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The Role of Thermoregulation in Lizard Biology: Predatory Efficiency in a Temperate Diurnal Basker

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Summary. Decreasing levels of simulated solar radiation have the following effects in the diurnal basking lizard *Lacerta vivipara:* (i) increase in time spent basking with a consequent decrease in time available for foraging (ii) decrease in speed of movement whilst foraging (iii) decrease in total foraging distance, and hence contact with potential prey (iv) decrease in searching efficiency in an experimental arena. Complete absence of simulated solar radiation accentuates these effects, and reduces the proportion of faster-moving prey in the diet. Time taken to swallow prey (handling time) increases exponentially with decreasing body temperature. It is concluded from these results that maintaining relatively high activity temperatures (30–36° C) is adaptive for the species because the loss of potential foraging time caused by lengthy periods of basking is offset by the following advantages: increased contact with and capture of prey, increased efficiency of prey handling, and availability of a wider range of prey types.

Introduction

Thermoregulation by behavioural means plays an important role in the biology of many species of diurnal lizards, and a considerable amount of time may be devoted to thermoregulatory activities. The body temperatures which are maintained during periods of activity are frequently high (>30° C) and relatively constant (Avery 1982); the precision with which they are controlled may vary between species, and also within species in different environments (Huey 1974). Such inter- and intra-specific variation has been analyzed in terms of cost-benefit models which demonstrate that high body temperatures will only be maintained in environments where the benefits, in terms of optimizing net energy gains, exceed the costs which are measured in terms of the time and energy expended in thermoregulatory behaviour (Huey and Slatkin 1976).

The costs of thermoregulation in cool climates are particularly high. The lizard *Liolaemus multiformis* at 4,300 m in the Peruvian Andes may often emerge from its burrow for less than 4.5 h/day; more than 80% of this time is spent thermoregulating by basking or by contact with sun-warmed rocks and other substrates, because of low air temperatures and a high frequency of thick cloud cover (Pearson and Bradford 1976). *Lacerta vivipara* from the cool oceanic climates of north-west Europe must also bask for long periods (Avery 1976). Individuals in the field usually maintain activity temperatures within the range 30–36° C (Avery 1971, Sveegaard and Hansen 1976), but laboratory observations show that feeding and other activities can occur at body temperatures as low as 10° C. What, then, are the benefits of high activity temperatures for this species?

There are a number of hypotheses about accurate thermoregulation around high body temperatures which might help to provide an answer to this question; they are not mutually exclusive, and include the following:

(i) The obvious physiological advantages of homeostasis, particularly for the functioning of enzyme systems. Optimization of digestive efficiency and oxygen transport in particular will have direct ecological consequences.

(ii) Increase in rapidity and efficiency of juvenile growth and the synthesis and deposition of yolk in gravid females.

(iii) Increase in the speed and efficiency of muscular contraction and neuromuscular coordina-

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tion, which will improve both the ability to capture invertebrate prey and the ability to escape from predators.

The purpose of the work reported in this paper is to test those aspects of the hypothesis which relate to feeding behaviour, by investigating the effects of different levels of simulated solar radiation and ambient air temperatures, and hence thermoregulatory capacities and body temperatures, on various aspects of foraging and prey capture. These are the time spent basking and foraging, the efficiency with which insect prey can be found and captured during foraging periods, and the efficiency with which it can be 'handled' after capture. The experimental lizard is *Lacerta vivipara,* which is particularly well adapted for life in temperate climates. It has a widespread distribution from north-west Europe to eastern Siberia, and is found further from the Equator than any other living species of reptile. It is a foraging predator, the diet in England consisting almost exclusively of small insects and other invertebrates (Avery 1962, 1966).

Material and Methods

Lizards were captured near Bristol and maintained in the laboratory in large plastic bowls under natural illumination. Heat to enable the animals to thermoregulate was provided from 275 W incubator bulbs which were switched on for 5 h/day. Food was available *ad libitum* and comprised larvae of *Tenebrio molitor,* crickets (*Acheta domestica*) and occasionally spiders or blowflies (*Calliphora* spp); drinking water was always available.

