Evolutionary rigidity of thermal physiology: the case of the cool temperate lizard Lacerta vivipara

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We compared the thermal dependence of sprint speed in two populations of the common lizard, *Lacerta vivipara,* from different altitudes Although field body temperatures in the montane population were consistently 3–5°C below those of the lowland population, we found no parallel shift in the optimal temperatures for sprint speed Lizards from both populations also selected similar temperatures in the laboratory In the field, lizards from the montane population were frequently active at body temperatures that seriously impair locomotion These observations give support to the static view of thermal physiology, which claims that thermal physiology is evolutionary stationary and resistant to directional selection

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Introduction

Temperature strongly affects a wide variety of physiological processes, ranging from elementary enzyme reactions up to whole-animal processes such as metabolism, growth and locomotion. Temperature curves for most processes typically include a range of temperatures around an optimum temperature at which performance for that process is at or near its maximum. Pough and Gans (1984) define this range as the thermal performance breadth (= TPB). Body temperatures that depart from this optimal temperature range should reduce ecological performance and hence fitness, natural selection should therefore favour animals that keep their body temperatures within the optimal range. This can be achieved in three fundamentally different ways: (1) through thermoregulation, i e by (physiologically or behaviourally) adjusting body temperatures until they are within the optimal range; (2) by acclimatization; or (3) by adaptation of the temperature curve (shifting optimal temperatures or widening the optimal range)

The first two mechanisms may operate within the life-span of individual organisms, while genetic adaptations to local conditions involves several consecutive generations.

In lizards that are confronted with geographical variation in thermal environments, behavioural thermoregulation is believed to be the primary compensatory mechanism In response to environmental changes, many species increase thermoregulatory effort to retain body temperatures near optimal. Such regulatory behaviours may include habitat shifts (Clark and Kroll 1974, Huey and Webster 1976, Hertz 1981, Hertz and Huey 1981), changes in activity times (Hertz 1981, Hertz and Huey 1981, Hertz and Nevo 1981) and increases in basking intensity (Huey and Webster 1976, Hertz 1981, Hertz and Huey 1981, Hertz and Nevo 1981)

Behavioural shifts, however, often cannot compensate entirely for the reduction in environmental temperatures encountered at high altitudes or latitudes (Brattstrom 1965, Clark and Kroll 1974, Huey and Webster 1976, Hertz 1981, Hertz and Nevo 1981, Hertz and

Huey 1981, Crowley 1985, van Berkum 1986, Van Damme et al. 1989). Thermoregulation may become too costly (Huey 1974, Huey and Slatkin 1976) or physical factors may impede the achievement of optimal temperatures (Van Damme et al. 1986). In such circumstances, we might expect a strong selection pressure towards lowering the physiological optimum temperatures and/or widening the optimal ranges (Hertz et al 1983). However, whereas the importance and existence of behavioural adjustments have been widely documented, the extent of long-term physiological adaptation is still under debate

Two contrasting views on the evolutionary lability of thermal physiology have been labeled the 'static' and the 'labile' view (Hertz et al. 1983) The static view claims that thermal physiology is evolutionarily stationary and resistant to directional selection. Support for this view comes largely from studies on temperate-desert lizards (Bogert 1949, King 1980, Hertz et al. 1983, Crowley 1985), but also on other ectotherms (Ushakov 1964, Brown and Feldmut 1971, Calhoun et al. 1981) The labile view arose from the studies on the lizard genus *Anolis*, in which thermal differentiation seems to be the rule rather than the exception (Ruibal 1960, Rand 1964, Ruibal and Philibosian 1970, Heatwole et al 1969, Huey and Webster 1976, Van Berkum 1986) In Australian skinks (Lygosominae) optimal temperatures seem to have evolved at a lower pace than thermal preferences (Huey and Bennett 1987) The flexibility of thermal physiology thus seems to differ between taxonomic and ecological groups, and the validity and generality of both contrasting views should be tested by studies on reptiles from other families and climatic regions

