The Thermal Dependence of Feeding Behaviour, Food Consumption and Gut-Passage Time in the Lizard Lacerta vivipara Jacquin

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The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin

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Abstract. Although the effects of temperature on ectotherm physiology have been generally recognized, consequences for animal performance in the field have seldom been assessed. We experimentally investigated the thermal dependence within the body temperature range 20–35 °C, of distinct behavioural and physiological functions related to feeding (sprint speed, prey-catching rate, prey-handling rate, gut-passage rate, voluntary food intake, mass change) in the lizard *Lacerta vivipara* Jacquin. All functions examined were strongly dependent on body temperature (T_b); their rate generally increased rapidly within the range 20–30 °C and then levelled. Exceptions were gut-passage rate and the amount of weight change, which exhibited a decline at 35 °C. Some small but consistent differences in thermal sensitivities between performance functions were evident. Gut-passage rate and weight change were maximal at $T_b \approx 30$ °C, which is slightly lower than the optimal temperature of the other functions (32–34 °C). Passage rate had the widest, whereas prey-catching rate and weight change had the narrowest 80% thermal performance breadth. These results indicate that no single T_b maximizes all behavioural and physiological processes and therefore supports the 'multiple optima' hypothesis. We predicted performance levels in the field by integrating results of the thermal sensitivity experiments with data on T_bs of field-active *L. vivipara*. Lizards seem to be able to achieve >80%

of their maximum capacity for most of the time, at least during sunny weather. Under cloudy/variable conditions, when lizards suffer impaired possibilities to thermoregulate, performance levels were reduced. This depression is less accentuated for gut-throughput rate and weight change. We discuss our results in the context of the overall thermal biology of this cool-climate lizard.

Introduction

Many lizard species thermoregulate behaviourally to keep their body temperatures (T_b) between lower and upper threshold temperatures (Berk & Heath, 1975; Barber & Crawford, 1977; van Berkum, Huey & Adams, 1986). The importance of maintaining T_bs within a narrow range is evident considering its direct influence on biochemical and physiological processes (Dawson, 1975). The ecological relevance of such 'low level' functions has however been questioned (Huey & Stevenson, 1979; Huey, 1982). These authors argued that attempts to integrate physiology and ecology should be based on studies of whole-animal functions such as sprint speed, growth rate, predation success, digestive efficiency, etc. Such information allows elaboration of some of the central themes in the thermal biology of ectotherms.

A first approach integrates laboratory data on the thermal dependence of behavioural performances with records of T_bs maintained in the field (Bennett, 1980; Hertz, Huey & Nevo, 1983; Huey, 1983; Crowley, 1985; Stevenson, Peterson & Tsuji, 1985; van Berkum, 1986; Huey *et al.*, 1989; Van Damme *et al.*, 1989; Van Damme, Bauwens & Verheyen, 1990). This allows examination of the degree of coincidence between the T_bs of active reptiles and the T_bs at which performance is maximized. Existing data indicate that most lizards are active at T_bs that maximize sprint speed, the best-studied performance trait, although some species or populations experience serious locomotor impairment at normal activity temperatures

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(Hertz *et al.*, 1983; Crowley, 1985; van Berkum, 1986; Huey & Bennett, 1987; Hertz, Huey & Garland, 1988; Van Damme *et al.*, 1980; Van Damme *et al.*, 1990).

A second approach examines whether different processes have similar optimal temperatures and thermal sensitivity profiles in single species. Many authors have implicitly or explicitly assumed that a single range of T_bs maximizes all performance functions. Both indirect observations (Huey, 1982) and direct evidence (Huey, 1982; Stevenson *et al.*, 1985) indicate that performance functions might differ in their thermal sensitivity.

In this study we investigate the thermal dependence of several components of the feeding system of the lizard *Lacerta vivipara* Jacquin. This lizard, which inhabits the subarctic and atlantic climatic regions (Spellerberg, 1976), occupies a thermal environment subject to strong seasonal and daily fluctuations. Both body temperatures selected in a laboratory thermogradient (Van Damme, Bauwens & Verheyen, 1986) and maintained in the field (Van Damme, Bauwens & Verheyen, 1987) show considerable seasonal variation. It therefore seemed a suitable species for studying the coincidence between temperatures at which performance functions are maximized and those maintained during activity. Avery and co-workers have previously examined the effects of thermoregulatory capacities on juvenile growth rates (Avery, 1984) and foraging distance (Avery, Bedford & Newcombe, 1982), and the consequences of low T_bs (<20°C) on prey-handling time (Avery *et al.*, 1982) and spontaneous voluntary running speed (Avery & Bond, 1989) in this species. However, these studies are not entirely conclusive with respect to the consequences of small T_b variations within the activity temperature range (25–36°C; Van Damme *et al.*, 1987). These considerations lead us to study the thermal dependence, within an ecologically relevant temperature range (20–35°C), of both short-term (running speed, prey catching, prey handling, food intake) and intermediate-term (gut-passage time, body-weight change) components of the feeding system in *L. vivipara*.