Foraging Behaviour and Hunting Efficiency

Experiments were carried out in the laboratory in aluminium-walled enclosures measuring 1.4 × 0.9 × 0.3 m. The floor of each enclosure was covered with white paper, ruled with a grid to facilitate recording the movements of the lizards. Twenty four wooden blocks of 4 cm cube and four clay bricks were placed in each enclosure; also a dish filled with foam rubber, which was kept saturated with water to enable the lizards to drink but to prevent the crickets from drowning, and a piece of folded cardboard to provide a hiding place for the lizards. The enclosures were surrounded by large screens to prevent disturbance; the animals were observed through a small slit cut in one of the screens. Heat was provided for 5.5 h/day from a 275 W incubator lamp suspended 1.18, 0.45 or 0.25 m (positions 1–3) above one end of each enclosure. Radiant heat beneath the bulb at position 3 was approximately 1.9 W cm^{-2}, falling in positions 2 and 1 by the ratios 0.3 and 0.05. Ambient temperature when the bulb was not switched on was approximately 20° C, and illumination was natural daylight received through the laboratory window.

The experimental animals were adult male *Lacerta vivipara* placed two to each enclosure; pairs were used because overall food consumption rates by single lizards are small and so subject to excessive sampling error and other variability. Each pair of lizards was allowed to settle in the enclosures for at least one week before observations and experiments were begun. In many lizard species, placing pairs of males together would confound experiments of this kind because of territorial behaviour, but male *L. vivipara* do not interact outside the breeding season (Avery 1976). During the settling period and observations of foraging behaviour, 12 mealworms were placed at randomly selected positions within each enclosure before the bulb was switched on each day to prevent the lizards from associating food with any particular location. During experiments on hunting efficiency each enclosure received either 20 mealworms (about 100 mg each), 30 small crickets (about 10 mg each) or 10 large crickets (about 100 mg each). The large crickets had the distal ends of each hind leg removed by cutting the femora, since otherwise the lizards had considerable difficulty in capturing them. All three quantities are larger than the normal daily consumption by two lizards, and the food remaining after the bulbs had been switched off was removed and counted. Observations on foraging behaviour were made during the period from one hour until two hours after the bulb had been switched on; this period was chosen to avoid recording behaviour during the long preliminary bask which takes place immediately after emergence once the bulb has been switched on, and which served to raise body temperatures from ambient to the activity level. Activity and movements were timed with a stopwatch, the positions of the animals at any time being recorded in relation to the coordinates of the grid.

Diet

These experiments utilized pairs of adult or one-year old lizards, maintained under conditions similar to those described above except that the incubator bulbs were at a height of 50 cm. Mixtures of small crickets and mealworms weighing about 50 mg were placed in each enclosure before the bulbs were switched on, and uneaten prey were removed after the bulbs had been switched off. Trials were carried out with the bulbs switched on for 4.5 h/day (thermoregulating lizards) or with the bulbs not switched on at all (non-thermoregulating lizards); in the latter case ambient temperatures remained throughout at 15° C (experiments with 1-year old lizards) or 20° C (experiments with adult lizards). On days when the bulbs were not switched on, feeding and removal of uneaten prey were carried out at equivalent times.

Handling Time

Previously weighed mealworms or crickets were placed with forceps about 1 cm in front of adult lizards, whose reactions were timed with a stopwatch. Different ambient temperatures were obtained by utilizing natural daily fluctuations or using a thermostatically-controlled room. The use of daily temperature fluctuations was deliberate, to prevent acclimation effects which might have occurred in any systematic schedule. After the completion of the experiment, a telethermometer and polystyrene-encased thermistor were used to check the assumption that cloacal temperatures of the lizards corresponded to ambient under the experimental conditions; body temperatures were not measured during the course of the experiments because of the possibility that the stress which is caused to the animals might affect their behaviour.

