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## To thermoconform or thermoregulate? An assessment of thermoregulation opportunities for the lizard *Zootoca vivipara* in the subarctic

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**Abstract** The general model of thermoregulation of ectotherms predicts that thermally challenging environments select for evolution of thermoconformity. Studies of reptilian thermoregulation at climatic extremes are rare and, in the subarctic zone, completely lacking. Thermal characteristics of the habitat of the lizard *Zootoca vivipara* were studied in the subarctic zone, at the northern margin of its distribution, where lizard density was already extremely low. We found that, during the activity period, the preferred body temperatures of *Z. vivipara* were not available for a thermoconformer, but available for 7 h for a thermoregulator in an average day. Therefore, thermoconformity is unbeneficial and accurate thermoregulation should be the appropriate strategy. We hypothesise that the extremely low lizard abundance at our subarctic study site is caused by the short activity season and the large daily temperature fluctuations, with night temperatures occasionally falling below zero even during the activity period.

### Introduction

The main cost of ectotherm thermoregulation is the time spent with thermoregulatory behaviour that is consequently not available for other activities (Huey and Slatkin 1976). The benefit of thermoregulation is to reach the thermal optimum for physiological processes (e.g. Stevenson 1985). There are two extreme strategies of

thermoregulation: thermoconformity (lack of behavioural regulation) and accurate thermoregulation (e.g. Huey and Slatkin 1976). The cost-benefit model of lizard thermoregulation predicts thermoconformity when costs are high and thermoregulation when costs are low as compared to its benefits (Huey and Slatkin 1976). If a thermoregulator is faced with a cooler than preferred thermal environment, it compensates behaviourally (Adolph 1990; Gvoždik 2002), but pays a cost of spending more time on it. From this, one can predict high thermoregulation costs at the northern limit of the distribution of a species that reaches high latitudes (Blouin-Demers and Weatherhead 2001).

The predictions of the model have not been widely studied in the thermal extremes (Shine and Madsen 1996; Blouin-Demers and Weatherhead 2001). Shine and Madsen (1996) have argued that, in the tropical regions, ecology and behaviour may be affected only trivially by thermoregulatory concerns. Luiselli and Akani (2002) found that, although thermoregulation in the tropics is less important, it still occurs and has consequences on activity and life-history attributes. At higher latitudes, the situation seems to be habitat dependent: in open, shallow marshes, the common habitat of water snakes (*Nerodia* sp.), the main constraint imposed by high latitudes was hypothesised to be the short activity season rather than a benign thermal environment (Brown and Weatherhead 2000). In forests, the common habitat of rat snakes (*Elaphe* sp.), daily activity was heavily constrained by temperature (Blouin-Demers and Weatherhead 2001). As far as we are aware, the last two studies are the only ones dealing with thermoregulatory strategies of populations at the northern margin of a given species' distribution range, but even these were conducted far below the Arctic Circle.

The European common or viviparous lizard, *Zootoca vivipara* (Jacquin 1787) has the largest known distribution range among lizards of the world (Avery 1982; Gasc et al. 1997). Thermoregulatory behaviour and hibernation of this cool-adapted species are well studied (e.g. Bauwens 1981; Avery and D'Eath 1986; Van

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Damme et al. 1987, 1990; Grenot et al. 2000; Voituron et al. 2002). It is known to be one of the most effective and most accurate thermoregulators under various environmental conditions (Gvoždik 2002), with evolutionarily rigid thermal tolerance limits (Van Damme et al. 1990; Gvoždik and Castilla 2001).

In this paper, we examined the characteristics of the thermal environment of common lizards in the subarctic zone close to the northern limit of its distribution. We sampled the thermal environment of the habitat of *Z. vivipara* using physical models. From the operative temperatures ( $T_e$ ; Bakken et al. 1981) provided by the physical models, we estimated the daily duration of the attainable, preferred body temperatures for a randomly moving thermoconformer and an accurate thermoregulator lizard such as *Z. vivipara*. We then fitted our results to the cost-benefit model to see whether the thermoconformer behaviour predicted by us—or the thermoregulator behaviour expected for *Z. vivipara*—is more beneficial in subarctic thermal environments. We also evaluated if the available  $T_e$  could explain the low lizard density in the subarctic, or whether other explanations for this should be sought.

