

Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta*

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Summary. We studied, in the field and laboratory, aspects of the thermal biology in two populations of the lizard *Podarcis tiliguerta* along a 1450 m altitudinal gradient. Body temperatures (T_b) at high altitudes average lower, are more variable, but are more elevated above environmental temperatures than at sea level. Lizards partially reduced the impact of altitudinal changes in thermal loads through presumable subtle behavioural adjustments. A comparison of the thermal preferences in the laboratory, the maximum operative temperatures predicted from a biophysical model, and the activity T_b's at both sites, indicates that the main response to changing environmental conditions is an active shift in thermoregulatory set points. Integration of field T_b's and laboratory data on temperature specific sprint speeds, predicts that the mountainous lizards experience reduced running abilities that are especially acute in the early morning. Despite this impairment of running performance, the thermal sensitivity of running speed has not evolved to match the T_b's experienced by both populations. This result supports the view that the thermal physiology of this lizard is evolutionarily conservative, but the lack of information on the relation between running performance and fitness components impedes rejection of alternative hypotheses.

Key words: Thermal biology – Altitudinal variation – *Podarcis tiliguerta*

Active reptiles attempt to maintain their body temperature between lower and upper threshold temperatures (Berk and Heath 1975; Barber and Crawford 1977) and rely primarily on behavioural adjustments to buffer short term variation in environmental heat loads (Avery 1982; Huey 1982). The resulting body temperatures directly affect physiological and whole-animal performances (Huey and Stevenson 1979) such as growth rate (Licht et al. 1969; Avery 1984), digestion (e.g. Harlow et al. 1976; Harwood 1979; Stevenson et al. 1985), predation success (Greenwald 1974; Avery

et al. 1982) and running speed (e.g. Bennett 1980; Hertz et al. 1983; Crowley 1985; van Berkum 1986, 1988). The ecological consequences of activity at suboptimal temperatures have been demonstrated by Christian and Tracy (1981), who found a clear relation between body temperature and abilities to evade hawk predation by hatchling Galapagos land iguanas.

Lizards may respond in several ways to long-term (geographical, seasonal) changes in thermal environments. Behavioural adjustments are generally considered as the primary compensatory mechanism. Such regulatory behaviours include habitat shifts (Clark and Kroll 1974; Huey and Webster 1976; Hertz 1981; Hertz and Huey 1981; Christian et al. 1983), changing times of activity (Huey and Pianka 1977; Hertz 1981; Hertz and Huey 1981; Hertz and Nevo 1981; Van Damme et al. 1987) and increasing basking intensity (Huey and Webster 1976; Hertz 1981; Hertz and Huey 1981; Hertz and Nevo 1981; Van Damme et al. 1987). Behavioural shifts may however not be entirely effective in buffering differences in thermal loads, or they could be too costly in terms of time and energy expended (Huey and Slatkin 1976). An ectotherm can then alter the regulatory set-point temperatures (Christian et al. 1983) or even abandon thermoregulation (Huey 1974; Huey and Webster 1976; Hertz and Huey 1981). If such responses result in reduced physiological capacities, selection should favour a shift in the physiological optimum temperatures to restore performance levels (Hertz et al. 1983; Huey and Bennett 1987).

The importance of each of these regulatory responses (behaviour, shifts in regulatory set-points, physiological adaptation) can be examined by comparing the thermal biology of organisms living in thermally distinct habitats. Conspecific lizard populations occurring along altitudinal gradients offer an excellent opportunity to tackle the problem.

Here we consider responses to variation in the thermal environment in two populations of the lacertid lizard *Podarcis tiliguerta* along a 1450 m altitudinal gradient. We examine variation induced by differential thermal regimes in: 1) regulatory behaviours; 2) thermal preferences (selected body temperatures in a laboratory thermogradient) and optimum temperatures of running performance; 3) constraints imposed by the physical environment in achieving these temperature levels; 4) body temperatures maintained in the field; and 5) predicted sprint performances, obtained through integrating data on activity body temperatures and on the temperature dependence of sprint speed. We discuss

the relevance of our results to questions on the extent of thermal physiology evolution (Hertz et al. 1983; Crowley 1985; van Berkum 1986, 1988; Huey and Bennett 1987).