Results

Foraging Behaviour and Hunting Efficiency

Wild *L. vivipara,* like many diurnal lizards which actively search for their prey, have a fairly consis-

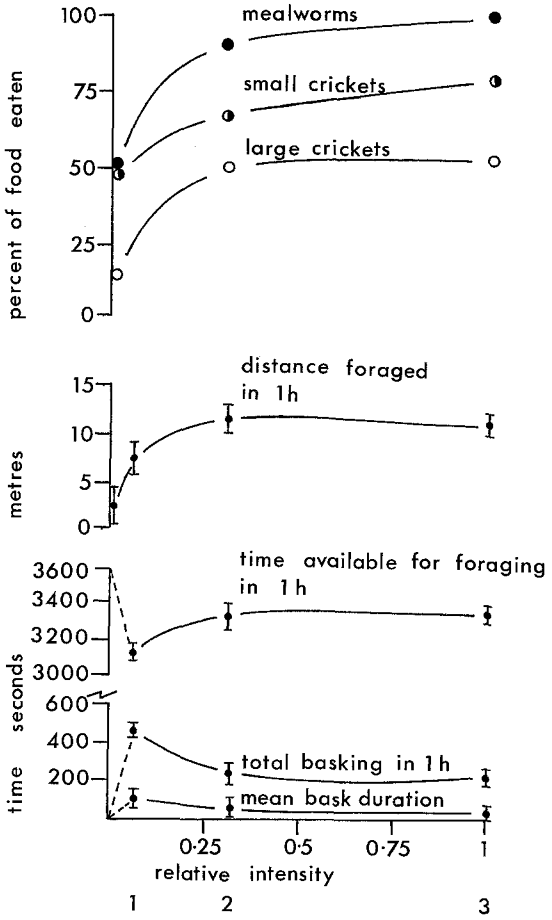

Fig. 1. Basking, foraging and hunting efficiency of *L. vivipara* in relation to the distance of the heating lamp from the substrate (expressed as relative intensity of radiant heat). Curves are fitted by eye. Vertical bars show ±1 S.E.

tent diel cycle of behaviour during sunny weather. The animals emerge from their overnight resting places at predictable times (Avery and McArdle 1973) and bask to raise their body temperature from ambient to the activity level. Thereafter their behaviour alternates between periods of foraging, during which body temperatures usually fall (at any rate in temperate climates), and basking, during which they rise. Lizards in the laboratory, when given the opportunity to bask beneath an incubator lamp, exhibit similar behaviour. The effects of varying the distance of the lamp from the substrate on a number of variables related to basking, foraging and hunting efficiency during the second hour of activity are shown in Fig. 1; also shown are values for days when the lamps were not switched on at all. The results illustrated in Fig. 1 may be summarized as follows:

(i) The mean duration of basking periods increased with decreasing radiant heat intensity, from 52.3 s with the bulb at position 3 to 138.9 at position 1 (one-way ANOVA: $F_s = 19.1$; 2,35 d.f.; $P < 0.001$). The difference between positions 2 and 3, however, is not significant (Student-Newman-Keuls test). The lizards did not bask on days when the bulb was not switched on.

(ii) Total time basking/hour also increased with decreasing heat intensity, from 221.7 s with the bulb at position 3 to 443.3 s at position 1 (one-way ANOVA: $F_s = 8.06$; 2,35 d.f.; $P < 0.01$). The difference between positions 2 and 3 is again not significant (Student-Newman-Keuls test). The time potentially available for foraging within the hour is the inverse of the time basking. The whole hour was potentially available for foraging on days when the bulb was not switched on.

(iii) The total distance moved during foraging activity decreased slightly with decreasing radiant heat intensity, from 12.1 m h^{-1}, to 8.8 m h^{-1}, but this is not significant (one-way ANOVA: $F_s = 1.26$; 2,35 d.f.; $P > 0.1$). There was also a small decrease in the mean speed of foraging; this is not shown in Fig. 1, but can be calculated from foraging times and distances.

(iv) The mean proportion of potential food which was found and eaten by two lizards (hunting efficiency) during the experimental periods was significantly lower for all three categories of food when the bulb was not switched on and the lizards could not thermoregulate (Mann-Whitney U-tests, $P < 0.001$).

Diet: Fast-Moving Versus Slow-Moving Prey

Figure 2 shows the proportion of crickets in the diet of pairs of lizards which were given various combinations of crickets and mealworms as potential food over 5-day periods. Lizards which were able to thermoregulate (open symbols) ate crickets in almost the same proportion as they were available (the dotted line shows exact proportionality). In lizards which were not able to thermoregulate and kept at 15 or 20° C (solid symbols) the proportion of crickets in the diet was smaller. No crickets were eaten at all in six of these experiments, and in 19 of the 21 experiments which can be paired for thermoregulation/no thermoregulation the proportion of crickets in the diet was smaller in the no thermoregulation condition ($P < 0.001$; binomial distribution).

