

The Italian wall lizard, *Podarcis siculus*, along the Tuscanian coast of central Italy: biometrical features and phenotypic patterns

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The Italian wall lizard, *Podarcis siculus*, has a wide distribution. However, information on several aspects of its ecology and biology are scarce, and relate mainly to insular populations. This paper describes the main morphological features of 123 individuals along a geographical gradient (five localities) in northwestern Tuscany (central Italy). Our results show a strong sexual dimorphism in most of the considered parameters, high geographic variation, low interaction between sex and locality and a similar distribution of external parasite load and tail autotomy between the sexes.

Key words: biometry, geographic variation, Italian wall lizard, *Podarcis siculus*

INTRODUCTION

The Italian wall lizard, *Podarcis siculus*, is among the commonest reptile species of the Italian peninsula. It is distributed from north of the Apennines throughout central and southern Italy, from coastal to hilly areas, reaching high altitudes in Sicily (Corti, 2006; Corti et al., 2010). Based on the EU Habitats Directive and the IUCN red list of the Mediterranean reptile fauna (Crnobrnja-Isailovic et al., 2008), the Italian wall lizard receives particular conservation attention. The available information on the species' biology is however often rather descriptive (e.g., atlases: Henle & Klaver, 1986; Corti, 2006) or based on small sample size (Lo Cascio & Corti, 2008). Recent further studies on this species' biology however suggest that *P. siculus* is a suitable model organism to study, for example, morphological and functional patterns of adaptive responses to habitat change (Bruner & Costantini, 2007; Herrel et al., 2008; Fulgione et al., 2008; Biaggini et al., 2009).

Knowledge about several *P. siculus* life-history traits is still scarce (see Corti et al., 2010 and literature therein), as are comparisons among populations (Lanza et al., 1993: meristic characters; Herrel et al., 2008: functional morphology; Biaggini et al., 2009: ecology and behaviour). Inter-specific comparisons within the genus *Podarcis* are mainly devoted to diet and the study of herbivory in an insular context (Perez-Mellado & Corti, 1993; Perez-Mellado et al., 2000). It would be desirable to investigate how *P. siculus* performs in natural versus anthropogenic habitats (Amo et al., 2006), which physiological responses can be recorded (Davis et al., 2008; French et al., 2008) and how it adapts its morphology to habitat characteristics and environmental change (Herrel et al., 2008). At present we ignore the degree and frequency of adaptive plasticity in *P. siculus*, and multiple comparisons and experimental analyses are needed (see Bombi et al., 2009).

This paper examines the extent of morphological (and likely functional) variation of *P. siculus* in central Italy. It aims at i) verifying patterns of body size variation at a local scale, ii) investigating the degree of sexual dimorphism among different areas, and iii) documenting the presence of external parasites.

MATERIALS AND METHODS

Study areas

We studied four localities from the south of Viareggio (province of Lucca) to the south of Pisa (a 23 km North-South transect along the coast of Tuscany), and a fifth locality 15 km east of Pisa, in the fields around the Museum of Natural History of the University of Pisa. Habitats at the study sites are represented by sandy dunes, wooded areas and uncultivated fields. Altitudes range from a few metres to about 50 m above sea level (Table 1).

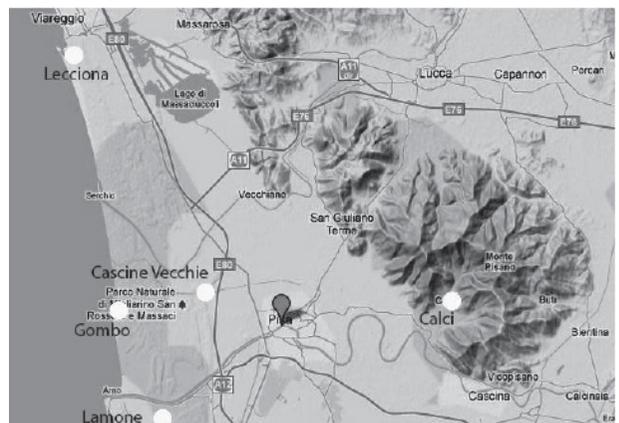


Fig. 1. Sampling areas in north-western Tuscany (Tyrrhenian Sea) (locality dots in white)

