

**MORPHOLOGICAL CORRELATES OF PREY CONSUMED BY *PODARCIS MELISELLENSIS* (BRAUN, 1877) AND *P. SICULUS* (RAFINESQUE, 1810) (SAURIA, LACERTIDAE) FROM TWO MAINLAND REGIONS IN THE EASTERN ADRIATIC AREA**

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**Abstract** – The correlation between trophic utilization and morphology was studied for two lizard species (*Podarcis melisellensis* and *P. siculus*) from two mainland localities in the eastern Adriatic area; this is the first report of trophic and morphometric data for *P. melisellensis* from mainland populations. Variance partitioning showed that most of the variation in morphological traits for the analyzed lizards was the result of differences between species, and to a lesser extent between sexes. Locality did not have a strong effect on the variation of morphological traits. Prey weight is the only characteristic of prey that generally exhibits correlations with morphological characteristics rather than prey size. The pattern of correlations is generally weaker for *P. melisellensis* than for *P. siculus*. Optimal foraging theory predictions were generally confirmed: *P. siculus* is more constrained by trophic resource availability, with a premium on larger and heavier prey consumed in the less productive locality (SM), which can be relaxed in more productive regions (KL). *P. melisellensis* shows such constraints only for males in the less productive region (SM). Females of both species consume heavier prey.

**Key words:** *Podarcis melisellensis*, *Podarcis siculus*, diet composition, morphological correlates, optimal foraging theory, trophic niche differentiation

## INTRODUCTION

Optimal foraging theory (OFT, MacArthur and Pianka, 1966; MacArthur, 1972) is one of the key theories in a body of theoretical models that have been developed following the formalization of the ecological niche concept by Hutchinson (1957). This set of models, now known as “classical niche theory”, has been recently reviewed and revitalized by Chase and Liebold (2003) and continues to remain in the forefront of ecological research. OFT predicts that actively foraging generalist species (“searchers”, to which the studied lizards belong) foraging in environments with limited food sup-

ing profits, expressed by energy per unit prey, and foraging costs, expressed by time spent on acquiring and consuming prey. This places a premium on capturing the most and largest palatable prey in as short a time as possible, with larger lizards presumably at an advantage. However, in very productive environments, where environmental pressures are relaxed, different tactics may evolve, and prey may be selected by other criteria. In studies of lizard trophic resource utilization and niche differentiation, head length, upper jaw length and snout-vent length have been, and still are, used as morphological indicators of trophic utilization, which, in turn, is indicated by prey size (Schoener, 1968; Roughgarden, 1972; Henle and Klaver, 1985, and refer-

ences therein, Pianka, 1993; Burke and Mercurio, 2002; Vitt and Pianka, 2004).

A wealth of bionomic data for both analyzed species was summarized by Tiedeman and Henle (1985, and references therein) for *Podarcis melisellensis* and Henle and Klaver (1985, and references therein) for *Podarcis siculus*. Arnold (1987), in a study of resource partitioning of lizards in southern Europe, reported detailed data on the resource use of these two species from localities in the eastern Adriatic. Both species of wall lizards are active heliotherms with generally unimodal (*P. siculus*) or bimodal (*P. melisellensis*) activity patterns, regulating their temperature by alternating between closed and open habitat structures. They are generalist predators that actively forage and search for mostly arthropod prey, although they occasionally take other prey items including plant food (especially *P. siculus* on islands). Both occupy a wide variety of structural habitats and microhabitats, tending to avoid dense forested areas and completely closed habitats, but utilizing the ecotones and edges of these structures. Human modified landscapes, especially if of high productivity, offer “supernormal” habitats (Arnold 1987) for both species so they both occur in and around agricultural areas and pastures. Competitive exclusion on islands, and habitat differentiation and displacement on the coast have been documented to exist where both species coexist. *P. melisellensis* tends to be of a cautious nature, foraging and basking in the vicinity of shelters. It avoids towns, swampy and marshy areas, rarely occurs in the littoral on the coast and islands, preferring open habitats covered by mosaic patches of stony, bushy, and grass-covered structures in which it occurs mostly close to the ground, being a poor climber. Its range is confined to the eastern Adriatic, from Trieste (Italy) to northern Albania, on the islands and the coast, and inland up to 800-1000 m altitudes. The populations studied nominally belong to *Podarcis melisellensis fumana*. *P. siculus* is a vigorous, opportunistic species, widely foraging within a large home range, frequently basking on rocky outcrops and walls. It is a good climber, prefers vertically structured microhabitats with somewhat denser vegetation structure, and frequently enters the littoral

zones on the coast to forage. It readily enters towns. Originating from Italy, by complex postglacial invasions (frequently human-induced), it established a discontinuous range on the islands and coast of the eastern Adriatic, ranging inland up to an altitude of 200 m. Nominally, the population studied in Croatia is assigned to *P. siculus campestris*, the population from Kotor (Montenegro) to *P. siculus cattaroi*.

