Keeping a cool mind: head–body temperature differences in the common wall lizard

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Abstract

Evidence of head–body temperature differences are known for many species of medium- to large-sized reptiles, but are scanty for small lacertid lizards. In this study, we heated 48 individuals of *Podarcis muralis* (19 males and 29 females) in order to investigate their ability to achieve and maintain local temperature differences between body parts. Lizards were put into polystyrene boxes and heated with incandescent lamps. Temperatures were measured with both an infrared thermometer and an infrared camera at four different body points every 20 min for 2 h. We found a statistically significant thermal gradient from the tip of the nose, the coolest part of the body, to the trunk, the warmest area, whereas the head achieved an intermediate temperature. We therefore hypothesize that *P. muralis* is able to physiologically regulate the heat distribution across its body. *Podarcis muralis* is sexually dimorphic, but neither sex nor body size are associated with temperature differences between individuals. The two measurement devices used responded differently to insulating material and to living animals, possibly indicating that infrared camera is able to detect dermal heat, while infrared thermometer detects mainly epidermal heat. This study shows for the first time that *P. muralis* can achieve and maintain temperature differences between the head and the body.

Introduction

Regional heterothermy consists in temperature differences among body parts and is a widespread phenomenon among reptiles. Local body temperature (T_b) differences were first demonstrated in *Phrynosoma cornutum*, which basks keeping the body under the sand and only the head exposed. As a result, its head may be 3–5°C warmer than its body (Heath, 1964). Since that pioneering work, head–body temperature differences have been reported for several species of lizards like varanids (Johnson, 1972), scincids (Hammel, Caldwell & Abrams, 1967), agamids (Heatwole, 1970), gekkonids (Webb, Johnson & Firth, 1972) and iguanids (Crawford Jr., Palomeque & Barber, 1977).

Head–body temperature differences are also known for snakes (Webb & Heatwole, 1971; Heatwole & Johnson, 1979; Gregory, 1990; Dorcas & Peterson, 1997), turtles (Webb & Johnson, 1972; Morgareide & Hammel, 1975) and crocodilians (Grigg & Alchin, 1976; Drane, Webb & Heuer, 1977). Some authors explained heterothermy by means of different surface/volume ratio between the head and the body (Pough & MacFarland, 1976), while others demonstrated that reptiles can actively maintain their heads and bodies at different temperatures with a combination of physiological and behavioural mechanisms like panting (Webb *et al.*, 1972), gaping

(Spotila, Terpin & Dodson, 1977), countercurrent vascular systems (Heath, 1966; Tattersall, Cadena & Skinner, 2006), controlling the regional blood flow (Amiel *et al.*, 2011) or exposure of certain body parts to solar radiation (Gregory, 1990). The reason why the head and trunk are kept at different temperatures is linked to the regulation of the nervous system, which is highly sensitive to fluctuation in temperature (Schmidt-Nielsen, 1997). Indeed, some authors suggested that local heterothermy in reptiles arises because the brain is the anatomical place where the temperature is perceived and regulated (Webb & Johnson, 1972; Webb *et al.*, 1972). At a low environmental temperature, the head may be kept at higher temperature than the body (Gregory, 1990), while at a higher environmental temperature the head is kept at lower temperature to prevent brain overheating (Crawford Jr. *et al.*, 1977; Dorcas & Peterson, 1997; Borrell, LaDuc & Dudley, 2005).

Most of the studies on this topic were focused on medium and large species, which show high thermal inertia and depends mostly on solar and thermal radiation as heat source. By contrast, temperature regulation of small species depend mostly on air temperature (T_a) (Pough *et al.*, 2004) and it is still unclear to which extent small reptiles are able to physiologically regulate T_b. Some authors stated that physiological regulation is important only for medium and large species, and believe that small ones rely exclusively upon behavioural

regulation of T_b (Crisp, Cook & Hereward, 1979; Fraser & Grigg, 1984). Other studies demonstrated that physiological control of T_b occurs even in small reptiles (McKenna & Packard, 1975).

There is little evidence that small lizards can achieve and maintain regional temperature differences. For example, Crawford Jr. *et al.* (1977) found that the tropical lizard *Anolis carolinensis* is able to maintain a head temperature lower than the body core temperature by panting. However, these authors observed that if panting does not occur, the circulation of blood is sufficient to balance head–trunk temperature differences. There is instead no evidence of such local temperature differences in temperate small lizards, for which thermoregulation may be more important than for tropical ones (Shine & Madsen, 1996) because their thermal biology is affected by great circadian and seasonal fluctuation of environmental features (Huey & Slatkin, 1976; Avery, 1978; Castilla, Van Damme & Bauwens, 1999; Blouin-Demers & Nadeau, 2005).

