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Experimental support for the cost–benefit model of lizard thermoregulation: the effects of predation risk and food supply

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Abstract Huey and Slatkin's (Q Rev Biol 51:363–384, 1976) cost–benefit model of lizard thermoregulation predicts variation in thermoregulatory strategies (from active thermoregulation to thermoconformity) with respect to the costs and benefits of the thermoregulatory behaviour and the thermal quality of the environment. Although this framework has been widely employed in correlative field studies, experimental tests aiming to evaluate the model are scarce. We conducted laboratory experiments to see whether the common lizard *Zootoca vivipara*, an active and effective thermoregulator in the field, can alter its thermoregulatory behaviour in response to differences in perceived predation risk and food supply in a constant thermal environment. Predation risk and food supply were represented by chemical cues of a sympatric snake predator and the lizards' food in the laboratory, respectively. We also compared males and postpartum females, which have different preferred or "target" body temperatures. Both sexes thermoregulated actively in all treatments. We detected sex-specific differences in the way lizards adjusted their accuracy of thermoregulation to the treatments: males were less accurate in the predation treatment, while no such effects were detected in females. Neither sex reacted to the food treatment. With regard to the two main types of thermoregulatory behaviour (activity and microhabitat selection), the treatments had no significant effects. However, postpartum females were more active than males in all treatments. Our results further stress that increasing physiological performance by active thermoregulation has high priority in lizard behaviour, but also shows that lizards can indeed shift their accuracy of thermoregulation in response to costs with possible immediate negative fitness effects (i.e. predation-caused mortality).

Keywords Body temperature · Thermoregulatory behaviour · Thermoregulatory strategy · *Zootoca vivipara*

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Introduction

In ectotherms, virtually all studied behavioural or physiological traits have been found to be body-temperature-dependent (e.g. Bennett 1980; Hertz et al. 1982; Huey 1982; Shine and Harlow 1993; Sinervo and Adolph 1994; Belliure et al. 1996; Angilletta 2001; Angilletta et al. 2002). The fact that terrestrial ectothermic vertebrates have the ability to maintain a relatively high and constant body temperature has long been recognised (Sergeyev 1939; Cowles and Bogert 1944). Thermoregulation includes both physiological and behavioural processes (Stevenson 1985a), and their relative contributions are highly size-dependent (Stevenson 1985a, 1985b). Small ectotherms undergo rapid heat exchange with their environment, so they can act as thermal opportunists and regulate their body temperature almost exclusively by behavioural means (Stevenson 1985a, 1985b; Adolph 1990; Bauwens et al. 1996). The timing of seasonal and daily activities seems to be the most critical factor determining body temperature for small-bodied heliotherms (i.e. ectotherms that gain heat directly from solar radiation), whereas thermal microhabitat selection is the predominant thermoregulatory behaviour during activity (e.g. Stevenson 1985a; Adolph 1990; Bauwens et al. 1996).

According to Huey and Slatkin's (1976) cost–benefit model of lizard thermoregulation, lizards (or ectotherms in a wider sense) should alter their thermoregulatory strategy with respect to the costs associated with the behaviour, the benefits of the achieved body temperature and the thermal quality of the environment. The model was based on the assumption that the extent of thermoregulation is adjusted to maximise net energy gain. However, Huey and Slatkin (1976) emphasised that thermoregulatory strategies are also influenced by other than energetic considerations, and their model would equally describe gains and losses of fitness with regard to any fitness-related activities (like mate search, predator avoidance or foraging) that conflict with accurate thermoregulatory behaviour. The two extremes of thermoregulatory strategy are active thermoregulation (reaching the optimal body temperature as the primary task) and thermoconformity (no regulation). The main benefit of maintaining the optimal body temperature is the optimisation of the physiological processes (e.g. Huey and Stevenson 1979; Angilletta et al. 2002). The associated costs are the time and energy devoted to the thermoregulatory behaviour that are consequently not available for other fitness-related activities like foraging or mate-searching, and an increased risk of predation (Huey and Slatkin 1976). The model is commonly used as a conceptual framework (e.g. Blouin-Demers and Nadeau 2005); hence, empirical tests of the model's predictions are of principal importance. While it has been shown experimentally that lizards bask less under high predation risk (Downes and Shine 1998; Downes 2001), the thermoregulatory strategy or the environmental and body temperatures were not studied in these experiments. Despite its high importance, empirical tests of the effects of manipulated costs on the thermoregulatory behaviour are extremely scarce (but see Withers and Campbell 1985).

