



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

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ARTICLE INFO

Article history:

Received 15 February 2012

Accepted 30 November 2012

Available online 22 December 2012

Keywords:

Body size

Competition

Density

Insularity

Thermal biology

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.

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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 km², 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 km²), 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.

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

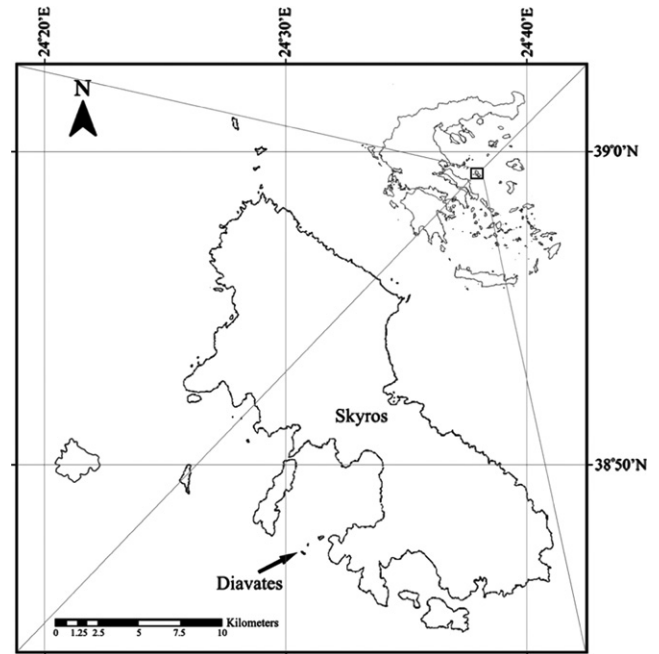


Fig. 1. Map of Skyros Archipelago in the Aegean Sea (East Mediterranean Sea). Arrow denotes Diavates islet.

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 \pm SE; slope = 1.043 ± 0.025 , intercept = -1.47 ± 0.707 , $r=0.999$, $N=24$, $P < 0.05$).

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