 (12)	.25 \pm .01 (12)	.21 \pm .008 (8)
Width tooth 2 (mm)	.31 \pm .01 (10)	.24 \pm .01 (12)	.25 \pm .01 (12)	.20 \pm .007 (7)
Width tooth 3 (mm)	.31 \pm .007 (9)	.25 \pm .01 (12)	.26 \pm .01 (11)	.21 \pm .01 (8)
Width tooth 4 (mm)	.33 \pm .01 (9)	.26 \pm .01 (12)	.27 \pm .01 (12)	.22 \pm .01 (7)
Height tooth 1 (mm)	.41 \pm .01 (10)	.34 \pm .01 (12)	.36 \pm .01 (12)	.33 \pm .01 (8)
Height tooth 2 (mm)	.42 \pm .01 (10)	.34 \pm .02 (12)	.37 \pm .01 (12)	.35 \pm .02 (7)
Height tooth 3 (mm)	.42 \pm .01 (9)	.36 \pm .008 (12)	.38 \pm .02 (11)	.35 \pm .02 (8)
Height tooth 4 (mm)	.43 \pm .01 (9)	.37 \pm .01 (12)	.41 \pm .02 (12)	.35 \pm .03 (7)

loss of cecal valves after having been fed an exclusively arthropod diet for 15 wk. Although parts of their gastrointestinal systems were still better developed than those of specimens feeding mainly on arthropods in the wild, it seems likely that a prolonged exposure to an animal-based diet would have erased even those differences. These observations call for a more flexible view of the digestive system in lizards. Plasticity of gastrointestinal morphology and function has long been described in birds (Savory and Gentle 1976a, 1976b; Karasov 1996; reviews in Starck 1999; McWilliams and Karasov 2001) and mammals (e.g., Sibly et al. 1990; Lee and Houston 1993; Munn et al. 2006). Gut morphology and performance in these animals vary seasonally in concert with changes in internal demand (e.g., reproduction, migration, hibernation) or environmental conditions (food availability, nutrient composition). In reptiles, there is evidence that digestive function may change in response to dietary demands on ontogenetic, seasonal, and instantaneous timescales. Many reptiles shift toward a more herbivorous diet as they age (Kennett and Tory 1996; Bjorndal 1997b; Rocha 1998; Spencer et al. 1998; Durtsche 2000; Fialho et al. 2000; Bouchard and Bjorndal 2006; but see Cooper and Vitt 2002 on the generality of this phenomenon). At least in some of the species studied, this ontogenetic dietary shift is accompanied by changes in digestive efficiency (Durtsche 2004; Bouchard and Bjorndal 2006). Reptiles living in a seasonal environment have been described as regulating their digestive apparatus according to activity or prey availability (Latif et al. 1967; Tracy and Diamond 2005; Naya et al. 2008; Iglesias et al. 2009). And in snakes and other reptiles with irregular feeding patterns, eating is followed by an immediate up-regulation of digestive functions, resulting in an increased mass of the small intestine and intensified enzyme activity and brush-border transport rates (Secor and Diamond 1995, 2000; Secor and Phillips 1997; Jackson and Perry 2000; Starck and Beese 2002; Ott and Secor 2007). All of these observations suggest that many lineages of vertebrates, including lizards, exhibit considerable phenotypic plasticity in the morphology and physiology of their digestive system. In these lineages, dietary shifts from carnivory to omnivory (as observed in many lizard families; Cooper and Vitt

2002) may constitute less of an evolutionary challenge than previously thought. It has been argued that the transition to exclusive herbivory (typically folivory) would require more substantial adaptations (Cooper and Vitt 2002). However, with the potential exception of the need for specialized dentition for cutting or reducing leaves, most of the changes deemed necessary in this context (elongation of the intestines, development of valves, prolonging retention time, acquisition of commensals, increasing digestive efficiency) have been shown to occur in a short to very short time span in this study and many of the studies cited above. Admittedly, the plasticity of the digestive system has been studied in only a handful of reptile species, and it seems likely that studies are biased to more flexible species. If future studies show that some species have more flexible digestive systems than others, it would be of great interest to know which evolutionary and mechanistic factors contribute to this variation (see Tracy and Diamond 2005). Differences in digestive flexibility may also determine the colonization success of species.

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