Table 1. Sampling sites for *Podarcis siculus* in northwestern Tuscany

Study area	Habitat	Distance from the sea (km)	Latitude	Longitude	Altitude (m)	Human presence
Lecciona	dunal	0.2	43° 50'	10° 14'	0	YES
Cascine Vecchie	uncultivated fields and ruins	5	43° 43'	10° 20'	2	YES
Gombo	retrodunal	0.1	43° 42'	10° 16'	0	NO
Calci	uncultivated fields and dry walls	20	43° 43'	10° 31'	46	YES
Lamone	uncultivated fields and dry walls	2	43° 39'	10° 18'	0	YES

Sampling

We captured lizards with a noose on a stick or by hand (i.e. when turning up stones and barks). Sampling occurred throughout the day, from May to August 2007 and from March to September 2009. We considered lizards to be adult at a minimum snout to vent length (SVL) of 51.7 mm (males) and 49 mm (females, see Henle & Klaver, 1986). Other age classes (i.e., subadults, juveniles, newborns) were not considered.

We took standard measurements of body size and head dimensions: head length (snout tip to pileus), head width, head height at the widest and highest point correspondingly (Kaliontzopoulou et al., 2007), maxilla length (from snout tip to the distal portion of the maxilla articular), inter-orbital distance (between the median point of the external margin of the supraoculars), internasal (between the inner margins of nostrils), distance between eye and nostril (from the anterior part of the eye to the posterior nostril margin) and eye diameter. We also measured SVL and tail length, and recorded tail status (as entire, damaged or regenerated) and body mass. We used a centesimal calliper and an electronic balance to record the above variables. Values were expressed as $\text{mm} \pm 1 \text{ SD}$ and $\text{g} \pm 1 \text{ SD}$, with an accuracy of $\pm 0.5 \text{ mm}$ and 0.5 g respectively. We took dorsal, lateral and ventral photographs of all captured lizards (head and abdominal region) to detect the presence of external parasites.

Statistical analyses

Normality of data (sexes pooled together) was tested prior to each analysis (Kolmogorov-Smirnov test, all with $P > 0.05$). Body mass of males ($7.384 \pm 2.19 \text{ g}$, $n=32$) and females ($4.682 \pm 1.34 \text{ g}$, $n=33$) with entire tails was comparable to males ($7.585 \pm 1.86 \text{ g}$, $n=34$) and females ($4.848 \pm 1.06 \text{ g}$, $n=21$) with regenerated tail (Student t -test, male = -0.402 , $df=64$, $P=0.689$; Student t -test, female = -0.478 , $df=52$, $P=0.635$). Thus, tail status did not affect body mass estimation and individuals were pooled for further analyses. We compared body mass, head length, maxilla length, eye diameter, nostril-eye distance, internasal and inter-orbital distances as dependent variables separately for each sex using t -tests and *Mann-Whitney U* tests (depending on normality of data). A multivariate General Linear Model (GLM, multi-way ANOVA) was

used to test for sexual and/or locality effects with SVL as covariate, and sex and capture locality as factors between sexes in each sampling locality. We excluded the individuals from Calci, because we had only three females from that site.

The distribution of tail status (entire, damaged, regenerated) was examined using *Mann-Whitney U* tests. Body condition index, calculated as body mass divided by SVL, was arcsine transformed, tested for normality and analysed with parametric statistics (GLM, univariate ANOVA, with sex and locality as independent factors and as interacting variables). The ratios of head width/head length and head height/head length were tested for differences among localities and between sexes using arcsine transformed values (excluding the Calci sample). Finally, we performed a GLM ANCOVA with sex as factor, latitude and longitude as covariates, considering the interaction sex*latitude and sex*longitude. We used SPSS v.13.0 for all statistical analyses, set α at 0.05, and all tests were two-tailed.