The standard methods for measuring reptile temperatures use contact thermometers with a thermocouple probe inserted in the cloaca. However, this procedure needs lizard capturing and handling, which may increase metabolic rate and physiological stress (Langkinde & Shine, 2006). This can also induce subsequent changes in the lizard's behaviour, potentially affecting the reliability of temperature records. A handheld infrared thermometer (IR) offers an alternative method that reduces handling, thus attenuating stress and decreasing reading time (Hare, Whitworth & Cree, 2007). IR has been shown to be effective for distant T_b measurements of lizards and frogs (Rowley & Alford, 2007; Bucklin *et al.*, 2010). Recently, Carretero (2012) questioned the uncritical use of IR, since temperatures estimated from IR tend to give progressively higher values than contact thermometer for higher temperatures. A further technique is offered by infrared thermocamera (TC) that measures the radiation emitted by a lizard's body to assess its temperature. Recent studies supported the reliability of the TC to investigate thermal ecology of reptiles (Tattersall, Andrade & Abe, 2009; Tattersall & Cadena, 2010) and skin temperatures recorded with TC have been shown to be strictly correlated to cloacal temperatures recorded with contact thermometer (Luna & Font, 2013). No previous study had investigated the relationship between IR and TC.

In this study, we used *Podarcis muralis* to investigate head–body temperature differences using both IR and TC measurement devices. Given its small body size, ecological characteristics and the lack of knowledge about possible heterothermy, *P. muralis* provides an excellent opportunity to study the ability of a small lizard to achieve and maintain local T_b differences. Due to its low thermal inertia, it is possible that *P. muralis*, exposed to high temperature, will show a weak thermal gradient across the body, as expected by physical models (Stevenson, 1985; Fei *et al.*, 2012), that is, the trunk should be the warmest area, followed by the head, which should show little or no difference with the trunk, and then by the limbs and the tail, which should be the coldest body parts. Any deviation from this expectation may indicate the presence

of a physiological (Amiel *et al.*, 2011) and/or behavioural (Borrell *et al.*, 2005) mechanism able to regulate the heat distribution in the body.

Material and methods

Podarcis muralis is a small lacertid lizard [snout-to-vent length (SVL) up to 75 mm] that occurs in Italy and widely across Europe, from Spain to Turkey and from Jersey Island to Greece (Arnold, Arribas & Carranza, 2007; Biaggini *et al.*, 2010) living in temperate, continental, Mediterranean and dry climates. Like many other lacertid species, it is sexually dimorphic (males with longer SVL and larger head, females with longer trunk). The thermal ecology of Italian populations is well known: the mean cloacal temperatures, recorded in the field during spring and summer, are 33 and 36°C, respectively (Avery, 1978). For a Spanish population, Braña (1991) reported a mean cloacal temperature of 33.8°C. Under laboratory conditions, provided a temperature gradient, the species sets its own T_b to 33.7°C (Tosini & Avery, 1994). It is possible that a certain degree of geographic variation in T_b among different populations exists (Kiefer, Van Sluys & Rocha, 2005).

We conducted the experiments at the Natural History Museum of Milan from April to October 2012. Forty-eight adult lizards (19 males, 29 females) were captured by noosing in Cesano Maderno, near Milan, in an urban park. All individuals were sexually mature (Sacchi *et al.*, 2012) and were sexed, measured and photographed for photoidentification to avoid replications (Sacchi *et al.*, 2010).

Lizards were housed in plastic terraria ($35 \times 23 \times 21$ cm) with the bottom covered by paper sheets. We provided a hollow brick as shelter, water *ad libitum* and food three times a week (*Tenebrio molitor* larvae). Food was removed each day at 16:00 h because the correlation between meal and subsequent T_b has been demonstrated (Tosini & Avery, 1994). Since previous research demonstrated that *P. muralis* completes the digestion of a mealworm in approximately 32 h (Pafilis *et al.*, 2007), we assumed that the effect of food on T_b on the following day was negligible. Each terrarium was positioned under a heating lamp in the afternoon every day, so that they reached an internal T_a of 27°C. All lizards were acclimatized for 2 days and the experiment was conducted on the third day.

