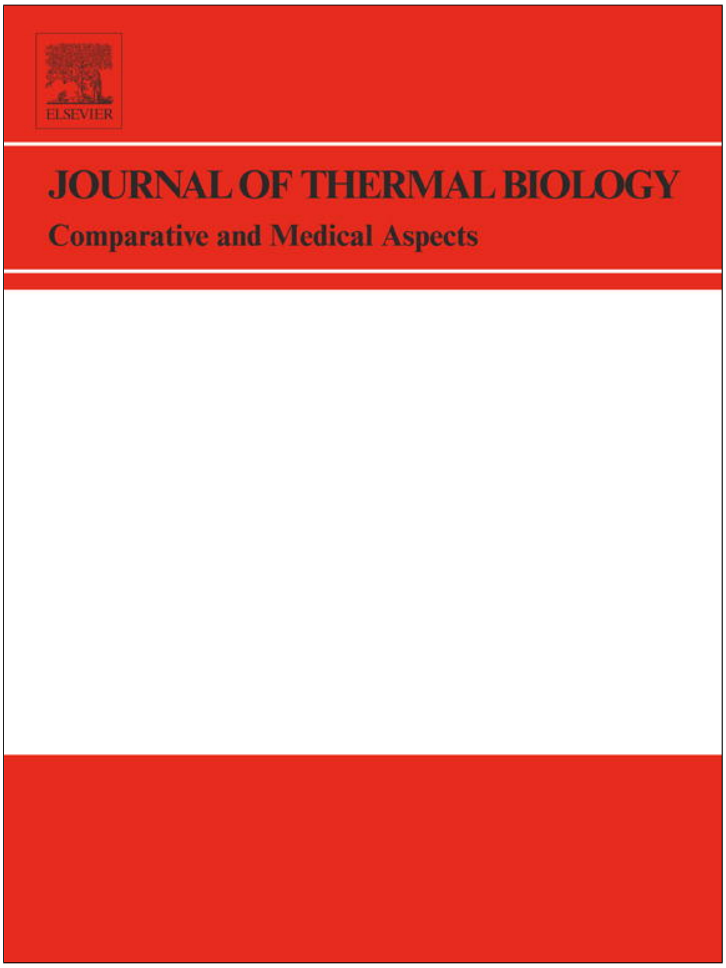
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The effect of body size on the thermoregulation of lizards on hot, dry Mediterranean islands

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ABSTRACT

Body size shapes the overall biology of organisms. We assessed the impact of size on temperature regulation in populations of normal-sized and large-bodied insular Mediterranean lizards (*Podarcis gaigeae*, Lacertidae). We hypothesized that large lizards would achieve higher body temperatures and thermoregulate more effectively than their smaller kin. Large- and small-bodied lizards share the same thermoregulation pattern, achieving similar body temperatures in the field. Large lizards, however, prefer higher set-point temperatures. Lizards in both populations thermoregulate effectively, but large lizards thermoregulated less effectively than normal-sized lizards. The particular conditions at the islet that harbors the large-bodied population (harsh intraspecific competition) seem to account for this pattern.

1. Introduction

Temperature is of pivotal importance for reptilian life, and governs most parameters of whole-animal performance and fitness (Bartholomew, 1982; Rome et al., 1992). Though unable to use metabolic heat for thermoregulation, reptiles effectively thermoregulate behaviorally (Avery, 1982; Zimmerman et al., 1994). This is crucial since physiological processes are strongly temperature sensitive and mostly occur within a narrow range of body temperatures (Huey, 1982; Peterson et al., 1993).

The effectiveness of thermoregulation depends, to a large extent, on body size (Huey and Stevenson, 1979). The body size-environment interaction is profound in ectotherms because they rely on external heat (Huey, 1982; Niewiarowski, 2001). Body size affects the rate at which heat is exchanged (Claussen and Art, 1981; Tracy, 1982). Small size favors faster heating and cooling rates (Hailey, 1982; Bowker et al., 2010) through conduction (Muth, 1977; Crawford et al., 1983). Large reptiles better control heat exchange rate by blood flow and exhibit thermal inertia supported by slower heating and cooling rates (Dzialowski and O'Connor, 1999). Large species can thus thermoregulate more accurately (O'Connor et al., 2000; Angilletta et al., 2002) but are also sensitive to overheating.