## Materials and methods

*Z. vivipara* is a small (adult snout-vent length 50–70 mm) diurnal, ground-dwelling, heliotherm, insectivorous lizard. Its distribution extends from northwest Spain to Sakhalin in the east, and well beyond the Arctic Circle in the north.

Our investigation was conducted at Kilpisjärvi (69°02'N; 20°48'E), Finnish Lapland, in late spring/early summer 2002. The study site was a wet meadow, surrounded by a short, open forest of *Betula pubescens cherepanovii* on the southwestern slope of the Saana fjeld at an elevation of 500 m a.s.l. The site was chosen because of numerous lizard observations in this site made by local researchers during the past 15–20 years.

To determine the macrohabitat composition and the substrate type, the study site (0.75 ha) was divided into 100 quadrats, and the composition of forest, scrub, open area and herbal substrate, rock substrate, bare soil and water surface were estimated to the nearest 5% in 33 randomly selected quadrats.

Light conditions were quantified on a “typical day” (Christian 1998; mostly clear, partly cloudy) in forest, scrub and open areas. Ten pieces of 15 cm×15 cm plastic panels were randomly placed in each macrohabitat. These were checked every 30 min from 8.00 a.m. to 8.00 p.m. The percentage of light-shade cover was estimated to the nearest 25%.

To explore thermoregulatory opportunities, the use of  $T_e$  instead of air or ground temperatures is necessary (Tracy and Christian 1986; Grant and Dunham 1988; Huey et al. 1989). For evaluating  $T_e$ , complex biophysical equations (Van Damme et al. 1987; Christian and Bedford 1995, 1996), or the more popular physical models (Bauwens et al. 1996; Grover 1996; Schauble and Grigg 1998; Grbac and Bauwens 2001) are used. The complexity of the models varies greatly, from PVC pipes with approximate colour match to the studied species (Adolph 1990) to hollow electroformed copper lizard models painted to the same spectral reflectance as lizards (Hertz 1992a, 1992b). The issue of which type of model to use is controversial (Walsberg and Wolf 1996; Shine and Kearney 2001), but recent studies suggest that model attributes are less important than previously thought (Vitt and Sartorius 1999; Shine and Kearney 2001).

Therefore, we used hollow copper pipes (65 mm long, 12 mm in diameter, 1 mm wall thickness) sealed with plastic caps, painted

brown to match approximately the colour of *Z. vivipara*. An external probe of a HOBO RH/Temp/Light/External H08-004-02 data-logger was inserted into the middle of the models.

Seven models were placed in the field as follows: (1) open area, exposed to full sun, herbal substrate (OSH), (2) open area, exposed to full sun, rock substrate (OSR), (3) open area, full shade (artificial covering, but not closed from the surrounding air), herbal substrate (OShH), (4) open area, full shade, rock substrate (OShR), (5) forest, rock substrate (FR), (6) forest, herbal substrate (FH), middle of scrub (S). The data-loggers recorded data every 15 min from 0.00 of 5 June to 0.00 of 25 June. Daily temperature fluctuation was estimated from the  $T_e$  of the main habitat types (S, FH, OSH) weighted with their relative abundance.

The actual  $T_e$  that a randomly moving thermoconformer lizard could experience ( $T_r$ ) was calculated from the equation (modified from Schauble and Grigg 1998):

$$T_r = T_{ef} F + T_{es} S + (T_{eosh} SC + T_{eosu} LC) O$$

Where  $T_{ef}$  is  $T_e$  in the forest,  $T_{es}$  is  $T_e$  in the scrub,  $T_{eosh}$  is  $T_e$  in the open areas in full shade, and  $T_{eosu}$  is  $T_e$  in the open areas in full sun.  $F$  was the proportion of forest in the study site,  $S$  the proportion of scrub in the study site,  $SC$  the mean percentage of shade cover in open areas,  $LC$  the mean percentage of light cover in open areas, and  $O$  was the proportion of open areas. The model temperature data were incorporated in every half-hour from 8.00 a.m. to 8.00 p.m. of the 20 sampled days according to the light condition samples.