Handling Time

'Handling time' is defined for present purposes as the time which elapsed between the first seizure of a prey invertebrate by a lizard, and the first

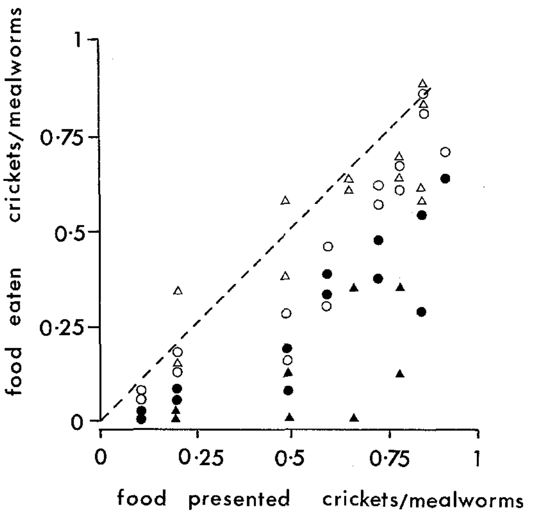

Fig. 2. Diet of *L. vivipara* in relation to the food presented (both expressed as the ratio crickets:mealworms). *Dotted line* shows exact proportionality. *Open symbols:* thermoregulating lizards. *Black symbols:* non-thermoregulating lizards (heating bulb not switched on). *Circles:* adult lizards. *Triangles:* one-year-old lizard

complete closure of the jaws after it had been swallowed. The process includes seizure of the prey in the jaws, shaking to stun and partially crush it, and manipulation (using the jaws and tongue, not the limbs) so that it is swallowed head first. Subsequent tongue extrusions, yawns, and movements of the head and neck to facilitate passage of the material through the oesophagus, were not included.

The relationships between handling time (H, in seconds) and temperature (T, °C) for crickets and mealworms of various weights (expressed for comparability as percentages of total lizard body weight) are shown in Fig. 3. Symbols in the Figure show mean handling times for each category of food; the complete data are too extensive to represent graphically. Temperatures are those of the ambient air, except when lizards were allowed to bask beneath an incubator bulb, in which cases a temperature of 32° C has been taken as representative of the mean body temperature of active lizards in the laboratory (Spellerberg 1976; Patterson and Davies 1978). Regression analysis showed that in all cases the best fit to the data is given by an exponential equation of the form

$$H = a\,[\exp(-bT)] \tag{1}$$

where a and b are constants, provided that values for $T < 10°$ C are ignored (see below). Table 1 shows values of a and b calculated by least-squares regression on the original data (not the means shown in Fig. 3).

Handling times for both mealworms and crickets increased with decreasing temperature. The effect was greater for larger prey, which at low temperatures were swallowed only with difficulty, and some could not be swallowed at all. The lower threshold temperature for mealworms weighing 2.0 and 2.5% of the lizards' body weight was 14.5° C, whereas smaller mealworms were sometimes eaten at 11.0° C (a mealworm weighing 2.5% of the lizard's body weight has an absolute weight of about 100 mg). Crickets were eaten at temperatures as