Though the impact of body size on thermoregulation is a hot spot in thermal biology studies (Dzialowski and O'Connor, 2001, 2004), the role of body size in thermoregulation of small lizards remains obscure (Carretero, 2008; Harlow et al., 2010). Large species have higher preferred body temperature and less variable temperatures (Stevenson, 1985). Nonetheless it is often thought that lizards have a single, species-specific, preferred T_b (Templeton, 1970, Bauwens et al., 1995). The thermal consequences of evolving drastic size differences within a single species are therefore unclear.

Intraspecific variation in body size is well known in lizards with some of the most striking cases occurring on islands (Meiri, 2007, Meiri et al., 2011). The "island rule" describes the existence of insular giants and dwarfs, predicting that large species tend to develop smaller forms whereas small-bodied species will evolve to be larger on islands (Van Valen, 1973; Lomolino, 2005) though the generality of that pattern has been debated (Meiri et al., 2006; Raia et al., 2010).

The thermal biology of reptiles is usually determined by three main values (Huey and Slatkin 1976; Hertz et al., 1993): First, body temperatures (T_b) are the temperature that animals achieve in the field under natural conditions. Second, set-point range (T_{set}) that animals achieve under specially designed thermal gradient in laboratory conditions where no constraints curtail the innate ability for accurate thermoregulation (Dzialowski, 2005). In the absence of other data T_{set} is considered the optimal temperature for performance. Third, operative temperatures (T_e), the predicted equilibrium temperatures of a non-thermoregulating animal, correspond to the temperature of the environment (Bakken et al., 1985; Bakken, 1992).

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To clarify the way body size affects thermoregulation within a single species, we evaluated the aforementioned thermal parameters of the endemic Skyros wall lizard (*Podarcis gaigeae*, Aegean Sea, Greece) and estimated the three aspects of thermoregulation (precision, accuracy and effectiveness, Hertz et al., 1993). Body size of *P. gaigeae* varies greatly (Valakos et al., 2008). In the small islet of Mesa Diavates (hereinafter "Diavates") individuals are ~40% longer, and weigh nearly thrice as much as their counterparts from 'mainland' Skyros (Pafilis et al., 2009). On Diavates, predation is minimal and population density is high, but intraspecific competition is harsh, including cannibalism. These factors, together with marine subsidies (sea-derived nutrients provided by sea birds—Polis and Hurd, 1996) seem to drive the evolution of larger body sizes (Pafilis et al., 2009). On Diavates large size is highly adaptive: hatchlings can escape cannibalism, adults are more effective predators and the largest males have better access to females, while the latter produce larger clutches comprising larger eggs (Pafilis et al., 2011). Does large size also confer a thermoregulatory advantage?

It is well established that body size affects the way large animals thermoregulate. Our aim was to assess the effect of body size on thermoregulation in a small lizard. We formulated two main hypotheses: First, Diavates large lizards would achieve (in the field) and prefer (in the lab) higher body temperatures than the small lizards of Skyros. Physiological requirements of body size in ectotherms imply that larger reptiles maintain higher body temperatures in order to ensure the smooth whole-animal performance (Turner and Tracy, 1986; Angilletta, 2009). Large-bodied lizards, as result of their size, may have a preference for higher T_{set} (Stevenson, 1985). Second, large-bodied lizards would be more effective thermoregulators, keeping their body temperature closer to, and within a narrow range around their thermal optimum. Larger reptiles spend less time in behavioral thermoregulation and maintain a more constant temperature thanks to their mass.

2. Materials and methods

2.1. Study sites and species

Podarcis gaigeae (Sauria, Lacertidae) is a small-bodied lizard (SVL = Snout–Vent Length around 60 mm, body mass 6.58 ± 1.3 g), occurring from the coastline up to 700 m above sea level, that feeds on a wide range of terrestrial invertebrates and is present in all habitats, including human settlements (Valakos et al., 2008). Lizards in all the islets surrounding the main island are larger compared to Skyros individuals (Pafilis et al., 2009).