RESULTS

We captured 123 adult *P. siculus*, including 68 males and 55 females. Normality was reached in all variables except head width and head height ($Z=1.484$, $P=0.024$ and $Z=1.372$, $P=0.046$ respectively). Males were longer, heavier and larger in all considered parameters (Student

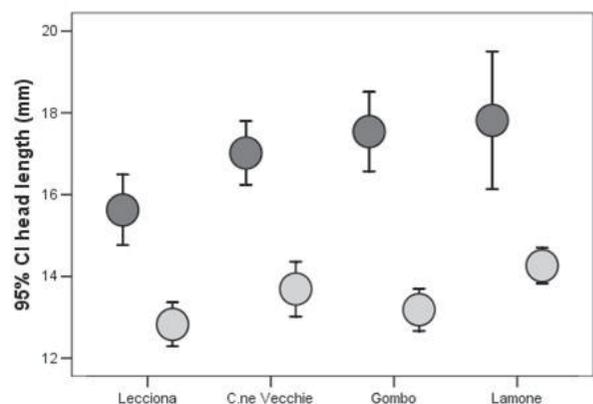


Fig. 2. Head length variation between sexes and among localities in *Podarcis siculus* (males in dark grey, females in light grey).

Table 2. Biometrical features of adult *Podarcis siculus* from northwestern Tuscany. Body mass in g, other variables in mm; for each locality: sample size; mean±1SD).

Variable	Sex	Lecciona	C.ne Vecchie	Gombo	Calci	Lamone
body mass	male	26; 7.6±1.9	16; 7.7±1.8	12; 7.8±1.9	8; 5.1±0.8	6; 8.9±2.4
	female	22; 4.7±1.4	12; 5.1±1.0	13; 4.2±1.1	3; 4.8±1.5	5; 5.6±0.3
SVL	male	26; 65.4±6	16; 67.6±5.8	12; 68.9±5.6	8; 60.0±1.9	6; 69.4±5.9
	female	22; 58.6±5.3	12; 61.9±4.5	13; 57.8±5.2	3; 54.7±3.0	5; 64.7±1.0
tail length	male	26; 118.2±25	16; 110.6±30.9	12; 116.0±30.0	8; 78.7±20.3	6; 121.5±34.7
	female	22; 93.3±23	12; 92.2±39.9	13; 102.2±15.4	3; 99.3±16.5	5; 102.4±16.4
head length	male	26; 15.6±2.1	16; 17.0±1.5	12; 17.5±1.5	8; 15.1±0.6	6; 17.8 ± 1.6
	female	22; 12.8±1.2	12; 13.7±1.1	13; 13.2±0.9	3; 12.8±0.1	5; 14.3±0.3
head width	male	26; 9.4±1.1	16; 10.0±0.9	12; 10.1±1.1	8; 8.9±0.3	6; 10.4±1.0
	female	22; 7.8±0.5	12; 8.1±0.4	13; 7.8±0.6	3; 7.8±0.2	5; 8.7±0.3
head height	male	26; 8.0±0.9	16; 8±1.0	12; 8.5±1.0	8; 7.4±0.4	6; 8.6±1.0
	female	22; 6.5±0.5	12; 6.6±0.5	13; 6.5±0.7	3; 6.4±0.2	5; 6.9±0.3
nostril eye	male	26; 4.6±0.4	16; 4.5±0.5	12; 4.8±0.4	8; 4.1±0.3	6; 4.8±0.4
	female	22; 4.2±0.4	12; 3.7± 0.4	13; 3.8±0.3	3; 3.5±0.1	5; 3.8±0.2
eye diameter	male	26; 3.4±1.1	16; 4.2±0.4	12; 4.0±0.4	8; 3.8±0.3	6; 4.8±0.7
	female	22; 2.6±0.8	12; 3.4±0.3	13; 3.4±0.3	3; 3.4±0.4	5; 3.6±0.3
inter-nasal	male	26; 2.1±0.3	16; 2.2±0.3	12; 2.4±0.3	8; 1.9±0.1	6; 2.3±0.3
	female	22; 1.7±0.2	12; 1.8±0.2	13; 1.8±0.2	3; 1.8±0.1	5; 1.9±0.1
inter-orbital	male	26; 6.2±0.5	16; 6.3±0.5	12; 6.4±0.5	8; 5.6±0.4	6; 6.5±0.6
	female	22; 5.1±1.2	12; 5.5±0.3	13; 5.2±0.3	3; 5.1±0.3	5; 5.6±0.1
maxilla	male	26; 17.9±2.1	16; 18.7±1.3	12; 19.4±1.7	8; 16.9±0.6	6; 19.2±2.3
	female	22; 14.3±1.8	12; 15.3±0.8	13; 14.5±0.9	3; 14.4±0.3	5; 16.3±0.2

t-tests with $P < 0.005$ to $P < 0.0001$ on the whole data set; Table 2). Head width and head height were also significantly larger in males ($U = -8.055$ and $U = -8.087$ respectively, both with $P < 0.0001$).

