

Effective thermoregulation in a newly established population of *Podarcis siculus* in Greece: a possible advantage for a successful invader

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Abstract. Temperature affects all aspects of reptilian biology. In order to colonize new habitats and support viable populations lizards have to successfully deal with their thermal environment. *Podarcis siculus* is a notorious example of a successful colonizer that has invaded numerous habitats outside its natural distribution range. Though certain features of its thermal biology have been assessed so far, the thermoregulatory abilities of the species remain poorly described. Here we investigated a recently discovered population in Greece and evaluated the effectiveness of thermoregulation measuring three main thermal parameters: set-point range, operative and field body temperatures. The Greek *P. siculus* appear to be accurate, precise and effective thermoregulators achieving $E = 0.96$. This effective thermoregulation may be used to explain, among other special characteristics, its spreading success.

Keywords. Temperature, thermoregulation, invasive species, Italian wall lizard, Greece.

INTRODUCTION

Thermoregulation is crucial in ectotherms, shaping all features of their overall biology (Bartholomew, 1982). In small reptiles like lizards, thermoregulation is most times achieved behaviorally through appropriate movements between warmer and cooler microhabitat sites, shade and sun (Avery, 1982; Stevenson, 1985). Systematic research of reptilian thermal biology dates back to the mid-1940s (Cowles and Bogert, 1944). In 1976, Huey and Slatkin introduced a concise and detailed model to evaluate thermoregulation in ectotherms. This paradigm remained in use for the next two decades until Hertz and his partners (1993) fundamentally changed the way thermoregulation was perceived and proposed a thorough research protocol to answer a question of paramount importance: how effectively do lizards thermoregulate?

In order to answer this question, Hertz et al. (1993) took into account three main parameters: body temperatures (T_b , the temperature that animals achieve in the field), operative temperatures (T_e , the temperature that a non-regulating animal would achieve in the field, measured with the use of models), and the species' set-point range (T_{set} , the temperature that animals select in a laboratory setting in the absence of any ecological constraints). Therefore T_b can be viewed as the result of the species' mean T_{set} , which is considered a thermal utopia under ideal conditions (Sagonas et al., 2013a) and its interactions with a biotope's T_e . By considering these variables together, we are able to assess the effectiveness, accuracy and precision of thermoregulation of any given species (Hertz et al., 1993).

The Italian Wall Lizard *Podarcis siculus* (Rafinesque-Schmaltz, 1810) (Sauria, Lacertidae) is definitely not any

given species. It is a small-bodied (snout-vent length, SVL, up to 90 mm; Corti and Lo Cascio, 2002), diurnal, heliothermic lacertid that feeds mainly on terrestrial invertebrates (Corti, 2006), although its diet may include unusual food resources such as rodents, geckos and even conspecifics (Capula and Aloise, 2011; Grano et al., 2011), revealing a flexible and opportunistic feeder (Zuffi and Giannelli, 2013), as most lacertids are (Scali et al., 2015). A native lizard of the Italian peninsula and north Adriatic coasts, *P. siculus* has recently expanded its distribution in many other Mediterranean countries by establishing numerous new populations (Crnobrnja Isailovic et al., 2009). Its excellent dispersal abilities (Vignoli et al., 2012) are underscored by the fact that it is the only *Podarcis* lizard that can be found in four continents: Europe, Asia, North America and Africa (Arnold and Ovenden, 2002; Kolbe et al., 2013; Tok et al., 2015). As such, *P. siculus* has been widely used as a model organism in numerous ecological, physiological, behavioral and phylogenetic studies (Fulgione et al., 2004; Podnar et al., 2005; Bonacci et al., 2008; Biaggini et al., 2009; Vervust et al., 2010; Raia et al., 2010). Several aspects of its thermal biology have been also studied (Avery, 1978; Ouboter, 1981; Van Damme et al., 1990; Tosini et al., 1992, 1996). However, its thermoregulation effectiveness (*sensu* Hertz et al., 1993) remains undetermined.

In this study, we worked with a new, recently established population in Greece (Adamopoulou, 2015). We focused on the thermoregulatory capacity of *P. siculus* by measuring the three main thermal features, that is T_b , T_c , and mean T_{set} . Furthermore, we compared the published data on set-point range temperatures from different sites within the species range. We hypothesized that since *P. siculus* is a highly successful colonizer capable of adapting easily to new habitats, it should achieve effective thermoregulation.