Material and methods

Anima Is

Podarcis tiliguerta is a small (adult body size: 45-65 mm; mass: 2-6 g), agile, diurnal, insectivorous wall lizard that is endemic to the Mediterranean islands Corsica and Sardinia and some adjacent smaller islets. *P. tiliguerta* is the most ubiquitous lizard on Corsica, where dense populations can be found in a wide range of habitats from sea-level up to more than 1800 meter. It is a shuttling heliotherm, that is partially ground-dwelling and partially saxicolous, using boulders, rocks, stone piles and staple-walls as basking and perching sites.

Field study

We studied lizards at two locations on Corsica that are ca 50 km apart. The first is situated ca 5 km SW of Calvi (42°32'N, 8°43'E; département Haute-Corse, France), at elevations 0-70 m, between the shoreline and the coastal road between Calvi and Galeria. This site is an unkempt meadow with small rocky outcrops, stone piles, stone walls and several small ruins standing scattered over the area. Vegetation consists mainly of grasses and small herbal plants, some shrubs (*Rubus sp.*, *Cistus criticus*, *C. monspeliensis*) and trees (*Pistacia lentiscus*, *Quercus ilex*). The site is surrounded by typical Corsican maquis. *P. tiliguerta* shares this habitat with the congeneric wall lizard *P. sicula*, the secretive little lizard *Algyroides fitzingeri*, two geckos (*Tarentola mauritanica* and *Phyllodactylus europaeus*) and the predatory snake *Coluber viridiflavus*, that was frequently observed here.

The second study plot is situated near the ski-centre Haut-Asco (42°25' N, 8°55' E; département Haute-Corse, Corsica, France), at 1450 m altitude. We sampled a SE-exposed hillside with vegetation consisting of grassy strips that alternate with large patches of dwarf-scrubs (*Juniperus nana*, *Genista labelli*). The site is scattered with seedlings of *Pinus nigra*, granite boulders and stones, rocky outcrops, stone piles and some (wooden) build ings. *P. tiliguerta*, which was present here in remarkably higher densities than at the Calvi-site, was the only lizard encountered. The snake *C. viridiflarns* was seen occasionally.

We sampled each of both sites during 7-10 days in May 1988. Data were collected between 7.30-18.00 h (Mean European Time) covering the entire daily activity period of *P. tiliguerta* at that time of the year. We randomly walked the study areas and captured active adult lizards (body size >45 mm) with a noose. We immediately measured body (cloaca!, = T_b), air (shaded bulb, = 3 cm above substrate, = T_a) and substrate temperatures (shaded bulb, = T) to the nearest 0.1°C with a thermocouple connected to a quick-reading electronic thermometer (DGT Digital thermometer). We also noted time of day, sex, weather conditions (sunny, cloudy/variable - either 5 or < 5 min of continuous sunshine before observation), amount of solar radiation at the spot of first sighting (full sun, sun filtered by vegetation, shade, overcast), whether or not the lizard was basking, and microhabitat characteristics. Microhabi-

tats were characterized by three parameters: substrate type (stony, vegetation, gravel, wood), perch height (< 25 cm, 25-50 cm, 50-100 cm, > 100 cm), and transit distance to the nearest spot of deep shade (< 0.5 m, 0.5-1 m, 1-2 m, 2-5 m, > 5 m). Wind speed was measured with an electronic anemometer (DGT-100 thermo-anemometer; to nearest 0.1 m/s), at the spot where the lizard was noosed.

Additional meteorological data were taken at 2 min intervals during a 24 h period at each study site. We measured air temperatures in deep shade and in full sun at 150 cm above the ground with copper-constantan thermocouples. Photosynthetically active solar radiation (400-700 nm) was measured with a quantum sensor (LI-190SB, LI-COR Inc.). Measurements were taken and registered with a portable data-logger (Squirrel SQ 16 meter/logger, Grant Instruments Ltd.).

Maximal operative temperatures

For each T_b measured in the field, we calculated a corresponding "maximal operative body temperature" (T_{max}). This is the maximal temperature that theoretically can be attained under ambient environmental conditions, and was simulated assuming that the lizard was in full sun and oriented so that it maximized solar radiation input. As the estimation of the maximal operative temperature assumes that the animal is in steady state with its environment and maximizes heat gains, the T_{max} values were estimated only for lizards that were captured during sunny weather.