Only light conditions from open areas were incorporated into the equation because sunlit and shaded patches changed fast in the forest, and light was strongly filtered in the scrub, so the physical models gave good temperature estimates without corrections.

For an accurately thermoregulating lizard, the average daily duration of the available thermal optima was simply the time during any of the models (those representing a combination of habitat and substrate with a relative abundance at least 5% of the study area) experiencing higher temperatures than the lower thermoregulatory set-point ( $LBT_{set}$ ; 26.7°C; Gvoždik 2002) of *Z. vivipara*.

To estimate the lizard abundance, we searched actively for lizards, walking slowly in suitable habitats (southern slopes of fjells, moors, etc.) by counting all sighted animals for 6 days between 5 and 15 June 2002. The lizard abundance was estimated as number of lizards encountered per hour. Standard error for this estimate was obtained by considering each day as an independent data point.

General meteorological data were obtained from the Kilpisjärvi Meteorological Station of the Finnish Meteorological Institute.

For statistical analyses, the STATISTICA 4.5 for Windows (StatSoft, Tulsa, Oklahoma 1994) program was used.

## Results

### Density of lizards

The lizard density was estimated to be very low as, on average, only 0.08 (SE=0.07,  $n=6$ ) specimens were encountered per hour (0.19; 0; 0.095; 0.095; 0 on the 6 days, respectively). Note that this estimate was based on only 5 observed specimens from more than 60 h searching by three researchers. Three of the encountered specimens were found in our study site, and the other two in similar habitats further away from the study site.

### Thermal habitat

The macrohabitat composition of our study area was 66% scrub, 29% forest and 5% open area. The scrub

was very dense and half a metre high on average. The forest was sparse, and consisted of relatively short (5–7 m) birches. The open areas were covered mainly with grass but sometimes also with moss. Bare soil, rocks and water surface composed less than 1% of the area.

Light-shade cover differed among the morning (from 8.00 a.m. to 11.00 a.m.), midday (from 11.00 a.m. to 4.30 p.m.) and evening (from 4.30 p.m. to 8.00 p.m.) periods (Friedman ANOVA:  $\chi^2_{2,30} = 11.13$ ;  $P = 0.004$ ), and between the macrohabitat types (Friedman ANOVA:  $\chi^2_{2,25} = 37.98$ ;  $P < 0.001$ ). The percentage of light cover was highest in the midday period and in the open area while the lowest in the morning and in the bush.

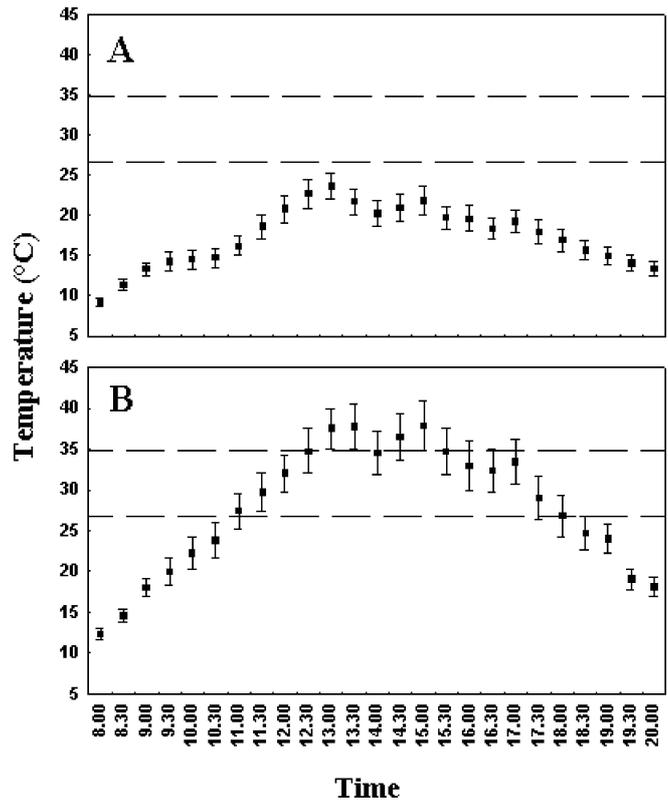
The daily means of the  $T_e$  recorded by the data-loggers for different habitat types were significantly different (Friedman ANOVA:  $\chi^2_{6,20} = 113.68$ ;  $P < 0.001$ ; Table 1). The  $T_e$  measured on herbal substrate and rock differed significantly only in forest (Wilcoxon matched pairs tests with Bonferroni correction: OSR–OSH:  $n = 20$ ;  $Z = 1.94$ ;  $P = 0.052$ ; OShR–OShH:  $n = 20$ ;  $Z = 0$ ;  $P = 1$ ; FR–FH:  $n = 20$ ;  $Z = 3.43$ ;  $P < 0.001$ ). The daily fluctuations of  $T_e$ , weighted by the macrohabitat type abundancies, were extremely high (mean = 23.93°C; min = 8.62°C; max = 33°C; SD = 6.53), and on three nights (15% of the sampled days) the mean temperature fell below zero, although the spring/summer period of 2002 was warmer than the long-term average (data from Finnish Meteorological Station not shown).