Skyros Island (207 km^2, N 38° 51′, E 24° 33′—Fig. 1) harbors varied Mediterranean habitats such as phrygana, maquis, pine forests, farmland and dunes. Diavates is a small islet (0.019 km^2), 1.4 km from Skyros, and its vegetation consists of few evergreen scrubs (*Pistacea lentiscus*) and mainly, of dense herbaceous vegetation characterized by nitrophilous species such as *Mercurialis annua* or species belonging to the family Malvaceae (Bohling et al., 2002). The predation regime on Skyros and Diavates is very different. Skyros hosts several specialized lizard predators, while Diavates is predator free (Pafilis et al., 2009). As a result a very dense population (850 individuals/ha compared to 120 individuals/ha on Skyros) has been established at Diavates.

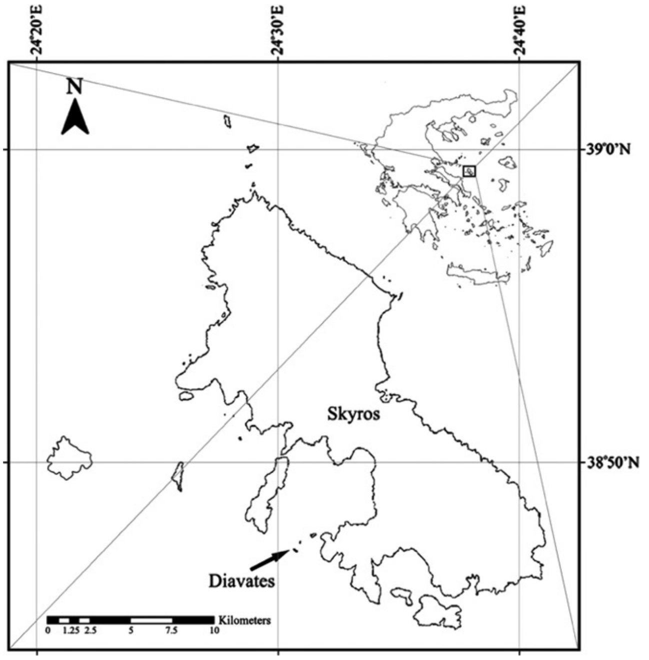

Fig. 1. Map of Skyros Archipelago in the Aegean Sea (East Mediterranean Sea). Arrow denotes Diavates islet.

2.2. Thermal measurements

2.2.1. Field measurements (T_b and T_e)

We sampled body temperatures (T_b) of as many individuals as we could within the time frame set for T_e (see below). Lizards were captured by hand and noose and T_b was then immediately measured with a quick-reading cloacal thermometer (T-4000, Miller & Weber, Inc., Queens, NY) to the nearest 0.1 °C. We then immediately obtained substrate and air temperatures (5 cm above the ground) from the spot each individual was captured (Avery, 1982; Lemos-Espinal et al., 1997). We made sure we captured lizards from all microhabitat types. We recorded time, age class, sex, mass, SVL for each animal. SVL (in mm) and mass (in g) were measured with Digital Calipers (Silverline 380244, accurate to 0.01 mm) and a digital scale (i500 Backlit Display, My Weight, accurate to 0.1 g), respectively.

We estimated the operative temperatures (T_e) of non-regulating, inactive lizards, by using hollow, electroformed copper models painted brownish green. Models were closed at both ends except for a narrow slot where the logger probes (HOBO U12 4-Channel External Data Logger—U12-008) were plugged in (Diaz, 1997). Models were tailored according to the average body size of each population and have the same size, shape and radiative properties as the study animal (Bakken, 1992). We calibrated the loggers following the manual (HOBO U12-008; *in silico* analyses were done with BoxCar Pro 4 software). In order to adjust the heat capacity of the models to that of the lizards, we added 2.5–3 ml of water into each model before placing them in the field (Grbac and Bauwens, 2001). At this point we need to stress out that the use of thermal models has been thoroughly applied to ecological problems (Bakken and Gates, 1975; Bakken et al., 1983).