Polystyrene boxes ($27 \times 18 \times 19$ cm) were used to reduce convective and conductive heat exchanges with the surrounding environment. The boxes were open on top to allow temperature measurements and a hole was made on one side to introduce a thermometer probe. A single lizard was put into each box and acclimatized for 30 min, then T_a was measured using a Thermo-Timer probe (TFA Dostmann GmbH & Co., Reicholzheim, Germany) (sensitivity: 0.1°C; precision: ± 1.5%). Lizard T_b was measured at a distance of 25 cm from each of the following four body points: (1) the tip of the nose, corresponding to the prefrontal shields; (2) the head temperature, corresponding to the interparietal shield; (3) the last third of the trunk on the back; and (4) the side (Fig. 1). After the first measurement of air and T_b (T_1), a heating lamp positioned at 40 cm height (Exo-Colour Spectrum Light,

Figure 1 The figure shows the four body points where temperatures were recorded. From left to right: prefrontal shields on the tip of the nose; the interparietal shield on the head; dorsally and on the side of the last third of the trunk.

Table 1 The table reports the mean values of body temperatures including standard deviation and minimum and maximum (in brackets) for all individuals (N). IR refers to infrared thermometer and TC to thermocamera. All temperature values are given in °C

Body point	N	IR	TC
Prefrontal	384	33.5 ± 3.6 (23.6–38.2)	33.1 ± 3.9 (21.6–38.4)
Intraparietal	384	34.1 ± 3.8 (23.6–39.0)	34.7 ± 4.4 (22.2–40.6)
Back	384	34.6 ± 3.8 (23.7–40.3)	36.3 ± 4.8 (22.3–42.5)
Side	384	34.6 ± 3.8 (23.7–40.2)	36.1 ± 4.7 (22.7–43.0)

www.exotica-decor.com) (75 W; spectrum: 300–800 nm), was lighted above each terrarium and measurements of T_a and T_b were repeated seven times (T_2–T_8) every 20 min. T_a reached constant maximum values of 32–34°C, similar to environmental temperatures experienced in the field during summer in the study area (our own data). When the experiment ended, lights were turned off and the lizards were left for 30 min in the boxes before moving them to the terraria. Each lizard was tested once and then was released at the capture site.

Temperatures were simultaneously recorded with two different devices: a handheld IR (Lafayette TRP-39, Lafayette Instrument Co., Lafayette, Indiana, USA) (sensitivity: 0.1°C; precision: ± 2%) and a TC (FLIR B-200, Flir Systems Inc., Wilsonville, Oregon, USA) (sensitivity: 0.08°C; precision ± 2%; IR image resolution 200×150 pixels). Because IR had a distance-to-spot (D : S) ratio of 50 : 1, the diameter of the measured area at 25 cm distance was 0.5 cm. These structural characteristics imply that background noise was inevitably added when measuring the temperature of the prefrontal area. To account for this effect, we used TC to obtain an independent measure of the same parameters, based on the different temperature detection mechanism: TC produces an image of the emitted infrared radiation and allows the capturing of the temperature values through the pointer function. All the images were analysed by FLIR Tools 3.1 (Copyright 1999–2013 FLIR Systems, Inc; http://www.flir.com). We cannot reliably estimate the temperature of small body parts such as the limbs and the tail with the devices used in this study. However, we examined the thermal images with FLIR Tools looking for predicted thermal patterns. We expected to find the limbs and tail almost always cooler than the head and the body, being smaller and with higher surface/volume ratio. In this case, data were qualitative and with no statistical meaning.

To account for possible differences between instruments, we carried out a control test with the same design described below, but measuring the temperature of the base of three different empty polystyrene boxes instead of the lizards' T_b.

To investigate which variables affect T_b, we applied a linear mixed model where T_b was the dependent variable, lizard identity (Id) was used as the random factor, and SVL, sex, measuring device (IR vs. TC), time (T_1–T_8), T_a, and body points (pos) were used as fixed factors. A three-way interaction (pos × time × sex) and all two-way interactions among these variables were also included in the model. The same analysis was used to check for significant differences between the two measuring devices: here, the substrate temperature (T_s) instead of T_b, was included in the model as the dependent variable, the polystyrene boxes (Box) was the random factor and a three-way interaction (T_a×device×time) and all two-way interactions were the predictors. The starting models were simplified in order to obtain the minimal adequate models (Zuur *et al.*, 2009).

We performed post hoc t-tests between the mean temperature of the four body points to assess the direction and magnitude of the thermal gradient. A further t-test was done between IR and TC values to assess if measured differences were statistically significant.

To investigate the relationship between temperatures recorded with IR and TC, we used standardized major axis regression (SMA) (Legendre & Legendre, 1998). We performed two different analyses. In the first one, we looked for a common slope between lizards and polystyrene regression lines. In the second, we checked for deviation from slope = 1 of the regression line between IR and TC in both polystyrene and lizard data. Analyses were performed under the R statistical environment (R Core Team, 2013) and reported values are means ± standard errors.