The study area in Croatia is located southeast of Split in central Dalmatia and is bounded by the only two permanent watercourses in the area (the rivers Žrnovnica and Cetina) from the north and south. It stretches from the coastal townships of Stobreč and Omiš in the east, to the ridges of Mt. Mosor in the west. It is mainly a tourist region along the coastline, while complex patterns of agriculture, vineyards, and cattle and sheep farming occur inland and on the ridges. Vegetationally it is much degraded, while agricultural complexes and farms are surrounded by tracts of ruderalized vegetation. The whole region is very heterogeneous in orography known for its pronounced and long summer droughts (Marković, 1970; Rodić 1989). The study area in Montenegro is located in the general region of the Boka Kotorska bay, encompassing the towns of Kotor and Tivat and their immediate surroundings in the north, and the valley of Grbalj southward to the township of Lastva Grbaljska, and to the bay at Jaz. From the east, it is bounded by the ridges of Mts. Lovćen and Njeguši, from the west by the ridges of Luštica. The coastline is dominated by an infrastructure supporting tourism, while the surrounding areas are mostly agricultural, with vineyards and orchards on the hillsides and cattle and sheep farming at higher altitudes. Several large agricultural complexes existed in the area that are now abandoned. The hydrography of the area is well developed, with several permanent watercourses and tracts of drainage and irrigation canals in abandoned agricultural complexes.

The aim of this study was to investigate the correlation patterns between the indicative morphological and prey characteristics of *P. siculus* and *P. melisellensis* in two regions differing in their ecological settings, specifically in productivity. We investigated

whether head and upper jaw length are reliable indicators of prey length consumed by these lizards, as is commonly assumed in the literature, and if not, which characters of lizard morphology were more reliable predictors of diet. For *P. melisellensis* this is the first report of trophic data for mainland populations, while for *P. siculus* it can be comparatively assessed with results from other studies.

#### MATERIALS AND METHODS

The bioclimatic (Hijmans et al, 2005; Ahn and Tateishi, 1994) and land cover data were extracted for the study areas (approximately 100 km<sup>2</sup>) and geotransformed to 25 ha square grids. Several parameters were analyzed from bioclimatic data (Hijmans et al, 2005; Ahn and Tateishi, 1994): BIO1 – annual mean temperature (°C), BIO9 – mean temperature of the driest quarter (°C), BIO12 – annual precipitation (mm), BIO17 – precipitation of the driest quarter (mm), ET – evapotranspiration (mm), PET – potential evapotranspiration (mm), AI – BIO12/PET, aridity index. Land cover data (CORINE land cover 2000 100 m ver9/2007 (<http://www.eea.europa.eu>) was extracted for 18 land cover classes and summarized for those habitat classes from which lizards were collected (URB – urban/suburban, AGRI – agricultural and OPEN – open habitats).

The lizards were collected in the field by the senior author from two localities Split-Mosor (SM) and Kotor-Lastva (KL), and deposited in his private collection. A total of 289 individuals were caught by hand, and measurements were taken with a digital caliper and a 100 g scale. Using digital calipers with a precision of 0.01 mm, the following morphological measurements were taken: head length (from pileus to rostrum) – HL; head width at the widest point of the head – HW; head height at the highest point – HH; upper jaw length – UJL; lower jaw length – LJL; front leg length – FLL; longest anterior toe length – LATL; hind leg length – HLL; longest posterior toe length – LPTL and snout-vent length – SVL.

Stomach contents were removed *in situ* through a ventral incision, and preserved in a 70% aqueous

ethanol solution. All prey items were sorted and identified using a binocular scope (4 x and 10 x). Lizards with empty stomachs or stomachs with almost fully digested contents were eliminated from further analyses. The weight of each stomach was measured on an analytical balance (accuracy of 10<sup>-4</sup> g) before and after removing the contents, and total net weight of prey was recorded. Stomach contents were identified to family or order level. The number of prey items found in each stomach was recorded. The length of each prey item was measured using digital calipers ( $\pm 0.01$  mm) and scored according to its percentage in the total volume of stomach contents. For each stomach the following measures were recorded: the number of ingredients in the stomach (NP); net weight of prey consumed (SW); maximum length of prey (Lmax); the average length of the largest 50% volume fraction of prey (L50%); mean prey length weighted by percentage of stomach volume (Lpon) and general mean length of prey (Lavg).