To verify the similarity of the temperature responses between an inanimate object and a living organism (Hertz, 1992), we placed, at the lab, a model and a lizard side by side under the same heat source (a 150 W lamp) and measured their temperatures at 5 min intervals. Six temperature equilibria were generated for each model-lizard pair, ranging from 10 to 35 °C, and four lizards were tested. Because of their lower heat capacity, copper models heated and cooled more rapidly than animals (Bakken and Gates, 1975, Hertz, 1992). The temperatures of the models (T_e) and lizards (T_b) did not differ significantly (t-test, $df = 28$, $P = 0.70$). Regression analysis of T_b on T_e suggests that the models and lizards have similar thermal responses (regression statistics ± SE; slope $= 1.043 \pm 0.025$, intercept $= -1.47 \pm 0.707$, $r = 0.999$, $N = 24$, $P < 0.05$).

We used 30 copper models in each biotope and placed them so as to cover all types of microhabitats available to lizards in the field (Huey, 1991). Temperature measurements were taken for two consecutive days starting from 8:00 to 19:00 at 30-minute intervals using Hobo digital logger thermometers.

2.2.2. *Lab measurements (T_{set})*

A total of 94 adult lizards (48 from Skyros Island and 46 from Diavates) were transferred at the laboratory facilities of the School of Biology at the University of Athens. Lizards were housed in pairs in vitreous terraria (20 cm × 25 cm × 15 cm) on a substrate of sand; bricks and stones were provided as hiding places. The lizards were held at 25 °C under a controlled photoperiod (12L: 12D) using fluorescent lights. Animals were provided with water ad libitum and had access to mealworms (*Tenebrio molitor*) every other day. By the end of the study the animals were released back into the field.

Set-point temperatures (T_{set}) were measured during summer only (Grbac and Bauwens, 2001; Gvozdik and Castilla, 2001), in a specially designed terrarium (100 × 25 × 25 cm). A thermal gradient ranging from 10 to 50 °C was achieved by placing two incandescent heating lamps (100 and 60 W) at one end and two ice bags at the other end of the terrarium (Van Damme et al., 1986). Lizards were allowed to acclimate for 30 minutes and their body temperatures were subsequently measured with a cloacal Miller–Weber thermometer every hour for three consecutive hours (Castilla and Bauwens, 1991). In all analyses we used the inter-quartile range of the body temperatures selected by lizards in the thermal gradient (Huey, 1982; Hertz et al., 1993).

2.3. *Effectiveness of thermoregulation d_b/d_e*

We evaluated the effectiveness of thermoregulation using the formula: $E=1-(\overline{d_b}/\overline{d_e})$, where $\overline{d_b}$ is the mean deviation of preferred field T_b from T_{set} and d_e is the mean deviation of field T_e from T_{set} (Hertz et al., 1993). The two indices in parenthesis provide important information on the ability of ectotherms to thermoregulate since $\overline{d_b}$ is considered as a measure of closeness of thermoregulation and d_e describes the thermal quality of the habitat. The values of E usually range from zero (perfect thermoconformers) to one (perfect thermoregulators).

3. Results

3.1. *Body size*

Lizards from Diavates are significantly longer (females: $t=16.8$, $df=91$, $P<0.001$; males: $t=22.7$, $df=83$, $P<0.001$) and heavier (females: $t=13.15$, $P<0.001$; males: $t=15.03$, $P<0.001$) than those from Skyros Island, with no overlap in SVL or in minimal mass (Table 1).

3.2. *Field measurements*

The Diavates population (94 adults) had slightly lower T_b and also experienced a greater range of T_e than on Skyros (84 adults) (Table 2). Body temperatures in both populations were statistically similar (Fig. 2, Table 2, $t=-1.74$, $df=176$, $P>0.05$) and differed from the environmental temperatures. Since T_b in both populations did not significantly differ between sexes, data were pooled for each population (Skyros: $t=1.01$, $df=82$, $P>0.05$ and Diavates: $t=0.07$, $df=92$, $P>0.05$).