Results

According to the linear mixed model, the following variables had a significant effect on T_b: Id [likelihood ratio (LR) test, LR = 1622; *P*-value < 0.0001; d.f. = 1], T_a (LR = 5037; *P*-value < 0.0001; d.f. = 1), pos (LR = 32.03; *P*-value < 0.0001; d.f. = 4), time (LR = 970; *P*-value < 0.0001; d.f. = 6), the interaction time×pos (LR = 18.46; *P*-value < 0.0001; d.f. = 3) and the device (LR = 270; *P*-value < 0.0001; d.f. = 1). There were no temperature differences associated with sex (LR = 0.289; *P*-value = 0.591; d.f. = 1) and SVL (LR = 3.270; *P*-value = 0.071; d.f. = 1). The four body points showed different temperatures (Table 1). In detail, there was a temperature gradient from the tip of the nose, representing the coolest part of the body, to the head at an intermediate temperature (t-value = 4.980; *P*-value < 0.0001; d.f. = 3015) and the trunk, that represented the warmest part of the body (t-value = 9.794; *P*-value < 0.0001; d.f. = 3015). Instead, there was no difference
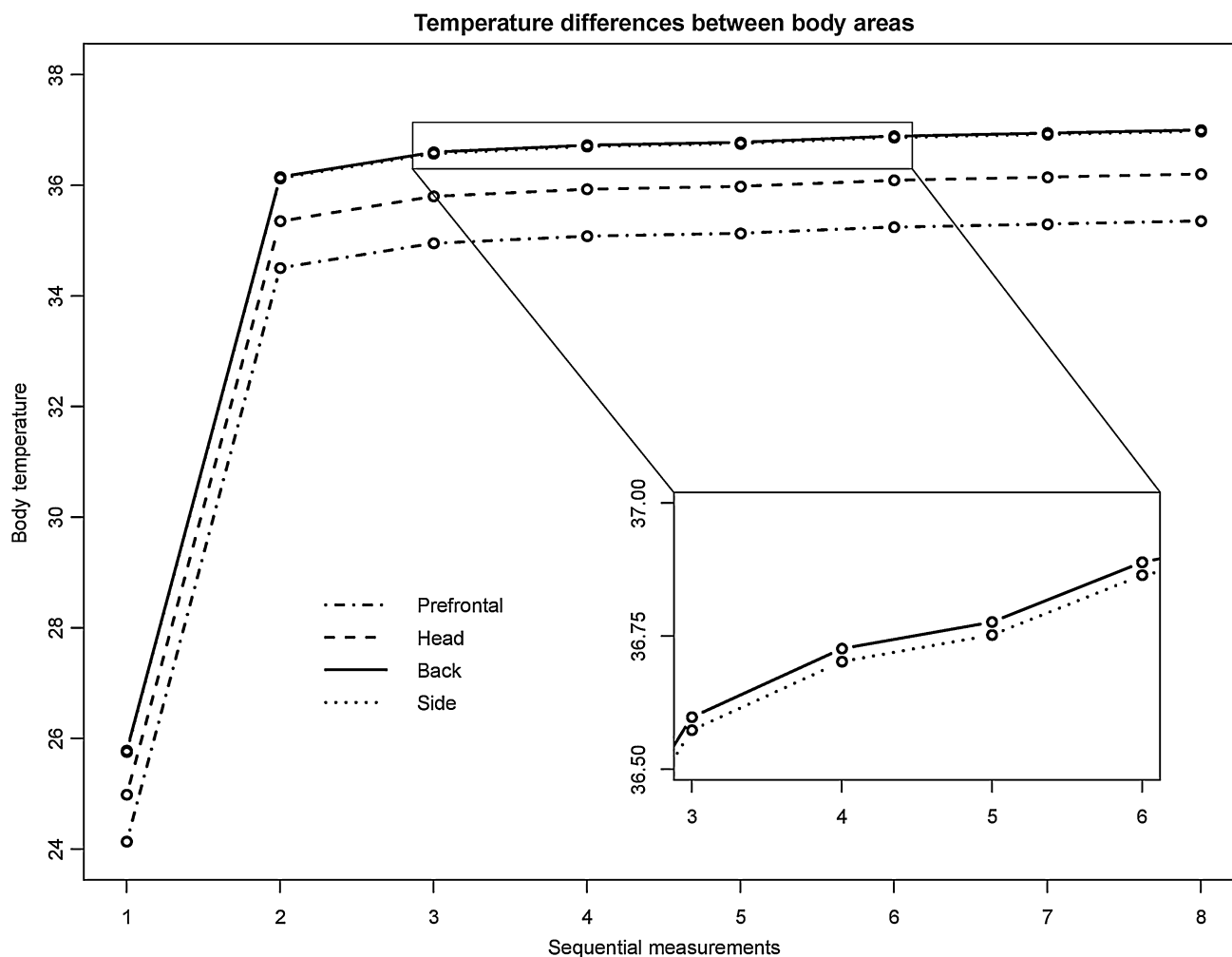
Figure 2 The temperature differences between the four body points as measured by the thermocamera. Lines represent the values predicted by the model for all individuals at the four points on the body, as experiment proceeds. Mean difference between lines are given in the results. The detail shows the little differences between the back and side temperatures. Please note the very different scale used for the plot and for the detail.