#### *Statistical analysis*

Bioclimatic variables were extracted from global datasets for the two localities, summarized and tested for differences between localities by one-way analysis of variance. For the prey properties and morphometric characteristics, several parameters of descriptive statistics (reported for non-transformed data) were calculated (means and standard errors). As a descriptive tool, model II nested analysis of variance was used to partition the variance of the prey properties and morphometric traits between species, among populations nested within species and between sexes nested within populations. This method showed which hierarchical level (species, population or sex) contributed the most to prey and morphometric variations. In order to elucidate the relationships between prey properties and morphometric traits, Pearson correlation coefficients were calculated. The correlation patterns were further explored by canonical correlation analysis, a multivariate method particularly suited for datasets from which two sets of measurements can be extracted. By performing a simultaneous ordination and regression of the two sets of measurements, a quantitative and visual anal-

ysis of correlation patterns between and among the measurements is possible. Here, the set of morphological measurements was regressed upon and correlated with the set of prey properties. All analyses reported were performed in the Statistica software package (StatSoft, 2011).

## RESULTS

As can be seen from Table 1, the bioclimatic signatures of the two study areas are distinctly different and statistically highly significant (except for BIO17), the SM area being cooler and markedly drier, with a higher water deficit than the KL area. The profiles of land cover data are not significantly different, although KL has a larger proportion of open habitats (including pastures), which are preferred habitats for these species. As the parameters of rainfall, water balance, evapotranspiration and potential evapotranspiration are widely used to predict productivity in terrestrial ecosystems (Rozenzweig, 1968, Herzog et al, 2005), from our results we can assess that the KL area in Montenegro is more productive than the SM area in Croatia. This has clear implications for the rest of our results.

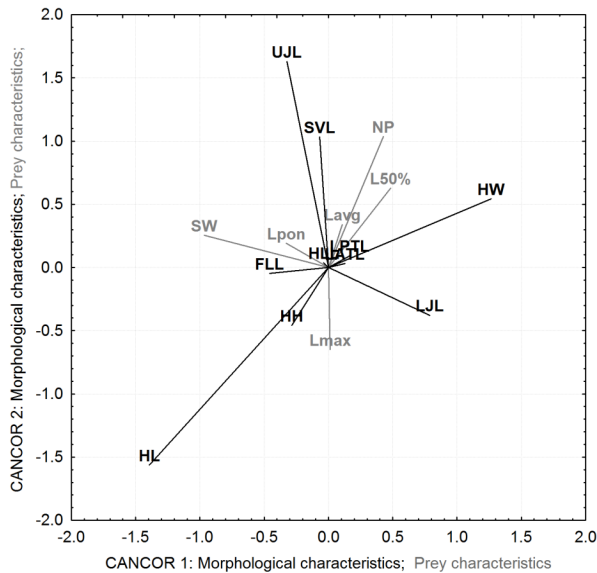
For *P. melisellensis*, a total of 530 items (in males 168, in females 212) was recorded in lizards from the Split-Mosor (SM) locality, and 150 items (in males 61, in females 89) in lizards from the Kotor-Lastva (KL) locality. For *P. siculus*, a total of 837 items (in males 410, in females 427) were recorded in lizards from the Split-Mosor (SM) locality, and 329 items (in males 101, in females 228) in lizards from the Kotor-Lastva (KL) locality. Summary statistics of prey consumed are given in Table 2.

The total sample of 289 lizards consisted of 146 males and 143 females. For *P. melisellensis* 72 lizards (40 males, 32 females) were from the Split-Mosor (SM) locality, and 65 lizards (30 males, 35 females) were from the Kotor-Lastva (KL) locality. For *P. siculus* 83 lizards (43 males, 40 females) were from the Split-Mosor (SM) locality, and 69 items (33 males, 36 females) were from the Kotor-Lastva (KL) locality. The summary statistics of prey properties and

morphometric traits are given in Table 2 and Table 3.

The results of model II nested analysis of variance are presented in Table 4 for prey properties and Table 5 for morphometric traits. The results of correlation analysis among the prey properties and morphometric traits are presented in Table 6 for *P. siculus* at both localities, and Table 7 for *P. melisellensis*.