Estimates were obtained by solving the steady-state energy balance equation of Tracy (1982) for body temperature. Air temperature was estimated by the measured T_a . Radiation flux density at the data and time of capture was calculated as described in McCullough and Porter (1971). The amount of solar radiation absorbed by the lizard was estimated as in Campbell (1977), using geometrical formulae for horizontal cylinders to calculate body areas exposed to radiation (Monteith 1973) and a short wave absorption coefficient equal to 0.84 (Knötig 1964). Thermal radiation was computed from the Stefan-Boltzmann equation (Tracy 1982). Convection was estimated as in Roughgarden et al. (1981), using the field measured wind velocity values. Metabolic heat production, evaporative heat loss and conductive heat flow were considered to be negligible (Muth 1977; Porter et al. 1973; Tracy 1982).

As our calculations of T_{max} are based on indirect estimates of radiation intensity, results should be regarded as crude estimates. Accordingly, our aim was not to obtain accurate estimates for each corresponding T_b -measurement, but rather to detect general patterns in the temperatures that lizards can attain.

Selected body temperatures

On 6 June 1988, 15 freshly caught males from each population were flown to the Field Biological Station at Kalmthout, Belgium. The lizards were housed in terraria (0.5 x 1.0 m) that were filled with sand, stones and grasses. No more than three lizards were placed in the same terrarium. A 150 W lightbulb was suspended above one end of the terraria, producing a gradient of air temperatures ranging 18-55°C. Food (house crickets, meal worms and fly larvae) and water were provided ad libitum.

We measured body temperatures of active lizards in the

terraria, with a minimum time interval of one hour between two measurements, using the same thermometer as that in the field. These T_b -readings were considered as estimates of selected or "preferred" body temperatures. We assume that selected body temperatures represent the temperatures that lizards would attempt to achieve in the field in the absence of physical and biotic restrictions (Licht et al. 1966).

Thermal sensitivity of sprint speed

Sprint speed seems an ecologically relevant process (Huey and Stevenson 1979) in *P. tiliquerta*, as it frequently uses quick short dashes to capture prey and to escape from (human) predators.

We examined thermal sensitivity of sprint speed in males from both populations that had been transported to our laboratory. Lizards selected for this experiment had intact or completely regenerated tails and were matched for body size (Calvi: $x=58.4$, $SD=1.8$, $n=9$; Haut-Asco: $x=59.9$, $SD=2.0$, $n=10$, t -test, $P>0.1$). We measured sprint speed at a fixed sequence of body temperatures (32.5, 25, 37.5, 35, 20, 27.5, 30°C) on a race track similar to those described by Bennett (1980) and Huey et al. (1981). Body temperature of lizards was controlled by placing them in an incubator at the appropriate test temperature during at least 1 h. Subsequently we chased an individual lizard down the track by hand. Nine pairs of photocells measured the time intervals needed to cover eight consecutive 0.25 cm intervals. Each lizard was tested three times per temperature, with a 1 h rest between races and a maximum of three trials a day. From the three trials at each body temperature, the fastest 0.5 m interval was selected and considered as the maximum sprint speed for that individual at that temperature.

After completion of the running experiment, we determined the critical thermal maximum (CT_{Max}) for 5 lizards from each population, as an estimate of the upper temperature for which locomotion is possible. Animals were heated continuously in an incubator while we observed their behaviour. The body temperature associated with a loss of right-

strom 1971).

ing response was used as an indicator of CT_{Max} (Bratt-

We used the procedure outlined by van Berkum (1986)

to obtain estimates, for each individual lizard, of the optimal body temperature for sprinting (temperature at maxi-

mal speed, = $T_{(p)}$) and of the 80% and 95% performance breadths (body temperature ranges over which speed is, respectively, at least 80% or 95% of its maximum).

Results

Diurnal variation in air temperatures and solar radiation at both sites during a predominantly sunny day in May is depicted in Fig. 1. Differences in air temperatures between the two locations were clear-cut. Solar radiation was somewhat higher in Haut-Asco, but during the afternoon the sun often became obscured by clouds and disappeared behind the mountain ridge at ca 16.30 h.