In an earlier study, we showed that the common lizard *Zootoca vivipara* thermoregulates with high accuracy as long as its preferred or "target" body temperature range [the body temperature range (central 80% in our case) that the study animals maintain in a zero cost thermal environment] is available, but turns into an almost perfect thermoconformer when not (Herczeg et al. 2006). *Z. vivipara* is an excellent model for experimental studies of thermoregulation as its thermal physiology and ecology are well documented. It is a very accurate and effective thermoregulator in different thermal environments (Van Damme et al. 1987; Gvoždik 2002) and has evolutionarily rigid thermal preference and tolerance limits (Van Damme et al. 1990a; Gvoždik and Castilla 2001; Uller and Olsson 2003). Furthermore, while the preferred body temperature range does not necessarily include optima for the different physiological functions (Huey and Bennett 1987), in the case of *Z. vivipara* it does (Van Damme et al. 1990a, 1990b; 1991). Hence, the physiological benefits of accurate thermoregulation can be assumed directly.

In the present paper, we test the hypothesis that *Z. vivipara* (an active thermoregulator in the field) adjusts its thermoregulatory strategy in response to different perceived costs of thermoregulation in a constant thermal environment where its preferred body temperature is available. It is noteworthy that Huey and Slatkin's (1976) model was formulated on energetic considerations, and that we use it in a wider sense to generate predictions (see below) about the effects of other than energetic costs on thermoregulatory behaviour. The main ecological costs associated with thermoregulatory behaviour besides energy are (1) the increased predatory risk and (2) the lost opportunities (e.g. foraging, mating). We tested the following predictions. First, lizards will decrease the accuracy of their thermoregulation under simulated predation risk or food shortage. Second, the expected response will be stronger under predation risk than under food shortage, as the former (as compared to the latter) treatment entails immediate fitness loss. Third, the response of postpartum females to the treatments should be weaker than that of males, as females can be expected to depend more strongly on optimal physiological performance to regain body condition and energy stores following parturition.

Materials and methods

Study organism and sampling

The European common or viviparous lizard, *Z. vivipara*, is a small [snout-vent length (hereafter SVL) ca. 25–70 mm (45–70 mm for adults); body weight (hereafter BW) ca. 0.35–6 g (2–6 g for adults)], diurnal, heliothermic lizard. It has the largest distribution amongst the world's reptiles; its distribution extends from northwest Spain to Sakhalin in the east, and well beyond the Arctic Circle in the north. It occurs at both high altitudes and latitudes (Gasc et al. 1997) and is one of the most effective thermoregulators among lizards (Gvoždik 2002).

We collected adult lizards from a population near Helsinki between 24 July and 27 August in 2006, during the experiments (see below). The habitat of the sampled population belongs to the humid habitat type of the species (see Lorenzon et al. 1999); it was a swampy meadow with short, sparse birch trees. Ground was covered with a thick layer of moss and/or grass. Lizards were collected by noosing or by hand; all individuals were released at the site of capture after the experiment. Although tail loss is unlikely to affect thermoregulatory behaviour in *Z. vivipara* (Herczeg et al. 2004), we used individuals with intact or fully regenerated tails. Altogether, 34 individuals (15 males and 19 postpartum females) were caught and used in the experiments. In some cases, especially in August, we could not judge by eye whether a female was postpartum or nonreproductive. However, since females reproduce annually in the study population according to our experience, all adult females were considered to be postpartum individuals.

Experimental design

We used eight 150 × 60 × 50 cm (length × width × height) rectangular glass terraria as experimental units. We established similar photothermal gradients in all terraria by suspending 75 W reflector bulbs (Exo Terra "Sun Glo" Broadspectrum Daylight Spot Lamp; Rolf C. Hagen Inc., Montreal, Canada) at one end of the terraria and placing ice boxes under the other end. The heating bulbs were switched on at 09:00 hours and off at 18:30 hours each day. Terraria walls were covered with brown paper such that lizards in different terraria could not see each other. We simulated shifting natural photoperiod conditions, starting with a 19:5 light:dark period on the 26 of July, changed it to 17:7 two weeks later and to 15:9 again after the next two weeks. The long light phase and the rapid change in late summer are natural at this latitude (ca. 60°10′N).