T_es at Diavates range from 23.3 °C at 08:00 (minimum) to 73.4 °C at 13:30 (maximum) and at Skyros Island the minimum temperature obtained was 22.6 °C at 8:00 to 74.3 °C at 13:00 (Table 2). Mean daily distribution of T_e is shown in Fig. 2. T_es on Diavates were significantly higher than on Skyros ($t=2.91$, $df=55$, $P<0.05$) suggesting that this is a warmer habitat.

3.3. *Set-point temperature range*

There were no significant differences between the T_{set} of males and females in either Skyros (ANOVA, $F_{1,46}=0.18$, $P>0.05$) or Diavates ($F_{1,43}=0.45$, $P>0.05$) and so we pooled body temperatures of males (Skyros: $T_{set}=33.9\pm0.6$ and Diavates: $T_{set}=34.7\pm0.8$) and females (Skyros: $n=28$, $T_{set}=33.8\pm0.6$ and Diavates: $n=30$, $T_{set}=34.6\pm0.5$). Lizards from Diavates achieved slightly higher temperatures than their Skyros peers (34.6 vs. 33.7 °C, ANOVA, $F_{1,91}=65.74$, $P<0.05$, Table 2) and this resulted to a lower mean daily distribution of T_{set} for the Skyros population (Fig. 2). Mean T_{set} was higher than the mean T_b in both populations (ANOVA, Skyros: $F_{1,130}=5.66$, $P<0.05$, Diavates: $F_{1,137}=51.049$, $P<0.05$, Table 2). Since body size differed significantly between populations, we repeated the analysis with SVL or mass as a covariate. When body size or mass were taken into account, differences in set-point temperature disappeared (ANCOVA, SVL: $F_{1,90}=2.60$, $P>0.05$ and Mass: $F_{1,90}=2.18$, $P>0.05$).

3.4. *Effectiveness of thermoregulation (E)*

The mean deviation of field T_e from T_{set} (d_e) was higher on Skyros Island than on Diavates (7.2 vs. 4.8 °C, $F_{1,55}=4.12$, $P<0.05$). The difference between field body temperatures and T_{set} (d_b) was higher on Diavates (1.9 vs. 1.0 °C, $F_{1,176}=12.73$,

Table 2
Values for the thermal parameters ruling thermoregulation. Operative (T_e) and body (T_b) temperatures (field measurements), deviation of T_e from the lab-measured set-point range (T_{set}), namely d_e, and deviation of T_b from T_{set}, namely d_b for the two *P. gaigeae* populations.

Population	Variable	*n*	Mean (°C)	Range (°C)	SD	SE
Diavates islet	T_e	26	40.7	23.3–73.4	9.3	0.29
	d_e	26	4.8	0–17.2	3.9	0.78
	T_b	94	32.3	27.5–37.3	2.2	0.23
	d_b	94	1.9	0–6.5	1.9	0.20
	T_{set}	45	34.6	34.0–35.8	0.5	0.07
Skyros Island	T_e	15	39.4	22.6–74.3	10.5	0.46
	d_e	15	7.2	0–14.2	3.7	0.94
	T_b	84	32.9	26.8–38.8	2.5	0.27
	d_b	84	1.0	0–5.5	1.3	0.14
	T_{set}	48	33.7	32.3–34.8	0.6	0.63

Table 1
Values for snout–vent length (in mm) and body mass (in g): means ± standard deviation; range. Sample size in parenthesis.

	Skyros		Diavates	
	Females (49)	Males (35)	Females (44)	Males (50)
SVL	51.66 ± 5.80; 44.4 – 57.5	57.58 ± 5.42; 52.4 – 65.2	71.77 ± 5.70; 59.8 – 82.8	81.94 ± 4.46; 67.7 – 93.2
Body mass	4.1 ± 0.6; 3.0–5.3	6.2 ± 1.3; 4.4 – 8.3	7.6 ± 1.8; 4.3 – 12.3	14.7 ± 3.2; 7.7 – 21.3