We address the following questions:

1 What is the thermal sensitivity of several behavioural and physiological performances related to the feeding ecology?

2 Are these performances maximized at T_bs maintained during activity in the field?

3 Do the different performance traits have similar thermal sensitivity profiles?

Material and methods

L. vivipara is a small (adult snout–vent length 45–65 mm; mass 3–4 g), ground-dwelling lizard that actively searches for a variety of invertebrate prey (Avery, 1966; Pilorge, 1982; Heulin, 1986). It is live-bearing, having a distinct annual reproductive and activity cycle (Bauwens & Verheyen, 1985) and most frequently inhabits well-vegetated and rather humid places. Daily activity patterns of this shuttling heliotherm depend largely on prevailing weather conditions, particularly the level of solar radiation (Avery, 1971, 1976; House, Taylor & Spellerberg, 1980; Van Damme *et al.*, 1987).

Animals used in this study (all adult males) were collected in the Belgian national nature reserve 'de Kalmthoutse Heide' (Kalmthout [51° 25′N, 4°25′E], province of Antwerp, Belgium). In this study area, field T_bs of active lizards average 29·9°C (SD = 3·5, n = 1063, age/sex groups pooled), but vary seasonally and among age/sex groups (Van Damme *et al.*, 1987). During May and June, the months in which the laboratory experiments were conducted, mean T_b of adult male lizards is 30·7°C (SD = 3·5, n = 97). In a laboratory thermogradient, *L. vivipara* selects T_bs between 25 and 37°C ($\bar{x}$ = 32·1, SD = 2·3, n = 1857, sexes and ages pooled); during May–June, selected T_bs of adult males average 32·2°C (SD = 2·1, n = 336) (Van Damme *et al.*, 1986).

Testing procedures

We conducted four experiments, each with a different group of adult male lizards. Animals were housed individually in soil-filled plastic terraria (60 × 35 × 22 cm) containing heather (*Calluna vulgaris* (L.) Hull) and mosses. A 75-W bulb suspended 20 cm above the substrate provided heat and light for 8 h day^{-1}. Food (crickets and mealworms) and water were provided *ad libitum*. All lizards were tested within 2 weeks of their capture.

We examined the thermal sensitivity of different behavioural and physiological processes by measuring the performances of individual lizards at six T_bs (20, 25, 27·5, 30, 32·5 and 35°C), covering the range of temperatures maintained by this lizard in the field. The sequence of temperatures was selected randomly for each performance function.

In the sprint speed experiment, we controlled the lizards' T_b by placing them in an incubator at the appropriate temperature for at least 1 h before testing.

For all other experiments, we introduced an individual lizard into a vivarium (50 × 50 × 20 cm) and controlled its T_b by placing the terrarium in a small (65 × 65 × 60 cm) constant-temperature room. This chamber was heated by a 100-W heat bulb mounted in the roof; temperature was controlled by a thermostat (ETAF 4, precision = 0·3 °C) connected to a thermistor located on the substrate in the centre of the vivarium. Prior to the experiments, we calibrated the thermostats by monitoring the body temperatures of dead lizards with an electronic thermometer (DGT, precision = 0·1 °C). Temperature was spatially uniform within the chambers. A 20-W cold TL-tube provided illumination in the chamber. The floor of the terrarium was covered with sand and mosses; eight wooden blocks (10 × 5 × 5 cm) were placed at random on the floor to increase environmental heterogeneity (Avery *et al.*, 1982). We observed behaviour through a one-way mirror located in the front side of the chamber.

Sprint speed

Lizards were chased down a racetrack (240 × 15 cm) similar to that described by Huey *et al.* (1981). Running times were measured by 10 sets of photocells positioned at 25-cm intervals along the track. Each lizard was run five times at each test temperature, with no more than three runs per day. From these five trials, we selected the fastest 50-cm track interval. This was used as an estimate of maximum sprinting ability at that temperature. This experiment was run with 20 lizards. Van Damme & Verheyen (1987) provide a preliminary report of the results; Van Damme *et al.* (1990) included the data into a broader sample of lizards from the present study area (Kalmthout).