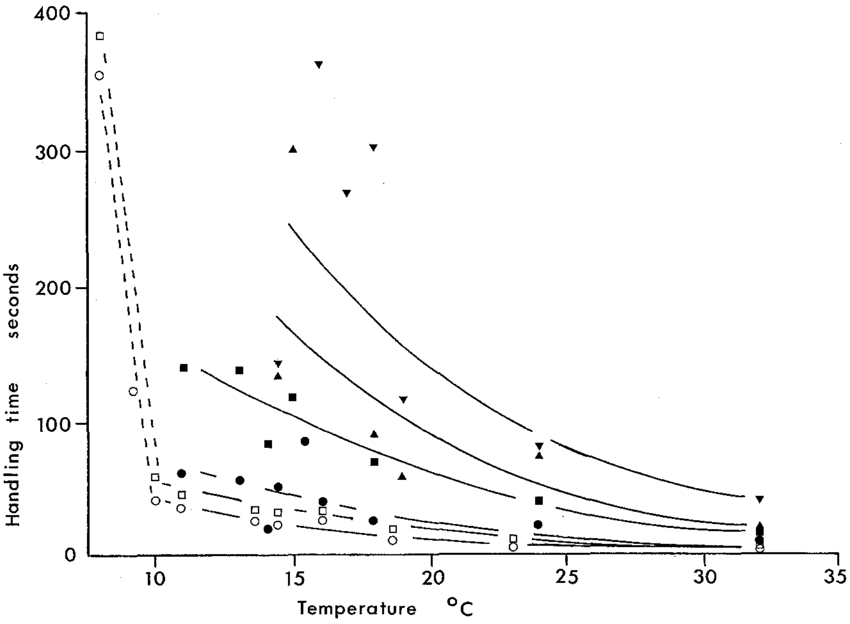

Fig. 3. Handling time in relation to temperature for crickets and mealworms of different sizes. Symbols are mean values, curves are exponentials fitted to raw data (see text). Key to symbols: ▼ mealworms 2.5% of predator's body weight; ▲ mealworms 1.5%; ■ mealworms 1.0%; ● mealworms 0.5%; □ crickets 1.2%; o crickets 0.8%

Table 1. Values for a and b in regressions $H=a\,[\exp(-bT)]$ relating handling time to temperature

Food type	Size (as % of predator body weight)	a	b	Variance ratio F_s	d.f.
Crickets	0.8	71.2 x	0.083	330.9	1,32
	1.2	144.9 x	0.098	61.0	1,61
Mealworms	0.5	194.6 x	0.096	87.3	1,25
	1.0	381.1 y	0.084	46.6	1,17
	1.5	755.9 z	0.100	61.1	1,16
	2.5	1,003.7 z	0.094	66.9	1,12

Values of a in groups x, y and z differ significantly between groups; comparisons within groups, and all comparisons for values of b, are not significant at $P=0.05$

low as 8.0° C, but below 10° C the rates were lower than those predicted by extrapolation from the equations in Table 1 (dotted lines in Fig. 3). Crickets larger than 1.2% of the lizards' body weight were not eaten, probably because the exoskeleton is too hard to be crushed by the jaws.

Discussion

Foraging Behaviour and Hunting Efficiency

The periods of time spent basking by the lizards in these experiments were smaller than basking times which are usually observed in the field, because of the high and constant intensity of the heat provided by the incubator lamps, and also because the ambient laboratory temperature was higher than the air temperature in the lizards' natural microhabitat for much of the activity season from March to October. The time devoted to foraging during any one hour period was probably greater, therefore, than in unrestrained wild animals, but since feeding had to be constrained within the 5.5 h period during which prey was presented, the overall contact rates of the predators with their prey were probably similar to field values.

From the standpoint of contact with stationary prey, however, the important variable is not the time potentially available for foraging, but the distance moved. The curves relating these two variables to intensity of radiant heat are different (Fig. 1). The explanation is that the behaviour of the lizards changed at low intensities, in two respects. Mean speed of movement during each burst of foraging activity fell slightly with decreasing intensity, although the differences are not significant (F-tests, $P>0.1$). With no radiant heat the mean foraging speed fell further, and the number of non-basking pauses between each burst of movement increased, resulting in a considerable drop in the distance moved (Fig. 1). This decrease in foraging distance is considered to be a major factor responsible for the decrease in hunting efficiency at 20° C. Other factors may also have contributed, however. They include the reduction in neuromuscular coordination which results in increased handling times, reduced ability to chase fast-moving prey (see Bennett 1980; Putnam and Bennett 1982), increase in the number of unsuccessful attempts to capture prey (see below) and possibly a decrease in general central nervous efficiency which results in fewer prey being perceived. The latter is an exceedingly difficult phenomenon to investigate experimentally, and almost all of the information which is available on the subject is anecdotal. Detection of prey by the racerunner (*Cnemidophorus sexlineatus*) in the field is less efficient at lower temperatures (Hardy 1962) and the "time to notice" locust prey by water dragons (*Physignathus cocinensis*) is affected by a number of environmental variables (Gillett and Gonta 1978 – but temperature was not investigated in these experiments). The decrease in hunting efficiency was not an artefact due to decreasing appetite or food requirements at lower temperatures, since it was shown on a number of occasions that the experimental animals were still hungry and would eat proffered food at the termination of the experimental periods.