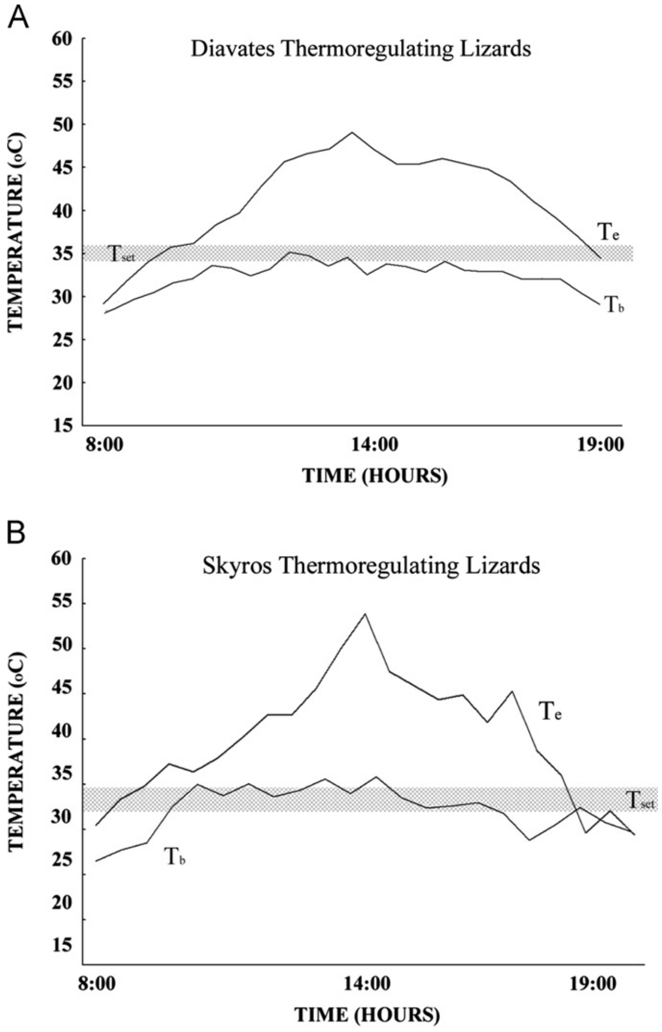

Fig. 2. Plots representing the daily variation for mean active body temperature in the field (T_b), the mean operative environmental temperature (T_e) obtained every 30 min and the set-point temperature range (T_{set}), measured every hour in the lab, for Diavates (A) and Skyros Island populations (B).

$P < 0.05$). The interquartile range of set-point temperatures for Skyros varied from 32.3 to 34.8 °C and for Diavates from 34.0 to 35.8 °C.

The mean d_b and d_e values (Table 2) in both populations were high indicating that habitats are not thermally ideal and lizards have to thermoregulate in order to achieve body temperatures close to the set-point range (Table 2). By entering these values to the equation $E = 1 - (\overline{d_b}/\overline{d_e})$, we estimated the effectiveness of thermoregulation for Skyros Island and Diavates as $E = 0.87$ and $E = 0.72$ respectively. Lizards in both populations actively thermoregulated and follow the same pattern, which was expected since body temperatures are closer to the T_{set} than operative temperatures are and therefore $\overline{d_b}$ and $\overline{d_e}$ are low and high, respectively.

4. Discussion

We tested whether large body size confers thermal advantages on small lizards. Large-bodied Diavates lizards did not achieve higher body temperatures and were less effective thermoregulators than small-bodied Skyros ones, rejecting our predictions. Diavates lizards achieved higher preferred (set-point) temperatures but thermoregulate less effectively than their Skyros kin with which they shared similar T_b in the field.

Since all physiological processes and the overall performance of an ectotherm are temperature sensitive, T_{set} is often used to define the thermal optima of organisms (Clusella Trullas et al., 2007). Lizards from the Diavates population selected higher temperatures. T_{set} is not fixed and may change with season, sex, age and reproductive status (Andrews et al., 1999; Carretero et al., 2005; Veríssimo and Carretero, 2009). Our results suggest that body size also affects set-point range.

We predicted that T_{set} would be higher in the large-bodied lizards because of their (presumed) higher thermal requirements. Physiological and biochemical procedures depend on temperature. In order to satisfy the increased metabolic needs of a larger body, we expected that body temperatures should be higher to facilitate procedures related to energy input, such as the temperature sensitive foraging (Van Damme et al., 1991; Diaz, 1994) and digestion (McConnachie and Alexander, 2004; Pafilis et al., 2007).