A general linear model with SVL as a covariate and sex and locality as fixed factors, including the interactions sex*locality and sex*SVL, showed that all variables were highly correlated with SVL ($P < 0.0001$ in all cases). The effect of sex after taking SVL into account was only significant for head length ($P = 0.032$; Fig. 2) and nostril-eye distance ($P = 0.027$; Fig. 3). The effect of locality was significant for all variables except inter-orbital and maxilla ($P = 0.995$ and $P = 0.06$, respectively). Sex and locality interacted significantly only for body mass ($P = 0.007$) and nostril-eye distance ($P = 0.038$). Sex and SVL interacted

significantly for all variables (P ranging from 0.025 to 0.002) with the exception of eye diameter ($P = 0.454$) and inter-orbital distance ($P = 0.998$).

Head width/head length and head height/head length ratios did not vary between sexes and were not affected by sex*locality, but significantly differed among localities ($F = 4.331$, $df = 3$, $P = 0.006$ and $F = 5.311$, $df = 3$, $P = 0.002$, respectively; Figs. 4 and 5). Head height/head width ratios did not show any variation in the model. After arcsine transformation of the ratio nostril-eye distance/head length and tested with a GLM analysis, we found locality effects ($F = 14.996$, $df = 3$, $P < 0.0001$) and SVL covariation ($F = 23.061$, $df = 1$, $P < 0.0001$), but no effects of sex or sex*locality.

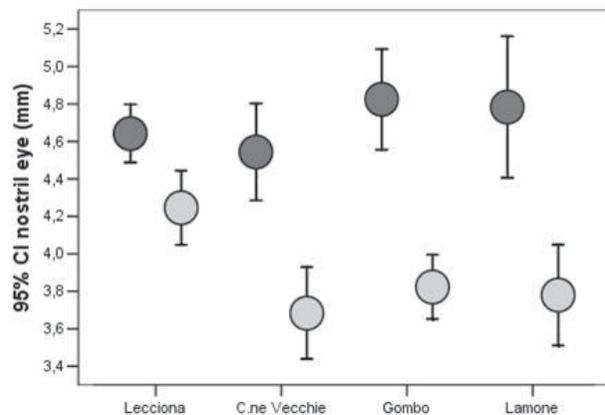


Fig. 3. Nostril-eye distance between sexes and among localities in *Podarcis siculus* (males in dark grey, females in light grey).

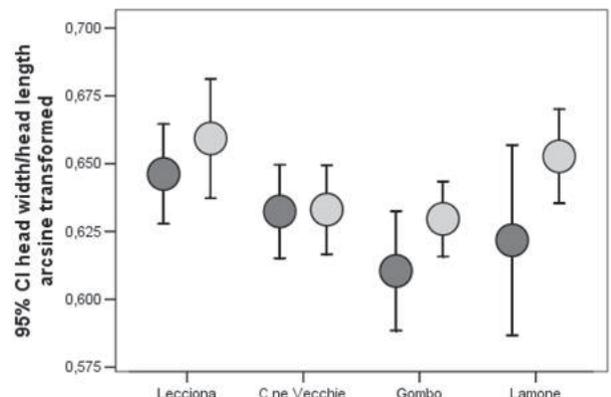


Fig. 4. Head width/head length variation among localities in *Podarcis siculus* (males in dark grey, females in light grey).

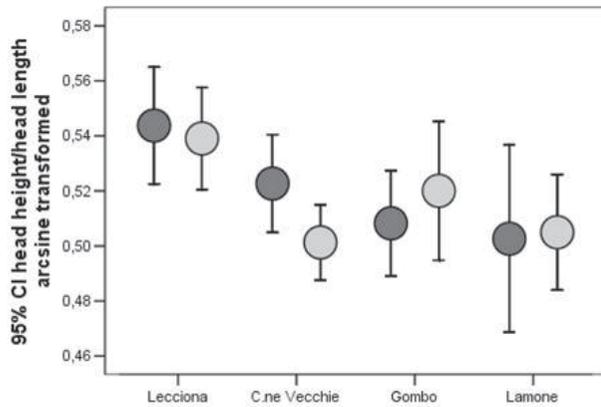


Fig. 5. Head height/head length distribution among localities in *Podarcis siculus* (males in dark grey, females in light grey).