Thermoregulatory behaviours

The number of lizards captured per hour in both populations is shown in Fig. 2. At sea-level (Calvi), the hourly

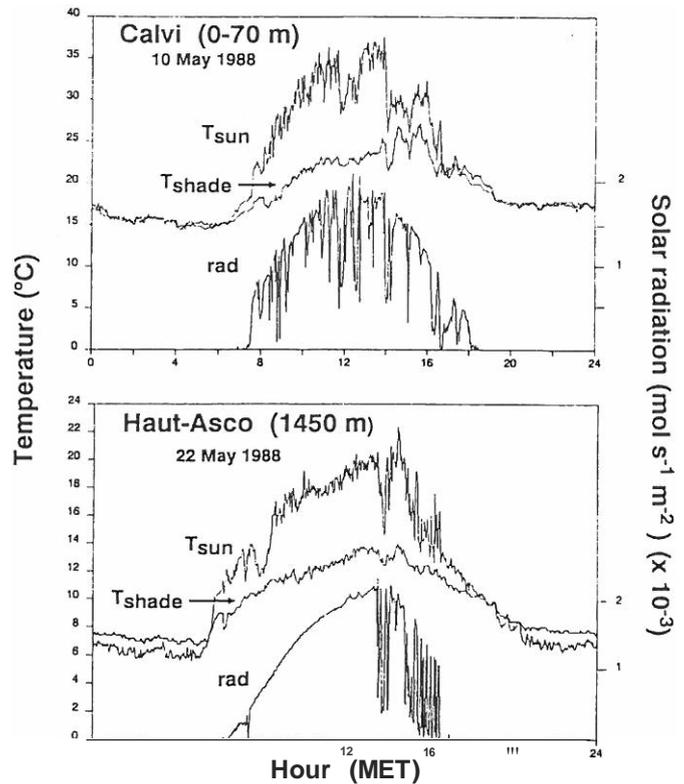


Fig. 1. Air temperatures in sun (T_{sun}) and shade (T_{shade}) and intensity of photosynthetically active solar radiation (rad) for a typical day during May at each of both study sites

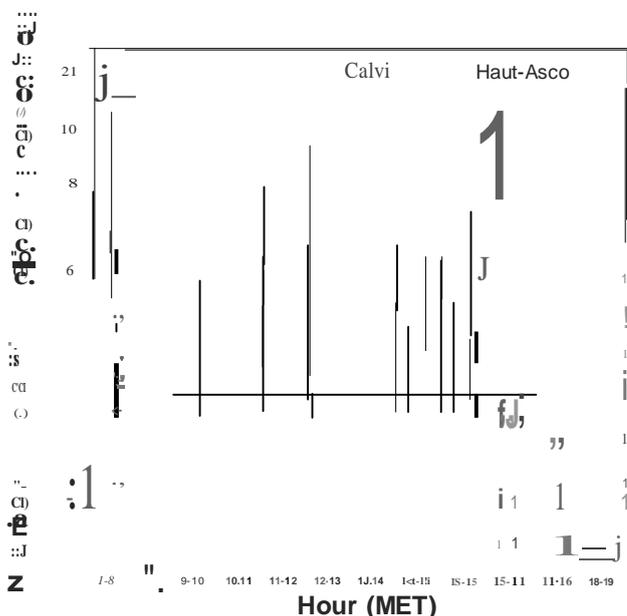


Fig. 2. Number of lizards captured per person hour at different times of day in both study areas

number of lizards captured exhibited a typical unimodal pattern, with more lizards active during the warmer hours. In the mountainous population, activity started and ceased rather abruptly. Activity times during the afternoon were restricted due to the early disappearance of the sun behind the mountain rim. The high number of animals caught immediately after 'sunrise' (i.e. when sunshine reaches the study site, see Fig. 1) may partly reflect increased catchability. Nevertheless, it was obvious that during early morning more lizards were active in the mountainous population than at the lowland site. Overall, the number of lizards

Table 1. Frequencies of lizards observed on different substrate types, perch height (cm) classes and transit distances (m) to nearest spot of deep shade. Data for periods of uninterrupted sunshine only

Substrate:	Stony	Vegetation	Gravel	Wood	
Calvi (0-70 m)	98	4	0	0	
Haut-Asco (1450 m)	104	8	11	7	
Height:	<25	25-50	50-100	>100 cm	
Calvi	32	21	28	10	
Haut-Asco	65	16	3	6	
Distance to shadow:	<0.5	0.5-1	1-2	2-5	>5 m
Calvi	89	3	4	3	3
Haut-Asco	98	2	10	10	10

captured per hour was distinctly highest at the high altitude area (Fig. 2). This probably reflects higher lizard abundance, higher visibility and a lower wariness of the lizards.

When weather conditions changed from sunny to cloudy, and when the sun disappeared in the afternoon, lizards initially remained exposed on stony substrates in a basking-like posture. Within one hour, most retreated to shelter. Lizards at the lowland site seemed to retreat faster than the high-altitude lizards, despite the more adverse ambient temperatures at the latter site.