MATERIALS AND METHODS

The study site (Palaio Faliro) is located along the back side of a sandy beach in the Athens, Greece (37°55'9.38"N, 23°42'0.50"E). It is a heavily modified habitat planted with oleanders, tamarisks and yuccas delimited by a crowded beach on the front and a highway avenue on the back. The only other reptile recorded on site was the Ocellated skink (*Chalcides ocellatus*). The site represents the only known location of *P. siculus* in Greece (Adamopoulou, 2015), which probably originates from the Adriatic region (Silva-Rocha et al., 2014).

In May 2015 we measured the operative temperatures of the site using 31 hollow, electroformed copper models that mimic the size, shape and reflectance of the species and were validated against live animals in the field (Bakken, 1992; Dzialowski, 2005). To simulate the heat capacity of the lizards, we

added 2.5-3 ml of water into each model, both ends of which were sealed with plasticine, except for a narrow opening where the probe of a data-logger (HOBO U12 4-Channel External Data Logger - U12-008) was inserted (Diaz, 1997; Grbac and Bauwens, 2001). The models were placed on various spots on site so as to cover all types of microhabitats available to lizards (Huey, 1991). We recorded T_c every 15 minutes for two consecutive days (09:00-19:00).

To ensure that the temperature responses between the copper models and the study animals were similar, we tested their cooling and heating rate (Lutterschmidt and Reinert, 2012). An adult male lizard and a copper model were placed side by side near a heating source (two 140 W lamps) for 45 minutes. Subsequently, the heating source was turned off and the subjects were left to cool down for 45 minutes, resulting in a total period of 90 minutes. During this period we recorded the temperature of the model and the lizard every five minutes with a Weber quick reading cloacal thermometer. A linear regression of T_b on T_c suggested that there was a good fit between the model and the animal responses (regression statistics \pm SE; slope = 1.305 ± 0.118 , intercept = -7.290 ± 3.557 , $r^2 = 0.928$, $P < 0.001$).

The body temperatures (T_b) of 30 individuals were measured on site during the same dates that T_c s were sampled. Lizards were caught by hand or noose from all occupied microhabitats and their temperature was measured within 20 seconds using a quick-reading cloacal thermometer (T-4000, Miller & Weber, Inc., Queens, NY) to the nearest 0.1 °C. For every lizard caught we also measured SVL with digital calipers (Silverline 380244, accurate to 0.01 mm) while sex was determined by inspection of the femoral pores.

Finally, 11 adult males (since sampling took place within the reproductive period we tried to avoid the impact of sex on set-point range temperatures; Carneiro et al., 2015) were transferred to the laboratory facilities of the Department of Biology at the University of Athens to measure T_{set} . The lizards were placed in a specially designed terrarium (100 x 25 x 25 cm) where a thermal gradient (10-60 °C) was achieved with the use of two incandescent heating lamps (100 W and 60 W) at one end and two ice bags on the opposite (Van Damme et al., 1991). Subsequently their body temperature was measured every 30 min for four consecutive hours (Castilla and Bauwens, 1991) using a quick-reading cloacal thermometer (T-4000, Miller & Weber, Inc., Queens, NY). We used the inter-quartile range of the body temperatures selected by lizards in the thermal gradient (Hertz et al., 1993).

To evaluate the effectiveness of thermoregulation we used the formula: $E = 1 - (\bar{d}_b/\bar{d}_e)$, where \bar{d}_b represents the mean deviation of field T_b s from mean T_{set} and \bar{d}_e provides a measure of thermoregulation accuracy and the mean deviation of T_c s from mean T_{set} (Hertz et al., 1993). Mean \bar{d}_b provides an index of the accuracy of thermoregulation whereas \bar{d}_e sketches out the thermal quality of the habitat. E may range from zero (perfect thermoconformers) to one (perfect thermoregulators).

Complementary to the classical evaluation of the thermoregulatory effectiveness (Hertz et al., 1993), we also employed an alternative approach that quantifies the extent of departure from perfect thermoconformity (Blouin-Demers and Weatherhead, 2001). In the latter, positive values of the differ-

ence between \bar{d}_e and \bar{d}_b describe thermoregulation, zero represents animals demonstrating perfect thermoconformity, and negative values describe animals avoiding habitats of high thermal quality. The magnitude of the difference ($\bar{d}_e - \bar{d}_b$) provides an index of the thermoregulatory effectiveness (Blouin-Demers and Weatherhead, 2001).

RESULTS

Our results (male SVL = 74.3 ± 3.5 mm, $n = 9$; female SVL = 65.3 ± 7.0 mm, $n = 20$; t-test, $t = -3.650$, $df = 27$, $P = 0.001$) corroborated the typical pattern of sexual body size differences according to which male *P. siculus* are larger than females (Henle and Klaver, 1986).