Field body temperatures of both *P. gaigeae* populations lie within the same range with other Mediterranean *Podarcis* islanders (Pérez-Mellado and Salvador, 1981; Pérez-Mellado, 1989; Castilla and Bauwens, 1991; Adamopoulou and Valakos, 2005). Since T_{set} for Diavates lizards is higher than the preferred (set-point) temperatures for Skyros population, one would expect that T_b for the large lizards would be higher as well, due to the same driving factor (large body size). However T_b of the two populations was similar. We believe that the underlying reason should be sought to the ecological factors preventing a lizard from achieving field T_b within its set-point range: food availability, predation and competition (Huey and Slatkin, 1976; Crowder and Magnuson, 1983).

Food abundance greatly influences thermoregulation (Angilletta, 2009; Schuler et al., 2011) and ectotherms drop their T_b when food is scarce (Elliot, 1982; Jonassen et al., 1999). Mediterranean islands often have limited food resources (Fuentes, 1984; Brown and Pérez-Mellado, 1994). However this is not the case for Diavates where a thriving colony of yellow-legged gulls (*Larus michahellis*) provides abundant marine subsidies through food remains, guano and decomposing carcasses (Pafilis et al., 2009, 2011). Predation regime affects also the time span for thermoregulation (Huey, 1982). Under strong predation pressure, lizards have to be cautious to avoid their enemies, decreasing hence the time for basking. Diavates is a predator free biotope (Pafilis et al., 2009) and thus large lizards should be able to bask to their thermal optima without fear (Case, 1982).

Though predation and food do not prevent large lizards from achieving the preferred T_b, intraspecific competition may. Population densities of insular lizard communities are often extremely high (Rodda et al., 2001; Pérez-Mellado et al., 2008; Novosolov et al., in press), triggering a strong intraspecific competition. This competition includes cannibalism, which is common among Mediterranean lacertids (Arnold, 1988; Pafilis et al., 2008). In Diavates adults eat juveniles and aggressive encounters between adults often end up in limb and tail amputations (Pafilis et al., 2009). Large-bodied lizards have to be incessantly vigilant in order to prevent an attack and defend themselves. That means they cannot dedicate enough time for an effective thermoregulation that would allow them to reach the T_{set}. Alternatively, predator and (interspecific) competitor-free and resource-rich Diavates may be a more benign environment, and thus the pressure to keep performance at its peak may be not that imperative. Thus Diavates lizards may be able to be active in sub-optimal temperatures, because selection for effective thermoregulation is relaxed.

Lizards in both populations thermoregulate effectively. Lizards with *E* values exceeding 0.5 are considered effective thermoregulators (Hertz et al., 1993). The *E* values for the two *P. gaigeae* populations are lying within the top percentile among Greek lacertids (Pafilis, 2003). Nonetheless, the thermoregulation effectiveness of large lizards was somewhat lower than that of Skyros animals (0.72 vs. 0.87), though the difference is not large. This can result from the higher T_{set} of the Diavates population (see above) and from the thermal qualities of the two habitats (as expressed by T_{e}).

Operative temperatures sketch the thermal profile of a habitat and, through the mean d_{e}, provide an index that allows representation of the complex thermal environment (Bakken, 1992; Hertz et al., 1993). While the biotope in Skyros Island, located in a mild slope, belongs to the typical phrygana ecosystem and provides a plethora of shelters and basking places, Diavates is homogenous, with few retreat sites and places available for temperature regulation.

In summary, both *P. gaigeae* populations followed the same strategy of thermoregulation with high activity T_{b} that varies within a narrow thermal window (high precision of body temperature), and high thermal preferences (T_{set}). Large-bodied lizards had a higher set-point range and live in a warmer habitat. Their higher values for T_{e} and T_{set} affect $\overline{d_{\mathrm{b}}}$ and $\overline{d_{\mathrm{e}}}$, and through them the thermoregulation effectiveness index. Their relative lower ability to reach their preferred temperature in the field means they are less accurate thermoregulators. Though predation pressure on Diavates is minimal and food is abundant, harsh intraspecific competition constrains large-bodied lizards from effectively regulating their temperature.

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