### Hypothesised success of the different strategies

A hypothetical thermoregulator lizard would reach significantly higher body temperatures than the hypothetical thermoconformer (Wilcoxon matched pairs test:  $n = 500$ ;  $Z = 19.37$ ;  $P < 0.001$ ). The preferred temperature range of *Z. vivipara* (26.7–34.8°C; Gvoždik 2002) was never reached by the mean of the calculated daily  $T_r$  profile of the thermoconformer (Fig. 1A). The hypothetical thermoconformer lizard could reach its  $LBT_{set}$  only on 7 out of the 20 sampled days. The duration of the thermal optimum was less than an hour on an average day. The mean of the daily available warmest  $T_e$

**Table 1** Operative temperatures (°C) of different macrohabitat types, substrate types and light intensities from 5 to 25 June 2002 (OSR open area, exposed to full sun, rock substrate; OSH open area, exposed to full sun, herbal substrate; OShR open area, full shade, rock substrate; OShH open area, full shade, herbal substrate; FR forest, rock substrate; FH forest, herbal substrate; S middle of scrub)

	Mean	Min.	Max.	Std. Dev.
$T_e$ (OSR)	17.52	−2.44	45.89	10.958
$T_e$ (OSH)	17.10	−7.85	57.24	14.834
$T_e$ (OShR)	10.20	−0.61	24.01	4.976
$T_e$ (OShH)	10.20	−2.44	25.17	5.696
$T_e$ (FR)	14.18	−0.61	41.99	7.938
$T_e$ (FH)	13.56	−1.97	47.96	9.059
$T_e$ (S)	11.59	−3.85	33.17	7.672



**Fig. 1A, B** The operative temperature that a randomly moving thermoconformer lizard would experience (A) and the available maximum operative temperatures for an accurate thermoregulator lizard (B) in the subarctic zone (mean  $\pm$  SE), at a latitude of 69°N on a summer day (note that the preferred range of *Z. vivipara* is between 26.7 and 34.8°C)

profile for an accurately thermoregulating lizard exceeded the  $LBT_{set}$  of *Z. vivipara* (Fig. 1B). The hypothetical thermoregulator lizard could reach its  $LBT_{set}$  on 19 out of 20 of the studied days. The duration of the thermal optimum was 7 h on an average day.

### Discussion

*Z. vivipara* is the reptile with the northernmost occurrence among the world's reptiles (Gasc et al. 1997), and it is known as an accurate thermoregulator with evolutionary rigid thermal preferences (Van Damme et al. 1990; Gvoždik and Castilla 2001; Gvoždik 2002). In spite of this, we predicted thermoconformity at the northern margin of its distribution, where the challenging thermal environment was hypothesised to be able to increase the time cost of behavioural thermoregulation to an extent that thermoregulation becomes remunerative. Our results contradict this prediction. In the open habitats of *Z. vivipara*, the thermoconformer strategy is a failure against the thermoregulator strategy (Fig. 1A, B) at least at high latitudes. This cannot be generalised for all reptiles due to the habitat-dependency of the two strategies' efficacy (Brown and Weatherhead 2000; Blouin-Demers and Weatherhead 2001). During the