Males did not differ from females in their T_b (t-test, $t = 0.758$, $df = 28$, $P = 0.455$) and achieved similar body temperatures in the field (mean T_b for males = 33.2, mean T_b for females = 32.6). The mean value for the pooled T_b data was 32.8°C (Table 1). The majority of T_b fell within the spectrum of mean T_{set} while the diel variation of body temperatures was limited (Fig. 1). Operative

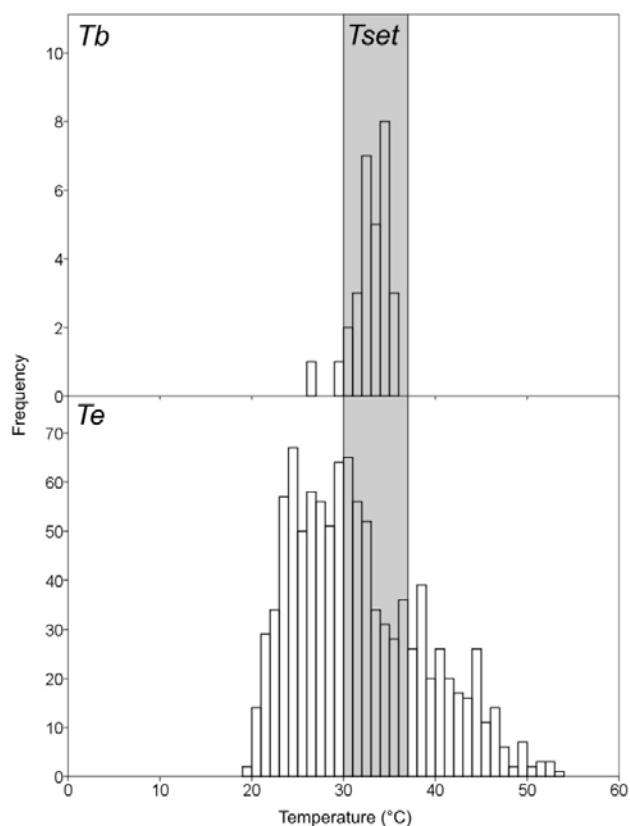


Fig. 1. Distribution of the mean body temperature in the field (T_b) and the mean operative temperature (T_e). The shaded area indicates the set-point range (T_{set}) measured in the laboratory.

Table 1. The thermal variables used in this study: operative temperatures (T_e), body temperatures in the field (T_b), set-point range (T_{set}), deviation of T_e from T_{set} (d_e) and deviation of T_b from T_{set} (d_b).

Variable	n	Mean (°C)	Range (°C)	SD	SE
T_e	31	31.7	19.5 – 53.4	7.10	0.22
d_e	31	3.2	0 – 16.4	3.30	0.10
T_b	30	32.8	26.8 – 35.8	1.94	0.35
d_b	30	0.1	0 – 3.2	0.59	0.11
T_{set}	11	33.8	30.0 – 37.0	2.25	0.30

temperatures ranged from 19.5 °C at 09:00 h (minimum) to 53.4 °C at 14:15 (maximum) and mean T_e was 31.7 °C (Table 1, Fig. 1). T_{set} values ranged from 30.0°C to 37.0 °C (Table 1). Lizards achieved a mean set-point temperature of 33.8 °C (Table 1). The mean deviation of T_b from mean T_{set} was 0.1 °C while the mean deviation of T_e from mean T_{set} was 3.2 °C (Table 1). These values were used to estimate the effectiveness of thermoregulation (*sensu* Hertz et al., 1993), that was $E = 0.96$. This value indicates that *P. siculus* is an active thermoregulator, as expected from the closeness of body temperatures to mean T_{set} . The complementary approach we used (Blouin-Demers and Weatherhead, 2001), also revealed high thermoregulatory effectiveness ($\bar{d}_e - \bar{d}_b = 3.1$)

DISCUSSION

This study provides a comprehensive analysis of the thermoregulation effectiveness of the Italian wall lizard. In line with our first hypothesis, *P. siculus* proved to be an effective thermoregulator and able to achieve body temperatures within mean T_{set} . Body temperatures that lizards achieve in the field vary considerably among different biotopes (Avery, 1978; Van Damme et al., 1990; Tosini et al., 1992), in accordance with our second prediction.

Operative temperatures at the study site revealed – at least during the study period – a benign habitat lacking extreme temperatures (Table 1). Nonetheless, the site offers the lizards the required thermal heterogeneity for behavioral thermoregulation. Mean d_e received a low value (3.2), indicating the high thermal quality of the habitat. In other words, lizards can easily achieve body temperatures within mean T_{set} .