Prey catching and prey handling

Lizards were starved for 1 day, placed individually in the environmental chambers and given 2 h to habituate to the new environment. Following introduction of three crickets (*Acheta domestica* (L.); mass adjusted to 7–10% of the lizard's weight; hind legs removed to prevent escape from the terrarium), behaviour was observed and timed with a stop-watch.

We defined 'catching time' as the period between introduction of the crickets and the first successful seizure of a prey. 'Handling time' is the period between the first seizure of the prey and the complete closure of the jaws after it has been swallowed.

If the lizard did not attempt to attack a cricket within 15 min, the trial was terminated and repeated after several hours and/or on the following day(s), until the lizard consumed the prey.

Each lizard was tested five times (successfully) at each of the six temperatures. From these five trials, we selected the shortest catching and handling time as estimates for maximal performance at that temperature. This experiment was performed with six lizards.

Gut-passage time

We marked crickets by introducing a small piece of plastic (3 × 2 × 0·1 mm) into their abdomen, and fed these crickets to the lizards. As soon as a lizard had consumed a cricket, it was placed in the environmental chamber at a given test temperature. The chamber was then inspected for the presence of faeces at 30-min intervals. Gut-passage time was defined as the time between the swallowing of the cricket and the appearance of the plastic tag in the faeces.

This experiment was performed with eight lizards, each was tested once at six temperatures.

Food consumption and assimilation

Lizards were starved for 3 days, weighed (to nearest 1 mg) and introduced individually into the constant-temperature room. We added five small (weight 0·10–0·15 g) and five large (weight 0·20–0·25 g) crickets. Lizards were maintained in the chamber for 3 consecutive days on a 9:15 L:D photoperiod regime. During the light phase the appropriate test temperature was maintained; during the dark phase temperature declined to 10–15 °C. On the fourth day, the lizard and the remaining crickets were removed from the terrarium and weighed. Faecal pellets were collected, parted from the uric-acid pledget (Avery, 1971), dried for 24 h at 60 °C and then weighed.

We estimated food consumption (*I*) by the difference between the total prey mass at the onset and at the end of the experiment. This quantity was converted to J assuming an energy content of 21·95 kJ g^{-1} dry weight and a dry weight/wet weight ratio equal to 0·347 (Avery, 1971).

Energy output (*E*) was estimated by weighing faecal output. Conversion assumed that the energy content of the excretory material is 8·94 kJ g^{-1} dry weight (Avery, 1971).

Apparent digestibility coefficients (ADC, *sensu* Throckmorton, 1973) were calculated as:

$$ADC = (I - E)/I$$

Body mass change was estimated by the difference in weight between the start and end of the experiment. It was converted to J assuming an energy content of tissue of $26 \cdot 35 \text{kJ g}^{-1}$ dry weight and a dry weight/wet weight ratio equal to 0·340 (Avery, 1971).

This experiment was conducted with six lizards (mean mass at onset of experiment, 3·14 g; range, 3·05–3·20 g); each individual was tested once at each of the six test temperatures.

Critical thermal maximum

The critical thermal maximum (CTMax), an estimate of the upper temperature for which locomotion is possible, was determined in five lizards. Animals were heated continuously in an incubator while we observed their behaviour. The body temperature associated with a transient loss of righting response was used as an indicator of CTMax (Lowe & Vance, 1955). All lizards recovered quickly from this experiment.

Estimation of thermal optima and thermal performance breadths

We standardized performances among lizards by dividing an individual's performance at each temperature through the maximum performance value recorded for that individual and function. A performance of 0 was assigned to the critical thermal maximum temperature, using the average value for all individuals. We plotted standardized performance against body temperature and used the procedure outlined by van Berkum (1986) to connect data points and to construct minimum polygons for each individual. These were then used to estimate the width and limits of the 80% performance breadth (TPB$_{80}$, body temperature range over which performance is at least 80% of its maximum) and the optimal body temperature (T_{opt}, temperature at maximal performance, calculated as the mid-point of the 95% performance interval) for each individual lizard. Performance breadths are a useful way of quantifying the degree of thermal specialization of a given trait.

We used the reciprocal of catching, handling and digestion times as estimates for the performance rates of these functions.