Sixty-five adults (32 males and 33 females) had undamaged tails, while three had recently damaged tails and 55 (34 males and 21 females) had regenerated tails. Excluding individuals with recently damaged tails, tail status was not affected by sex ($U=-1.375$, $P=0.169$) or locality (Median test= 2.090 , $df=4$, $P=0.719$). The Gombo locality was characterized by a high proportion of lizards with undamaged tails (16 undamaged and 9 regenerated tails).

From images taken from 94 lizards (49 males, 45 females), the proportion of lizards parasitized by ticks was similar between sexes (28.57% in males and 35.55% in females). Similarly, no correlation was found among locality, sex, body size, tail status and the presence of external parasites (detailed data not shown).

The body condition index showed a marked sexual dimorphism, with males having significantly higher values ($F=82.753$, $df=1$, $P<0.0001$). There were no significant effects due to locality ($F=1.496$, $df=3$, $P=0.22$), nor any interaction between sex and locality ($F=0.356$, $df=3$, $P=0.785$) (Fig. 6). A relationship close to significance was found with latitude ($P=-0.949$, $df=4$, $P=0.051$) suggesting a possible geographical cline in body status.

There was a marked latitudinal effect especially on head size and a significant sex*latitude interaction on nostril-eye distance (corrected models, $df=5$, P

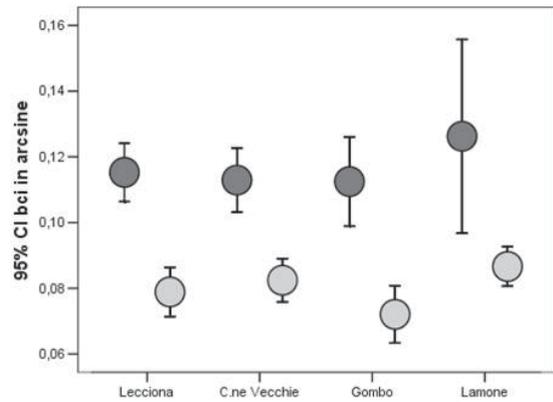


Fig. 6. Body condition index (bci/SVL) in *Podarcis siculus* (males in dark grey, females in light grey).

ranging from 0.0025 to 0.0001, see Table 3). Longitude significantly affected only one variable (nostril-eye, $F=5.534$, $P=0.002$), without any interaction with sex.

DISCUSSION

Adult Italian wall lizards display strong sexual differences, a pattern well known in lizards (Henle & Klaver, 1986; Herrel et al., 2008). Our results revealed sexual size dimorphism (SSD) in head size, as already found in other *Podarcis* and *Lacerta* species (Olsson et al., 2002; Rubolini et al., 2006; Bruner & Costantini, 2007; Kaliontzopoulou et al., 2007). However, in *Podarcis* the variation of SSD among localities has been rarely tested (but see Kaliontzopoulou et al., 2007; Herrel et al., 2008). Extensive analyses on the evolution of SSD, its proximal causes and possible adaptive hypotheses have been recently discussed (Watkins, 1996; McBrayer, 2004; Bruner et al., 2005; Johnson et al., 2005). Our results clearly indicate a general pattern of covariation of all traits due to the influence of SVL, a strong sexual differentiation and a significant interaction of sex*SVL, thus suggesting differential allometric patterns between sexes.

Geographical variation is significant for many parameters, mainly along a latitudinal cline, but we cannot

Table 3. Geographical effect on body size features of *Podarcis siculus* from northwestern Tuscany.