We established thermal gradients where the preferred body temperature (including the physiological optima in *Z. vivipara*; Van Damme et al. 1990a, 1991) of the species was available, but only under the basking bulb, to provide a challenging thermal environment. We used preferred body temperature range data recorded in late July in 2004 using lizards from the same population (central 80% of body temperatures recorded in a zero cost thermal gradient; males 30.7–34.7 °C; postpartum females 31.9–37.4 °C; Herczeg et al. 2006). Each terrarium was divided into three equal-sized sectors: sector 1 was directly under the bulb and termed "warm", sector 2 was in the middle of the arena and termed "medium", and sector 3 was above the ice boxes and termed "cool". We measured the operative temperature (an estimate of body temperature for an organism that does not exhibit behavioural or physiological thermoregulation, and has reached thermal equilibrium; Bakken et al. 1985; Hertz et al. 1993) in the terraria with the aid of physical models (Hertz et al. 1993). Although the importance of model attributes is debated (Walsberg and Wolf 1996; Vitt and Sartorius 1999; Shine and Kearney 2001; Dzialowski 2005), considering the size of *Z. vivipara* and the aims of our measurements, we used simple hollow copper pipes (65 mm long, 12 mm in diameter, 1 mm in thickness) sealed with plastic caps, painted brown with a small hole drilled in the middle, through which a K-type thermocouple connected to a TESTO 925 digital thermometer (TESTO, Lenzkirch, Germany) could be inserted. First, we set the minimum and maximum operative temperature in each terrarium (mean ± SD: minimum = 13.87 ± 0.65 °C, maximum = 34.99 ± 0.20 °C). Second, we measured operative temperature in a randomly chosen terrarium in more detail by randomly placing ten models into each sector after substrate, refuges, etc. (see below) were in place. The operative temperature differed between sectors ($F_{(2,27)} = 21.27$, $P < 0.001$; mean ± SD: "warm" sector = 29.22 ± 3.37 °C; "medium" sector = 25.02 ± 0.96 °C; "cool" sector = 19.95 ± 4.25 °C).

Bases of the terraria were covered with an approximately 2-cm layer of wet turf–soil mixture. If the substrate was not changed (according to the experimental protocol, see below), it was moistened by spraying water once a day, before starting the measurements. We provided six (two per sector) plastic flower-pot halves as refuges. Water was provided ad libitum in six (two per sector) Petri dishes. Mealworms (*Tenebrio molitor* larvae) were provided (according to the treatments, see below) in six (two per sector) Petri dishes.

We applied three treatments: "predation", "food" and "control". In the "predation" treatment, we used chemical stimuli from a common predator of *Z. vivipara*, the adder (*Vipera berus*), which occurs in sympatry with *Z. vivipara* in our study population. *Z. vivipara* is known to react to the chemical cues of *V. berus* (Thoen et al. 1986; Van Damme et al. 1990b); even naive newborn juveniles do so (Van Damme et al. 1995). We caught four adult adders and kept them in two plastic boxes (two in each). Water was provided ad libitum and heating bulbs offered the possibility of thermoregulation. The adders were fed with rat sucklings weekly and released at the point of capture following the experiment. We placed two 20 × 30 cm pieces of absorbent paper on the base of each plastic box housing the adders for 24 h. To set up the "predation" treatment, we placed one paper containing adder scent directly under the heating bulb in the experimental terrarium. The paper was fixed onto a similarly sized wooden panel with drawing pins. Similar papers without scent were placed in the middle of the "medium" and "cool" sectors. In this way we presented high potential predation risk in the only good basking spot. One could argue that the chemical cues of the predator might fade under the bulb relatively fast, but we assumed that the treatment was adequate in representing an area that is more frequently used by potential predators than other areas within the terraria. Our assumption was supported by the facts that (1) we detected a thermoregulatory response to this treatment and (2) the accuracy of thermoregulation did not increase during the day (actually, we found a slight decrease; see "Results").

In the "food" treatment, we used chemical stimuli from mealworms. We kept large numbers (>100) of mealworms in two plastic boxes. Two 20 × 30 cm pieces of absorbent paper were placed on the base of each plastic box for 24 h. We placed one paper containing mealworm scent in the middle of the "cool" sector and two papers without scents in the middle of the "medium" and "warm" sectors. Papers were fixed on similarly sized wooden panels with drawing pins. Here, we mimicked good foraging areas in the sectors with the lowest thermal quality.

