To heat or to save time? Thermoregulation in the lizard *Zootoca vivipara* (Squamata: Lacertidae) in different thermal environments along an altitudinal gradient

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Abstract: Behavioural regulation of body temperature in thermally heterogeneous habitats requires different amounts of time that could otherwise be dedicated to foraging and social activities. In this study I examined how four populations of the lizard *Zootoca vivipara* along an altitudinal gradient (250–1450 m) adjust their thermal-physiology traits and thermoregulatory behaviour to compensate for increasing time costs of thermoregulation. I focused on variation in several physiological (set-point temperature, heating rate) and behavioural traits (microhabitat selection, basking frequency, extent of thermoregulation). To estimate potential time spent basking and foraging by lizards that were not employing any behavioural compensatory mechanism, I used a simple biophysical model of thermoregulation, including information about operative temperatures at the study sites, selected temperature range, and heating/cooling rates. Time costs of thermoregulation for each population were calculated as potential time spent basking relative to time spent foraging. Operative temperatures varied among study sites, resulting in different time costs of thermoregulation. Lizards at 1450 m should spend about 50% more time basking than those at 250 m. I found that the only mechanism which potentially compensated for the higher time costs incurred at high altitudes was a shift in the choice of basking sites. Lizards thermoregulated with similar accuracy and effectiveness over the 1200-m altitudinal range, indicating that there were no adjustments in the extent of thermoregulation. The observed basking frequencies of lizards were highly correlated with potential time spent basking without behavioural adjustments, suggesting a minor compensatory effect of thermoregulatory behaviour. Lizards responded to higher time costs of thermoregulation primarily by allocating different amounts of time to basking. These results suggest that *Z. vivipara* regulated body temperature at the expense of time that could be devoted to other activities.

Résumé : Le contrôle comportemental de la température du corps dans les habitats où prévalent des températures hétérogènes entraîne des dépenses variables de temps qui pourrait être utilisé à d'autres fins, comme la recherche de nourriture et les activités sociales. J'ai tenté de déterminer comment les lézards *Zootoca vivipara* de quatre populations réparties le long d'un gradient thermique altitudinal (250–1450 m) ajustent leurs caractéristiques physiologiques thermiques et leur comportement thermorégulateur pour compenser les coûts croissants en temps de la thermorégulation. J'ai examiné plus particulièrement la variation de plusieurs caractéristiques physiologiques (températures de consigne, taux de réchauffement) et comportementales (choix d'un microhabitat, fréquence des bains de soleil, importance de la thermorégulation). Pour estimer la durée potentielle du temps consacré aux bains de soleil et à la recherche de nourriture chez les lézards qui n'avaient pas recours à des mécanismes comportementaux compensatoires, j'ai utilisé un modèle biophysique simple de thermorégulation dans lequel il y avait des informations sur les températures effectives aux sites de l'étude, l'étendue des températures préférées et les taux de réchauffement/refroidissement. Le coût en temps de la thermorégulation pour chaque population a été calculé comme le rapport entre la durée potentielle des bains de soleil et le temps consacré à la recherche de nourriture. Les températures effectives variaient d'un site à l'autre et cette variation a donné lieu à des coûts en temps différents selon le site. Les lézards qui vivent à 1450 m devraient passer au moins 50 % de plus de leur temps au soleil que les lézards vivant à 250 m. J'ai constaté que le seul mécanisme qui puisse compenser les coûts en temps plus élevés à haute altitude est la variation dans le choix des sites de repos au soleil. Les lézards ont une thermorégulation aussi précise et aussi efficace à toutes les altitudes le long du gradient de 1200 m, ce qui indique qu'il ne se fait pas d'ajustement de l'importance de la thermorégulation. La fréquence des bains de soleil des lézards était en forte corrélation avec le temps potentiel qu'ils peuvent consacrer aux bains de soleil sans ajustements comportementaux; on peut voir là l'effet compensatoire peu important du comportement de thermorégulation. Les lézards ont réagi aux coûts en temps plus élevés de la thermorégulation surtout en consacrant des périodes de

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temps variables aux bains de soleil. Ces résultats semblent indiquer que Z. *vivipara* gère sa température par des dépenses de temps qui pourrait être alloué à d'autres activités.

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Introduction

Many lizards regulate their body temperature predominantly by using various behavioural mechanisms (e.g., Cowles and Bogert 1944; Heath 1965; Adolph 1990; Bauwens et al. 1996). Although ectothermy requires a much lower energy investment than endothermy (Pough 1980), behavioural thermoregulation of ectotherms is time-consuming and thus may constitute an important part of a lizard's time budget (Dunham et al. 1989). How much time a lizard spends thermoregulating (shuttling between sun and shade, finding suitable basking sites, basking) depends primarily on the thermal properties of its habitat. Variation in the thermal environment, through its effect on thermoregulatory behaviour and activity time, may therefore have a profound and direct impact on the time budgets of lizards, and ultimately on their life histories (Dunham et al. 1989; Adolph and Porter 1993, 1996).

In several papers the effects of energetic costs on the extent of thermoregulation have been examined in the field and the laboratory (Huey 1974; Lee 1980; Withers and Campbell 1985). In accordance with the cost–benefit model of thermoregulation (Huey and Slatkin 1976), these studies showed that some lizards regulate their body temperature less carefully in a high-cost environment, and this resulted in a shift of the mean body temperature maintained during activity. However, some species of lizards do maintain similar body temperatures even at different altitudes, i.e., under different costs, by means of effective, mostly behavioural, compensatory mechanisms (Burns 1970; Hertz and Huey 1981; Waltner 1991; Lemos-Espinal and Ballinger 1995). In addition, shifts in body temperature during activity do not necessarily indicate changes in the extent of thermoregulation. Such shifts may also be induced by environmental constraints or arise as a result of behavioural shifts in set-point temperature (Van Damme et al. 1989; Tosini et al. 1995). Recent conceptual and methodological advances in the study of thermoregulation (Hertz et al. 1993; Bauwens et al. 1996; Christian and Weavers 1996), however, allow us to discriminate between these possibilities and thus shed more light on thermoregulatory responses of lizards to different thermal environments.

Unlike energetic costs, the time costs of thermoregulation have attracted only limited attention. The main objective of this paper is to determine whether lizards compensate for different time costs of thermoregulation in various thermal environments. For this purpose I compared the thermal biology of four populations of the lizard *Zootoca vivipara* (Lacertidae) living at different altitudes. The mean field body temperature of this species is 4.3°C lower at high altitude (2000 m) than at low altitude (25 m) (Van Damme et al. 1990). However, the reasons for this variation remain largely unknown. Seasonal variation in the thermal environment had no obvious effect on the extent of thermoregulation, and differences in monthly mean body temperatures resulted from constraints imposed by the thermal environment (Van Damme et al. 1987). However, thermoregulatory responses to seasonal variability at a single location may be quite different from

mechanisms compensating for long-term differences in the thermal environment along latitudinal and altitudinal gradients (Huey and Bennett 1990). Short-term fluctuations (e.g., day to day) should be compensated for by behavioural means, whereas long-term ones (e.g., seasonal or among years) should be compensated for by acclimation or adaptations in thermal physiology.

The lizard species studied thermoregulates actively by basking and by shuttling between sunlit and shaded sites (Avery 1976). This thermoregulatory behaviour can be described using a simple biophysical model (Bakken and Gates 1975). The model predicts that the time spent thermoregulating may be reduced by physiological or behavioural adjustments of two traits: set-point temperature and heating rate. Additionally, lizards may compensate for higher time demands by less careful regulation of their body temperature (Huey and Slatkin 1976). Based on the above facts, I made five non-mutually exclusive predictions concerning the thermoregulatory responses of lizards to altitudinal variation in time costs: (1) lizards physiologically adjust thermoregulatory set-points, (2) they physiologically adjust heating rates, (3) they increase heating rates behaviourally by adjusting microhabitat selection for basking, (4) they shift relations between body temperature, operative temperature, and set-point temperature range (i.e., causing a shift in accuracy and effectiveness of thermoregulation (sensu Hertz et al. 1993)), and (5) they allocate different amounts of time to basking.

Materials and methods

Study organism and study sites

Zootoca vivipara is a small (adult snout–vent length (SVL) ca. 65 mm; body mass ca. 6.5 g) diurnal insectivorous lizard. Because this species has the largest distribution known among lizards (Avery 1982) and inhabits a wide variety of thermal environments from sea level to an altitude of 3000 m, its life history varies considerably among populations (see Bauwens et al. 1986). In the Czech Republic, females give birth to 3–10 juveniles in July–August. Maturity is reached in their second or third year of life (L. Gvoždík, unpublished data).