Set-point range temperatures are critically important in reptiles as they determine the optimal overall performance of the animal (Clusella-Trullas et al., 2007). Many factors, such as season, sex, age, reproductive status, body size and habitat may affect T_{set} (Andrews et al., 1999; Car-

Table 2. Studies on mean set-point range (T_{set}) and effectiveness of thermoregulation (E) in *Podarcis* lizards.

Species	Location	E	T_{set}	Reference
<i>P. siculus</i>	Athens, Greece	0.96	33.8	This study
<i>P. liolepis</i>	Columbretes Island, Spain	0.95	34.2	Bauwens et al., 1996
<i>P. milensis</i>	Milos Island, Greece	0.95	33.4	Adamopoulou and Valakos, 2005
<i>P. lilfordi</i>	Menorca Island, Spain	0.88	35	Ortega et al., 2014
<i>P. gaigeae</i>	Skyros Island, Greece	0.87	33.7	Sagonas et al., 2013a
<i>P. levendis</i>	Pori Island, Greece	0.84	33.9	Lymberakis et al., 2015
<i>P. muralis</i>	Cres, Croatia	0.81	31.9	Grbac and Bauwens, 2001
<i>P. peloponnesiacus</i>	Peloponnese, Greece	0.76	34	Pafilis, 2003
<i>P. erhardii</i>	Andros Island, Greece	0.66	35.1	Pafilis, 2003
<i>P. melisellensis</i>	Cres, Croatia	0.63	33.5	Grbac and Bauwens, 2001
<i>P. tiliguerta</i>	Corsica, France		35.47	Van Damme et al., 1990
<i>P. bocagei</i>	Spain		35.15	Bauwens et al., 1995
<i>P. tauricus</i>	Peloponnese, Greece		33.8	Pafilis, 2003
<i>P. vaucheri</i>	Ketama, Morocco		33.43	Verissimo and Carretero, 2009
<i>P. hispanicus</i>	Bellaterra, Spain		33.07	Carretero et al., 2006
<i>P. hispanicus</i>	Galera, Spain		31.65	Carretero, 2012

retero et al., 2005; Carretero, 2008; Veríssimo and Carretero, 2009; Sagonas et al., 2013 a, b). The mean T_{set} for *P. siculus* was 1°C lower than the only other value reported in literature (Avery 1978) and falls within the upper percentile of the thermal range of other *Podarcis* species (Table 2).

To the best of our knowledge there are three published studies that present data on the set-point range and body temperatures of *P. siculus* (Avery, 1978; Van Damme et al., 1990; Tosini et al., 1992). The Greek population achieved higher T_{bs} in the field than lizards in Pisa (32.04 °C, Tosini et al., 1992) but lower compared to the populations from Tuscany (35.16 °C, Avery, 1978) and Corsica (33.89 °C, Van Damme et al., 1990). In regard to set-point range temperatures the mean T_{set} in the Italian population is approximately 1 °C higher (34.79 °C, Avery, 1978) than the one estimated in the present study.

An interesting finding was that T_{bs} did not vary considerably during the day, contrary to other *Podarcis* lizards (e.g., Adamopoulou and Valakos, 2005; Sagonas et al., 2013a), a feature that was also reported by previous studies (Van Damme et al., 1990; Tosini et al., 1992). The limited range of T_{bs} is an indication of high precision in thermoregulation (Hertz et al., 1993). As predicted by the low \bar{d}_e that was mentioned above, an impressive 93% of all T_{bs} fell within the measured range of mean T_{set} . This corresponded to a very low mean d_b (0.1), which suggests high thermoregulation accuracy (Hertz et al., 1993). Thus, *P. siculus* appears to be not only a precise thermoregulator (Van Damme et al., 1990; Tosini et al., 1992) but also an accurate one.

The index of thermoregulation effectiveness took a high value ($E = 0.96$), which is among the highest that have been reported so far, not only for *Podarcis* lizards (Table 2) but among all lacertids. When animals are unable to thermoregulate, E will approach zero, whereas when they can successfully regulate their body temperature, E will be close to one (Hertz et al., 1993). According to our results, *P. siculus*, at least in the study ecosystem, is actively thermoregulating with great success. This is directly related to the small deviation of T_{bs} from mean T_{set} . At this point we have to stress out that the evaluation of E was based on mean T_{set} that was calculated from exclusively male individuals and also that a limited number of T_{bs} were obtained in a short period of time.