Diet

Crickets are more difficult for a lizard to capture than mealworms, because they move faster and can jump. This is undoubtedly the reason why the proportion of crickets in the diet fell when the lizards could not thermoregulate (Fig. 2). Reduced ability to capture fast-moving prey at low body temperatures could have been a major selective force leading to the evolution of thermoregulatory behaviour in Reptiles. It would hence be of considerable interest to know whether the results of the laboratory experiments are consistent with the effects of ability to thermoregulate or not (which depends on weather conditions) on ability to feed in the field. No method could be devised, however, by which the necessary sampling could be carried out non-destructively, and the killing of a large number of lizards could not be justified for this purpose (direct observation of feeding behaviour in wild lacertid lizards is not usually possible – see Avery 1962, 1966).

Handling Time

Most reptilian body functions are sensitive to temperature, and the exponential relationships shown in Fig. 3 demonstrate that handling times for various kinds of prey are not an exception. The clumsy and often unsuccessful attempts to feed at low temperatures are similar to the results of observations on strike efficiency in gopher snakes (Greenwald 1974). The experimental lizards were tame and habituated to the laboratory protocol, and the prey were presented at a distance of only 1 cm; animals in the field may be less successful at obtaining prey at low temperatures (see Avery 1971). The limited data which are available for other species of lizard show that lower temperature thresholds for successful feeding in the field may vary enormously: in the gecko *Hemidactylus brookii* the threshold is 22–27° C (Avery 1981), in the chameleon *Chamaeleo pumilus* it is at least as low as 3.5° C (Burrage 1973). *Sceloporus cyanogenys* will feed in the laboratory at temperatures which are lower than those at which spontaneous foraging occurs (Greenberg 1976).

General Considerations

Diurnal Reptiles in cool or temperate climates must function at a range of body temperatures, but the majority of species maintain temperatures during a major part of their periods of activity at the surface which have been called "eccritic temperatures", "preferred body temperatures", "activity temperatures" or "activity temperature range" (Huey and Slatkin 1976, Huey and Stevenson 1979).

Many studies have demonstrated that the efficiency of various physiological functions may be optimal within the activity range (review: Dawson 1975). Less, however, is known about the ecological significance of thermoregulation. The results of the experiments reported here demonstrate that maintaining high activity temperatures increases the food intake of a cool climate lizard, because the increased food-gathering efficiency more than offsets the reduction in time available for feeding caused by the necessity to bask. It does so by enabling the animal to move further and faster whilst foraging, and so search a bigger area for potential prey; to capture a wider range of invertebrates than would otherwise be available by the inclusion of more of the faster-moving species; and to capture and handle prey more rapidly. These conclusions are empirical; the experiments give no detailed information on the precise mechanisms by which feeding efficiency is increased, nor do they demonstrate (other than by inference) that the same arguments apply to lizards in the field. A detailed analysis of the first of these problems would be impossible at present, since it would require an understanding of how the sum of the relationships of body temperature to individual physiological mechanisms affect overall performance in ways which have ecological consequences. The second problem relates to the applicability of laboratory-based results. The design of the feeding experiments was carefully chosen to simulate natural conditions so far as possible. It was for this reason that the trials were carried out in comparatively large enclosures; earlier attempts to perform them in smaller areas were not successful. The large numbers of wooden blocks in the arenas simulated the relatively densely vegetated conditions of the habitats in which *L. vivipara* usually occur in nature, where the animals must search for their food in a spatially complex environment. They cannot survey large areas, and so the experimental arenas provided obstacles to direct vision. A further function of the wooden blocks was to elicit a high level of spontaneous foraging, which occurs only in diversified environments; captive *L. vivpara* in simple cages do not forage spontaneously with the same frequency.