In this paper, we examine the extent of thermal physiology evolution in the cool temperate lacertid lizard, *Lacerta vivipara*. The geographic range of *L vivipara* is probably the largest of any living lizard (Avery 1982). It extends from Ireland in the west to the Sakhalin Island (USSR) in the east, and from northern Spain in the south to within the Arctic cycle. Within this huge area, populations of *L vivipara* inhabit very different thermal environments *Lacerta vivipara* therefore offers an excellent opportunity to play off both views on the flexibility of thermal physiology within one species. We contrast characteristics of temperature dependence of a whole-animal trait (running speed) in a lowland and a montane population. Body temperatures at the latter site are consistently 3–5°C below those maintained by the lowland lizards. The labile view of thermal physiology would predict a parallel shift of the optimal temperature or a broadening of the optimal temperature range. The static view forecasts the conservatism of thermal sensitivities. We examine these sets of contrasting predictions on the flexibility of thermal physiology

Material and methods

Study sites

The lowland population inhabits a patch of moist heathland in the Belgian national nature reserve "de Kalmthoutse heide" [Kalmthout (51°25′N, 4°25′E), province of Antwerp, Belgium, elevation 25 m]. The vegetation is dominated by crossleaved heath (*Erica tetralix*), purple moor-grass (*Molinia caerulea*) and bog asphodel (*Narthecium ossifragum*) Birch (*Betula pendula*) and pine (*Pinus sylvestris*) stand isolated and form small thickets. Activity in this population starts in early March (adult males) or April (subadults and adult females) and ceases by late September or early October. Aspects of the demography and thermal relations for this population have been published elsewhere (Bauwens 1985, Van Damme et al. 1986, 1987).

Broers and Clerx (1981, Clerx and Broers 1983) have studied *Lacerta vivipara* at high altitudes near Serfaus (47°02′N, 10°33′E) in the Austrian Alps. They reported on field body temperatures and some demographic parameters for two populations, one at 2000 m and the second at 2150–2200 m altitude The population at 2000 m inhabits a patch of heath (*Calluna*) surrounded by wet hayfields. Thickets of alders (*Alnus viridus*) and numerous ant-hills and rocks stand scattered over the area. The other population occurs on a rather steep (>30°) SE-facing slope vegetated with *Vaccinium* sp and *Rhododendron* sp. and surrounded by moist grassland (mostly *Deschampsia* sp.) At these sites, activity is restricted to four months (June–September) as snow covers the area from September until late May.

Field body temperatures (T_b)

T_b used in this paper come from an extensive study on the Kalmthout population (Van Damme et al 1987) and from data collected by Broers and Clerx in the Serfaus populations In both cases, active lizards were caught by hand and their cloacal body temperatures were measured to the nearest 0.1°C with electronic thermometers Air temperature was measured with the same device, a few cm above the substrate on which the lizard was caught

Because T_b did not differ significantly between both montane populations (t-test, P>0 1) we have lumped the data to contrast them to the lowland data

Selected body temperatures (T_{sel})

In September 1987, we collected 9 female and 8 male adult *Lacerta vivipara* at the 2000 m location in Serfaus and transported them to the Field Biological Station in Kalmthout, where we measured their selected body temperatures (T_{sel}) and running performance within two weeks after arrival T_{sel} for lizards of the lowland population have previously been reported by Van Damme et al (1986).
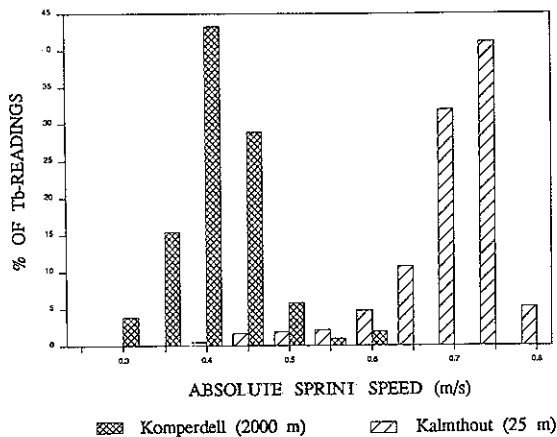
Fig. 3. Distribution of predicted absolute sprint speeds in lowland (hatched) and montane populations (crossed) of *Lacerta vivipara*