The results of the canonical correlation (CAN-COR) analysis are presented in Figs. 1–3. Five canonical roots were extracted with a determination coefficient of  $R^2=0.624$  (test for randomness,  $\chi^2=401$ ,  $p<0.001$ , significantly non-random) with two significant roots accounting for 86% of the determination coefficient. As can be seen from inspection of Fig. 1, the first root, according to the prey measurements, is a negatively unipolar factor of prey weight consumed per lizard (SW), while the second is a bipolar factor of number of prey consumed (NP) versus maximum length of prey (Lmax) per lizard. According to the morphological measurements, the first root is a bipolar factor contrasting head width (HW) and lower jaw length (LJL) with head length (HL), while the second root, also bipolar, contrasts upper jaw length (UJL) and snout-vent length (SVL) with head length (HL) of lizards. The lizards' scores on prey characteristics shown in Fig. 2 portray a diffuse, loosely organized cluster, with lizards of both species from the Kotor-Lastva locality scoring higher on the axis defined by prey weight. On the second axis, *P. siculus* from both regions generally scores higher on the pole defined by number of prey consumed, in contrast to *P. melisellensis*, which generally scores higher on the pole defined by maximum prey length. The pattern of scores on morphometric measurements (Fig. 3) show a separation of localities on the first axis, with lizards from the Kotor-Lastva locality scoring higher on the pole defined by head length, as opposed to lizards from the Split-Mosor locality with higher scores on the head width and lower jaw length pole. Generally, *P. siculus* from both regions scores higher on the second axis pole defined by upper jaw and snout-vent length, while *P. melisellensis* generally scores higher on the pole defined by head

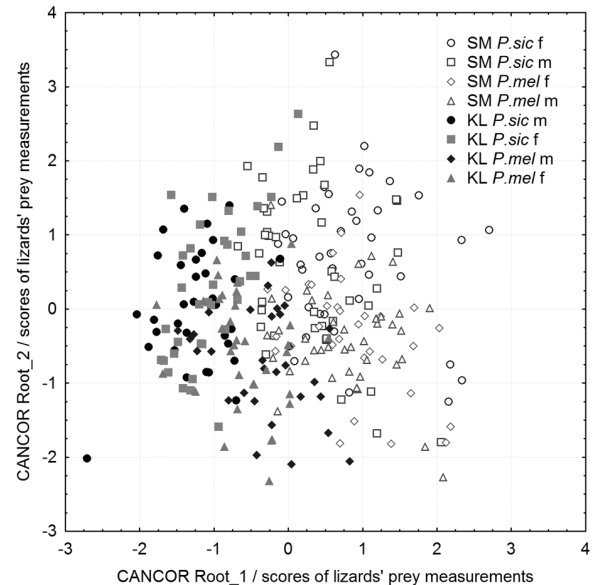


**Fig. 1.** Biplot of canonical correlation (CANCOR) weights of lizards' morphometric measurements (black shade; HL – head length, HW – head width, HH – head height, UJL – upper jaw length, LJJ – lower jaw length, FLL – front leg length, LPTL – longest anterior toe length, HLL – hind leg length, LPTL – longest posterior toe length, SVL – snout-vent length) and measurements of prey consumed (grey shade; NP – number of prey consumed, SW – net weight of prey consumed, Lmax – maximum length of prey, L50% – average length of the largest 50% volume fraction of prey, Lpon – mean prey length weighted by percentage of stomach volume, Lavg – mean length of prey) for the two significant roots of the analysis.

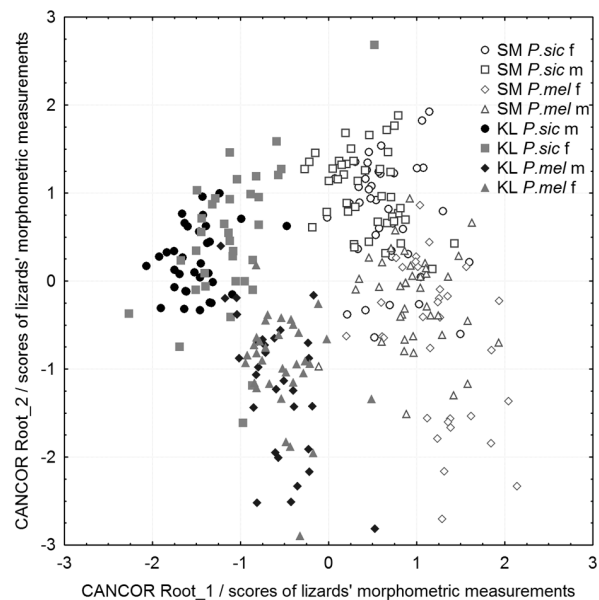
length. Overall, the prey ordination is less clearly defined than the morphometric one, and the ordinations are only broadly concordant with respect to species, sexes and localities. However, the general complex pattern of correlations presented in Tables 6 and 7 is borne out.

## DISCUSSION

From our analyses, we can see that the differences in the ecological signatures of the studied localities have bearing on both patterns of prey consumed by both species and their morphometric properties. Variance partitioning showed that most of the variation in morphological traits for the analyzed lizards was the result of differences between species, and to a lesser extent between sexes. Locality did not have



**Fig. 2.** Canonical scores of lizards according to prey measurements grouped by locality (Split – Mosor: SM, and Kotor – Lastva: KL), species (*P. siculus*: *P. sic*, and *P. melisellensis*: *P. mel*) and sex (males: m, and females: f) for the two significant roots of the analysis.