I investigated populations of Z. *vivipara* at four study sites along an altitudinal gradient: (1) Raduň (250 m; 49°53′N, 17°12′E): three small dried-up ponds (0.4 ha), well vegetated by grasses (*Calamagrostis* sp., *Deschampsia* sp., *Juncus* sp.) and nettles (*Urtica dioica*) up to 2 m high; (2) Ostravice (550 m; 49°34′N, 18°25′E): a meadow (7.5 ha) on a southeast-oriented slope surrounded by forest (*Fagus sylvatica*, *Picea abies*); (3) Slunečná (800 m; 49°50′N, 17°28′E): a forest clearing (3 ha) with planted young *P. abies* up to 3 m high on a south-oriented slope; (4) Vysoká Hole (1450 m; 50°02′N, 17°12′E): a subalpine meadow (6 ha) with scattered trees (*P. abies*, *Pinus mugo*) on a south-southeast-oriented slope. For simplicity I will refer to the study sites only by their altitude. Climatic characteristics (Fig. 1) were obtained from the nearest meteorological stations (Czech Hydro-

Fig. 1. Mean precipitation (*a*), air temperature (*b*), and sunshine hours (*c*) for each study site by month (I–XII). Because air temperatures at 550 m were not available, temperatures were adjusted for differences in altitude between the study site and the meteorological station at the theoretical adiabatic cooling rate of 0.6°C per 100 m of altitude in moist air (Begon et al. 1996).
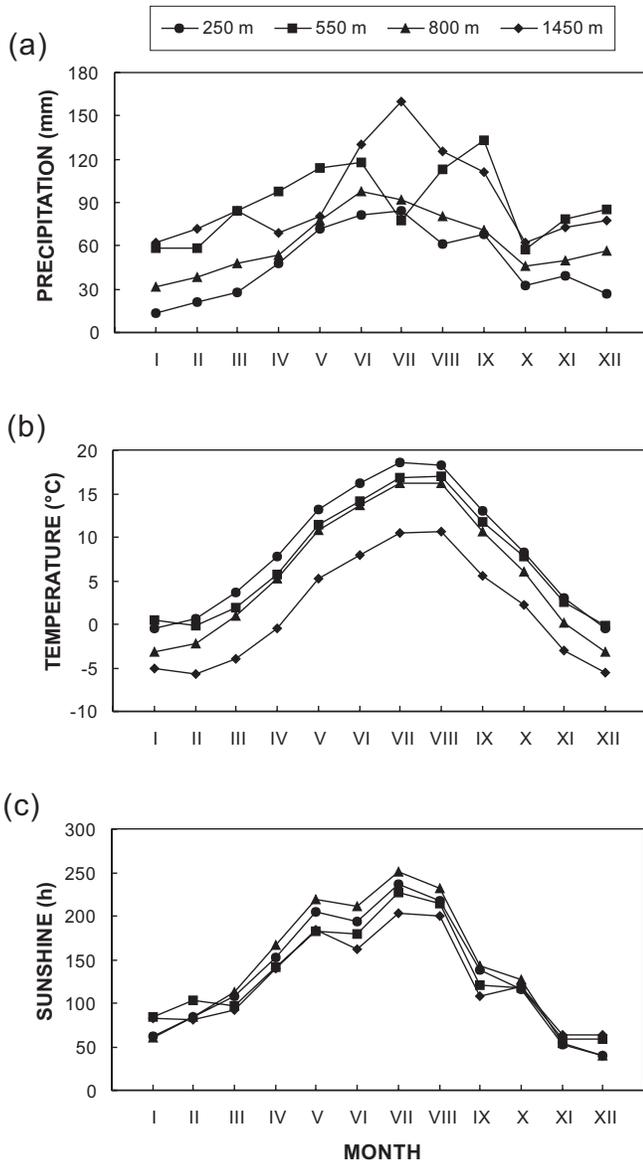
meteorological Institute, Ostrava branch) situated at altitudes (±50 m) similar to those of the study sites.

Thermoregulatory set-points

I estimated thermoregulatory set-points from measurements of preferred body temperatures (T_p) in a laboratory photothermal gradient (100 × 50 × 50 cm). A 100-W reflector bulb was suspended 15 cm above the substrate as the source of heat and light, and the opposite side of the gradient was cooled from beneath with ice. Under these conditions, operative temperatures (T_e's) of lizard models (see below for a description) ranged from 18 to 80°C, a range that is substantially wider than all reported T_p ranges in this species (Patterson and Davies 1978; Van Damme et al. 1986). Because humidity may affect thermoregulatory behaviour (Lorenzon et al.

1999), the substrate (Lignocel) was maintained equally moist over the whole gradient (for details see Gvoždík and Castilla 2001). As shelters I placed several pieces of bark along the gradient. Drinking water and food (crickets, *Acheta domestica*, mealworms, *Tenebrio molitor*) were provided ad libitum. I assume that abiotic and biotic constraints on thermoregulation were absent under these conditions. Animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care (1993).

To measure T_p, I took two samples (June and August) of six lizards from each locality so that lizards of both sexes and different age groups (adults and subadults) and reproductive conditions (gravid and nongravid) were represented. I measured body temperatures of surface-active (i.e., not in shelters) lizards by inserting a K-type thermocouple probe (0.5 mm in diameter) connected to a digital microprocessor thermometer (HH 21, Omega Engineering, Stamford, Conn., U.S.A.) 5 mm into its cloaca immediately after capture. Body temperature was measured hourly for each of 12 lizards per population. As the upper thermoregulatory set-point (UBT_{set}) and lower thermoregulatory set-point (LBT_{set}), I determined the 10th and 90th percentile of each individual's T_p distribution, respectively. The set-points were averaged for each population. Following arguments of Bauwens et al. (1995), I consider the central 80% of T_p's, rather than the central 50% (e.g., Hertz et al. 1993), to be a biologically more realistic estimate of the set-point temperature range (T_{set}) for *Z. vivipara*. However, because the determination of T_{set} bounds is somewhat subjective (Wills and Beaupre 2000), I additionally calculated T_{set} bounds as the central 50% of T_p's (50% T_{set} bounds) to explore the extent to which differences in T_{set} estimation may affect comparisons of thermoregulatory indices.

Heating rates

I used six lizards from each population to measure heating rates. Each lizard was fixed on a white plastic board (12 × 25 cm) by two bands of transparent adhesive tape. A K-type thermocouple (0.25 mm in diameter) connected to the same thermometer used for measuring T_p was inserted into its cloaca. The lizard was then cooled to 19°C and placed under a 100-W reflector lamp suspended 20 cm above the centre of its body. When the body temperature (T) reached 20°C, I started to record T at 15-s intervals until it equalled 35°C. The operative (equilibrium) temperature of a lizard model measured under identical conditions was 42°C. All measurements were taken at an ambient room temperature of 19 ± 1°C (for further details see Gvoždík 1999).

To compare heating rates among populations I calculated the thermal time constant for heating (τ_h). This constant was estimated for each individual using the nonlinear equation describing the heating curve of an ectotherm (Bakken and Gates 1975):

$$T(t) = T_e + [T(t_0) - T_e]e^{-t/\tau_h}$$

where $T(t)$ is the body temperature at time t, T_e is the operative (equilibrium) temperature, $T(t_0)$ is the body temperature at time 0, and t is the elapsed time (min). Heating constants were obtained by fitting a straight line to the plot of $\ln(T_e - T)$ versus time.

Operative temperatures and habitat description

I used physical models of lizards to measure T_e (Bakken 1992). Models were made from copper cylinders (10 mm in diameter, 60 mm long) whose ends were sealed with plastic plugs. In the middle of the ventral side a 1 mm wide opening was drilled for inserting the thermocouple probe. Cylinders were painted to match the colour of the lizards. The paint (Balakom, Opava, Czech Republic) was prepared using colour coordinates (400–700 nm) obtained from colour measurements (Dataflash 100®, Datacolor International, Lucerne, Switzerland) from 10 lizards. I verified thermal responses of randomly chosen models by comparing their equilibrium temperatures with those of four freshly killed lizards under different exposures to sunshine (full sun, partial sun, shade). As no significant differences were found (paired Student's t test, $t_{[11]}$ = 0.71, P = 0.51; difference 0.1 – 1.4°C), I considered the models to be sufficiently reliable for measuring T_e.

To measure the distribution of T_e's available to lizards during their activity period, I chose the first cloudless day with moderate or no wind at each site during the same period and year for measuring field body temperatures (T_b's). Every hour, I placed 24 models around the spot where the first lizard was observed. Models were placed around the spot on 8 lines intersecting at 45° angles. On each line I placed three models, with random orientation to compass direction, in the places with differing exposure to sunshine (full sun, partial sun, shade) that were nearest to the central spot. After 15 min their temperature was measured. Because of the high conductivity of the copper body, models were held only by their plastic ends during manipulation. If the metal part was touched, the temperature reading was discarded. I assume that T_e's measured in this way estimate the overall distribution of T_e's in the lizard's habitats.