Statistical analyses

We used two-way ANOVA without replicates to test for differences among temperatures and individuals, using the raw data of the distinct perform-

ance functions. One-way ANOVA and Duncan's new multiple range (DNMR) tests were used to assess significance of differences among performance functions in their T_{opt} and the width and limits of the TPB$_{80}$. The standard criterion of statistical significance was $\alpha = 0 \cdot 05$.

Results

Sprint speed

Sprint speed increased rapidly within the temperature range 20–32·5 °C and then levelled (Table 1). The critical thermal maximum temperature averaged 40·1 °C (SE = 0·3, $n = 5$). Hence locomotor abilities must decrease quickly between 35 and 40 °C. Burst speed varied considerably among individuals. A significant fraction of this variance could be attributed to interindividual differences that were preserved across test temperatures (Table 1).

Prey catching and prey handling

All lizards handled the relatively large prey in a similar way. Most often, the crickets were not killed by the first bite and resisted vigorously; the lizards then braced themselves on their forelimbs and shook their prey to stun it. Often, the crickets were laid down for a few moments and then taken up again. The lizards then progressively moved their grip towards the prey's head and swallowed it head first. In some cases, cricket extremities were ripped off before ingestion.

The number of trials that were stopped and had to be repeated because the lizard failed to attack the cricket, differed between test temperatures ($\chi^2 = 70 \cdot 202$, 5 d.f., $P < 0 \cdot 001$; Table 1), indicating that T_b has an important effect on whether or not the lizards attempted to feed. Attacks that did not result in prey capture at the first attempt tended to be more common at low temperatures (Table 1). Both catching and handling time varied significantly among test temperatures (Table 1). A significant fraction of the variation in catching and handling times was attributable to individual differences (Table 1), indicating that relative performances of individual lizards tended to be similar at the different test temperatures.

Gut-passage time

Gut-passage time decreased between 20 and 32·5 °C and increased again at 35 °C (Table 1). Note that at all T_bs the plastic tag, and presumably the

Table 1. Temperature dependence of distinct behavioural/physiological traits related to feeding in *Lacerta vivipara*.

	Units	n	20°C	25°C	27·5°C	30°C	32·5°C	35°C	P_{tem}	P_{ind}
Sprint speed	m s⁻¹	20	0·40 ± 0·02	0·53 ± 0·03	0·61 ± 0·03	0·73 ± 0·04	0·82 ± 0·05[a]	0·83 ± 0·05[a]	***	***
Catching time	s	6	249 ± 60	126 ± 23[a]	101 ± 41[ab]	40 ± 6[b]	83 ± 34[ab]	57 ± 26[b]	***	*
Handling time	s	6	308 ± 62	205 ± 32[a]	196 ± 25[a]	163 ± 16[ab]	158 ± 22[ab]	132 ± 15[b]	***	**
Hunting efficiency	No. failing attacks	6	0·77 ± 0·20	0·43 ± 0·13	0·50 ± 0·11	0·20 ± 0·09	0·30 ± 0·13	0·33 ± 0·13	0·09	
No. unsuccessful trials			32	12	2	6	3	1		
Gut-passage time	h	8	18·8 ± 1·9	13·5 ± 1·3[a]	14·0 ± 1·4[a]	11·2 ± 0·8[ab]	10·0 ± 0·8[b]	13·5 ± 0·7[a]	***	NS
Energy intake	J day⁻¹	6	660 ± 241[a]	793 ± 186[a]	1049 ± 135[ab]	1519 ± 207[c]	1373 ± 318[bc]	1625 ± 225[c]	**	NS
Faecal output	J day⁻¹	6	60 ± 18[a]	73 ± 15[a]	80 ± 13[a]	90 ± 21[a]	87 ± 12[a]	154 ± 31	*	NS
ADC	%	6	86 ± 5	86 ± 5	92 ± 1	92 ± 4	92 ± 2	89 ± 3	NS	NS
Body mass change	J day⁻¹	6	−142 ± 152[a]	95 ± 93[ab]	321 ± 50[bc]	212 ± 82[bc]	351 ± 205[c]	30 ± 78[a]	*	NS