**Fig. 3.** Canonical scores of lizards according to morphometric measurements grouped by locality (Split – Mosor: SM, and Kotor – Lastva: KL), species (*P. siculus*: *P. sic*, and *P. melisellensis*: *P. mel*) and sex (males: m, and females: f) for the two significant roots of the analysis.

**Table 1.** Summary of the statistics for bioclimatic (means and standard deviations and ANOVA results) and land cover (km<sup>2</sup> and chi-square test) data for the two studied regions. For abbreviations see Material and Methods section. \* P <0.05; \*\* P <0.01; \*\*\* P <0.001; ns – non-significant.

	SM		KL		Test statistic (df)	P-value
	mean	SD	mean	SD	F (1,683)	significance
Bioclimatic						
BIO1	13.4	2.2	14.4	1.0	84	0 ***
BIO9	21.7	2.4	22.2	0.9	16	0 ***
BIO12	949	68.1	1408	15.4	> 100	0 ***
BIO17	156	20.1	154	9.3	5	0.03 *
WB	382	18.7	1502	10.3	> 100	0 ***
ET	516	2.5	580	1.5	> 100	0 ***
PET	846	5.3	835	3.8	> 100	0 ***
AI	1.12		1.68		n/a	%
Land Cover	km <sup>2</sup>	% total	km <sup>2</sup>	% total	Kruskal-Wallis H (1,6)	
URB	10.2	9.6	11.5	10.5		
AGRI	20.2	19.2	18.6	16.9		
OPEN	27.1	25.4	43.8	39.9		
Total	57.5	106.5	74	109.8	0.048	0.83 ns

**Table 2.** Summary of the statistics (means and standard errors - SE) of prey properties for *P. siculus* and *P. melisellensis* in stomach contents (m – males, f – females). For prey properties' abbreviations see the Materials and Methods section.

		P. siculus				P. melisellensis			
		SM		KL		SM		KL	
		m	f	m	f	m	f	m	f
NP	Means	7.84	10.75	3.06	6.33	4.08	6.25	2.10	2.40
	SE	1.19	1.46	0.36	1.28	0.39	0.83	0.26	0.26
SW	Means	151.68	95.43	436.89	376.21	64.68	53.66	137.75	157.57
	SE	18.27	12.93	40.65	32.97	10.66	7.48	20.33	15.99
Lmax	Means	13.91	12.88	13.27	10.86	11.58	9.28	10.47	10.60
	SE	0.96	0.68	1.13	0.56	0.91	0.62	0.75	0.98
L50%	Means	13.28	11.79	11.99	10.19	11.11	8.46	10.32	10.35
	SE	0.91	0.58	0.86	0.56	0.85	0.62	0.76	0.99
Lpon	Means	11.27	9.46	11.50	9.42	8.14	7.17	9.91	9.62
	SE	0.80	0.42	0.84	0.53	0.58	0.60	0.69	0.89
Lavg	Means	9.22	7.32	10.40	8.13	7.58	6.19	9.10	8.36
	SE	0.71	0.42	0.75	0.49	0.48	0.51	0.66	0.70

**Table 3.** Summary of the statistics (means and standard errors - SE) of morphometrics traits (in mm) for *P. siculus* and *P. melisellensis* (m – males, f – females). For morphometric traits' abbreviations see the Materials and Methods section.

		P. siculus				P. melisellensis			
		SM		KL		SM		KL	
		m	f	m	f	m	f	m	f
HL	Means	18.33	14.61	18.98	15.71	13.25	10.72	12.39	11.01
	SE	0.26	0.22	0.26	0.24	0.26	0.24	0.36	0.15
HW	Means	11.29	8.86	9.05	7.73	8.26	6.63	6.46	5.72
	SE	0.18	0.15	0.16	0.13	0.17	0.16	0.18	0.08
HH	Means	9.54	7.20	9.69	7.60	6.61	5.20	6.21	5.42
	SE	0.20	0.17	0.24	0.19	0.15	0.12	0.21	0.09
UJL	Means	15.65	12.50	15.50	13.19	11.00	8.96	9.91	9.02
	SE	0.23	0.22	0.25	0.28	0.20	0.22	0.30	0.13
LJL	Means	16.30	13.33	14.91	12.61	11.90	9.86	9.59	8.74
	SE	0.21	0.20	0.24	0.27	0.22	0.23	0.31	0.13
FLL	Means	17.10	14.48	19.96	17.09	12.22	10.36	12.81	12.01
	SE	0.35	0.30	0.33	0.24	0.31	0.40	0.40	0.19
LATL	Means	8.31	7.16	8.19	7.06	5.97	5.20	5.23	5.04
	SE	0.16	0.16	0.16	0.11	0.15	0.19	0.18	0.13
HLL	Means	30.02	24.32	30.09	25.89	21.78	17.70	18.40	16.97
	SE	0.49	0.37	0.57	0.40	0.56	0.64	0.57	0.33
LPTL	Means	14.71	12.52	15.82	13.85	10.77	9.30	9.75	8.59
	SE	0.28	0.22	0.34	0.28	0.28	0.26	0.28	0.17
SVL	Means	73.70	67.04	72.38	69.32	55.87	48.84	50.74	50.42
	SE	1.03	1.32	0.94	1.28	1.07	1.47	1.86	0.95