activity season, *Z. vivipara* can reach its preferred temperature range easily on almost every day, but only with accurate thermoregulation. This is important for physiological processes (e.g. Stevenson 1985) and for different behavioural traits, such as prey handling time (Avery and Mynott 1990), locomotor performance (Avery and Bond 1989; Van Damme et al. 1990; Du et al. 2000) and escape behaviour (Smith 1997; Cooper 2000).

A habitat with low  $T_e$ , or the lack of sufficient variation among different patches, necessary for accurate thermoregulation (Grant and Dunham 1988; Tosini and Avery 1996; Witz 2001), should be inappropriate for *Z. vivipara*. The habitat we studied offered a large variety of  $T_e$  among habitat types (Table 1), and the  $LBT_{set}$  of *Z. vivipara* was available for 7 h on an average day for a thermoregulator lizard, while overheating as a danger did not occur (in shaded parts of the open area the temperature was always below  $LBT_{set}$ ). Significant difference in  $T_e$  between herbal and rock substrate was found only in forest, with higher maximum and lower minimum  $T_e$  on herbal substrate (Table 1) suggesting that rocks may not play an important role as substrates in the basking behaviour.

Irrespective of the continuous daylight in the subarctic zone during the summer, lighting patterns and temperature follow a daily cycle. The configuration of terrain and the angle of incident rays have the main influence on these patterns.

Despite the benign thermal environment during daytime in the Kilpisjärvi area, the lizard density was very low, about 0.08 specimens encountered per hour by one man as opposed to the great abundance (0.06 specimen/m<sup>2</sup>) in Kalmthout, Belgium (51°25'N; 4°25'E) reported by Bauwens (1981). In our study period, every model experienced  $T_e$  below zero at night (Table 1), which could be part of the explanation for the low lizard densities. There are basically two strategies dealing with subzero temperatures in lizards: supercooling and freeze tolerance, and *Z. vivipara* may use both (Grenot et al. 2000). These strategies need cryoprotectant molecules against freezing of body water, and *Z. vivipara* is known to have a fourfold level of blood glucose during hibernation (Grenot et al. 2000). Although not known for our study population, blood glucose levels show seasonal rather than daily patterns of fluctuations (Grenot et al. 2000). Keeping high glucose levels during summer or losing freeze tolerance and the ability for supercooling may decrease fitness as well. Another disadvantage of subzero temperatures is that recovery from freezing or supercooling may last more than 40 h (Voituron et al. 2002).

At high latitudes, large body size seems to be advantageous for survival over the winter period (e.g. Adolph and Porter 1993), and due to the shorter activity season, there might be a serious time constraint on growth (e.g. Merilä et al. 2000) linked with increased mortality (Sorci et al. 1996). Blouin-Demers and Weatherhead (2001) called 5 months a very short activity season. In the Kilpisjärvi area, the average

duration of snow cover has been 236 days in the last 5 years (Finnish Meteorological Institute), which translates to a potential activity period of 3–4 months in the study site. This phenomenon, considering the low lizard density found in Kilpisjärvi, supports the opinion of Brown and Weatherhead (2000) that the short activity season is the most serious challenge in the north for reptiles that occur in open habitats. This constraint may explain the low lizard density found in Kilpisjärvi. We hypothesise that the wide daily temperature fluctuations including the subzero temperatures at night, irrespective of the benign thermal environment during daytime, might also play an important role in shaping the density patterns.

*Z. vivipara* is known to be one of the most effective thermoregulators of all reptiles. Considering that our results prove there is an opportunity for thermoregulation even in the subarctic zone (69°02'N), the rigidity of its thermoregulatory behaviour can be interpreted from an evolutionary point of view. We suggest that its thermoregulatory behaviour, besides the freeze tolerance and the ability for supercooling, is one of the most important traits enabling *Z. vivipara* to reach the largest distribution area and the northernmost occurrence among the lizards of the world.

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