I assessed the availability of substrates at each study area by walking along 5 randomly chosen 30 m long transects and recording the type of substrate (e.g., bark, grass, stone) every 0.5 m.

Body temperatures and behaviour in the field

I sampled lizards from June to August during two consecutive seasons, 1996 and 1997 (250 and 550 m in 1996; 800 and 1450 m in 1997). The average air temperatures were similar at the same weather station during these 2 years. Because weather conditions may affect body temperature (Avery 1982) and surface activity of lizards (Van Damme et al. 1987), I restricted sampling to fully sunny days. However, because the study site at 1450 m was characterized by a very small number of fully sunny days (Fig. 1c), I also sampled there during partially cloudy weather. Under these conditions I measured T_b's not later than 5 min after clouds covered the sky and not sooner than 15 min after continuous sunshine began.

On each sampling day I walked haphazardly across a study site from sunrise until the end of lizard activity, i.e., 1 h after I saw last active lizard. Lizards were captured by hand or with a noose. Immediately after capture I measured the lizard's T_b using the same apparatus as for measuring T_p. Each lizard was individually marked and SVL (to 0.1 mm with plastic dial callipers), body mass (BM, to 0.1 g with Pesola scales), date and time of capture, whether basking

(motionless position, often with body flattened, of a lizard exposed to sun; see also Figs. 2–5 in Avery 1979) or not, substrate type, vertical position (in centimetres above the ground), and sun exposure (sun, partial sun, shade/overcast) were recorded. To avoid pseudoreplication (Hurlbert 1984), only one observation per individual was used for further analyses. Based on their body size (SVL and BM), sex, and reproductive condition, lizards were classified as subadult male, adult male, subadult female, gravid female, or nongravid female.

Indices of thermoregulation

To describe thermoregulation I used three indices (Hertz et al. 1993): (1) Accuracy of thermoregulation ($\bar{d}_b$): $d_b = T_b -$ UBT$_{set}$ for $T_b >$ UBT$_{set}$, $d_b =$ LBT$_{set} - T_b$ for $T_b <$ LBT$_{set}$, and $d_b = 0$ for LBT$_{set} = T_b =$ UBT$_{set}$. This index indicates how closely lizards maintain their body temperature to T_{set}. The higher the mean d_b, the lower the accuracy of thermoregulation of lizards. (2) Thermal quality of a habitat ($\bar{d}_e$), i.e., the mean deviation of T_e's from the T_{set} range, was calculated analogously to d_b, with T_e instead of T_b. (3) The effectiveness of thermoregulation (E) was calculated as $E = 1 - \bar{d}_b/\bar{d}_e$. Values of E approaching 1 indicate active thermoregulation, while values approaching 0 indicate thermoconformity.

Estimates of potential duration of basking and foraging

To examine whether lizards compensate for different time demands for thermoregulation, it is necessary to use some quantitative estimate of time costs that can be compared among study sites. For *Z. vivipara* thermoregulating (i.e., maintaining their T_b between LBT$_{set}$ and UBT$_{set}$) by basking and shuttling between warmer and colder microsites, I determined the potential time costs of thermoregulation by calculating the potential duration of basking and foraging episodes. The potential duration of basking is the time (t_{bask}) spent by a lizard to increase its body temperature from LBT$_{set}$ to UBT$_{set}$ (Bakken and Gates 1975):

$$t_{bask} = -\tau_h \ln\left(\frac{UBT_{set} - T_e}{LBT_{set} - T_e}\right)$$

where $T_e >$ UBT$_{set}$.

The potential duration of foraging is the time (t_{forage}) during which a lizard's body temperature decreases from UBT$_{set}$ to LBT$_{set}$:

$$t_{forage} = -\tau_h \ln\left(\frac{LBT_{set} - T_e}{UBT_{set} - T_e}\right)$$

where $T_e <$ LBT$_{set}$ and τ_c is the thermal time constant for cooling. The constant was derived from the known ratio between τ_c and τ_h ($\tau_c/\tau_h = 1.56 \pm 0.03$ (mean ± SE, $n = 10$) determined in another study (L. Gvoždík, unpublished data). Because τ_h and τ_c are functions of BM, the constants were adjusted for the mean BM of each population category and study site. Their values are valid for windless conditions only, because wind speed affects τ_c and τ_h through convection (Stevenson 1985).

The longer the mean t_{bask} and the shorter the mean t_{forage}, the higher the time costs of thermoregulation. To facilitate

Table 1. Lower and upper bounds of set-point temperature ranges (°C) estimated as the central 50% (50%LBT$_{set}$, 50%UBT$_{set}$) and 80% (LBT$_{set}$, UBT$_{set}$) of preferred body temperatures of *Zootoca vivipara* at different altitudes.

Altitude (m)	n	50%LBT$_{set}$	50%UBT$_{set}$	LBT$_{set}$	UBT$_{set}$
250	12	29.1 ± 0.5	33.8 ± 0.3	26.8 ± 0.6	34.8 ± 0.4
550	12	29.5 ± 0.4	32.9 ± 0.4	27.2 ± 0.5	34.3 ± 0.3
800	12	29.2 ± 0.4	33.0 ± 0.4	26.7 ± 0.5	34.3 ± 0.3
1450	12	29.7 ± 0.6	33.1 ± 0.5	27.2 ± 0.6	34.2 ± 0.5

Note: All values are given as the mean ± SE.

comparisons among the study sites I used the fraction of potential activity time (hours per day that lizards could potentially be active, given the general thermal environment) used for basking (Dreisig 1985) as a measure of the time cost of thermoregulation (c_t):

$$c_t = \frac{\bar{t}_{bask}}{\bar{t}_{bask} + \bar{t}_{forage}}$$

The c_t values are an estimate of the proportion of total time that a lizard spends thermoregulating in a particular thermal environment without behavioural adjustments of its heating rate. Additionally, I used this estimate as a "null hypothesis" (no time compensation) for comparisons with actual frequencies of basking lizards. If the actual values varied like the calculated ones, this would indicate that time-compensation mechanisms employed by lizards were minor ones.

Statistical analyses

For comparing continuous variables (temperature and time measurements) I used appropriate standard least-squares models (analysis of variance (ANOVA), analysis of covariance (ANCOVA), multiple regression) after examining the validity of assumptions of normality and homogeneity of variance (Sokal and Rohlf 1995). In cases of significant departures from homogeneity and normality, the data were transformed using Box–Cox transformation or rank transformation (Potvin and Roff 1993; Sokal and Rohlf 1995). The Tukey–Kramer HSD test was used for multiple comparisons. The Kolmogorov–Smirnov two-sample test was used to compare distributions of continuous variables.

Frequencies of used and available substrates, occurrence above ground, and basking were compared using a *G* test. Effects of continuous factors, nominal factors, and their interactions on nominal variables were modelled by logistic regression.

The comparison of the indices *E* and c_t was based on a method proposed by J. Felsenstein (Hertz et al. 1993). Indices were calculated 1000 times from pseudovalues generated by bootstrap resampling (Manly 1997) the original samples (d_b, d_e, t_{bask}, t_{forage}) using formulas described above. The pairs of resulting bootstrap estimates of *E* and c_t were compared between populations. Because of multiple comparisons an experimentwise error rate was specified for each comparison using the Dunn–Šidák method (Sokal and Rohlf 1995).

A significance level of $\alpha = 0.05$ was used for all statistical tests. When an observed difference was judged to be nonsignificant and the result was important for drawing conclu-

Table 2. Thermal time constants (min) of *Z. vivipara* at different altitudes.

Altitude (m)	Adjusted mean	SE	Mean
250	6.9	0.3	7.5
550	6.7	0.3	7.0
800	6.3	0.3	5.5
1450	6.9	0.3	6.3

Note: Adjusted (least squares) means were used to remove an effect of body mass (ln-transformed).

sions, I provide information about the statistical power ($1 - \beta$) of the test and the least significant number (LSN), which is the minimum sample size necessary for obtaining a significant result at $\alpha = 0.05$ and $1 - \beta = 0.80$ (Cohen 1988; for a similar approach see also Forsman 1996).

Statistical analyses were performed using JMP 3.2 statistical software (SAS Institute Inc., 1995) and Statistica for Windows 5.5 (StatSoft, Inc. 2000). Bootstrap resampling was carried out using programs written by D. Bauwens and J. Díaz (for *E* comparisons) in BASIC and by M. Gvoždík (for c_t comparisons) in C++.