**Table 4.** Variance components from a nested analysis of variance in prey properties (see Material and Methods for abbreviations). Each component is expressed as the percentage of the total variance (%). Error variation represents variation within populations plus basic error variance (m – males, f – females). \* P <0.05; \*\* P <0.01; \*\*\* P <0.001; ns – non-significant.

	Between species		Among populations		Between sexes		Error
	%	P	%	P	%	P	%
NP	0.0	ns	30.4	***	6.3	***	63.3
SW	0.8	***	52.3	***	0.1	ns	46.8
Lmax	10.8	***	0.1	ns	1.6	ns	87.6
L50%	7.5	***	0.9	ns	2.8	*	88.8
Lpon	7.3	***	6.5	**	3.4	*	82.8
Lavg	0.0	ns	8.0	***	8.9	***	83.1

**Table 5.** Variance components from a nested analysis of variance in morphometric traits (see the Materials and Methods for abbreviations). Each component is expressed as the percentage of the total variance (%). Error variation represents variation within populations plus basic error variance (m – males, f – females). \* P < 0.05; \*\* P < 0.01; \*\*\* P < 0.001; ns – non-significant.

	Between species		Among populations		Between sexes		Error
	%	P	%	P	%	P	
HL	67.0	***	0.7	ns	18.6	***	13.6
HW	44.8	***	19.3	***	44.8	***	16.1
HH	58.2	***	0.0	ns	22.0	***	19.8
UJL	69.7	***	0.5	ns	14.9	***	14.9
LJL	62.3	***	8.3	***	13.9	***	15.4
FLL	61.7	***	9.1	***	9.4	***	19.8
LATL	66.9	***	1.2	*	7.3	***	24.6
HLL	67.7	***	2.0	ns	11.8	***	18.5
LPTL	69.7	***	3.1	ns	9.1	***	18.1
SVL	71.0	***	0.1	ns	3.6	***	25.2

a strong effect on the variation of morphological traits. These results could indicate that previous genetic differentiation between the two lizard species is followed by morphological differentiation. Although no studies integrating genetics and morphology have, to our knowledge, been reported for these species in this area, the results of Clover (1979) on phenetic differentiation of these species in the area and Gorman et al (1975) on their evolutionary genetics (albeit mainly for island OTU's) as well as their molecular genetics and phylogeographic reconstruction reported by Podnar et al (2004, 2005), seem concordant with these results. Morphological variability and sexual dimorphism is well documented in these species (Henle and Klaver, 1985; Tiedeman and Henle, 1985). The absence of a clear geographic pattern of morphological variation (low effect of population in variance partitioning analysis) is expected due to the relatively close proximity of the sampled localities (220 km). Such a low influence of locality on morphological traits variation could be consequence of low environmental variability, or constant environmental fluctuations across different populations, which at the moment we cannot assess from our data. Most of the variation in prey characteristics for the analyzed lizards was allocated at an individu-

al level, meaning that the variation in sample is very high and a clear pattern of diet cannot be accessed. However, for average prey consumed per lizard (NP) and stomach weight (SW), most of the variation is allocated at the population (locality) level, meaning that there are substantial differences among localities for these two traits (e.g. the SM population has the highest NP, KL the lowest NP, KL the highest SW, and SM the lowest SW).

From our identification of the Kotor-Lastva locality (KL) as being more productive, we can interpret these results in terms of the optimal foraging theory (OFT). In KL, lizards have many opportunities to forage at leisure, and thus acquire a small number of heavy prey that does not necessarily have to be the largest – it can be, for example fatter, and they could spend more time foraging for such items. The correlation pattern between prey and morphometrics for both species and localities presented in Tables 6 and 7, as well as in Figs. 1–3, generally support these findings. Although the reported significant correlations are moderate in strength, their non-determination coefficients are high ( $1-r^2=0.10-0.40$ ), indicating that any functional relationship described (e.g. by linear regression) will have a large



**Table 6.** Pearson correlation coefficients among prey properties and morphometric traits for *P. siculus*. For abbreviations see the Materials and Methods section. Significant correlations are in bold type.