A MANOVA (repeated measurements, SPSS) revealed a highly significant effect of temperature ($P<0.0001$) and altitude ($P<0.0001$) on sprint speed. Mean sprint speed was consistently lower in the highland population (Fig. 1). The interaction effect between both factors was not significant, indicating that the temperature dependence of sprint speed is similar in both populations. Accordingly, optimal temperatures, widths and limits of thermal performance breadths did not differ between both populations (t-tests, Tab 2).

We predicted absolute and relative (% Vmax) sprint speed for each field body temperature recorded for adult lizards in June, July, August and September by interpolation in the thermal sensitivity curves of each individual raced in the laboratory, and then averaged performances among individuals. Lizards at high altitudes were frequently active at body temperatures that impede running at more than 75% of maximal capacity whereas low altitude lizards generally obtained body temperatures that fall within the TPB-80-range (Fig. 2). The combined effects of body temperatures and the differences in absolute sprint velocity cause the extreme between-population difference in predicted absolute speeds (Fig. 3)

Discussion

Our results coincide with the predictions of the static view on the evolution of thermal physiology. Field body temperatures were considerably reduced in the high altitude population, even during the warmest part of the activity season. The observed differences in T_b's are among the largest reported within a single lizard species, with the possible exception of some *Anolis* (Ruibal and Philibosian 1970, Huey and Webster 1976). Never-

theless, we found no differences between both populations in any of the parameters derived from the sprint performance curves

In the absence of data on operative temperatures (Bakken and Gates 1975) for the montane population, we cannot determine whether low T_b's in this population result from ineffective thermoregulation or are induced by physical constraints that prevent lizards from achieving higher temperatures. However, the huge amount of time that lizards at high altitudes spent basking inclines us to the latter supposition. In an open air terrarium-study performed by Broers and Clerx (1981, 1983) at Serfaus, *Lacerta vivipara* individuals bask for 38 (male) to 54% (female) of their time spent above ground.

Why have optimal temperatures and TPB's not been become adapted to the highland thermal environment? Evolution of any trait requires three basic conditions: (1) there must be interindividual variation for the trait within the population; (2) this variation must have a genetic component and (3) interindividual differences should have an effect on fitness. Interindividual variation is a topic that has largely been overlooked and only recently received more attention (Bauwens et al. 1987, Bennett 1987). Especially studies on thermal physiology rarely address the topic of variation between individuals (but see Huey and Kingsolver 1989). Interindividual variation in T_b and field thermoregulatory behaviour have been reported only in the lizard *Conolophus pallida* (Christian et al. 1983, 1985) and in African lizards from different families (Bowker 1984). Body temperatures selected in thermogradients differed between individual *Dipsosaurus dorsalis* (DeWitt 1967) and *Podarcis sicula* (Spellerberg and Smith 1975). We know of no studies that actually examine consistent interindividual differences in thermal sensitivity curves

Equally few studies examine the second prerequisite for the occurrence of evolution: the genetic basis of variation in physiological performance. In reptiles, significant heritabilities have been found for important whole-animal function such as burst speed, stamina (Garland 1985, Van Berkum and Tsuji 1987) and antipredator behaviour (Arnold and Bennett 1984) but the only heritability estimates for thermoregulatory behaviour come from studies on mice (Becker and Hegmann 1972, Lacy and Lynch 1979)

Finally, evolution of optimal temperatures for sprint speed also requires an adverse effect of locomotor impairment on fitness. Although such an effect seems intuitive, indirect or direct evidence has been provided only in a small number of cases. Greenwald (1974) showed a positive relation between body temperature, strike velocity and predatory success in the gopher snake (*Pituophis melanoleucus*). Avery et al. (1982) demonstrated that, in *Lacerta vivipara*, low body temperatures reduce speed of movement while foraging, and decrease total foraging distance and hence contact with potential prey. In juveniles of the same species,