Results

Thermoregulatory set-points

Upper and lower thermoregulatory set-points were not significantly correlated within populations ($r = 0.29$–0.40, df = 12, $P = 0.20$–0.37) and were therefore tested separately. LBT$_{set}$ values did not differ significantly among or within populations (ANOVA, effect of population: $F_{[3,28]} = 0.63$, $P = 0.6$, $1 - \beta = 0.16$, LSN = 282; effect of population category (sex, age, and reproductive condition): $F_{[4,28]} = 1.61$, $P = 0.19$; effect of interaction: $F_{[12,28]} = 1.78$, $P = 0.1$). UBT$_{set}$ values did not differ significantly among populations (ANOVA, $F_{[3,28]} = 1.63$, $P = 0.20$, $1 - \beta = 0.38$, LSN = 111) and there was no significant interaction between the effects of population category and population ($F_{[12,28]} = 0.86$, $P = 0.59$).

Means of 50%T_{set} bounds were 1–2.3°C lower/higher than those of T_{set} bounds (Table 1). There was a strong relationship between 50%T_{set} and T_{set} bounds within populations (LBT$_{set}$: $r = 0.70$–0.90, df = 12, $P < 0.01$–0.0001; UBT$_{set}$: $r = 0.78$–0.97, df = 12, $P = 0.03$–0.0001).

Heating rates

The thermal time constant increased with BM (linear regression of ln-transformed values, $F_{[1,22]} = 65.1$, $P < 0.0001$).

Fig. 2. Distribution of operative temperatures (T_e) at 250 m (*a*), 550 m (*b*), 800 m (*c*), and 1450 m (*d*). The vertical lines indicate the lower (LBT$_{set}$) and upper (UBT$_{set}$) thermoregulatory set-points.
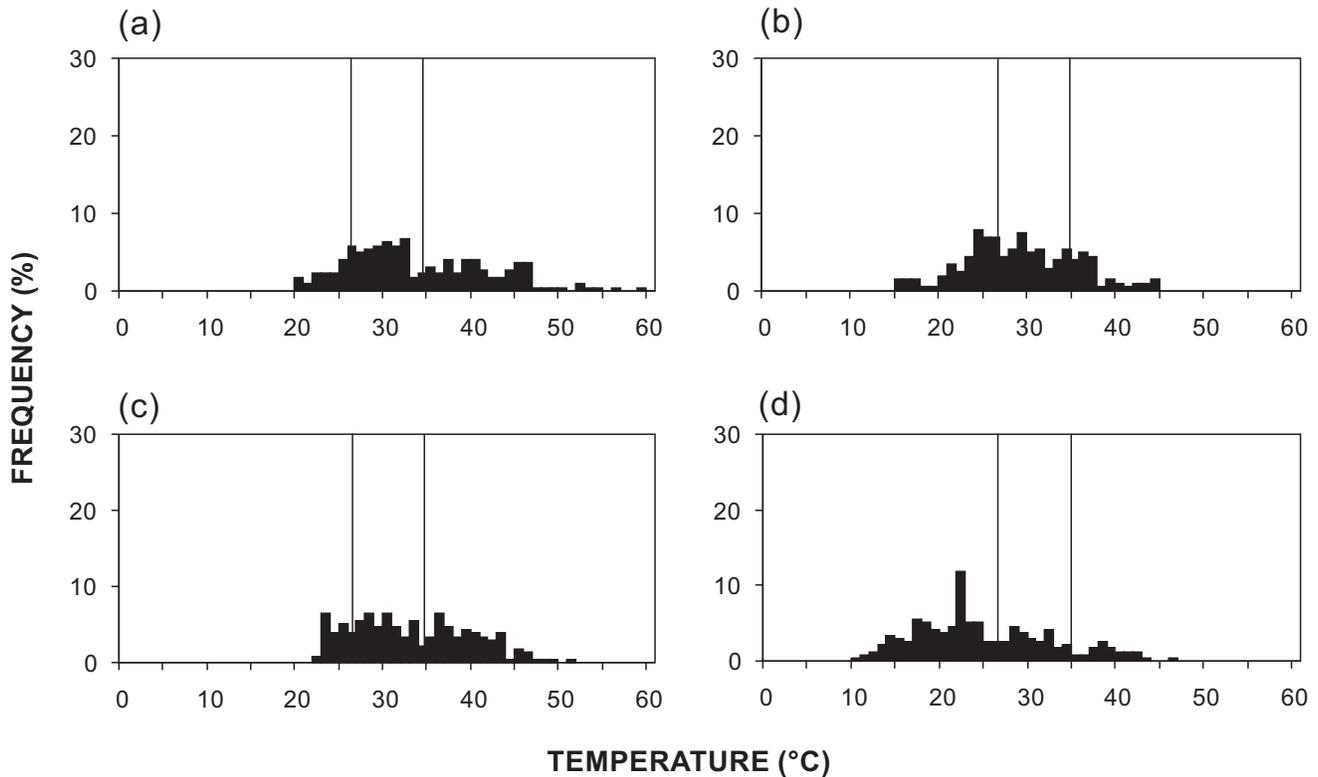

Table 3. Operative temperatures (T_e) and field body temperatures (T_b) of *Z. vivipara* at different altitudes.

Altitude (m)	T_e (°C)			T_b (°C)		
	Mean ± SE	Range	*n*	Mean ± SE	Range	*n*
250	33.5 ± 0.6	19.5–66.9	222	31.1 ± 0.3	23.6–37.3	95
550	28.4 ± 0.4	14.2–43.9	202	31.0 ± 0.4	17.2–36.0	91
800	32.4 ± 0.4	21.2–51.0	235	31.0 ± 0.6	22.7–35.2	30
1450	24.1 ± 0.5	9.8–45.4	238	28.7 ± 0.5	19.9–34.8	50

There were no significant differences in heating rates (τ_h) among populations when the effect of BM was controlled for (ANCOVA, population: $F_{[3,16]} = 0.93$, $P = 0.45$; BM: $F_{[1,16]} = 31.5$, $P < 0.0001$; interaction: $F_{[3,16]} = 0.84$, $P = 0.49$; Table 2).

Operative temperatures

Sun exposure (full sun, partial sun, and shade) and time of day influenced T_e (ANOVA, effect of sunshine: $F_{[2,837]} = 334.88$, $P < 0.0001$; effect of time: $F_{[4,837]} = 104.33$, $P < 0.0001$), their effects being additive ($F_{[24,837]} = 1.46$, $P = 0.07$). T_e's varied among study sites (ANOVA, $F_{[3,837]} = 58.31$, $P < 0.0001$). In particular, T_e's at 550 and 1450 m were lower than those at 250 and 800 m (Tukey–Kramer HSD test, $P < 0.05$ for all comparisons; Table 3). T_e's were similar at 250 and 800 m ($P > 0.05$). Distributions of T_e's were platykurtic (Fig. 2), indicating that surface-active nonthermoregulating lizards could potentially reach T_b's within the range 29.7–47.4°C under similar weather conditions. Except for 08:00 and 10:00 at 1450 m, maximum T_e's from

hourly samples were above UBT$_{set}$ (Fig. 3), suggesting that lizards were rarely constrained by available T_e's to maintain their T_b's within T_{set}.

The index of thermal quality of the habitat ($\bar{d}_e$) varied among sites (ANOVA, $F_{[3,893]} = 21.68$, $P < 0.0001$). In particular, $\bar{d}_e$ was higher at 1450 m than at other altitudes (Tukey–Kramer HSD test, $P < 0.05$; Table 4). This resulted from a higher number of T_e's lying below T_{set} (G test, $G_{[6]} = 129.39$, $P < 0.0001$; Fig. 4*a*). In contrast, the relatively high d_e at 250 m was primarily a result of a high proportion of T_e measurements that were above T_{set}. Proportions of T_e's lying below, within, and above T_{set} varied among study sites ($G_{[6]} = 129.39$, $P < 0.0001$). The lowest proportion of T_e's lying within T_{set} was at 1450 m, indicating that thermal conditions were less favourable there than at other sites.
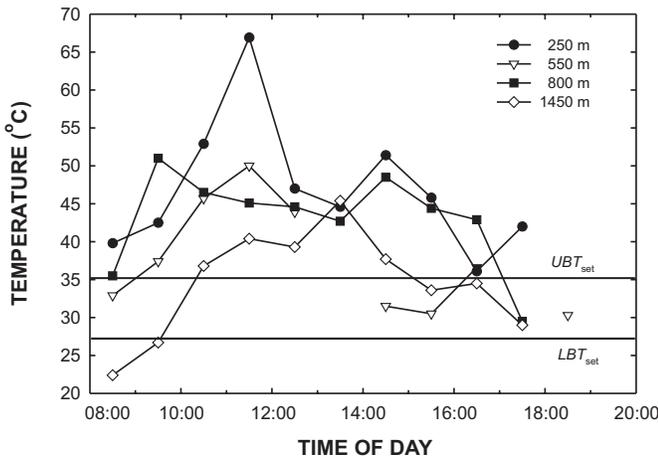
Mean indices of habitat quality calculated using 50%T_{set} bounds (50%d_e's) were 1.1–1.4°C higher than mean d_e's calculated using 80% bounds (Table 4). A comparison of 50%d_e's among study sites yielded a result similar to that for d_e's (ANOVA, $F_{[3,893]} = 22.27$, $P < 0.0001$).