<i>P. siculus</i>	HL	HW	HH	UJL	LJL	FLL	LATL	HLL	LPTL	SVL
SM males										
NP	-0.02	0.07	0.19	0.10	-0.06	-0.13	0.07	-0.13	0.01	0.07
SW	<b>0.45</b>	<b>0.45</b>	<b>0.55</b>	<b>0.48</b>	<b>0.40</b>	0.28	0.00	<b>0.44</b>	0.05	<b>0.49</b>
Lmax	<b>0.40</b>	<b>0.35</b>	<b>0.35</b>	<b>0.39</b>	<b>0.32</b>	0.18	-0.02	<b>0.31</b>	-0.05	<b>0.37</b>
L50%	<b>0.39</b>	<b>0.32</b>	<b>0.32</b>	<b>0.37</b>	<b>0.33</b>	0.19	-0.04	<b>0.32</b>	-0.05	<b>0.35</b>
Lpon	<b>0.39</b>	<b>0.32</b>	<b>0.32</b>	<b>0.39</b>	<b>0.32</b>	0.22	-0.02	<b>0.36</b>	-0.04	<b>0.35</b>
Lavg	0.29	0.23	0.20	0.28	0.27	0.21	0.01	<b>0.30</b>	0.04	0.26
SM females										
NP	0.22	<b>0.33</b>	0.22	0.19	0.22	0.02	0.24	0.19	-0.08	0.24
SW	<b>0.59</b>	<b>0.62</b>	<b>0.42</b>	<b>0.51</b>	<b>0.63</b>	<b>0.66</b>	<b>0.36</b>	<b>0.58</b>	0.23	<b>0.54</b>
Lmax	<b>0.42</b>	<b>0.47</b>	0.31	<b>0.34</b>	<b>0.45</b>	<b>0.48</b>	<b>0.32</b>	0.31	<b>0.46</b>	<b>0.43</b>
L50%	<b>0.41</b>	<b>0.48</b>	<b>0.34</b>	<b>0.33</b>	<b>0.47</b>	<b>0.45</b>	0.31	<b>0.33</b>	<b>0.40</b>	<b>0.42</b>
Lpon	<b>0.39</b>	<b>0.40</b>	0.27	<b>0.34</b>	<b>0.46</b>	<b>0.51</b>	0.19	0.30	<b>0.51</b>	<b>0.40</b>
Lavg	0.13	0.03	0.01	0.08	0.15	<b>0.36</b>	-0.03	0.14	0.30	0.04
KL males										
NP	-0.21	-0.20	-0.25	-0.26	-0.26	<b>-0.35</b>	-0.10	-0.18	-0.30	<b>-0.38</b>
SM	-0.20	-0.22	-0.15	-0.16	-0.17	-0.08	0.07	0.03	-0.26	-0.23
Lmax	-0.03	-0.15	-0.14	-0.04	-0.02	-0.11	-0.14	0.02	-0.34	-0.16
L50%	-0.14	-0.21	-0.22	-0.11	-0.08	-0.23	-0.24	-0.12	-0.32	-0.19
Lpon	-0.03	-0.15	-0.11	-0.02	0.00	-0.04	-0.12	0.03	-0.23	-0.09
Lavg	0.17	0.05	0.07	0.17	0.20	0.17	0.05	0.15	-0.16	0.16
KL females										
NP	0.17	<b>0.36</b>	<b>0.38</b>	<b>0.48</b>	<b>0.43</b>	<b>0.45</b>	0.08	<b>0.39</b>	0.16	0.28
SW	<b>0.43</b>	<b>0.37</b>	0.27	0.32	0.33	<b>0.45</b>	0.23	0.28	0.27	0.23
Lmax	0.08	0.02	0.08	0.07	0.13	0.27	0.04	0.00	0.28	0.03
L50%	-0.07	-0.09	-0.04	-0.07	-0.02	0.14	-0.07	-0.10	0.19	0.05
Lpon	-0.01	-0.20	-0.09	-0.16	-0.08	0.03	-0.10	-0.16	0.17	-0.08
Lavg	0.01	-0.27	-0.21	-0.29	-0.21	-0.17	-0.10	<b>-0.37</b>	0.01	-0.15

associated variability. We also found no consistent pattern among these correlations. In the Split-Mosor locality, the males of both species showed significant correlations with morphology, with prey weight being as strongly or more strongly correlated than prey size characteristics, although we see that larger prey is preferred. The pattern for females is similar for

*P. siculus*, but for *P. melisellensis* females in the area significant correlations were exhibited only for prey weight. In the Kotor-Lastva area, males of both species showed no correlation pattern whatsoever. *P. melisellensis* females exhibited a correlation pattern for prey weight, while *P. siculus* females exhibited this pattern for prey numbers consumed. Prey weight is

Table 7. Pearson correlation coefficients among prey properties and morphometric traits for *P. melisellensis*. For abbreviations see the Materials and Methods section. Significant correlations are in bold type.