At both sites, the vast majority of lizards was seen on stony substrates (Table 1). The difference in substrate use between locations ($G = 23.103.3$ df, $P < 0.001$) can be attributed to the variable number of observations on gravel and wood, substrate types that were not available at the low-elevation site. Perch height distributions also differed: in Haut-Asco, a larger proportion of lizards was active near ground level ($G = 37.380$, 4 df, $P < 0.001$, Table 1). The lower perch heights at high altitude can, at least partly, be attributed to the absence of stone walls at that site; these habitats were the lizards' favourite perching and basking sites at sea-level. Although relatively less high altitude lizards were found in the immediate neighbourhood of shade (Table 1), the difference between sites was not significant ($G = 7.857$, 4 df, $P > 0.05$).

All mountainous lizards ($n = 130$) and most (97% of $n = 102$) individuals seen in the lowland area during sunny weather, were in full sun when first sighted. The proportion

of lizards seen basking showed typical U-shaped patterns during the course of the day in both populations. The overall proportion of basking lizards was similar in both populations (Calvi: 50%, Haut-Asco: 46%, $G = 0.394$, 1 df, $P > 0.50$).

Body and air temperatures

We found no differences in T_b 's between males and females at either of both sites (two-way ANOVA: $P > 0.10$) and therefore lumped data for further analyses. As was to be expected in an heliothermic lizard, availability of sunshine has a profound effect on T_b in both populations (Table 2). To reduce the effect of short-term variations in weather conditions, we will only consider sunny weather data in subsequent analyses.

Body temperatures of high altitude lizards were significantly lower and more variable than in the low elevation population (Table 2). Mean T_b and T_a were also significantly lower at high elevations. No differences in wind speed between locations were evident (Table 2).

Slopes of regression lines of T_b on T_a were remarkably similar in the two populations ($b = 0.31$ in both cases) and significantly smaller than 1 ($P < 0.001$). The mean difference between T_b and T_a was highest at the high altitude site (Table 2), indicating that T_b was high relative to T_a at the cooler site.

In both populations T_b varied with time of day (ANOVA: Calvi: $P = 0.03$; Haut-Asco: $P < 0.001$; Fig. 3). This variation is most apparent at the high elevation site.

Maximal operative temperatures

Our estimates (Table 2) reveal a considerable altitudinal variation in maximal operative temperatures. At sea level, $T_{m'}^o$ -values were close to, or exceeded the critical thermal maximum (see Table 4) during most of the day (Fig. 3). Hence, it is not surprising that measured body temperatures were well below the predicted maxima. In the mountainous populations, mean T_b 's closely approached mean values of T_{max} during the early morning hours (Fig. 3). During the rest of the day, field T_b 's were well below the theoretical maxima, although the latter seldom exceeded the critical level. It should be noted that during most of the day, $T_{m'}^o$ -values at the high altitude site were above T_b 's recorded in the lowland population. Hence, physical factors alone

Table 2. Statistics (mean \pm 1 SE, range in parentheses, sample size) of body (T_b), air (T_a), substrate (T_s) and maximal operative temperatures ($T_{m'}^o$) ($^{\circ}C$) and wind speed (m/s) recorded at both field sites and selected body temperatures (T_{cl}) in a laboratory thermogradient. Data for sunny weather samples only, except where indicated

	Field study							Thermogradient
	T_b (cloudy)	T_b	T_s	T_s	wind	$T_b - T_a$	$T_{m'}^o$	T_{cl}
Calvi (0-70 m)	30.20 \pm 0.55 (23.6-36.8) 31	34.02 \pm 0.29 (25.7-39.2) 102	23.58 \pm 0.29 (17.9-32.2) 102	27.17 \pm 0.35 (18.7-37.3) 102	0.46 \pm 0.05 (0.0-2.7) 102	10.44 \pm 0.34 (1.4-17.5) 102	43.19 \pm 0.33 (34.4-51.9) 102	35.47 \pm 0.20 (33.0-38.2) 40
Haut-Asco (1450 m)	25.42 \pm 0.46 (20.3-32.1) 39	30.51 \pm 0.34 (21.5-37.5) 130	15.06 \pm 0.26 (8.0-23.5) 130	22.01 \pm 0.45 (11.5-37.0) 130	0.48 \pm 0.04 (0.0-1.9) 130	15.75 \pm 0.38 (5.0-24.6) 130	35.28 \pm 0.40 (25.0-44.7) 130	35.50 \pm 0.17 (32.7-38.4) 56
P means	<0.001	<0.001	<0.001	<0.001	>0.05	<0.001	<0.001	>0.05
P variances	>0.05	<0.001	>0.05	<0.001	>0.05	>0.05	<0.001	>0.05