Table 4. Indices of thermal quality of habitat (d_e), accuracy (d_b), and effectiveness (E) of thermoregulation and their values ($50\%d_e$, $50\%d_b$, and $50\%E$) calculated using $50\%T_{set}$ bounds in *Z. vivipara* at different altitudes.

Altitude (m)	n^a	d_e (°C)	$50\%d_e$ (°C)	n	d_b (°C)	$50\%d_b$ (°C)	E	$50\%E$
250	222	3.9 ± 0.4	5.0 ± 0.4	95	0.5 ± 0.1	1.1 ± 0.2	0.86 (0.80–0.92)	0.78 (0.72–0.85)
550	202	2.6 ± 0.2	3.8 ± 0.3	91	0.6 ± 0.2	0.9 ± 0.1	0.78 (0.64–0.90)	0.76 (0.67–0.83)
800	235	2.8 ± 0.2	3.9 ± 0.2	30	0.6 ± 0.2	1.5 ± 0.3	0.79 (0.62–0.93)	0.62 (0.47–0.80)
1450	238	5.6 ± 0.3	7.0 ± 0.3	50	0.9 ± 0.3	1.2 ± 0.2	0.85 (0.75–0.93)	0.83 (0.78–0.90)

Note: Indices d_e, d_b, $50\%d_e$, and $50\%d_b$ are presented as the mean ± SE and E and $50\%E$ as the mean with 95% confidence intervals in parentheses.
[a]Number of measurements.

Fig. 3. Maximum hourly operative temperatures at different altitudes. Horizontal lines indicate the lower and the upper thermoregulatory set-points.

Fig. 4. Frequency of operative temperatures (*a*) and field body temperatures (*b*) below (shaded columns), within (open columns), and above (solid columns) the set-point temperature range (T_{set}) at different altitudes.
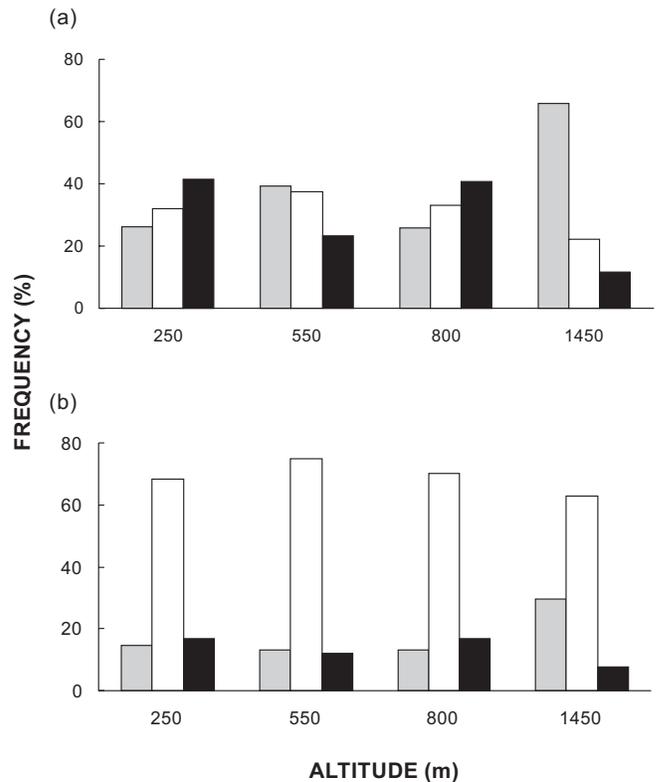

Field body temperatures and indices of thermoregulation

Sun exposure and time of day significantly affected T_b (ANOVA, effect of sunshine: $F_{[2,232]} = 16.91$, $P < 0.001$; effect of time: $F_{[4,232]} = 7.67$, $P < 0.0001$), but an interaction of these effects with that of study site was not significant ($F_{[24,254]} = 0.22$, $P = 0.80$). T_b's varied among populations (ANOVA, $F_{[3,254]} = 3.62$, $P = 0.01$). In particular, lizards from 1450 m had lower T_b's than those from other altitudes (Tukey–Kramer HSD test, $P < 0.05$; Table 3). To examine whether this low T_b resulted from purely environmental constraints, I repeated the analysis with a smaller subset of data including only T_b's measured at those times of day when $T_e > \mathrm{UBT_{set}}$ (Fig. 3). The test yielded similar results (ANOVA, $F_{[3,192]} = 4.71$, $P = 0.003$), suggesting that the decrease in T_b was not caused by lower ambient temperatures that prevented lizards from reaching $\mathrm{UBT_{set}}$ at high altitude.

Distributions of T_b's at 250, 550, and 800 m were leptocurtic and left-skewed, whereas the distribution at 1450 m was symmetrical (Fig. 5). The distributions of T_b's were much narrower than those of T_e's (Kolmogorov–Smirnov test, $P < 0.001$ for all comparisons), suggesting that lizards actively regulated their T_b.

The indices of accuracy of thermoregulation did not vary significantly among populations (ANOVA, $F_{[3,262]} = 0.824$, $P = 0.48$, $1 - \beta = 0.21$, LSN = 1240; Table 4). Because lizards at 1450 m were constrained to reach T_{set} during a restricted period of the day, d_b could be confounded there. Therefore, I recalculated d_b's using only T_b's measured out-

side this period. The new comparison of d_b's among populations gave similar results to the previous test ($F_{[3,255]} = 1.23$, $P = 0.30$; $1 - \beta = 0.33$; LSN = 769). Low d_b's indicate that lizards in all populations thermoregulate with a high degree of accuracy. Proportions of T_b's below, within, and above T_{set} did not differ significantly among populations (G test, $G_{[6]} = 8.39$, $P = 0.21$; Fig. 4*b*). The index of "effectiveness" of thermoregulation ranged from 0.78 to 0.86 (Table 4). Multiple paired comparisons of E pseudovalues generated by bootstrapping revealed no significant differences among populations.

Mean indices of accuracy of thermoregulation calculated using the central 50% of T_p values ($50\%d_b$'s) were 0.9–1.5°C higher than mean d_b's (Table 4). Comparisons of $50\%d_b$'s among populations showed results similar to comparisons of d_b's (ANOVA, $F_{[3,262]} = 0.57$, $P = 0.64$, $1 - \beta = 0.17$, LSN = 1710). The index of effectiveness of thermoregulation based

Fig. 5. Distribution of field body temperatures (T_b) at 250 m (*a*), 550 m (*b*), 800 m (*c*), and 1450 m (*d*). The vertical lines indicate the lower (LBT$_{set}$) and upper (UBT$_{set}$) thermoregulatory set-points.
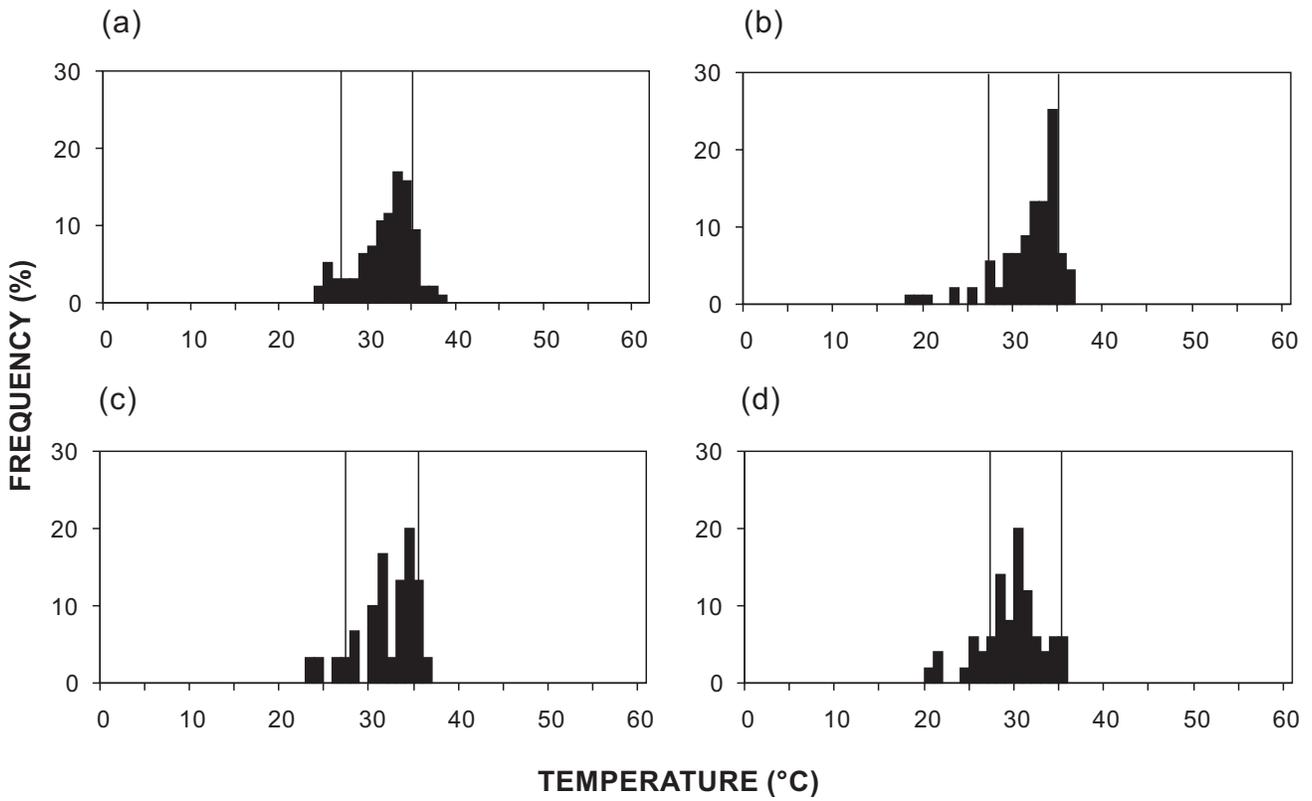