Although all of the actively foraging insectivorous lizards studied were found to identify prey scent (e.g. Cooper 1995; Cooper et al. 2000; Cooper and Pérez-Mellado 2001, 2002), as far as we are aware, *Z. vivipara* has not been studied in this respect. Hence, we conducted a pilot experiment to test whether *Z. vivipara* can distinguish between distilled water (scentless control), 9:1 water:cologne solution (pungency control; Cooper et al. 2002) and mealworm scent. We randomly selected eight lizards (four males and four females that had fed on mealworms before) and presented the different stimuli 1–2 cm from the lizards' snouts in a random order using cotton swabs on the tip of 15-cm-long wooden applicators. After the first tongue-flick, the number of tongue-flicks was recorded for 60 s. If the lizard moved its snout more than 5 cm away from the cotton swab, the experiment was terminated. A minimum waiting time of 20 min between subsequent testing of the same individual was applied. We found that the lizards responded with a higher number of tongue-flicks to the mealworm scent than to any of the control scents (repeated measures ANOVA: $F_{(2,14)} = 7.45$, $P = 0.006$; number of tongue-flicks ± SE: distilled water = 3.25 ± 1.22; cologne = 6.62 ± 1.37; mealworm = 12.12 ± 3.07), and the only two biting attempts were observed in response to mealworm scent, and thus we assumed that they can identify their prey's scent.

In the "control" treatment, one scentless paper was presented in the middle of each sector. Following one day of acclimation, each lizard met the treatments in random order. In addition to the acclimation day, there was a starvation day before the "food" treatment. Food was always provided ad libitum, but in the "food" treatment or in the starvation days (prior to "food" treatment) there was no food at all. Between treatments, lizards were randomly redistributed between the available terraria, substrate was changed and the refuges and Petri dishes were washed. There was a day for re-acclimation between the treatments. Scentless papers were presented in the acclimation, re-acclimation and starvation days in all sectors. As the absorbent paper backs were covered with plastic, we did not wash or change the wooden panels. We note that lizards did not experience real costs in our treatments. We attempted to provide situations where lizards, based on chemical information, could alter their accuracy of thermoregulation with respect to the perceived predation risk or food supply, or in other words, could decide between (1) thermoregulation and predator avoidance and (2) thermoregulation and foraging.

Data collection and analysis

To avoid the disturbance caused by the repeated handling and cloacal body temperature measurements, we measured temperature of the body surface of the experimental lizards with a Raynger ST80 ProPlus non-contact infrared thermometer (Raytek® Santa Cruz, CA, USA). This method gives close estimates of the cloacal body temperature measurements in *Z. vivipara* (as shown in detail in Herczeg et al. 2006; see also Shine et al. 2002 for similar inference).

Including all treatments, acclimation, re-acclimation and starvation days, one experiment lasted for seven days. Due to the number of available terraria, eight lizards could be tested simultaneously in isolation. We ran three full runs with eight lizards, one with seven lizards, and one with three lizards. Lizards were caught two or three days before the start of the experiment, kept in plastic boxes with water and food provided ad libitum, and a heating bulb that allowed thermoregulation was also present.

Lizards were individually marked by paint codes and introduced to the terraria in the evening before the first acclimation day. On the treatment days, lizards were monitored from 10:00 to 18:00 hours at hourly intervals. We recorded body temperature, activity (individuals in retreats or dug in the substrate were counted as inactive) and sector preference of the individuals (representing thermal microhabitat preference). If a lizard was found to be inactive, we gently lifted the refuge and measured lizards' body temperature. If they were hidden in the substrate and we could not locate them, body temperature and sector preference measurements were left unscored. This method resulted in 890 body temperature and sector preference records (682 measurements during activity) and 918 activity records.

We estimated the accuracy of thermoregulation as the mean absolute deviation of body temperatures from the boundaries of the preferred body temperature range (Hertz et al. 1993). Likewise, the thermal quality of habitat was estimated as the mean absolute deviation of operative temperatures from the boundaries of the preferred body temperature range (Hertz et al. 1993). For these indices, we used preferred body temperature data measured in the same population in the same season in 2004 (Herczeg et al. 2006). To test for the extent of thermoregulation we compared individual mean accuracy of thermoregulation with thermal quality of habitat (e.g. Díaz and Cabezas-Díaz 2004). Because the sample sizes of operative temperature measurements were artificial and not independent, we calculated the mean accuracy of thermoregulation for each individual, and simply compared them (for the sexes and treatments separately) with the mean thermal quality of habitat, applying one-sample *t* tests. Here, we used data only from active individuals, as quantifying the thermoregulatory strategy makes sense in active individuals (Huey and Slatkin 1976; Hertz et al. 1993). As the thermal environments were the same, we did not calculate the different indices describing the effectiveness of thermoregulation (Hertz et al. 1993; Blouin-Demers and Weatherhead 2001); in this case accuracy of thermoregulation was informative alone.