between back and side temperatures (t-value = 0.122; P-value = 0.903; d.f. = 3015; Fig. 2). Mean temperature differences between body parts were the following: 0.77 ± 0.16°C between the tip of the nose and the head; 0.75 ± 0.16°C between the head and the back; 0.02 ± 0.16°C between the back and the side.

When tested on polystyrene, the two instruments showed no difference in detected temperatures (LR = 0.020; P-value = 0.886; d.f. = 6). When used to measure T_b of living animals, the two instruments detected different temperatures. In particular, TC detected higher temperatures, with a mean difference of 0.84 ± 0.05°C (t-test = 16.81; P-value < 0.0001; d.f. = 3015). In Fig. 4, the occurrence of a temperature gradient across the body is easily noticeable.

The regression lines for the lizard data and the polystyrene test did not share common slopes (LR = 57.76; P-value < 0.0001; d.f. = 1; Fig. 3), implying that the correspondence

between measures obtained by TC and IR is affected by the properties of the material being measured. The SMA regression performed for polystyrene test found no deviation from slope = 1 (r_{27} = −0.05043; P-value = 0.795; slope = 0.99; confidence interval [CI] 95% = 0.96–1.03), suggesting that the two devices were reading the same temperature. Instead, the slope resulted statistically higher than 1 for lizard data (r_{1338} = 0.35; P-value < 0.0001; slope = 1.29; CI 95% = 1.24–1.34), that is, TC detected temperature values progressively higher than IR with increasing T_b.

Discussion

There is a lot of evidence that many reptile species are able to achieve and maintain local temperature differences among body parts (Hammel *et al.*, 1967; Heatwole, 1970; Johnson,
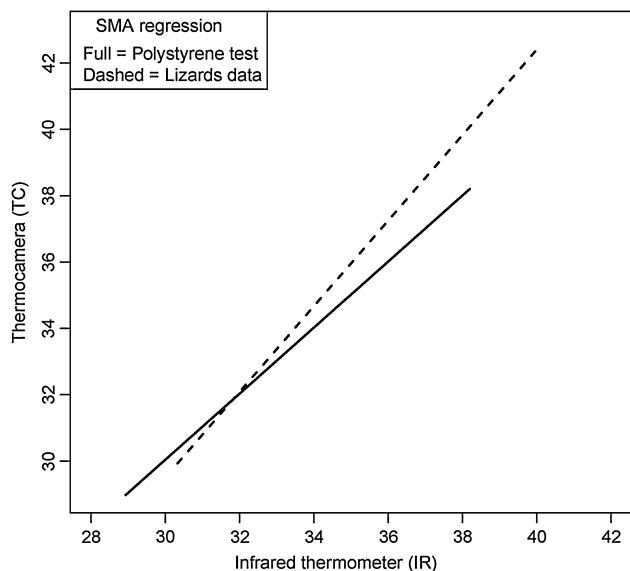
Figure 3 SMA regression lines for both polystyrene test (full line; slope = 0.99; CI 95% = 0.96–1.03) and lizard data (dashed; slope = 1.29; CI 95% = 1.24–1.34). At progressively higher temperature of the lizards, TC measures higher temperatures than IR. CI, confidence interval; IR, infrared thermometer; SMA, standardized major axis regression; TC, thermocamera.

1972; Webb *et al.*, 1972; Crawford Jr. *et al.*, 1977; Castilla *et al.*, 1999; Borrell *et al.*, 2005; Amiel *et al.*, 2011). Before the present study, however, there was no evidence of such a phenomenon in temperate, small body-sized lacertid lizards.

Our findings clearly showed the occurrence of a thermal gradient from the tip of the nose, the coolest part of the body, to the trunk, the warmest area. Head temperature was intermediate between them (Fig. 4). This thermal gradient was supported by data from both measuring devices (Table 1) and was maintained throughout the experiment (Fig. 2).

The head–body temperature gradient may be explained by means of different surface/volume ratios between head and trunk, as some authors found for *Iguana iguana* (Pough & MacFarland, 1976). Alternatively, the gradient could be actively maintained by physiological or behavioural mechanism, as several studies on lizard have proved (Heath, 1966; Hammel *et al.*, 1967; Heatwole, 1970; Johnson, 1972; Webb *et al.*, 1972; Crawford Jr. *et al.*, 1977).