Fig. 6. Frequency of substrates available (solid columns) and used (open columns) by lizards at 250 m (*a*), 550 m (*b*), 800 m (*c*), and 1450 m (*d*). B, bark; DV, dead herb vegetation; IP, iron plate; S, soil; ST, stone; T, tar; V, living herb vegetation; W, wood.
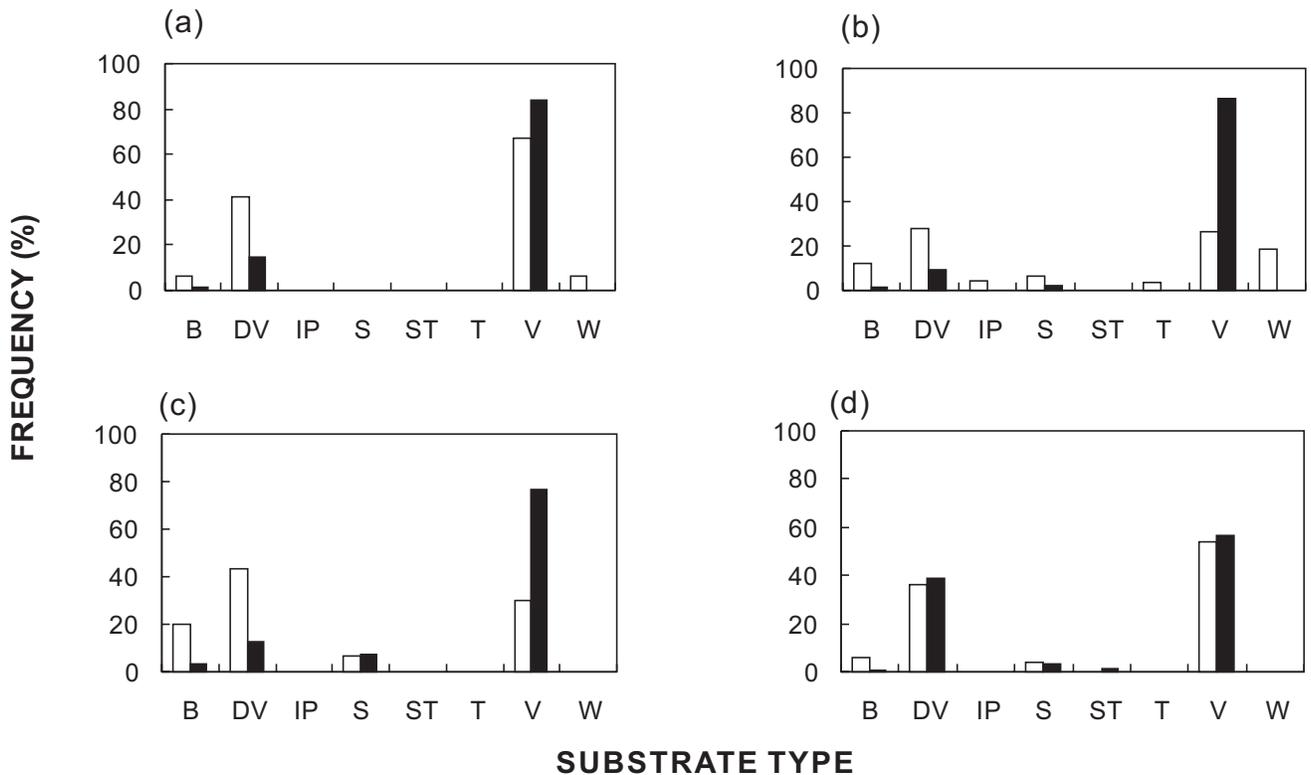
Fig. 7. Frequency of occurrence of basking lizards on different substrates at different altitudes.
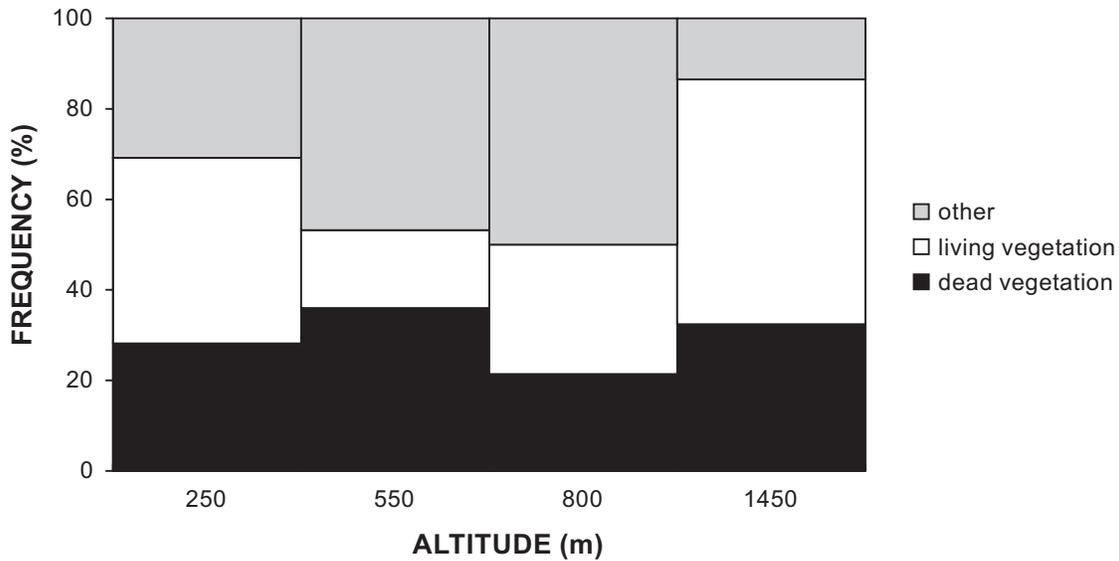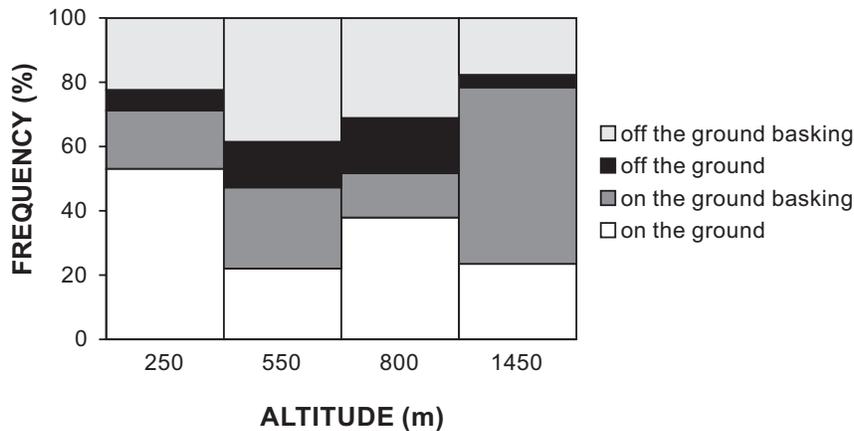

Fig. 8. Frequency of occurrence of basking and nonbasking lizards on and off the ground at different altitudes.

on $50\%d_b$ and $50\%d_e$ indices ($50\%E$) was lower than E in all populations (Table 4). Multiple paired comparisons of $50\%E$ pseudovalues revealed significant differences between populations at 800 and 1450 m, which differed in 99% of paired comparisons.