We used general or generalised linear mixed models (GLMMs) in PROC MIXED of SAS (Littell et al. 2006) in the analyses of accuracy of thermoregulation, activity and sector preference patterns. We set individual as the random factor in these models to account for the nonindependence in our data (repeated measurements of the same individuals). As we conducted five rounds of experiments (one round lasted for one week; a maximum of eight experiments ran simultaneously) we included round as a fixed factor (no interactions were computed) in the models to control for its potential effect. To analyse accuracy of thermoregulation, we applied GLMM with activity, sex and treatment as fixed factors and time (time of measurement within day) as a covariate. Here, we included activity in the model in order to see whether choosing inactivity during the daily activity period has an effect on the body temperature. To analyse activity, we applied GLMM with binomial error (applying the GLIMMIX macro, Littell et al. 2006), as each lizard in each measurement was counted as either active or inactive. We set sex and treatment as fixed factors and time as a covariate. To describe sector preference we calculated an index as follows:

$$I = (n_1 + 2n_2 + 3n_3)/(n_1 + n_2 + n_3)$$

where n_1 = number of times a lizard was found in sector 1, n_2 = number of times a lizard was found in sector 2, and n_3 = number of times a lizard was found in sector 3 on a given day (Herczeg et al. 2006). In the GLMM we set the index of sector preference as the dependent variable, and sex and treatment as fixed factors. Here, we only analysed active individuals, as analysing sector preference as a variable describing thermoregulatory behaviour makes sense in active individuals (Huey and Slatkin 1976; Hertz et al. 1993). In all GLMM models we included only the biologically interpretable two-way interactions and the single explanatory variables.

All statistical analyses were performed with SAS 9.1 (SAS Institute Inc., Cary, NC, USA) and Statistica 6.1 (StatSoft Inc., Tulsa, OK, USA) software packages.

Results

Thermoregulatory strategy

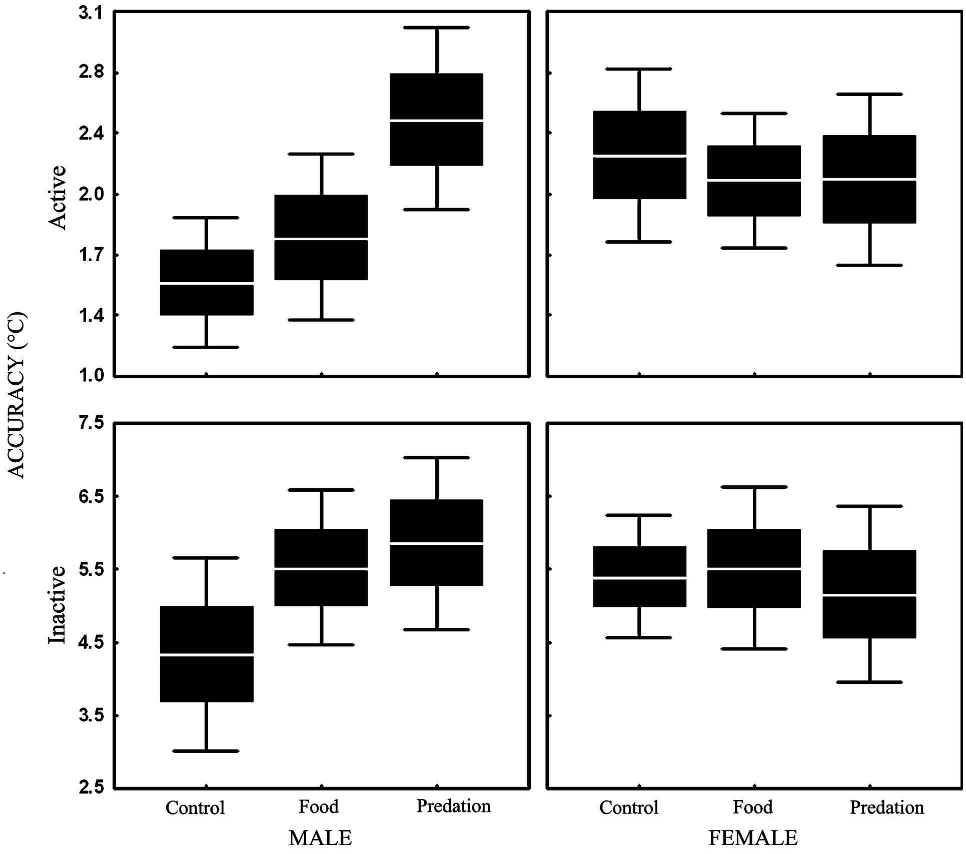
In all treatments, the accuracy of thermoregulation was higher (closer to zero) than the mean thermal quality of habitat in both sexes (males: $t_{14} < -11.08$, $P < 0.001$; females: $t_{18} < -11.62$, $P < 0.001$). The results remained the same after applying the sequential Bonferroni correction (Rice 1989) for each sex. These results indicate active thermoregulation in all treatments by both sexes.