Covariate	dependent variable	F	df	P
latitude	head length	7.579	1	0.007
	head width/head length	5.452	1	0.021
	eye diameter	11.812	1	0.001
	internarial	10.397	1	0.002
	maxilla length	4.105	1	0.045
longitude	nostril-eye	5.534	1	0.020
sex*latitude	nostril-eye	6.138	1	0.015

deduce what could have generated the results we recorded. The whole organismal variation should be furthermore studied in depth (McBrayer, 2004; Bruner et al., 2005; Herrel et al., 2008, 2009). We also found that locality and sex interacted significantly only on head length and on distance between nostril openings and the anterior margin of the eye. These different patterns of head features likely relate to a different size of pre-maxillary and maxillary bones, the corresponding anatomical parts. Tail status patterns suggest that disturbed and/or attacked individuals, divided per sex, are likely in the same percentage across localities. Tail autotomy, usually induced by predation attempts or environmental, human dependent stress (Amo et al., 2006; French et al., 2008), is shared between sexes at similar frequency. Not surprisingly, the highest percentage of intact tails was observed in an undisturbed area (see Table 1). It is, however, important to underline that direct measures or indirect interactions among environmental features (i.e., vegetation coverage, food availability) and biological characteristics of the species (i.e., male-male fights, nesting habitat selection) remained unrecorded, preventing a hypothesis-driven analysis (e.g. Sacchi et al., 2009).

Parasite load has been shown to influence population biology and ecology, ranging from the change of haematocrit formula and favouring the occurrence of haematoparasites to alteration of reproductive frequency and fitness or displacement performance (Davis et al., 2008; Roca & Galdón, 2010). Nevertheless, we are not able to speculate on possible effects of parasites on the sampled lizards. The ratio between SVL and body mass was not affected by any measured parameters.

Given the fact that comparative information on *P. siculus* is scarce (see Biaggini et al., 2009; Corti et al., 2010), further research from ecological and functional perspectives as well as on reproductive and behavioural patterns is desirable (Olsson et al., 2002; Fulgione et al., 2008; Sacchi et al., 2009).

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REFERENCES

- Amo, L., López, P. & Martín, J. (2006). Nature-based tourism as a form of predation risk affects body condition and health state of *Podarcis muralis* lizard. *Biological Conservation* 131, 402–409.
- Biaggini, M., Berti, R. & Corti, C. (2009). Different habitats, different pressures? Analysis of escape behaviour and ectoparasite load in *Podarcis sicula* (Lacertidae) populations in different agricultural habitats. *Amphibia-Reptilia* 30, 453–461.
- Bombi, P., Salvi, D., Luiselli, L. & Bologna, M.A. (2009). Modelling correlates of microhabitat use of two sympatric lizards: a model selection approach. *Animal Biology* 59, 109–126.
- Bruner, E. & Costantini, D. (2007). Head morphological variation in *Podarcis muralis* and *Podarcis sicula*: a landmark-based approach. *Amphibia-Reptilia* 28, 566–573.
- Bruner, E., Costantini, D., Fanfani, A. & Dell’Omo, G. (2005). Morphological variation and sexual dimorphism of the cephalic scales in *Lacerta bilineata*. *Acta Zoologica* 86, 245–254.
- Corti, C. (2006). *Podarcis sicula*. In *Atlante degli Anfibi e dei Rettili d’Italia/Atlas of Italian Amphibians and Reptiles*. Sindaco, R., Doria, G., Razzetti, E. & Bernini, F. (eds.), Societas Herpetologica Italica, 486–489. Firenze: Edizioni Polistampa.
- Corti, C., Biaggini, M. & Capula, M. (2010). *Podarcis siculus* (Rafinesque-Schmalz, 1810). In *Fauna d’Italia. 47. Reptilia*, 407–417. Corti, C., Capula, M., Luiselli, L., Razzetti, E. & Sindaco, R. (eds.), Ministero dell’Ambiente e Tutela del Territorio, Direzione Protezione della Natura: Calderini Gruppo 24 Ore.
- Crnobrnja-Isailovic, J., Vogrin, M., Corti, C., Pérez Mellado, V., Sá-Sousa, P., Cheylan, M., Pleguezuelos, J., Sindaco, R., Romano, A. & Avci, A. (2008). *Podarcis siculus*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.1. <www.iucnredlist.org>. Downloaded on 03 August 2011.
- Davis, A.K., Maney, D.L. & Maerz, J.C. (2008). The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. *Functional Ecology* 22, 760–772.
- French, S.S., Fokidis, H.B. & Moore, M.C. (2008). Variation in stress and innate immunity in the tree lizard (*Urosaurus ornatus*) across an urban-rural gradient. *Journal of Comparative Physiology B* 178, 997–1005.
- Fulgione, D., Guglielmi, S., Odierna, G., Ripa, D., Caliendo, M.F. & Rastogi, R.K. (2008). Morphological differentiation and genetic structure in island lizard populations. *Zoological Science* 25, 465–474.
- Henle, K. & Klaver, C.J.J. (1986). *Podarcis sicula* (Rafinesque-Schmalz, 1810) – Ruineidechse. In *Handbuch der Reptilien und Amphibien Europas, 2/II. Echsen (Sauria) III (Lacertidae III: Podarcis)*, 254–342. Böhme W. (ed.), Wiesbaden: AULA-Verlag.
- Herrel, A., Huyghe, K., Vanhooydonck, B., Backeljau, T., Breugelmans, K., Grbac, I., Van Damme, R., Duncan, J. & Irschick, D.J. (2008). Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. *Proceedings of the National Academy of Science* 105, 4792–4795.
- Herrel, A., Schaerlaeken, V., Moravec, J. & Ross, C.F. (2009). Sexual shape dimorphism in Tuatara. *Copeia* 4, 727–731.
- Johnson, J.B., McBrayer, L.D. & Saenz, D. (2005). Allometry, sexual size dimorphism, and niche partitioning in the mediterranean gecko (*Hemidactylus turcicus*). *The Southwestern Naturalist* 50, 435–439.
- Kaliontzopoulou, A., Carretero, M.A. & Llorente, G.A. (2007). Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. *Journal of Morphology* 268, 152–165.
- Lanza, B., Garavelli, P. & Corti, C. (1993). Clinal variation in some meristic characters of the Italian wall lizard *Podarcis sicula* (Rafinesque-Schmalz, 1810). In *Lacertids of the Mediterranean region*, 43–49. Valakos, E.D., Böhme, W., Perez-Mellado, V. & Maragou, P. (eds.), Hellenic Zoological Society.
- Lo Cascio, P. & Corti, C. (2008). Indagini sull’ecologia dei rettili sauri della R.N.O. e del S.I.C. “Isola di Lampedusa”. *Naturalista siciliano, S. IV*, 32, 319–354.
- McBrayer, L.D. (2004). The relationship between skull