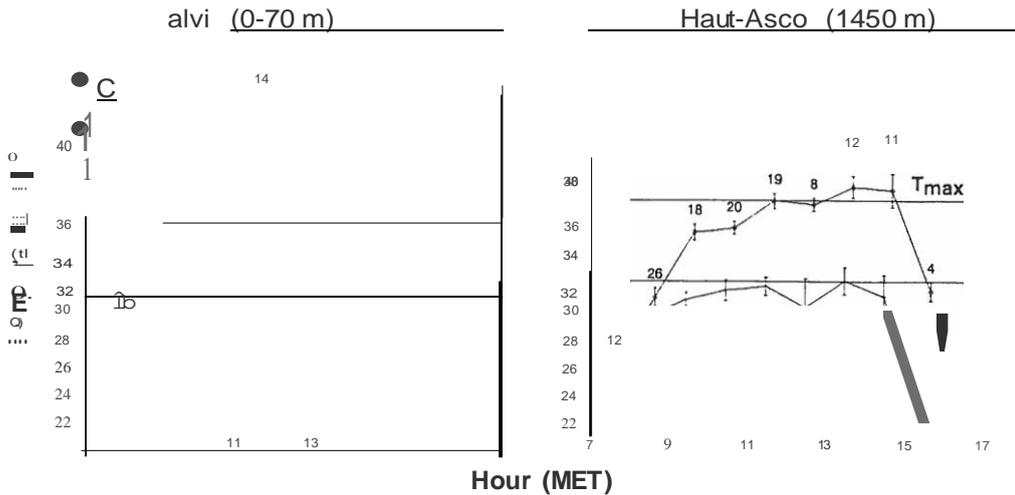


Fig. 3. Body temperatures (T_b) and predicted maximal operative temperatures (T_m'') at different times of day in both study areas. Shown are mean values (± 1 SE) and sample sizes. The stippled area depicts the range of selected body temperatures

Table 3. Sprint speeds (m/s) at various body temperatures ($^{\circ}$ C) of lizards from both study areas. Values are means ± 1 SE

	Body temperature							N
	20	25	27.5	30	32.5	35	37.5	
Calvi (0--70 m)	1.16 \pm 0.09	1.74 \pm 0.12	2.11 \pm 0.15	1.99 \pm 0.14	2.19 \pm 0.22	2.16 \pm 0.16	2.49 \pm 0.19	9
Haut-Asco (1450 m)	1.07 \pm 0.05	1.66 \pm 0.05	1.82 \pm 0.08	1.78 \pm 0.09	1.90 \pm 0.09	2.21 \pm 0.10	2.34 \pm 0.11	10

Table 4. Parameters of thermal sensitivity of sprint speed in both populations: optima! temperature (T_{0p}), the 95% and 80% performance breadths (B95, B80) and their lower limits (L95, L80), and critica! thermal maxima (CTMax) ($^{\circ}$ C). Values are means ± 1 SE

	B95	L95	B80	L80	N	CTMax	N
Calvi (0--70 m)	35.5 \pm 1.1	6.1 \pm 1.1	32.4 \pm 1.3	12.9 \pm 1.0	9	42.4 \pm 0.3	5
Haut-Asco (1450 m)	36.3 \pm 0.7	5.8 \pm 1.0	33.4 \pm 1.1	12.4 \pm 1.2	10	43.0 \pm 0.4	5

do not impede the maintenance of similar temperatures at both sites.

Selected body temperatures

Body temperatures selected in the thermal gradient, were similar for lizards of both populations (Table 2). A comparison of field T_b 's recorded during sunny weather with selected body temperatures, reveals that the proportion of T_b 's that fell within the selected body temperature range, was significantly higher at high elevations (66%) than in the lowland area (42%) ($G=12.581$, 1 df, $P<0.001$).

Thermal dependence of sprint speed

A two way ANOVA showed significant effects of temperature ($P<0.0001$) and of sampling location ($P=0.02$) on absolute sprint speed. High altitude lizards consistently had the lowest sprint velocities (Table 3). There was no significant temperature \times site interaction effect, indicating that temperature sensitivity curves for sprint speed are similar in both populations. Accordingly, parameters derived of the sprint performance curves (Table 4) showed no significant differences between the two populations (Hest, all $P>0.1$).