Values are means ± 1SE. *n*, number of lizards tested; P_{tem} and P_{ind}, significance of variation between temperatures and individuals (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, NS, $P > 0.05$). Superscripts common in a row denote values that do not differ significantly (Duncan's new multiple range test).
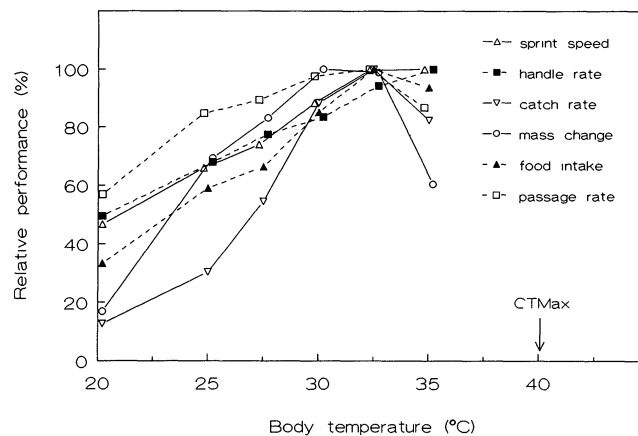
Fig. 1. Relative performance of distinct behavioural and physiological functions at various body temperatures in *Lacerta vivipara*. Shown are averages of the data used in the minimum polygon analyses (see van Berkum, 1986, for selection criteria) and of values obtained through interpolation at each body temperature. CTMax, critical thermal maximum temperature.

food material, had passed the gut within 24 h, i.e. at the beginning of the next activity day.

Avery (1973) estimated stomach evacuation rates for *L. vivipara* kept at 20 and 30 °C, by measuring stomach volumes of lizards that were killed at known times after feeding. The time taken to empty the stomach was 11 h at 30 °C and 24 h at 20 °C (estimated from Fig. 4 in Avery, 1973), whereas 85% of the food was evacuated from the stomach in 7 h at 30 °C and in 19 h at 20 °C (Avery, 1973). These figures coincide surprisingly well with our estimates (Table 1).

Food consumption and assimilation

Voluntary food intake increased within the range 20–30 °C and then levelled (Table 1). Results of Avery (1971) provide an independent estimate of the *ad libitum* food consumption by *L. vivipara* in the laboratory. Substitution of our lizards' body weight into equation (8) of Avery (1971) yields an estimated energy intake of 1225 J day^{-1}, which is

slightly lower than our measurements at 30–35 °C. This suggests that food intake by our lizards was at or near its maximal rate at these temperatures. Apart from the quantitative effect of T_b on food intake, we also noted a qualitative effect: lizards tended to consume relatively more large crickets at higher temperatures (G-test, $P = 0.07$).

The energy lost in faeces was approximately constant within the interval 25–32.5 °C, and increased abruptly at 35 °C (Table 1). Apparent digestibility coefficients did not change significantly with T_b (Table 1).

Observed changes in lizard body mass can be considered as an estimate of the net energy gain, i.e. the gross energy intake minus the energy lost in faeces, as nitrogenous excreta and as costs of maintenance and activity metabolism. An important assumption is that weight changes are not affected by the food volume that possibly remained in the digestive tracts at the end of the experiment. Estimates of gut-throughput times indicate that stomachs will be emptied within

Table 2. Parameters of the thermal-dependence curves of distinct performance functions.

	T_{opt}	TPB$_{80}$	LL$_{80}$	UL$_{80}$
Sprint speed	34·2 ± 0·3^c	8·8 ± 0·5^b	28·9 ± 0·4^a	37·7 ± 0·2^b
Catching rate	32·4 ± 0·9^b	4·2 ± 0·6^a	30·4 ± 0·8^a	34·6 ± 1·1^a
Handling rate	34·1 ± 0·9^c	8·2 ± 1·0^b	29·6 ± 1·0^a	37·9 ± 0·6^b
Gut-passage rate	30·2 ± 1·0^a	10·7 ± 1·8	24·9 ± 1·4	35·6 ± 0·7^a
Energy intake	33·7 ± 0·6^{bc}	7·7 ± 1·2^b	28·9 ± 1·2^a	36·5 ± 0·7^b
Body-mass change	30·4 ± 1·0^a	4·4 ± 0·4^a	27·7 ± 1·1^a	32·1 ± 0·9
ANOVA	$P < 0.001$	$P < 0.001$	$P < 0.005$	$P < 0.001$

Means ± 1SE optimal temperature (T_{opt}), and the width (TPB$_{80}$) and lower (LL$_{80}$) and upper (UL$_{80}$) limits of the 80% thermal performance breadth. Superscripts common in a column denote values that do not differ significantly (Duncan's new multiple range test).

Table 3. Per cent of body temperatures recorded in the field during sunny ($n = 57$) and cloudy conditions ($n = 40$), associated with the indicated relative (% of maximum) performance levels for each of the distinct behavioural and physiological functions.