Tab 2. Selected body temperatures (T_{sel}), critical thermal maxima (CTmax), optimal temperatures (T_{opt}), the 95% and 80% performance breadths (TPB95, TPB80) and their upper (U95, U80) and lower limits (L95), L80) for sprint speed in lowland (Kalmthout, 25 m) and montane (Komperdell, 2000 m) populations of *Lacerta vivipara*. Values are means ± 1 SE

	Kalmthout (h = 25 m)	Komperdell (h = 2000 m)
T_{sel}	32 3± 0 2 (151)	32 1±0 3 (92)
CTMax	40 4± 0.4 (5)	40 7±0 5 (5)
T_{opt}	34 1± 0 4 (34)	35 0±0 2 (17)
TPB95	4 5± 0 4	4 6±0 4
lower limit	31 9± 0 5	32 7±0 3
upper limit	36 3± 0 5	37 3±0 2
TPB80	9 5± 0.4	9 0±0.7
lower limit	28 2± 0.5	29 0±0.5
upper limit	37 7±0 02	38 0±0 3

Fig 1. Thermal dependence of maximal sprint speed in two populations of the lizard *Lacerta vivipara*. Means (± 1 SE) are for the Komperdell (altitude = 2000 m, n = 17, triangles) and for the Kalmthout population (altitude = 25 m, n = 34, circles).

Results

A comparison of the monthly mean T_b's in distinct sex/age groups (adult males, adult females, subadults) revealed few differences in the lowland population (in April, mean T_b of adult females was higher than in adult males and subadults, Van Damme et al. 1987) and none in the highland population. Selected temperatures measured during September, optimal temperatures and TPB-limits did not vary among sex/age classes in either population

Therefore, we have lumped data for the three sex/age classes in subsequent analyses

Field body temperatures

Monthly mean air temperatures at the high altitude location were consistently 5 to 10°C below corresponding lowland values (Tab. 1). Monthly mean T_b's were also significantly lower in the highland population (Kolmogorov-Smirnov-test, all P<0.01, Tab 1) but the altitudinal difference in T_b was less than that for T_a. During July and August, T_b's were more variable in the montane than in the lowland population (F-tests, both P<0 01, Tab 1). The difference between T_b and air temperature was highest in the highland population (Kolmogorov-Smirnov-test, P<0 01)

Selected body temperatures

Temperatures selected by montane *Lacerta vivipara* from Austria were similar to the T_{sel} recorded during September in the lowland population (t-test, P>0.1, Tab 2) To what extent do field T_b's maintained by lizards in both populations match the selected temperatures? High altitude lizards maintained activity T_b's that were well below their T_{sel}: 79% of all T_b's taken in September were below the T_{sel}-range In the lowland
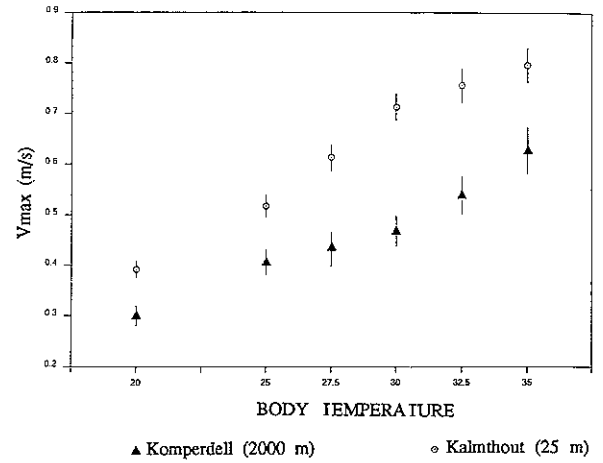
population only 19% (17/90) of the T_b measured in September fell below the T_{sel}-range. Throughout the activity season, 46% of all T_b of active lowland *Lacerta vivipara* (n = 1063) were below the T_{sel}-range, 50% fell within and 4% fell above (we took into account the intrapopulational and seasonal variation in T_{sel} (Van Damme et al. 1986) when calculating these percentages) When T_{sel} measured in September for the highland population are considered representative for the whole activity season, 64% (171/266) of all T_b measured are below the T_{sel}-range