If *P. muralis* is not able to regulate the heat distribution across its body and behaves as a passive heat exchanger, little differences between head and trunk temperatures should be expected (Stevenson, 1985; Fei *et al.*, 2012). Furthermore, the limbs and tail should be cooler than the head due to their higher surface/volume ratio. Instead, we found that the head is significantly cooler than the trunk (Fig. 4) and the limbs are almost always warmer than the head at high temperatures (Fig. 5). These results suggest the occurrence of an active mechanism that allows *P. muralis* to regulate, to a certain extent, the heat distribution. Such a mechanism could be

either physiological or behavioural or a combination of them. Behavioural strategies take advantage of convective and conductive heat exchanges and are well known for free ranging lizards which, for example, can shuttle between sunny and shady patches, use rodent or insect burrows, or climb on trees to expose the body to wind (Pough *et al.*, 2004). However, our experimental design prevented conductive and convective heath exchanges with the external environment and shadow patches were not available. Therefore, our results suggest that *P. muralis* physiologically regulates the heat distribution across its body and is consequently able to maintain local temperature differences. We observed that the coolest area of the body was the tip of the nose, which could indicate that respiratory cooling was occurring. In snakes, this mechanism has proven to be effective for the regulation of head temperature (Borrell *et al.*, 2005; Tattersall *et al.*, 2006) and this process may as well explain the temperature gradient that we observed in *P. muralis*. Actually, respiratory cooling is more of a physical phenomenon than a physiological process, but reptiles can increase or reduce lung ventilation to modify the rate of respiratory cooling (Al-Ghamdi, 2005). Other physiological mechanisms that allow the establishment of head–body temperature differences include countercurrent vascular systems (Heath, 1966) and blood shunts (Farmer, 2011). We cannot exclude that those mechanisms might also work in *P. muralis*, but no data are available for supporting nor rejecting this hypothesis. Physiological regulation of heat distribution is reinforced by the finding that limbs showed higher temperatures than the head. This result is contrary to the expectations, if no regulation does occur. It is thus possible that at high temperature, *P. muralis* exploits its limbs as heat radiator, as previously found for other reptiles (Dzialowski & O'Connor, 1999, 2004).

A second relevant result of this study is the lack of difference in T_b between the sexes, or with increasing body size. Huey & Pianka (2007) observed only minimal T_b differences between the sexes in 56 lizard species. Our data could therefore reflect a true absence of differences in thermal needs between males and females in *P. muralis*, but we cannot completely exclude the possibility that lack of sexual difference in thermal response was an effect of the experimental condition. We also did not find temperature differences associated with body size. Our experimental design specifically involved only adult lizards (SVL range: 52–71 mm), and was consequently able to reveal only large effects of body size. Therefore, we cannot exclude that temperature differences associated with body size might occur in wild populations, especially between juvenile and adult lizards (Vasconcelos, Santos & Carretero, 2012).