	Sunny			Cloudy/variable			
	<80%	80–95%	>95%	<80%	80–95%	>95%	P
Sprint speed	14	40	46	43	35	23	<0·01
Catching rate	42	42	16	73	20	8	<0·02
Handling rate	23	32	46	50	28	22	<0·02
Gut-passage rate	7	75	18	23	50	28	<0·05
Energy intake	18	39	44	43	40	18	<0·01
Body-mass change	53	33	14	58	25	18	>0·50

P denotes significance of difference in performance distribution between sunny and cloudy conditions (*G*-test).

24 h, even at the lowest experimental temperature. This implies that our estimates of net energy gain are probably not biased by incomplete digestion of food material. A second assumption is that mass changes are unaffected by differential water uptake at the distinct experimental temperatures. Our data do not allow us to examine the validity of this assumption. Observed body-mass changes increased rapidly between 20 and 27·5 °C, levelled between 27·5 and 32·5 °C, and decreased dramatically at 35 °C (Table 1).

Optimal temperatures and thermal performance breadths

We found significant differences among the performance functions in all parameters of the thermal dependence curves (Table 2, Fig. 1). The T_{opt} was significantly lower for gut-passage rate and body mass change than for the other processes. Prey-catching rate and weight change had the narrowest TPB$_{80}$, whereas gut-throughput rate had the broadest TPB$_{80}$. The lower limit of the TPB$_{80}$ for gut-passage rate is inferior to that of the other performance functions. Weight change exhibited a surprisingly low value for the upper limit of its TPB$_{80}$.

Performance in the field

To predict performance by active lizards in the field, we integrated results of thermal sensitivity experiments with data on activity T_bs of *L. vivipara* (source of data, Van Damme *et al.*, 1987). We distinguished between T_bs taken during sunny (>5 min of continuous sunshine before capture of the lizard) and cloudy/variable weather (<5 min of continuous sunshine). For each performance function, we calculated the proportion of T_bs recorded in adult males during May–June that were asso-

ciated with performance levels <80%, 80–95% or >95%.

Distributions of predicted performances (Table 3) differed between the behavioural/physiological functions both for T_bs recorded during sunny ($G = 72·90$, $P < 0·001$) and during cloudy weather ($G = 24·57$, $P < 0·01$). In both cases, lizards achieved >80% of maximum performance most frequently for gut-throughput rate and least frequently for prey-catching rate and the amount of mass change. For most of the functions studied, low predicted performances (<80%) were almost exclusively induced by T_bs that were below the TPB$_{80}$. The remarkable exception is weight change, where the vast majority of the T_b recordings (29/30 for sunny, 9/23 for cloudy weather) with low associated performance exceeded the TPB$_{80}$ for this function. Predicted performance levels were lower during cloudy/variable than during sunny weather for most functions, with the exception of the rate of body-mass change (Table 3). Estimated performances during cloudy/variable weather were relatively high for gut-passage rate (77% of the T_bs fell within the TPB$_{80}$), indicating that this process is less depressed under suboptimal conditions than the other functions (Table 3).

Discussion

Body temperature has a profound effect on all components of the feeding system studied. Most of the functions experience a rapid increase in performance over the temperature interval 20–30 °C, and were maintained at relatively constant levels within the range 30–35 °C.

Our study and those of Avery (Avery, 1973; Avery *et al.*, 1982; Avery, 1984; Avery & Bond, 1989) provide a comprehensive analysis of the quantitative and qualitative effects of thermoregulatory abilities and/or T_b on the feeding behaviour,

food intake and food passage rate in L. vivipara. At low T_bs lizards often fail to attack their prey, reflecting a lowered willingness to feed and/or poor abilities to detect or recognize potential prey. Decreased abilities to thermoregulate, induced by low levels of simulated solar radiation, reduce the time devoted to foraging and the total distance moved, and probably result in decreased probabilities to contact potential prey (Avery et al., 1982). Abilities to capture prey increase with T_b, as evidenced by a decrease in the number of unsuccessful prey attacks, higher prey-catching rates, and a dietary shift from small to large crickets (this study) and from slow- (mealworms) to fast-moving prey (crickets) (Avery et al., 1982). The higher rate of contacting prey, an increase in the number of feeding attempts, increased abilities to capture and handle prey, and decreased gut-throughput times are factors that contribute to an increase of the voluntary food intake with T_b. Avery (1971) showed that on changeable days food intake by lizards in the field was only about 60% of that on sunny days, and suggested (Avery, 1976) that this was due to a decrease in the time available for foraging. Our results indicate that other factors are also involved. During changeable weather, lizards maintain relatively low T_bs (Van Damme et al., 1987) that are associated with reduced performances for most of the functions contributing to food consumption.