A GLMM revealed that males and females adjusted their accuracy of thermoregulation differently in response to the treatments (treatment: $F_{(2,851)} = 0.53$, $P = 0.591$; sex: $F_{(1,197)} = 0.10$, $P = 0.753$; treatment × sex: $F_{(2,844)} = 4.36$, $P = 0.013$; Fig. 1). In other words, males reacted to the "predation" treatment by lowering their accuracy of thermoregulation, whereas females did not (Fig. 1). Active individuals maintained their body temperature closer to their preferred range than did the inactive ones (activity: $F_{(1,859)} = 41.58$, $P < 0.001$; Fig. 1). We found a weak, nonsignificant decrease in accuracy of thermoregulation within day (time: $F_{(1,857)} = 3.30$, $P = 0.070$; data not shown). Timing of the experiment had no effect on the accuracy of thermoregulation (round: $F_{(4,27.9)} = 0.58$, $P = 0.680$). The individual effect was significant ($Z = 2.52$, $P = 0.006$). All other interactions were nonsignificant (treatment × activity: $F_{(2,863)} = 1.04$, $P = 0.356$; treatment × time: $F_{(2,847)} = 0.72$, $P = 0.487$; sex × activity: $F_{(1,863)} = 0.03$, $P = 0.866$; sex × time: $F_{(1,861)} < 0.01$, $P = 0.957$; activity × time: $F_{(1,860)} = 0.44$, $P = 0.509$).

Activity and sector preference

A GLMM revealed that the general activity level decreased during the day in both sexes, while postpartum females were active more of the time than males (time: $F_{(1,904)} = 87.04$, $P < 0.001$; sex: $F_{(1,246)} = 2.49$, $P = 0.116$; sex × time:

Fig. 1 Accuracy of thermoregulation [mean ± SE (boxes) ± 95% CI (whiskers)] of *Z. vivipara* in the different treatments. Accuracy of thermoregulation is the mean absolute deviation of body temperatures from the preferred body temperature range (0 means perfect thermoregulation)



$F_{(1,904)} = 9.59$, $P = 0.002$; Fig. 2). Activity did not differ among treatments ($F_{(2,874)} = 0.45$, $P = 0.635$) and none of the remaining interactions were significant (treatment × sex: $F_{2,874} = 0.13$, $P = 0.875$; treatment × time: $F_{(2,874)} = 0.32$, $P = 0.723$). Timing of the experiment did not affect activity (round: $F_{(4,25.1)} = 0.93$, $P = 0.464$). The individual effect was significant ($Z = 2.34$, $P = 0.009$).

According to the third GLMM, none of the single explanatory variables or the interaction had a significant effect on sector preference (treatment: $F_{(2,64)} = 1.15$, $P = 0.322$; sex: $F_{(1,31)} = 0.97$, $P = 0.332$; treatment × sex: $F_{(2,64)} = 1.52$, $P = 0.226$; round: $F_{(1,31)} = 0.06$, $P = 0.804$). The individual effect was also nonsignificant ($Z = 1.04$, $P = 0.149$).

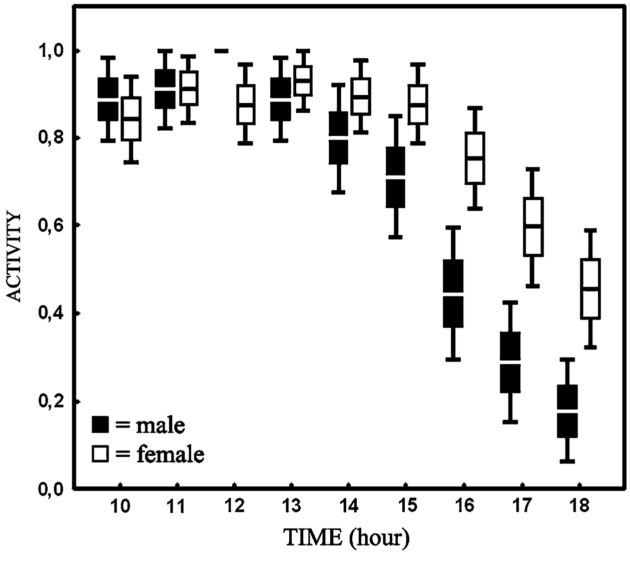


Fig. 2 Daily activity patterns [mean ± SE (boxes) ± 95% CI (whiskers)] of *Z. vivipara*. One denotes 100% activity, zero denotes perfect inactivity