In order to invade new ecosystems and establish viable populations, animals have to fulfill certain requirements (Kolar and Lodge, 2001). Ectotherms need to furthermore meet additional thermal demands: they have to adapt swiftly to the environmental temperatures of the new biotope while, at the same time, perform close to optimal levels (Kraus, 2009). Thermal specialists, which achieve optimal performance in a narrow range of temperatures, are less apt to invade new habitats than thermal generalists (Angilletta et al., 2003; Angilletta, 2009). The Italian wall lizard is a successful colonizer thanks to the quick acclimatization and adaptability to the environmental conditions of the new “home” and to the numerous ways of dispersal (Deichsel et al., 2010; Valdeón et al., 2010; Silva-Rocha et al., 2012, 2014). Our findings suggest that *P. siculus* is able to effectively, accurately and precisely regulate its body temperature. Thanks to this

effective thermoregulation, it may overcome the thermal challenges of new environments.

As *P. siculus* settles new populations, there is strong evidence that it competes with native lacertids. Downes and Bauwens (2002) found that *P. siculus* is more aggressive and dominant than *Podarcis melisellensis* and occupies better thermal microhabitats. In laboratory experiments, *P. siculus* was also more aggressive and eventually suppressed activity levels in *Podarcis tiliguerta* (Vanhooydonck et al., 2000). Furthermore, *P. siculus* hybridizes with other endemic *Podarcis* lizards (Capula, 1993; Capula, 2002; Capula et al., 2002). The above considerations highlight the risk that *P. siculus* poses for autochthonous species, above all for Greece, which is home to seven endemic lacertids (Valakos et al., 2008). Since *P. siculus* has become established in Athens, it is only matter of time before it invades places that host endemic lizards (e.g., Peloponnese, Milos, Skyros, Crete). To eliminate the danger of further dispersal and the concomitant negative effects, the investigated Athens population of *P. siculus* needs to be exterminated. The Hellenic Herpetological Society inaugurated an eradication project in spring 2015. More than 150 individuals have been captured so far indicating that the initially estimated 50-60 animals (Adamopoulou, 2015) have multiplied to a much larger actual population in only a couple of years.

This study, in spite of sampling flaws in field and lab temperature measurements, paves the way for delineating the particular features of ectotherms, which, like *P. siculus*, rapidly expand their distribution. Further research that will assess the thermoregulation pattern of *P. siculus* in diverse habitats throughout its range is badly required. Effectiveness of thermoregulation and mean T_{set} should be the focal points. Thereby it will be clarified whether the successful dispersal of the species is due to a standardized, conservative thermal pattern (the “static” view, Bogert, 1949) or just a response to environmental factors (the “labile” view, Huey, 1982). If E will receive equally high values and mean T_{set} will be similar to the studied population, then *P. siculus* will be indeed an effective thermoregulator with a conservative thermal physiology. Our results are the first step to this end.

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REFERENCES

- Adamopoulou, C. (2015): First record of *Podarcis siculus* (Rafinesque-Schmaltz, 1810) from Greece. *Herpetozoa* **27**: 187-188.
- Adamopoulou, C., Valakos, E.D. (2005): Thermal ecology and activity cycle of *Podarcis milensis* in a sandy coastal area. *Isr. J. Zool.* **51**: 39-52.
- Andrews, R.M., Mendez de la Cruz, F.R., Villagran-Santa Cruz, M., Rodriguez-Romero F. (1999): Field and selected body temperatures of the lizard *Sceloporus aeneus* and *Sceloporus bicanthalis*. *J. Herpetol.* **33**: 93-100.
- Angilletta, M.J. (2009): Thermal adaptation: A theoretical and empirical synthesis. Oxford University Press, Oxford.
- Angilletta, M.J., Wilson, R.S., Navas, C.A., James, R.S. (2003): Tradeoffs and the evolution of thermal reaction norms. *Trends Ecol. Evol.* **18**: 234-240.
- Arnold, E.N., Ovenden, D.W. (2002): A field guide to the Reptiles and Amphibians of Britain and Europe. Harper Collins Publishers Ltd, London.
- Avery, R.A. (1978): Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from central Italy. *J. Anim. Ecol.* **47**: 143-158.
- Avery, R.A. (1982): Field studies of body temperatures and thermoregulation. In: *Biology of the Reptilia*, Vol. 12: Physiology C, Physiological Ecology, pp. 93-166. Gans, C., Pough, F.H., Eds, Academic Press, New York.
- Bakken, G.S. (1992): Measurement and application of operative and standard operative temperatures in ecology. *Am. Zool.* **32**: 194-216.
- Bartholomew, G.A. (1982): Physiological control of body temperature. In: *Biology of the Reptilia*, Vol. 12: Physiology C, Physiological Ecology, pp. 167-211. Gans, C., Pough, F.H., Eds, Academic Press, New York.
- Bauwens, D., Garland, Jr., T., Castilla, A.M., Van Damme, R. (1995): Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* **49**: 848-863.
- Bauwens, D., Hertz, E.E., Castilla, A.M. (1996): Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* **77**: 1818-1830.
- 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.
- Blouin-Demers, G., Weatherhead, P.J. (2001): Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a ther-