Microhabitat selection

Substrate availability varied among study sites (G test, $G_{[6]} = 178.8$, $P < 0.0001$). The most frequent available substrates were living and dead herb vegetation (Fig. 6). Because other substrates were relatively scarce, I pooled them into one category ("other"). Substrate frequencies used by lizards differed from those available at 250 m ($G_{[2]} = 13.87$, $P = 0.001$), 550 m ($G_{[2]} = 134.88$, $P < 0.0001$), and 800 m ($G_{[2]} = 27.43$, $P < 0.0001$), whereas they did not differ at 1450 m ($G_{[2]} = 1.88$, $P = 0.39$; Fig. 6). These results indicate substrate selection by lizards at some of the study sites. To find out whether substrate selection was of thermoregulatory importance, I compared frequencies of lizards basking on different substrates (Fig. 7). Because overall log-linear analysis revealed significant interaction between study site and substrate (likelihood ratio (L-R), $\chi^2_{[6]} = 22.31$, $P = 0.001$), the degree of association between substrate and basking fre-
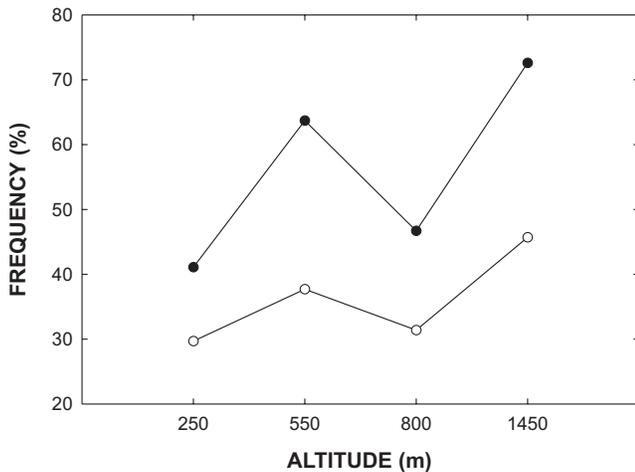
quency was tested separately for each population. Lizards basked more often on dead vegetation and other substrates than on living vegetation at 550 m ($G_{[2]} = 15.34$, $P = 0.0005$) and 800 m ($G_{[2]} = 9.02$, $P = 0.01$). No significant differences in occurrence of basking were found at 250 m ($G_{[2]} = 0.76$, $P = 0.69$) or 1450 m ($G_{[2]} = 0.56$, $P = 0.75$).

The proportion of lizards captured off the ground varied among populations (G test, $G_{[3]} = 19.22$, $P < 0.0002$; Fig. 8). The probability of being captured off the ground increased with t_{bask} (logistic regression, $\chi^2_{[1]} = 8.57$, $P = 0.001$) but not with t_{forage} ($\chi^2_{[1]} = 0.41$, $P = 0.52$). Lizards off the ground basked more frequently than those on the ground (G test, $G_{[1]} = 23.0$, $P < 0.0001$; Fig. 8). These results suggest that the occurrence of lizards off the ground was a thermoregulatory adjustment to longer basking time.

Observed basking times and potential time costs of thermoregulation

The frequency of occurrence of basking lizards changed during the day (log-linear analysis, L-R, $\chi^2_{[2]} = 10.43$, $P = 0.005$) but interaction between time of day and population was not significant (time of day × population: L-R, $\chi^2_{[6]} = 11.78$, $P = 0.07$). The proportion of lizards that basked

Fig. 9. Observed frequencies of basking lizards (●) and potential time costs of thermoregulation, i.e., the relative proportion of time spent basking (○), at different altitudes.

Fig. 10. Potential calculated heating (●) and cooling (○) times of lizards at different altitudes. Values are presented as the mean ± SE.

varied among study sites (*G* test, $G_{[3]}$ = 17.75, *P* = 0.0005; Fig. 9), except between those at 250 and 800 m ($G_{[1]}$ = 0.29, *P* = 0.59).

Based on my estimates of t_{bask}, lizards at different study sites should spend different amounts of time basking (ANOVA, $F_{[3,361]}$ = 4.07, *P* = 0.007). In particular, lizards at 550 m should bask longer than those at 250 m (Tukey–Kramer HSD test, *P* < 0.05; Fig. 10). The potential mean duration of foraging episodes varied among populations (ANOVA, $F_{[3,440]}$ = 65.47, *P* < 0.0001). In particular, for lizards at 550 and 1450 m, t_{forage} should be lower than for lizards at other sites (Tukey–Kramer HSD test, *P* < 0.05; Fig. 10). Differences in mean t_{forage}'s were more pronounced than those in mean t_{bask}'s, indicating that the differences in total time costs were determined mainly by t_{forage}. The correlation between mean t_{bask} and t_{forage} was not significant (r_S < 0.0001, df = 2, *P* > 0.99).

According to c_t's (Fig. 9), lizards should spend from 29.7% (250 m) to 45.7% (1450 m) of the daily time budget basking. Paired comparisons of 1000 pseudovalues of c_t from each site revealed significant differences between all study sites (differences from 98.4 to 100% of all pairs), except for 250 vs. 800 m. In this case, c_t's were higher in only 19% of all pairs that were compared. The observed relative frequencies of occurrence of basking lizards were highly correlated with c_t, i.e., the predicted relative proportion of time spent basking (r_S > 0.99, df = 2, *P* < 0.0001; Fig. 9).

Discussion

To maintain similar T_b's in thermally different habitats, lizards may either employ various physiological and behavioural adjustments or spend more time thermoregulating (Hertz 1981; Hertz and Huey 1981; Hertz and Nevo 1981; Van Damme et al. 1989; Adolph 1990; Díaz 1997). The results of this study indicate the latter response by *Z. vivipara*. First, I will mention some methodological issues in evaluating the extent of thermoregulation. Then I will consider the advantages and limitations of the method of estimating potential time costs that was used. Finally, I will discuss the
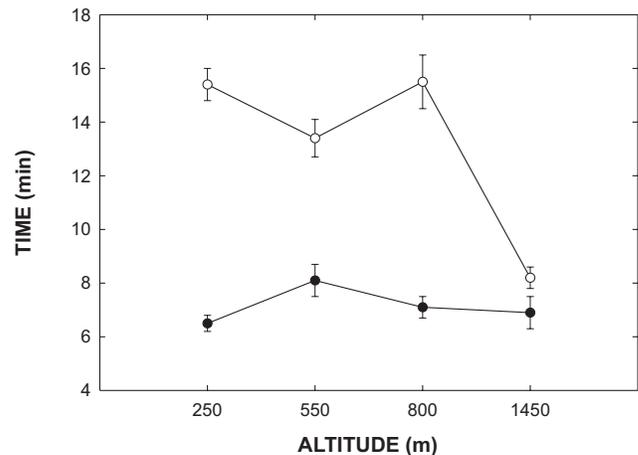
contributions of various physiological and behavioural mechanisms to compensate for the higher time costs of thermoregulation according to the predictions stated in the Introduction.

The limitations of comparing thermoregulatory indices

A comparison of the thermoregulatory indices of *Z. vivipara* and other lizards (Hertz et al. 1993; Christian and Weavers 1996; Bauwens et al. 1996; Díaz 1997; Schäuble and Grigg 1998) showed that this species, like other known lacertids (for a review see Castilla et al. 1999), is one of the most accurate and effective thermoregulators. Nevertheless, available data are still very limited and, moreover, thermoregulatory-index values must be compared with caution because of methodological inconsistencies. Herein, I note two methodological modifications, used in this study, that affected index values irrespective of the extent of thermoregulation.

First, I estimated T_{set} as the central 80% of all body temperatures preferred in the gradient, although the central 50% of T_p's was also used elsewhere (e.g., Hertz et al. 1993; Christian and Weavers 1996; Schäuble and Grigg 1998). The arbitrary determination of T_{set} was recently criticized (Wills and Beaupre 2000) because of its unknown effect on thermoregulatory-index values. To demonstrate how the estimation of T_{set} may affect these values, I additionally calculated the indices using the central 50% of T_p's as the estimate of T_{set}. Generally, compared with original values, mean $50\% d_b$'s and $50\% d_e$'s were higher, whereas mean $50\% E$'s were lower (Table 4). However, the extent of these shifts varied among indices and populations, owing to differences in data distribution (Figs. 2, 5). An important finding was that a statistical comparison of "50% indices" among populations yielded similar results to those obtained with original variables, showing that in this case, the thermoregulatory indices were little affected by arbitrary determination of the T_{set} range. Nevertheless, because of an unpredictable effect of different T_b and T_e distributions on comparisons of thermoregulatory indices, at least two estimates of thermoregulatory set-points should be used for calculating them.

Second, because the surface activity of lizards may vary in space and time for reasons in addition to thermoregulation (Rose 1981), I measured T_e in habitat surrounding surface-active lizards only instead of creating a thermal map of the whole study site. Even though lizards may thermoregulate in shelters (for a review see Huey 1982), I could not measure T_b and T_e there and I therefore restricted the evaluation of the extent of thermoregulation to a period of surface activity only. As a result, I got fewer but biologically more realistic T_e values. It is likely that T_e's, measured in this way were less extreme than those measured in other studies that yielded lower d_e and E values.