The third main result concerns the responses of IR and TC. The two measurement devices showed no differences in detected temperatures when applied on insulating material like polystyrene, while they noticed statistically different temperatures on lizards, with TC reading higher values than IR. Both devices are supposed to measure the superficial temperatures (Rowley & Alford, 2007; Bucklin *et al.*, 2010), but our data suggest that this might not be the case when T_b increases. Indeed, the thickness of the body surface radiating
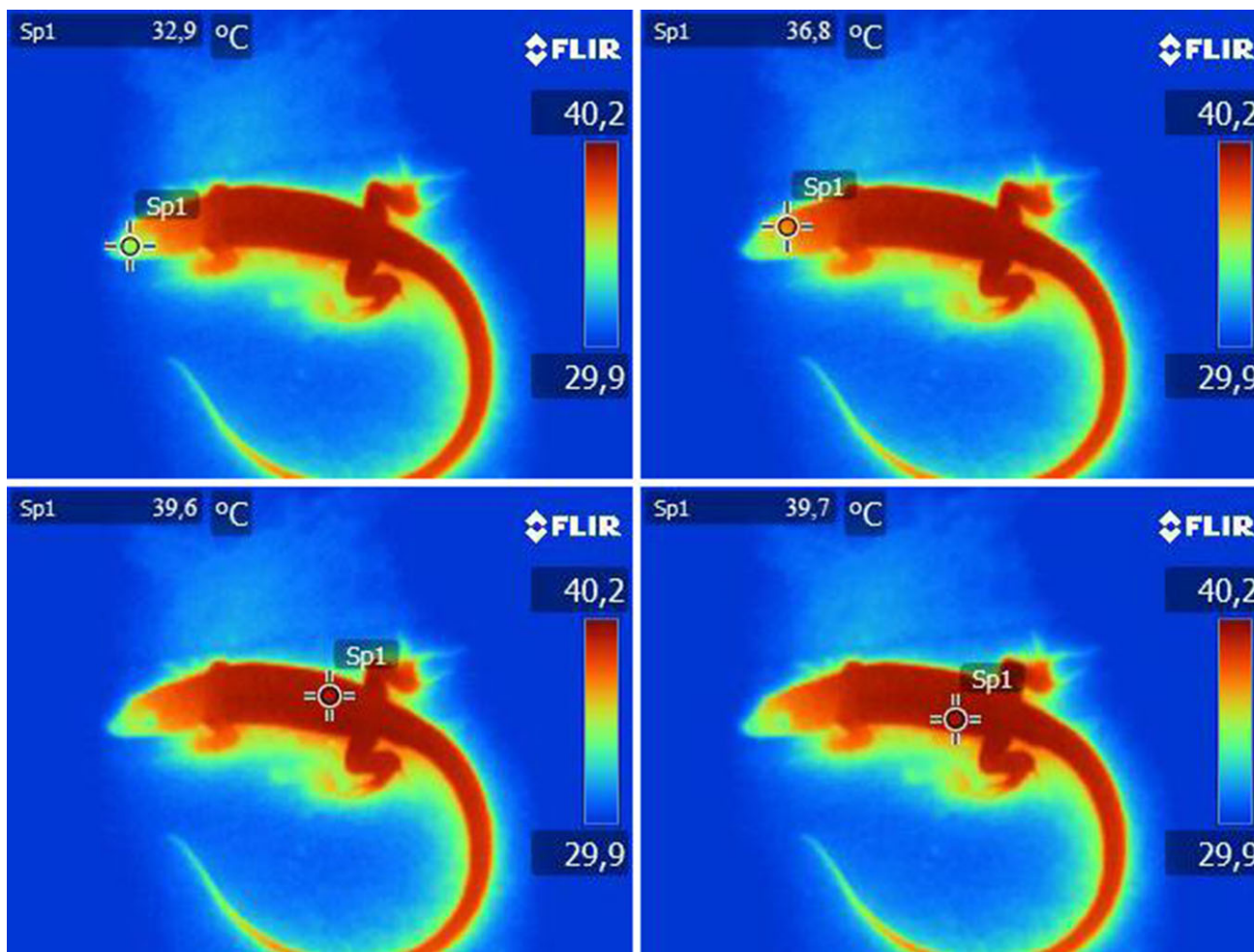
Figure 4 Infrared pictures showing body temperatures of a female lizard at the time T4. Clockwise, from top left: prefrontal, head, side and back temperatures. The mark 'Sp1' is the thermocamera pointer that reads body temperature at the shown point. The measured value is reported in the top left corner of each picture. Also, the temperature-to-colour scale that was used is shown on the right-hand side of each picture. We used FLIR tools 3.1 in order to show the same picture and moved the pointer to highlight the four body points chosen in this study. A temperature gradient reaching from the tip of the nose via head to the trunk is evident. Please note that the limb temperatures appear to be warmer than the head temperature.

heat detected by TC and IR may play an active role in the measuring process. Therefore, it is possible that TC is able to detect not only the temperature of the epidermis, but also some amount of the dermis heat, where the blood flow occurs (Tattersall *et al.*, 2009; Tattersall & Cadena, 2010). Carretero (2012) questioned the use of IR in small lacertid lizards, since he found that IR reads progressively greater values than cloacal thermometer with higher T_b. Our data do not support this assumption as we found that the properties of the surfaces being measured differently affect the correlation between the readings of the two devices. As stated before, we ascribed this effect to the thickness of skin surface, particularly to the heat radiated by the dermis, which is possibly detected by TC but not by IR. If the thickness of the skin can cause these effects, it is quite unlikely