- mally challenging environment. *Ecology* **82**: 3025-3043.
- Bogert, C.M. (1949): Thermoregulation in reptiles, a factor in evolution. *Evolution* **3**: 195-211.
- Bonacci, T., Aloise, G., Brandmayr, P., Zetto Brandmayr, T., Capula, M. (2008): Testing the predatory behavior of *Podarcis sicula* (Reptilia: Lacertidae) towards aposematic and non-aposematic prey. *Amphibia-Reptilia* **29**: 449-453.
- Capula, M. (1993): Natural hybridization in *Podarcis sicula* and *P. wagleriana* (Reptilia: Lacertidae). *Biochem. Syst. Ecol.* **21**: 373-380.
- Capula, M. (2002): Genetic evidence of natural hybridization between *Podarcis sicula* and *Podarcis tiliguerta* (Reptilia). *Amphibia-Reptilia* **23**: 313-321.
- Capula, M., Luiselli, L., Bologna, M.A., Ceccarelli, A. (2002): The decline of the Aeolian wall lizard, *Podarcis raffonei*: causes and conservation proposals. *Oryx* **36**: 66-72.
- Capula, M., Aloise, G. (2011): Extreme feeding behaviours in the Italian wall lizard, *Podarcis siculus*. *Acta Herpetol.* **6**: 11-14.
- Carneiro, D., García-Muñoz, E., Kaliontzopoulou, A., Llorent, G.A., Carretero, M.A. (2015): Comparing ecophysiology traits in two *Podarcis* wall lizards with overlapping ranges. *Salamandra* **51**: 335-344.
- Carretero, M.A. (2008): Preferred temperatures of *Tarentola mauritanica* in spring. *Acta Herpetol.* **3**: 57-64.
- Carretero, M.A. (2012): Measuring body temperatures in small lacertids: infrared vs. contact thermometers. *Bas. Appl. Herpetol.* **26**: 99-105.
- Carretero, M.A., Roig, J.M., Llorente, G.A. (2005): Variation in preferred body temperatures in an oviparous population of *Lacerta (Zootoca) vivipara*. *Herpetol. J.* **15**: 51-55.
- Carretero, M.A., Marcos, E., de Prado, P. (2006): Intraspecific variation of preferred temperatures in the NE form of *Podarcis hispanica*. In: Mainland and insular lacertid lizards: a Mediterranean perspective, p. 55-64. Corti, C., Lo Cascio, P., Biaggini, M., Eds, Firenze University Press, Florence.
- Castilla, A.M., Bauwens, D. (1991): Thermal biology, microhabitat selection, and conservation of the insular lizard *Podarcis hispanica atrata*. *Oecologia* **85**: 366-374.
- Clusella Trullas, S., Terblanche, J.S., van Wyk, J.H., Spotila, J.R. (2007): Low repeatability of preferred body temperature in four species of Cordylid lizards: Temporal variation and implications for adaptive significance. *Evol. Ecol.* **21**: 63-79.
- Corti, C. (2006): *Podarcis sicula*. *Lucertola campestre*, Italian wall lizard. In: Atlante degli Anfibi e dei Rettili d'Italia. Atlas of Italian Amphibians and Reptiles, pp. 486-489, Sindaco, R., Doria, G., Razzetti, E., Bernini, F., Eds, Polistampa, Firenze.
- Corti, C., Lo Cascio, P. (2002): The Lizards of Italy and Adjacent Areas. Chimaira Verlag, Frankfurt am Main.
- Cowles, R.B., Bogert, C.M. (1944): A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. Nat. Hist.* **83**: 265-296.
- Crnobrnja Isailovic, J., Vogrin, M., Corti, C., Pérez Mel-lado, V., Sá-Sousa, P., Cheylan, M., Pleguezuelos, J., Sindaco, R., Romano, A., Avci, A. (2009): *Podarcis siculus*. The IUCN Red List of Threatened Species 2009: e.T61553A12515189.
- Deichsel, G., Nafis, G., Hakim, J. (2010): *Podarcis siculus* (Italian Wall Lizard) USA: California. *Herpetol. Rev.* **41**: 513-514.
- Diaz, J.A. (1997): Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. *Funct. Ecol.* **11**: 79-89.
- Downes, S., Bauwens, D. (2002): An experimental demonstration of direct behavioural interference in two Mediterranean lacertid lizard species. *Anim. Behav.* **63**: 1037-1046.
- Dzialowski, E.M. (2005): Use of operative and standard operative temperature models in thermal biology. *J. Therm. Biol.* **30**: 317-334.
- Fulgione, D., Milone, M., Capriglione, T., Guarino, F.M., Rippa, D., Odierna, G. (2004): Genetic analysis in a mainland melanistic lizard (*Podarcis sicula*) population from Cilento and Vallo di Diano National Park (Campania, Italy). Supplement 2. *Ital. J. Zool.* **71**: 25-28.
- Grano, M., Cattaneo, C., Cattaneo, A. (2011): A case of cannibalism in *Podarcis siculus campestris* De Bette, 1857 (Reptilia, Lacertidae). *Biodiv. J.* **2**: 151-152.
- Grbac, I., Bauwens, D. (2001): Constraints on temperature regulation in two sympatric *Podarcis* lizards during autumn. *Copeia* **2001**: 178-186.
- Henle, K., Klaver, C.J.J. (1986): *Podarcis sicula* (Rafinesque-Schmaltz, 1810) - Ruineneidechse. In: Handbuch der Amphibien und Reptilien Europas, Echsens III (*Podarcis*), pp. 254-342. Böhme, W., Ed, Aula-Verlag, Wiesbaden.
- Hertz, P.E., Huey, R.B., Stevenson, R.D. (1993): Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* **142**: 796-818.
- Huey, R.B. (1982): Temperature, physiology, and the ecology of reptiles. In: *Biology of the Reptilia*, Vol. 12: Physiology C, Physiological Ecology, pp. 25-91. Gans, C., Pough, F.H., Eds, Academic Press, New York.