<i>P. melisellensis</i>	HL	HW	HH	UJL	LJL	FLL	LATL	HLL	LPTL	SVL
SM males										
NP	-0.11	0.00	-0.21	-0.02	-0.15	0.10	-0.01	-0.07	0.19	-0.13
SW	<b>0.38</b>	<b>0.32</b>	<b>0.31</b>	<b>0.32</b>	0.30	<b>0.40</b>	<b>0.41</b>	0.30	0.21	<b>0.35</b>
Lmax	<b>0.40</b>	<b>0.35</b>	<b>0.46</b>	<b>0.38</b>	<b>0.33</b>	<b>0.36</b>	0.23	0.28	0.13	<b>0.36</b>
L50%	<b>0.40</b>	<b>0.33</b>	<b>0.43</b>	<b>0.37</b>	<b>0.34</b>	<b>0.37</b>	0.27	0.29	0.11	<b>0.36</b>
Lpon	0.22	0.15	<b>0.38</b>	0.20	0.20	0.11	0.03	0.08	-0.03	0.22
Lavg	0.29	0.20	<b>0.40</b>	0.26	0.30	0.22	0.14	0.21	-0.02	0.28
SM females										
NP	0.23	0.26	0.07	0.35	0.28	0.34	0.32	<b>0.35</b>	0.29	0.26
SW	<b>0.48</b>	<b>0.36</b>	<b>0.36</b>	<b>0.43</b>	<b>0.45</b>	0.33	<b>0.41</b>	<b>0.42</b>	<b>0.41</b>	<b>0.51</b>
Lmax	0.27	0.18	0.25	0.21	0.27	0.07	0.00	0.16	0.13	0.24
L50%	0.24	0.13	0.19	0.17	0.21	0.02	-0.03	0.08	0.13	0.16
Lpon	0.11	0.02	0.13	0.00	0.08	-0.12	-0.11	0.00	0.07	0.11
Lavg	0.10	0.02	0.12	-0.03	0.07	-0.13	-0.11	-0.05	0.02	0.09
KL males										
NP	0.00	-0.06	-0.02	-0.04	-0.02	0.03	-0.15	-0.06	-0.16	0.05
SW	0.18	0.14	0.08	0.19	0.18	0.21	-0.15	0.00	0.09	0.12
Lmax	-0.04	-0.10	-0.06	-0.03	-0.05	0.03	-0.08	-0.06	0.08	0.04
L50%	-0.03	-0.09	-0.05	-0.02	-0.04	0.03	-0.08	-0.07	0.07	0.04
Lpon	0.05	-0.01	0.03	0.05	0.02	0.07	-0.02	0.02	0.15	0.10
Lavg	0.01	-0.04	0.00	0.02	-0.01	0.04	-0.01	0.00	0.14	0.08
KL females										
NP	0.10	-0.08	0.09	-0.08	-0.07	-0.06	-0.11	0.00	0.21	0.02
SW	<b>0.58</b>	<b>0.40</b>	<b>0.40</b>	<b>0.58</b>	<b>0.59</b>	0.27	0.13	<b>0.47</b>	0.33	<b>0.57</b>
Lmax	0.20	0.11	0.22	0.23	0.23	0.22	0.17	0.27	<b>0.35</b>	0.28
L50%	0.22	0.14	0.22	0.24	0.23	0.20	0.15	0.27	0.32	0.29
Lpon	0.17	0.11	0.16	0.21	0.20	0.17	0.14	0.25	0.26	0.25
Lavg	0.09	0.08	0.11	0.19	0.18	0.16	0.19	0.20	0.23	0.18

the only characteristic of prey that generally exhibits correlations with morphological characteristics rather than prey size, unless they are by themselves correlated. Furthermore, the pattern of correlations is generally weaker for *P. melisellensis* than for *P. siculus*. From OFT predictions we can surmise that *P. siculus* is more constrained by trophic resource avail-

ability (SM), with a premium on larger and heavier prey consumed, which can be relaxed in more productive regions (KL), where it feeds on heavier prey that is not necessarily larger. *P. melisellensis* shows such constraints only for males in the less productive region (SM) – in KL it may feed on whatever is available exhibiting no correlation pattern at all, with fe-

males consuming heavier prey. Bearing in mind that females generally have a high reproductive investment effort, they presumably have to consume prey with the highest energy returns, i.e. heavier prey, as heavy as they can acquire during foraging. Obviously detailed further analyses have to be conducted to confirm these conclusions.

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