Advantages and limitations of calculating c_t

This study showed that the biophysical model of thermoregulation (Bakken and Gates 1975; Dreisig 1985) can easily be used for calculating the potential relative time spent basking by lizards that are not employing any behavioural compensation mechanism. This "null hypothesis" of time demands for thermoregulation without behavioural adjustments can then be compared with the actual proportions of basking lizards or, even better, with observed proportions of time they spent basking. Such a comparison may help to determine whether or not thermoregulatory adjustments actually compensated for time spent thermoregulating. Besides this advantage, calculated potential time spent basking and foraging is a suitable measure of the thermal quality of a habitat. In an ideal thermal habitat, most T_e measurements should be within T_{set}, which means that a lizard should spent no time thermoregulating. However, if a proportion of T_e's lie outside T_{set}, then a more thermally suitable habitat is one that maximizes foraging and minimizes basking episodes, provided that the proportion of microhabitats with T_e outside T_{set} is not so high as to constrain the surface activity of lizards. Using this criterion, the best thermal habitats were at 250 and 800 m (Fig. 10). However, based on the d_e value, I obtained a different result: the highest thermal quality was in the habitats at 550 and 800 m (Table 4).

On the other hand, I must mention some limitations of this approach. First, the biophysical model of thermoregulation used is necessarily an oversimplification. The model is based on the assumption that a lizard does not leave a site with a particular equilibrium temperature during basking and foraging. In fact, a lizard moves across various sites, especially during foraging. The resulting cooling curve is therefore composed of a number of cooling and heating curves, depending on the time a lizard spent at sites with different equilibrium temperatures. In any event, I believe that estimates of mean time spent basking and foraging in a particular habitat do not differ markedly from actual values measured in the field.

Second, because the spectrum of radiation from the sun differs from that of an incandescent bulb, heating rates measured under laboratory conditions may differ from those measured in the field. This may affect estimates of time spent basking. However, Díaz et al. (1996) found that two lacertids increase their body temperature at similar rates under field and laboratory conditions. Because I used a similar method for measuring heating rates as those authors, I assume minor differences between heating rates measured under both conditions in this study also.

Compensation for the higher time costs of thermoregulation

According to the sequential responses of organisms to environmental stress (Slobodkin and Rapoport 1974; Huey and Bennett 1990; Hoffmann and Parsons 1991), I predicted that lizards would cope with long-term fluctuations in environmental temperature through acclimation or adaptation of thermal-physiology traits (thermoregulatory set-points and (or) heating rates). However, the present study showed minor variation in thermoregulatory set-points and heating rates among *Z. vivipara* populations. These findings, along with the previous ones (Gvoždík and Castilla 2001), suggest that differences in thermal environment across 1200 m altitude were too low to induce physiological adjustments in this species. A similar conclusion was reached by Van Damme et al. (1990). Their study, although based on a comparison of two populations, included an even larger altitudinal gradient. There are at least four hypothetical explanations for these findings. First, a minor variation of thermal-physiology traits was also found among populations of other active thermoregulating lizards along altitudinal gradients, suggesting the evolutionarily conservative character of these traits; that is, they respond slowly to directional selection (Bogert 1949; Hertz and Nevo 1981; Hertz et al. 1983; Crowley 1985; van Berkum 1988; Van Damme et al. 1989). Second, because populations of thermoconformers show greater variation in thermal physiology than active thermoregulators, careful behavioural thermoregulation may reduce selection pressure on these traits (Hertz 1981). Third, high gene flow between populations at different altitudes may prevent local adaptation of thermal-physiology traits (e.g., Kirkpatrick 1996). However, this is less probable in the species studied, because negligible differences in thermal physiology were also found between isolated populations from Great Britain and populations in this study (Gvoždík and Castilla 2001). Finally, the absence of adaptation may be due to various anti-adaptive forces, e.g., genetic correlation, developmental constraints, or phylogenetic inertia (Van Damme et al. 1990).

Physiological heating rates can be increased behaviourally by selecting substrates with different thermal conductivities (Heatwole 1970; Pearson and Bradford 1976; Stevenson 1985; Bakken 1989). I found that lizards selected substrates nonrandomly for basking at 550 and 800 m, which is consistent with my prediction and previous observations (House et al. 1980; Hailey 1982). Surprisingly, I found no evidence of nonrandom substrate selection at the site with the highest c_t, i.e., at 1450 m, which suggests that microhabitat choice was also influenced by factors other than thermoregulation. Because of the lack of additional information, I hypothesize that this was a consequence of (*i*) the short potential foraging times (Fig. 10), making the time costs of finding a suitable basking site higher than the potential benefits of heating faster on more suitable substrates (Hailey 1982), or (*ii*) a compromise between the thermoregulatory benefits of basking, requirements for other resources, and cost of predation (Bakken 1989; Huey 1991). Lizards can increase physiological heating rates not only by selecting microhabitats for basking, but also by changing body shape or orientating the body plane perpendicular to the sun (Heath 1965; Stevenson 1985; Díaz 1992; Martín et al. 1995). In this study the observed relative frequencies of basking were highly correlated with

c_t, i.e., the predicted proportion of time spent basking in the absence of any behavioural compensation. Provided that observed frequencies of basking lizards reflect the actual proportion of time spent basking, this result implies that the relative contribution of these unexplored behavioural adjustments to increase heating rates was negligible.

Most behavioural adjustments serve to increase heating rates (for a review see Stevenson 1985), and hence reduce basking time, not heat loss. However, closer examination of time costs among study sites revealed that the differences in potential time spent thermoregulating were mainly due to differences in foraging time (Fig. 10). Although lizards may reduce heat loss by avoiding microhabitats with low T_e during foraging, use of this strategy is very unlikely in habitats like those in this study, where dense herb cover created a very diversified thermal mosaic of sun/shade patches. Alternatively, lizards could physiologically change the blood flow to their appendages during cooling, but this adjustment has little effect in small-bodied lizards (Dzialowski and O'Connor 1999). Thus, the hypothetical reason why lizards at 1450 m insufficiently compensated for higher time costs was that their ability to reduce the higher rates of heat loss they experienced during foraging was limited.

Another way to reduce time costs of thermoregulation is to shift the extent of thermoregulation (Huey and Slatkin 1976). Contrary to this prediction, my results showed negligible differences in thermoregulatory indices among populations. This could have resulted from three facts: (1) time costs were compensated for by using various behavioural and physiological adjustments, (2) the extent of thermoregulation was not a function of time costs, or (3) time costs were too small to induce a shift in the extent of thermoregulation. The absence of differences in the accuracy and effectiveness of thermoregulation under different environmental conditions implies that during activity, lizards carefully maintained their body temperature within the preferred range, irrespective of the time spent thermoregulating. This finding is consistent with the "static concept of thermoregulation", i.e., lizards thermoregulate carefully whenever possible (Bogert 1949), and the suggestion of Dunham et al. (1989) that "requirements for thermoregulation, because of immediate effect of temperature on organism biochemical functions and physiological performance, should usually have precedence over the requirements of foraging and maintaining social status". These views are also supported by the fact that some lizards, including *Z. vivipara*, thermoregulate carefully despite the various costs involved under controlled laboratory conditions (Avery 1976, 1985; Cabanac 1985; Balasko and Cabanac 1998). The lack of thermoregulatory response to a shift in time costs may result from an unknown relationship between the currency used, time, and the ultimate currency of cost–benefit models, fitness. Using the true currency, fitness, the results of this study imply that for this species, the benefit gained from careful thermoregulation is higher than the associated costs across various thermal environments. It may also be argued that the time costs were too small to induce any thermoregulatory shift. However, the variation in d_e's among study sites is comparable to that which induced shifts in the extent of thermoregulation in other species (Hertz et al. 1993; Christian and Weavers 1996), suggesting that the differences in thermal environments, and hence in c_t, were sufficiently high in this study.

Consistent with my last prediction, the results of this study showed that lizards in cooler habitats compensated for higher time costs of thermoregulation by allocating more time to basking than to other activities. This fact, together with a shorter activity season, should therefore affect the energy budget, and ultimately the reproductive success, of lizards in high-altitude populations (Dunham et al. 1989; Adolph and Porter 1993, 1996). Furthermore, these results confirm that lizards, either within or among populations, cope with temporal and altitudinal variation in the thermal environment in the same way, by increasing the frequency of basking (Van Damme et al. 1987). Thus, the time scale and severity of fluctuations in the thermal environment seem to have a negligible effect on the kind of thermoregulatory compensation employed and the extent of thermoregulation in *Z. vivipara*.

Acknowledgements

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