- Huey, R.B. (1991): Physiological consequences of habitat selection. *Am. Nat.* **137**: S95-S115.
- Huey, R.B., Slatkin, M. (1976): Cost and benefits of lizard thermoregulation. *Q. Rev. Biol.* **51**: 363-384.
- Kolar, C.S., Lodge, D.M. (2001): Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* **16**: 199-204.
- Kolbe, J.J., Lavin, B.R., Burke, R.L., Rugiero, L., Capula, M., Luiselli, L. (2013): The desire for variety: Italian wall lizard (*Podarcis siculus*) populations introduced to the United States via the pet trade are derived from multiple native-range sources. *Biol. Invasions* **15**: 775-783.
- Kraus, F. (2009): Alien Reptiles and Amphibians: A scientific compendium and analysis. Springer, New York.
- Lutterschmidt, W.I., Reinert, H.K. (2012): Modeling body temperature and thermal inertia of large-bodied reptiles: Support for water-filled biophysical models in radiotelemetric studies. *J. Therm. Biol.* **37**: 282-285.
- Lymberakis, P., Valakos, E.D., Sagonas, K., Pafilis, P. (2015): The first ecological data for *Podarcis lewendis*, one of the most rare lizards in Europe. In: Abstracts of the International Congress on the Zoogeography and Ecology of Greece and Adjacent Regions, p. 147. Poulakakis N., Antoniou, A., Karameta, E., Psonis, N., Vardinoyannis K., Eds, Hellenic Zoological Society, Irakleio.
- Ortega, Z., Pérez-Mellado, V., Garrido, M., Guerra, C., Villa-García, A., Alonso-Fernández, T. (2014): Seasonal changes in thermal biology of *Podarcis lilfordi* (Squamata, Lacertidae) consistently depend on habitat traits. *J. Therm. Biol.* **39**: 32-39.
- Ouboter, P.E. (1981): The ecology of the island-lizard *Podarcis sicula salfi*: correlations of microdistribution with vegetation coverage, thermal environment and food-size. *Amphibia-Reptilia* **2**: 243-257.
- Pafilis, P. (2003): Adaptations of lacertid lizards based on their thermal biology, metabolic rate and phylogenetic history. Ph.D. Thesis, National and Kapodistrian University of Athens, Greece.
- Podnar, M., Mayer, W., Tvrtković, N. (2005): Phylogeography of the Italian wall lizard, *Podarcis sicula*, as revealed by mitochondrial DNA sequences. *Mol. Ecol.* **14**: 575-88.
- Raia, P., Guarino F.M., Turano, M., Polese, G., Rippa, D., Carotenuto, F., Monti, D.M., Cardi, M., Fulgione, D. (2010): The blue lizard spandrel and the island syndrome. *BMC Evol. Biol.* **10**: 289.
- Sagonas, K., Valakos, E.D., Pafilis, P. (2013a): The impact of insularity on the thermoregulation of a Mediterranean lizard. *J. Therm. Biol.* **38**: 480-486.
- Sagonas, K., Meiri, S., Valakos, E.D., Pafilis, P. (2013b): The effect of body size on the thermoregulation of lizards on hot, dry Mediterranean islands. *J. Therm. Biol.* **38**: 92-97.
- Scali, S., Sacchi, R., Mangacotti, M., Pupin, F., Gentili, A., Zucchi, C., Sannolo, M., Pavesi, M., Zuffi, M.A.L. (2015): Does a polymorphic species have a “polymorphic” diet? A case study from a lacertid lizard. *Biol. J. Linn. Soc.* **117**: 492-502.