In summary, the major conclusion from this work is that allowing a *L. vivipara* to thermoregulate in the laboratory increases its gross energy intake. It seems a reasonable extrapolation to conclude that this is also true for unrestrained animals in the field. The effects on *net* energy gains (i.e. of energy which is available once the costs of metabolism and activity have been met) are not known. They would be difficult to determine because neither the spatial distribution of potential prey nor the energy expenditure needed to acquire a unit of food intake, can be readily measured. Since the increases in foraging distance and food intake are large (Fig. 1), however, it is likely that net intake also increases. If this is so, it represents an adaptive advantage which would help to explain the evolutionary persistence of basking behaviour in cool climate lizards. The increased range of invertebrate prey made available (Fig. 2) may also be adaptive; *L. vivipara* have a greater range of invertebrate prey available to them than weakly thermoregulating sympatric amphibians such as newts which during their terrestrial phases may occupy the same habitats. Thermoregulation may also, of course, have many other adaptive advantages for Reptiles. It is important, in this as in all evolutionary arguments, to be careful not to lose sight of the fact that the adaptiveness of a character may relate simultaneously to a number of environmental variables. Behavioural ecologists have sometimes forgotten this in their enthusiasm to devise intellectually satisfying models, a point which has recently been emphasized from an entirely different angle by Janetos and Cole (1981).

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References

Avery RA (1962) Notes on the ecology of *Lacerta vivipara*. Br J Herpetol 3:36–38

Avery RA (1966) Food and feeding habits of the Common lizard in the West of England. J Zool 149:115–121

Avery RA (1971) Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. J Anim Ecol 40:351–365

Avery RA (1976) Thermoregulation, metabolism and social behaviour in Lacertidae. In: Bellairs Ad'A, Cox CB (eds) Morphology and biology of reptiles, Linnean Society of London Symposium Series no 3. Academic Press, London New York, pp 245–259

Avery RA (1981) Feeding ecology of the nocturnal gecko *Hemidactylus brookii* in Ghana. Amphibia-Reptilia 1:269–276

Avery RA (1982) Field studies of body temperatures and thermoregulation. In: Gans C, Pough FH (eds) Biology of the Reptilia, vol 12, Physiology C. Academic Press, London New York San Francisco, pp 93–166

Avery RA, McArdle BH (1973) The morning emergence of the Common Lizard *Lacerta vivipara* Jacquin. Br J Herpetol 5:363–368

Bennett AF (1980) The thermal dependence of lizard behaviour. Anim Behav 28:752–762

Burrage BR (1973) Comparative ecology and behaviour of *Chamaeleo pumilus pumilus* (Gmelin) and *C. namaquensis* A. Smith (Sauria: Chamaeleontidae). Ann S Afr Mus 61:1–158

Dawson WR (1975) On the physiological significance of the preferred body temperatures of Reptiles. In: Gates DM, Schmerl RB (eds) Perspectives of biophysical ecology. Ecological studies, vol 12. Springer, Berlin Heidelberg New York, pp 443–473

Gillett SD, Gonta E (1978) Locusts as prey: factors affecting their vulnerability to predation. Anim Behav 26:282–289

Greenberg N (1976) Thermoregulatory aspects of behaviour in the blue spiny lizard *Sceloporus cyanogenys*. Behaviour 59:1–21

Greenwald OE (1974) Thermal dependence of striking and prey capture by gopher snakes. Copeia 141–148

Hardy DF (1962) Ecology and behavior of the six-lined racerunner, *Cnemidophorus sexlineatus*. Univ Kansas Sci Bull 43:3–73

Huey RB (1974) Behavioral thermoregulation in lizards: importance of associated costs. Science 184:1001–1003

Huey RE, Slatkin M (1976) Costs and benefits of lizard thermoregulation. Q Rev Biol 51:363–384

Huey RB, Stevenson RD (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am Zool 19:357–366

Janetos AC, Cole BJ (1981) Imperfectly optimal animals. Behav Ecol Sociobiol 9:203–209

Patterson JW, Davies PMC (1978) Preferred body temperature: seasonal and sexual differences in the lizard *Lacerta vivipara*. J Therm Biol 3:39–41

Pearson OP, Bradford DF (1976) Thermoregulation of lizards and toads at high altitudes in Peru. Copeia 155–170

Putnam RW, Bennett AF (1982) Thermal dependence of isometric contractile properties of lizard muscle. J Comp Physiol 147B: 11–20

Spellerberg IF (1976) Adaptations of Reptiles to cold. In: Bellairs Ad'A, Cox CB (eds) Morphology and biology of reptiles, Linnean Society of London Symposium Series no 3. Academic Press, London New York, pp 261–285

Sveegaard B, Hansen IL (1976) Temperature regulation in lizards (*Lacerta vivipara, L. agilis* and *L. pityusensis*). Norw J Zool 24:232