Thermal sensitivity of running

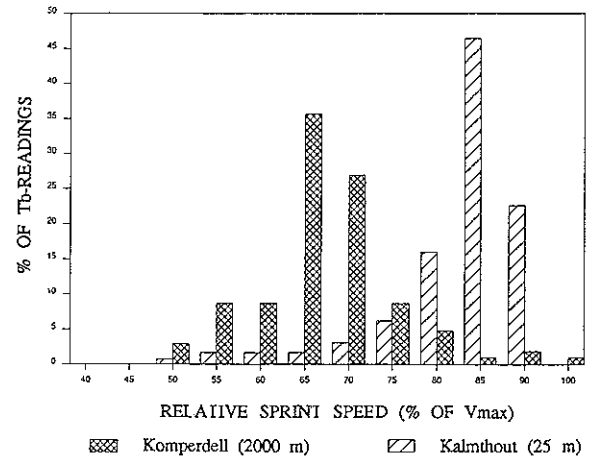We found no differences in CTMax between populations (t-test, P>0 1, Tab 2)

Fig 2. Distribution of predicted relative (% of Vmax) sprint speeds in lowland (hatched) and montane (cross hatched) populations of the lizard *Lacerta vivipara*

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behavioural thermoregulation increases growth rates through increasing food intake (Avery 1984). The most direct demonstration of the dramatic effects of locomotor impairment due to low body temperatures, comes from Christian and Tracy (1981), who found that the ability of hatchling land iguanas (*Conolophus pallidus*) to avoid hawk predation clearly depended on body temperature. On the other hand, several studies have failed to demonstrate a relation between variation in complex physiological characters such as sprint speed or metabolism and fitness (Feder 1987).

In *Lacerta vivipara*, several factors may weaken or nullify the supposed relation between speed and fitness. First, the ecological relevance of high speed may vary between populations because of differences in selection pressure. This may occur if food items are more abundant or more easy to catch, and/or if predation pressure is reduced at high altitudes. We have no data on either of these factors, but the observation that absolute speed of the high altitude lizards was reduced (see Hertz et al. 1983 and Crowley 1985 for comparable findings), seems to support the idea that high running speed is less important at high altitudes. Second, the repercussions of activity at low body temperatures may be minimized by compensatory shifts in antipredator or foraging behaviour. In our lowland population, locomotion in gravid females is seriously hampered by the mass of the clutch (Van Damme et al. 1989). They offset for this by shifting their behaviour from fleeing towards a more extensive use of crypsis (Bauwens and Thoen 1981). As no increase in mortality during gestation is apparent (Bauwens 1985), this shift in escape behaviour seems to compensate effectively for the reduced locomotor abilities. A distinct, temperature-induced shift in anti-predator behaviour has been described in *Agama* (Hertz et al. 1982) and *Gambelia wislizenii* (Crowley and Pietruszka 1983). The detrimental effects of low temperature on foraging abilities may be compensated by parallel effects on the escape capacity of the prey. *Lacerta vivipara* hunts on insects and spiders (Avery 1966, Itämies and Koskela 1971), ectotherms that may experience similar reductions in awareness or locomotor abilities due to low environmental temperatures. A shift from active foraging towards sit-and-wait predation also seems a possible adaptation.

Assuming that all three conditions for the evolution of temperature dependence curves are met, the absence of an adaptive shift may be caused by anti-adaptive forces, such as genetic correlation, developmental constraints (Alberch 1980), chance (Wright 1932, Bock 1959) or phylogenetic inertia (Wilson 1975, Ridley 1983). Deciding whether the lack of genotypical variation in thermal characters, the absence of a directive selection pressure, or a counter-adaptive force is responsible for the observed discrepancy between T_b and optimal temperatures in *Lacerta vivipara* (and other lizards) will require the investigation of interindividual variation in thermal physiology, heritability-estimates for temperature-curve-characteristics and estimating fitness (components) for animals with known thermal characteristics in natural conditions.

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