- morphology, biting performance and foraging mode in Kalahari lacertid lizards. *Zoological Journal of the Linnean Society* 140, 403–416.
- Olsson, M., Shine, R., Wapstra, E., Ujvari, B. & Madsen, T. (2002). Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* 56, 1538–1542.
- Perez-Mellado, V. & Corti, C. (1993). Dietary adaptation and herbivory in Lacertid lizards of the genus *Podarcis* from Western Mediterranean islands (Reptilia: Sauria). *Bonner Zoologische Beiträge* 44, 193–220.
- Perez-Mellado, V., Ortega, F., Martín-García, S., Perera, A. & Cortázar, G. (2000). Pollen load and transport by the insular lizard, *Podarcis lilfordi* (Squamata, Lacertidae) in coastal islets of Menorca (Balearic islands, Spain). *Israel Journal of Zoology*, 46, 193–200.
- Roca, V. & Galdón, M.A. (2010). Haemogregarine blood parasites in the lizards *Podarcis bocagei* (Seoane) and *P. carbonelli* (Pérez-Mellado) (Sauria: Lacertidae) from NW Portugal. *Systematic Parasitology* 75, 75–79.
- Rubolini, D., Pupin, F., Sacchi, R., Gentilli, A., Zuffi, M.A.L., Galeotti, P. & Saino, N. (2006). Sexual dimorphism in digit length ratios in two reptile species. *Anatomical Record A* 288A, 491–497.
- Sacchi, R., Pupin, F., Gentilli, A., Rubolini, D., Scali, S., Fasola, M. & Galeotti, P. (2009). Male-male combats in a polymorphic lizard: residency and size, but not color, affect fighting rules and contest outcome. *Aggressive Behaviour* 35, 274–283.
- Watkins, G.G. (1996). Proximate causes of sexual size dimorphism in the iguanian lizard *Microlophus occipitalis*. *Ecology* 77, 1473–1482.

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