We integrated results of temperature dependence of sprint speed with field data to assess the effects of observed geographical differences in T_b 's on locomotor performance. We calculated absolute and relative (% of maximal) speed of each individual raced in the laboratory, at each of the T_b 's recorded at its site of origin and then averaged performances among individuals. Resulting distributions of predicted performances at both study sites are shown in Fig. 4.

At sea level, virtually all lizards (98%) had T_b 's allowing them to run at 80% of their maximal speed; most (82%) of the recorded T_b 's were associated with speeds within 10% of their maximal capacity (Fig. 4). In the mountainous population, a considerable proportion (35%) of the active lizards were predicted to run at <80%, some at only 50% of their maximal speed. At this site, we separately considered the T_b 's recorded after 9.00 h, when estimates of T_m'' were within the selected temperature range. During this period, most lizards (81%) ran at 80% of their maximal capacity (Fig. 4).

Differences between sites in absolute speeds were even more pronounced (Fig. 4): the high elevation lizards did not achieve the predicted modal speed of their lowland conspecifics! In short, the mountainous lizards experience reduced sprint speeds, because they are often active at temperatures that reduce sprint capacity, and because they have lower maximal velocities at each body temperature.

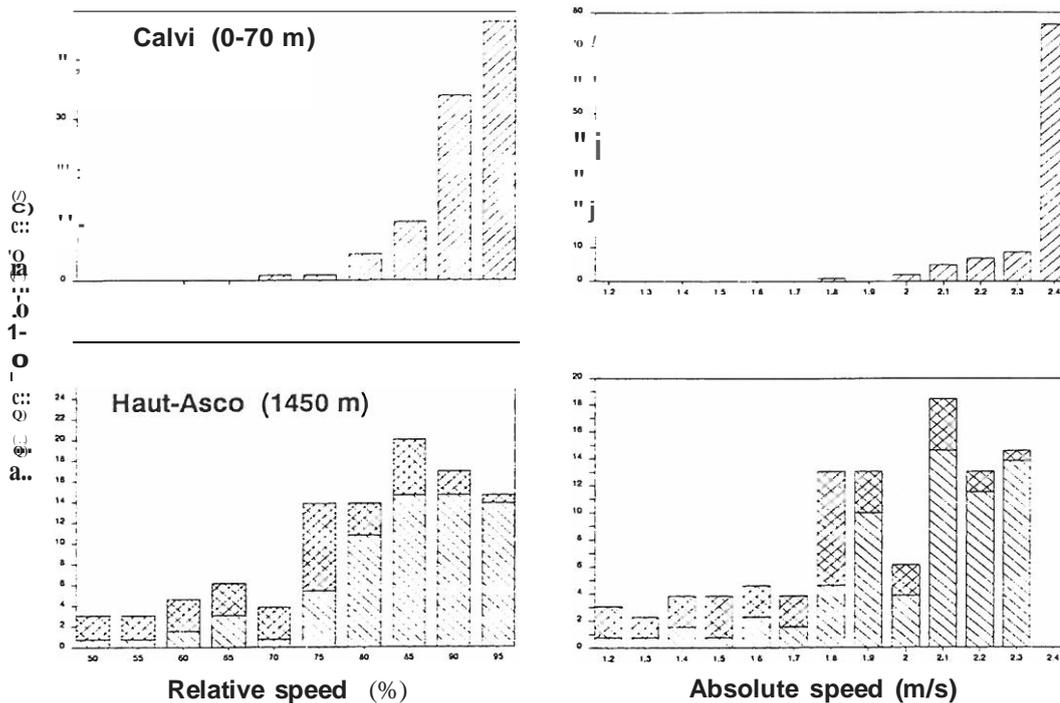


Fig. 4. Distributions of predicted relative (% of maxima!) and absolute sprint speeds of *Podarcis tiliguerta* at both study sites. For the Haut-Asco population, speeds predicted to occur before (*crossed*) and after 09.00 h (*hatched*) are given separately (see text for explanation)

Discussion

The most pronounced changes in thermal environmental with altitude were a decrease in air temperature and a reduction of the daily duration of direct solar insulation. The first is a general feature of high altitude locations (McCullough and Porter 1971), the second is attributable to peculiarities of local topographical and meteorological conditions.