Discussion

Although the cost–benefit model of lizard thermoregulation (Huey and Slatkin 1976) has been, and still is, widely used as conceptual framework in studies of thermoregulation (e.g. Blouin-Demers and Weatherhead 2001; Gvoždik 2002; Blouin-Demers and Nadeau 2005), its validity has seldom been tested experimentally. Withers and Campbell (1985) employed an operant conditioning technique in a shuttle box with heating lamps at both ends to see whether desert iguanas (*Dipsosaurus dorsalis*) are capable of changing their accuracy of thermoregulation as a response to increased energy costs of active thermoregulation. The lamps turned on when the experimental lizard broke a light beam (produced by photodiodes and monitored by photodetectors) under the given lamp, and the radiant heat provided by the lamps could only be exploited alternately. By manipulating ambient temperature and the thermal reinforcement time provided by a given lamp upon activation, Withers and Campbell (1985) were able to manipulate the time and energy needed for precise thermoregulation. Their results provided support for the cost–benefit model of thermoregulation (Huey and Slatkin 1976). In a preliminary study, we showed that *Z. vivipara* can change its thermoregulatory strategy in a zero cost environment and turn into an almost perfect thermoconformer when its preferred body temperature is unavailable (Herczeg et al. 2006). Hence, the question of whether lizards can change their thermoregulatory strategy with respect to the main ecological costs (increased predatory risk and lost opportunities) in environments where maintenance of preferred body temperature and, consequently, optimal physiological performance is possible, remained open.

The results of the present work show that lizards can alter their accuracy of thermoregulation in response to certain ecological costs, supporting the cost–benefit model of lizard thermoregulation (Huey and Slatkin 1976). However, we could not detect a total strategy change from active thermoregulation to thermoconformity in our treatments where the preferred body temperature of the experimental lizards was available (although the availability was limited to a small basking spot). By modelling fitness landscapes of thermal generalists and specialists in different environments, Gilchrist (1995) concluded that thermal specialists are favoured in environments where the thermal variation is low among generations (but can be high within generation). Furthermore, the benefits of accurate thermoregulation might be higher for thermal specialists than for thermal generalists (Huey and Slatkin 1976; Gilchrist 1995; for a review see Angilletta et al. 2006). Hence, the lack of a total strategy change is not surprising. Such strategy changes might occur rarely (if ever) in environments where the mean thermal quality is low, but the preferred body temperature is available. The responses to the increasing costs are likely to manifest as slight shifts in a continuum between the extreme strategies without a drastic decrease in performance. In our case, the shift in the accuracy of thermoregulation of male *Z. vivipara* in the “predation” treatment translates to a minor decrease in locomotor performance (Van Damme et al. 1990a) and a larger but still moderate decrease in behavioural and physiological traits related to feeding (Van Damme et al. 1991). The expected total strategy change in environments where the preferred body temperature is unavailable (Herczeg et al. 2006) must represent a case that normally does not occur in natural lizard habitats in the temperate zone, as available maximum operative temperatures exceed the preferred body temperature range even in the most extremely cool *Z. vivipara* habitats during the activity season (Gvoždik 2002; Herczeg et al. 2003). On days, or even during shorter within-day periods, when the preferred body temperature is unavailable due to bad weather, *Z. vivipara* simply becomes inactive (e.g. Van Damme et al. 1987), which might also be a response to some permanent threat like continuous predator presence. However, in tropical regions, where lizards inhabit areas where their preferred body temperature is unavailable but the operative temperature is generally close to the lower boundary of their preferred range, otherwise actively thermoregulating lizards were shown to adopt the thermoconformer strategy (Huey 1974).