Net energy gains, as indexed by the amount of body-mass change, increased with T_b within the interval 20–30°C, reflecting a parallel increase in voluntary food intake. Body-mass changes exhibited a spectacular drop at 35°C. This is probably induced by metabolic expenditures which rise exponentially with increasing T_b (Patterson & Davies, 1978). Avery (1984) likewise demonstrated a reduced net growth conversion efficiency in juvenile L. vivipara that were kept continuously at 33°C and attributed this to stress induced by prolonged exposure to high temperatures.

Most of the observed variation in performances is induced by T_b. However, a significant fraction of the total variance in sprint speed and in the rates of prey capture and handling could be attributed to interindividual differences that were preserved across experimental temperatures. Interindividual variation in whole-animal performances has rarely been studied in reptiles (Bennett, 1987). Available studies nevertheless demonstrate individual constancy in a variety of complex functions such as running speed (e.g. Bennett, 1980; Huey & Hertz, 1984; Garland, 1985; Huey & Dunham, 1987; van Berkum et al., 1989), antipredator responses

(Arnold & Bennett, 1984; Thoen, Bauwens & Verheyen, 1986), thermoregulatory behaviour and body temperatures (DeWitt, 1967; Christian, Tracy & Porter, 1983, 1985) and length-adjusted clutch size (Bauwens & Verheyen, 1987). Our present results complement these findings.

A major finding of our study is that different performance functions show slight but consistent differences in thermal sensitivities. The optimal temperatures for gut-passage rate and body-mass change were lower than that of the other functions. In addition, rate of prey capture and body-mass change had a relatively narrow, while gut-throughput rate had a rather broad thermal performance breadth. It should be pointed out that differences in the shape of performance curves are as relevant as diverging optimal temperatures within the context of thermal physiology (Huey, 1982). Our results therefore support the 'multiple optima' hypothesis (Bustard, 1967; Lang, 1979; Pough, 1980; Huey, 1982), which challenges the widely held view that each species has a narrow zone of temperatures that maximizes all physiological and behavioural traits. Until now, most support for this hypothesis was inferred from behavioural data, while few studies actually compared the thermal sensitivities of different performance functions (exceptions: Huey, 1982; Stevenson et al., 1985).

The functions that we examined in L. vivipara differ in the physiological and biochemical mechanisms involved in their action. Differences in thermal sensitivity profiles of whole-animal functions may hence be related to differential temperature susceptibility of the underlying reactions at tissue or lower levels. Although our study did not address this issue, we can suggest some hypotheses.

Both sprint speed and prey handling are functions that are likely to be influenced by skeletomuscular, nervous and respiratory systems (Mars & Bennett, 1986; de Queiroz et al., 1987), although it seems fair to assume that both rely primarily on the action of skeletal muscles. It is therefore perhaps not surprising that we found a high resemblance in the thermal sensitivity profiles of both functions. Prey catching, on the other hand, involves a complex integration of nervous and muscular actions. The relatively narrow thermal performance breadth found for this activity may reflect the thermal sensitivity of the nervous system. Alternatively, we may have underestimated the lizards' prey-catching rate at high T_bs due to the supposed increased abilities of

their ectotherm prey to evade predation at these temperatures.

Gut-passage rate, which is presumably the result of physiological and biochemical actions involved in digestion, differed from the other functions in having a low optimal temperature and a broad thermal performance breadth. These findings suggest that the reactions underlying the digestive process may have a relatively low thermal sensitivity. It is noteworthy that, although gut-passage rate was temperature dependent, we found no effect of temperature on the apparent digestibility coefficient. This result might be an artefact induced by assuming a temperature-independent energy content of lizard faeces. This assumption has however been validated empirically in several lizards, including *L. vivipara* (Avery, 1971; Harlow, Hillman & Hoffman, 1976; Harwood, 1979). A negative relation between temperature and energetic content of faeces has been found in two other lizards (Harwood, 1979). If such a relation exists in *L. vivipara*, high temperature ADCs would have resembled the ADCs at low temperatures even more closely. We therefore conclude that ADCs in *L. vivipara* are insensitive to temperature (see also Avery, 1971).