that core and skin temperatures may not be different, even in a small lizard. We therefore remain cautious on the criticism by Carretero on the use of IR, since it is possible that each measurement device measures temperatures using heat radiated through different processes that, as we have shown, do not necessarily share the same response with the increase of T_b. It is not possible, in our opinion, to validate or invalidate a given thermal device through the comparison of its readings with those of a second measurement device using a living organism as measuring object. However, our results are not in contrast with Carretero's conclusions concerning potential errors of IR with small lizards due to the pointer area, which can capture some amount of noise and lead to underestimate the actual temperature of the lizard's body. Further, more investigations are needed to understand to
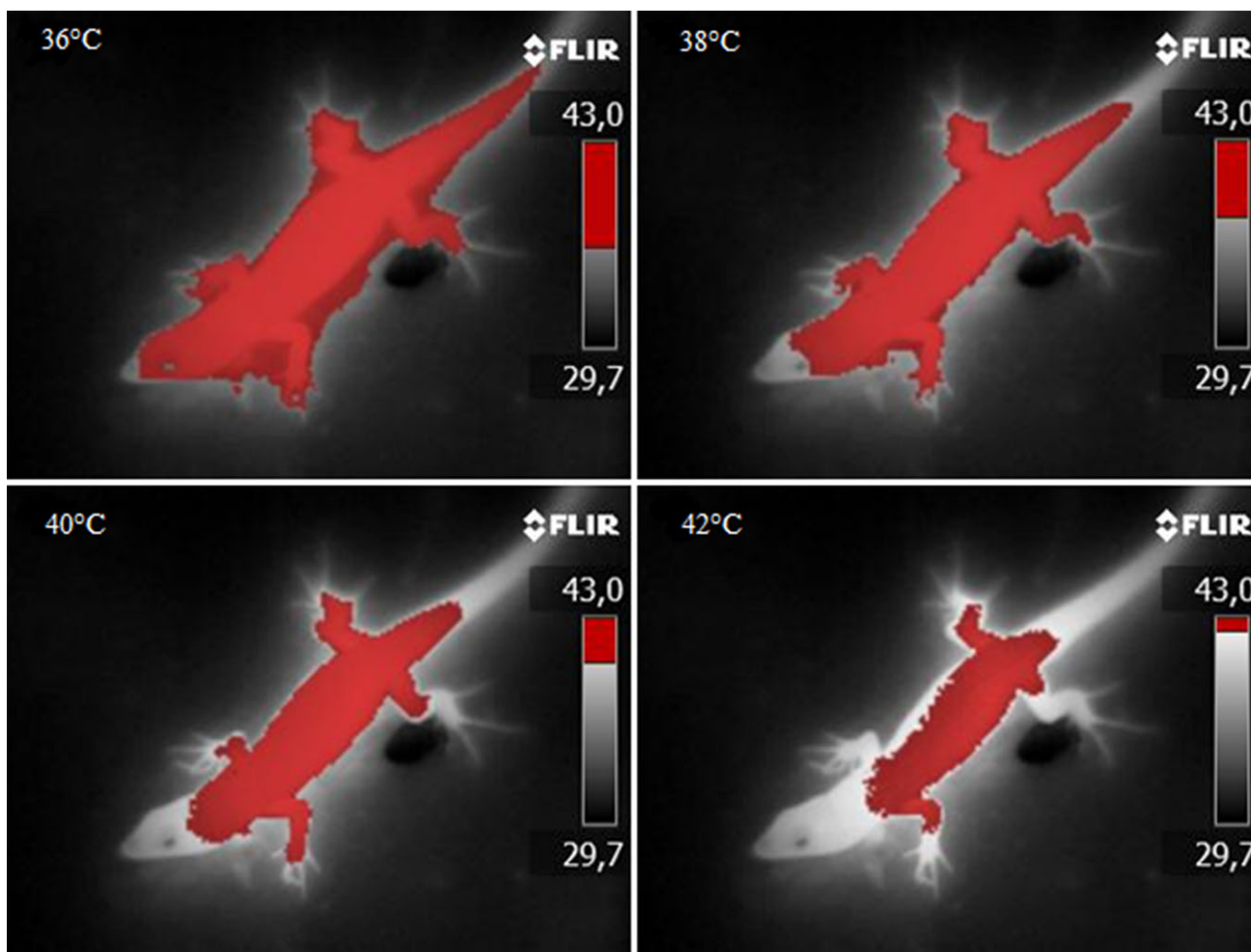
Figure 5 Pictures of a male lizard at time T4 showing distribution of body temperatures in relation to four selected thresholds. Threshold values are indicated in the upper left corner of each picture. The red parts of the body have temperatures above the threshold and the gray parts have temperatures below the threshold. The bar on the right in each picture indicates the position of the threshold (border between red and gray) in relation to the range of temperatures during the heating experiment. Note that in the lower left picture, the temperature of the head is lower than that of most parts of the limbs.

which extend TC is able to measure both superficial and dermal temperatures in living animals.

In conclusion our experiments showed for the first time that a small temperate lacertid lizard, the common wall lizard *P. muralis*, is able to achieve and maintain local temperature differences across body parts. Probably, respiratory cooling plays a major role, but we found support for the occurrence of interactions between physical, physiological and/or anatomical mechanisms in maintaining local temperature gradients. Future researches are needed to disentangle the contribution of those different mechanisms.

Acknowledgements

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