We found that lizards altered their accuracy of thermoregulation only in the “predation” treatment, but not in the “food” treatment. They either did not react to the “food” treatment, or changed their behaviour without sacrificing thermoregulation. For instance, they might have frequently visited the cool end of the terrarium for foraging but then return to the basking spot to warm up when necessary (which may be the case in nature too). This suggests that only costs with immediate negative effects on the individual fitness have the potential to override the benefits of optimised physiological performance accomplished by accurate thermoregulation. As the benefits of maintaining the optimal body temperature are greater for thermal specialists (favoured in habitats with low among-generation thermal variation) than for thermal generalists (Huey and Slatkin 1976; Gilchrist 1995), one would predict that apparently costly mechanisms of behavioural thermoregulation greatly increase fitness in ectotherms living in thermally challenging environments. Indeed, field studies conducted in cool environments indicate that lizards are ready to invest more time and energy into thermoregulation in order to maintain their optimal body temperature (e.g. Hertz and Huey 1981; Christian 1998; Gvoždik 2002; Huey et al. 2003). Furthermore, a recent meta-analysis revealed that lizards living in environments with low thermal quality are thermoregulating with higher effectiveness than lizards in high-quality environments (Blouin-Demers and Nadeau 2005). On the other hand, costs with immediate negative effects on fitness (i.e. predation or reproduction) seem to be able to override the need for accurate thermoregulation (Downes and Shine 1998; Shine et al. 2000; Downes 2001; Herczeg et al. 2007).

Male *Z. vivipara* responded to the predator’s scent in the basking place by decreasing their accuracy of thermoregulation, but postpartum females did not, suggesting that the cost–benefit relations differed between males and females in the same situation. It is unlikely that *V. berus* represent less of a threat to female than to male *Z. vivipara*; hence, the physiological benefits most probably differ between the sexes. Besides the many costs of reproduction in female reptiles (Shine 1980), viviparous reptiles living at high altitudes or latitudes may simply die from an energy deficit after parturition (Luiselli 1992; Madsen and Shine 1992). Hibernation is fuelled by stored fat in *Z. vivipara* (Avery 1970). Hence, the need to regain body condition and build-up energy stores for hibernation (ca. seven months in our population) may be responsible for the sexual difference found in our "predation" treatment (where food was provided ad libitum); females took greater risk in order to take up as much energy as possible. For this reason they needed permanently high body temperatures (postparturition females have a higher preferred body temperature range than their conspecifics; Le Galliard et al. 2003; Herczeg et al. 2006) for optimised feeding and digestive performances (Avery et al. 1982; Avery and Mynott 1990; Van Damme et al. 1991). This hypothesis is strengthened by the fact that females maintained considerably higher daily activity in all treatments than males (lower daily activity meant lower body temperature).

The main options in behavioural thermoregulation are (1) adjusting daily and seasonal activities to the environmental opportunities and (2) thermal microhabitat selection during activity (Stevenson 1985a). We found no treatment effects on activity or sector preference. Since activity patterns are strongly affected by the thermoregulation opportunities provided by the environment (Van Damme et al. 1987; Herczeg et al. 2006), we expected treatment differences in sector preference. In fact, the decreased accuracy of thermoregulation in male *Z. vivipara* reflected their avoidance of the basking spot. The resolution of the method we used to detect differences in microhabitat preference was most likely too low; males could avoid the basking spot but still occur in the "warm" sector. However, we found a difference in the daily activity patterns of the sexes (irrespective of treatment): activity decreased during the day in both sexes, but it did so more steeply in males than in females.

Similarly to our earlier experiment (Herczeg et al. 2006), we found highly significant individual effects on accuracy of thermoregulation and activity. Furthermore, Gvoždik and Castilla (2001) reported considerable individual variation in the thermal preference and tolerance limits of *Z. vivipara*, while they found no differences in an altitudinal interpopulation comparison. These observations do not suggest a simple explanation, and this source of variation deserves further investigation.

In summary, the results of this study provide experimental support for our predictions drawn from the wider concept of the cost–benefit model of lizard thermoregulation (Huey and Slatkin 1976), showing that the ecological costs of thermoregulation can alter the lizards' behaviour in a constant thermal environment. We suggest that total change in thermoregulatory strategy, i.e. from active thermoregulation to thermoconformity, rarely or never happens in environments with low mean thermal quality but available preferred body temperature, due to the high physiological costs. Rather, slight shifts towards thermoconformity in the continuum between the extreme strategies as a response to certain costs are supported by our findings. It seems that only the risk of immediate fitness loss has the potential to alter the accuracy of thermoregulation of actively thermoregulating lizards, and even that can be overriden by the physiological benefits in certain cases. Further studies are needed, both in the field and in the lab, to explore the biological significance of the large individual variation found in both the thermal physiology and thermoregulatory behaviour of *Z. vivipara*.

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