How well do the T_bs maintained during activity match the thermal sensitivities? During sunny weather, the majority (80–90%) of the T_bs recorded in the field ($\bar{x} = 32 \cdot 0$ °C, range $26 \cdot 7$–$37 \cdot 5$, $n = 57$; data from Van Damme *et al.*, 1987) enabled the lizards to achieve 80% of their maximum capacity for most functions examined. Exceptions were the rates of prey catching and of mass change, for which only 50–60% of the T_bs fell within the TPB_{80}. Predicted performances were generally reduced during cloudy/variable weather, when lizards suffer impaired possibilities to thermoregulate and maintain lower and more variable T_bs ($\bar{x} = 29 \cdot 1$ °C, range $20 \cdot 6$–$35 \cdot 9$, $n = 40$). The depressing effects of suboptimal weather were less obvious for mass change and gut-passage rate than for the other functions.

Among the functions examined, the largest differences in thermal sensitivities are the relatively low T_{opt} and wide TPB_{80} for gut-throughput rate and the low T_{opt} for the rate of mass change. What are the possible advantages of these differences in thermal sensitivities? A first factor relates to the amount of time spent under suboptimal conditions or in retreats, and the associated reduction in performance levels. *L. vivipara* inhabits a climatic region that is characterized by low and strongly fluctuating ambient temperatures and a variable level of direct sunshine. It attempts to maintain constant T_bs by restricting its activity to times with favourable weather conditions, by raising its T_b through overt basking and by shuttling between sun and shade (Avery, 1976; House *et al.*, 1980; Hailey, 1982; Van Damme *et al.*, 1987). However, physical factors periodically prevent this lizard from achieving T_bs within its 'preferred' range (Van Damme *et al.*, 1987) and heavy cloud cover impedes or severely restricts activity during 40–55% of the days within the 7-month activity period (Avery, 1976). Rocks or other objects that retain heat and thereby enhance overnight thermoregulatory abilities (Huey *et al.*, 1989) are absent in the usual habitats of *L. vivipara*. It therefore seems reasonable to assume that their T_bs during inactivity drop to cool ambient levels. Low optimal temperatures and broad thermal performance breadths will diminish the detrimental effects of low and fluctuating T_bs on performances. This might be especially important for processes such as digestion, that operate for long periods of time and cannot be restricted to instants where high T_bs can be maintained. Accordingly, gut-passage rate was less depressed in field-active lizards, especially at suboptimal conditions (cloudy/variable weather). It may be significant that our results contrast to those obtained for the lizards *Sceloporus occidentalis* and *Dipsosaurus dorsalis* (Huey, 1982) and the snake *Thamnophis elegans* (Stevenson *et al.*, 1985), where the TPB_{80} of digestion is narrower than that of other functions. However, these species seem to be able to maintain T_bs associated with near-maximal digestion rates during most of their daily activity period (Huey, 1982; Stevenson *et al.*, 1985), and even in their night-time retreats (Huey *et al.*, 1989).

A second factor relates to the costs of thermoregulation. Precise thermoregulation at high T_bs will maximize voluntary food intake by enhancing performances related to foraging behaviour (sprint speed, rates of prey catching and handling), which all have a relatively high T_{opt}. However, the maintenance of high temperatures through behavioural thermoregulation implies energetic and time costs and may increase risks of predation (Huey & Slatkin, 1976). Relatively broad TPBs and a low T_{opt} for functions that operate continuously will allow an ectotherm to diminish thermoregulatory precision without incurring an important performance depression. Lowering of the T_b after feeding would reduce costs of thermoregulation, and at the same time enhance gut-throughput rate and the rate of net energy gain. If true, we expect that lizards will thermoregulate

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carefully during foraging, but will become less thermophilic once a certain amount of prey has been swallowed. Two lines of evidence corroborate this suggestion. First, Avery (1985) continuously monitored active *L. vivipara* and found that their T_bs during foraging were maintained between an upper threshold temperature (36·3 °C, initiation of foraging) and a lower limit (32·9 °C, end of foraging and initiation of basking). This temperature interval lies well within the limits of the TPB_{80} for food intake rate, sprint speed and prey-handling rate. Second, in a preliminary laboratory study, individual *L. vivipara* that had consumed a relatively large amount of prey abandoned their 'normal' alteration of basking and foraging bouts, and positioned themselves in the vegetation, away from the heat of a light bulb (R. Van Damme, unpublished observations).

We suggest that enhanced physiological capacities over a broader range of body temperatures and reduced costs of thermoregulation should constitute selective advantages favouring the evolution of large TPBs in long-term performance functions, at least in environments where the costs of thermoregulation are high. Comparative studies involving phylogenetically closely related species, or populations from a single species, subject to differing climatic conditions, are needed to test this hypothesis.

Acknowledgments

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