- Silva-Rocha, I., Salvi, D., Carretero, M.A. (2012): Genetic data reveal a multiple origin for the populations of the Italian Wall lizard *Podarcis sicula* (Squamata: Lacertidae) introduced in the Iberian Peninsula and Balearic Islands. *Ital. J. Zool.* **79**: 502-510.
- Silva-Rocha, I., Salvi, D., Harris, D.J., Freitas, S., Davis, C., Foster, J., Deichsel, G., Adamopoulou, C., Carretero, M.A. (2014): Molecular assessment of *Podarcis sicula* populations in Britain, Greece and Turkey reinforces a multiple-origin invasion pattern in this species. *Acta Herpetol.* **9**: 253-258.
- Stevenson, R.D. (1985): The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am. Nat.* **126**: 362-386.
- Tok, C.V., Çiçek, K., Hayretdag, S., Tayhan, Y., Yakin, B.Y. (2014): Range extension and morphology of the Italian wall lizard, *Podarcis siculus* (Rafinesque-Schmaltz, 1810) (Squamata: Lacertidae), from Turkey. *Turk. J. Zool.* **38**: 1-7.
- Tosini, G., Foà, A., Avery, R.A. (1992): Body temperatures and exposure to sunshine of ruin lizards *Podarcis sicula* in central Italy. *Amphibia-Reptilia* **13**: 169-175.
- Tosini, G., Foà, A., Avery, R. (1996): Pinealectomy increases thermoregulatory set point temperatures in the lacertid lizard *Podarcis sicula*. *J. Herpetol.* **30**: 104-106.
- Valakos, E.D., Pafilis, P., Lymberakis, P., Maragou, P., Sotiropoulos, K., Foufopoulos, J. (2008): The Amphibians and Reptiles of Greece. Edition Chimaira, Frankfurt am Main.
- Valdeón, A., Perera, A., Costa, S., Sampaio, F., Carretero, M.A. (2010): Evidencia de una introducción de *Podarcis sicula* desde Italia a España asociada a una importación de olivos (*Olea europaea*). *Bol. Asoc. Herpetol. Esp.* **21**: 122-126.
- Van Damme, R., Bauwens, D., Castilla, A.M., Verheyen, R.F. (1990): Comparative thermal ecology of the sympatric lizards *Podarcis tiliguerta* and *Podarcis sicula*. *Acta Oecol.* **11**: 503-512.
- Van Damme, R., Bauwens, D., Verheyen, R.F. (1991): The thermal dependence of feeding behavior, food consumption and gut passage time in the lizard *Lacerta vivipara*. *Funct. Ecol.* **5**: 507-517.
- Vanhooydonck, B., Van Damme, R., Aerts, P. (2000):

- Ecomorphological correlates of habitat partitioning in Corsican lacertid lizards. *Funct. Ecol.* **14**: 358-368.
- Veríssimo, C.V., Carretero, M.A. (2009): Preferred temperatures of *Podarcis vaucheri* from Morocco: intraspecific variation and interspecific comparisons. *Amphibia-Reptilia* **30**: 17-23.
- Vervust, B., Pafilis, P., Valakos, E.D., Grbac, I., Van Damme, R. (2010): Anatomical and physiological changes associated with a recent dietary shift in the lizard *Podarcis sicula*. *Physiol. Biochem. Zool.* **83**: 632-642.
- Vignoli, L., Vuerich, V., Bologna, M.A. (2012): Experimental study of dispersal behaviour in a wall lizard species (*Podarcis sicula*) (Sauria Lacertidae). *Ethol. Ecol. Evol.* **24**: 244-256.
- Zuffi, M.A.L., Giannelli, C. (2013): Trophic niche and feeding biology of the Italian wall lizard, *Podarcis siculus campestris* (De Betta, 1857) along western Mediterranean coast. *Acta Herpetol.* **8**: 35-39.