In many lizards, behavioural shifts are the primary mechanism that compensate for geographical (and seasonal) changes in thermal environments (Hertz and Huey 1981; Hertz and Nevo 1981; Huey 1982). Such compensatory behaviours include selection of more open habitats, restriction of activity times and a more frequent use of regulatory behaviours (see references in Introduction). *P. tiliguerta* exhibited surprisingly few conspicuous behavioural shifts. Observed differences in microhabitat use were small and possibly induced by differential microhabitat availability. Both study areas, which differed in the presence of structural elements such as trees, shrubs and stone-walls, were open sites where large sunlit patches were readily available. We definitely did not observe an obvious shift to open habitats, such as that exhibited by other lizards as a response to lower temperatures at high elevations (Burns 1970; Huey and Webster 1976; Hertz 1981; Hertz and Huey 1981).

Main differences in activity rhythms were the early afternoon retreat and the early morning emergence of the high elevation lizards. The latter implies, as evidenced by estimates of T_{mw} that they temporarily exposed themselves to suboptimal thermal conditions. Hence lizards at the lowland site, but not in the mountainous population, restricted their activity to times when ambient conditions enabled the achievement of body temperatures near selected or optimal

levels. This result contrasts common expectations (Hertz and Huey 1981; Huey 1982). The relative number of lizards observed basking, a crude index of the time invested in behaviours that tend to increase T_b , did not differ with altitude.

In short, we are unable to document obvious behavioural shifts that may compensate for changes in the thermal environment. This however does not imply that compensatory behaviours were absent. High altitude lizards maintained T_b 's that were more elevated above ambient temperatures; precision of thermoregulation, as indexed by the regression slope of T_b on T_o was similar in both populations. We infer from these results that lizards partially reduced the impact of thermal conditions by subtle behavioural adjustments which remained unquantified by us.

The main response to changing environmental conditions seems to be an active shift in the set points of thermoregulation. This interpretation is based upon a comparison of the lizards' thermal preference in the laboratory, the maxima! operative temperatures and the actual activity body temperatures at both study sites. The similarity of selected body temperatures indicates that, in the absence of physical and biotic restrictions, lizards from both populations regulate their T_b between identical upper and lower set points. Estimates of T_{max} predict that climatic conditions at sea-level enable lizards to maintain T_b 's near selected levels throughout the daily activity period. Accordingly, a considerable proportion of the T_b -readings were within the selected range. At the mountainous site, physical factors prevented the attainment of selected temperatures during the early morning hours. The close agreement between T_b 's and maxima! operative temperatures during this interval indicates that lizards maintain body temperatures as high as it physically possible. During the rest of the day, the

high altitude lizards could theoretically achieve their selected temperatures, but they were most often active at lower T_b 's. Geographic differences in body temperatures therefore appear to represent an active shift in regulation rather than a purely passive result induced by differences in thermal regimes.

Following, not mutually exclusive hypotheses can explain this regulatory response. First, achievement of selected temperature levels by the high altitude lizards is possible only at the expense of considerable investment in thermoregulatory behaviours. We adopt this assertion because T_{max} -values were simulated assuming that the lizard remained fully exposed to solar radiation. Regulation of their T_b near T_{mm} within the selected range, would therefore seriously reduce the time available for other important activities, and seems not feasible within the actual ecological context (Huey and Slatkin 1976; Huey 1982).

It may also be suggested that the high altitude lizards regulate at lower T_b 's in order to maximize the daily period during which they can maintain a constant body temperature (Christian et al. 1983). At high elevations, lizards can achieve their selected temperatures only for a relatively short period of the day (::::: 6 h, Fig. 3). By regulating at a temperature slightly below the selected level, they can increase the number of hours (::::: 7-8 h) during which they can maintain their T_b constant.

To what extent does the observed geographic shift in T_b 's influence sprint performance of active lizards? In the lowland population, the vast majority of T_b -readings were associated with high (> 90%) relative running capacities. The mountainous lizards accepted activity at much lower performance levels. Major running impairments were however predicted to occur primarily during the early morning hours, when physical factors impede attainment of higher body temperatures. During the rest of the day, most lizards were active at T_b 's that enabled them to run at 80% of their maximal capacity. These lizards hence seem to shift thermoregulatory set-points to a level associated with a rather limited decrease in running performance, at least when the physical environment does not inhibit them of doing so. This regulatory zone is supposed to be a compromise between minimizing the risks associated with a decreased performance and maximizing the time available for non-thermoregulatory activities and/or the period during which T_b can be maintained constant.

Our results bear some relevance to discussions on the extent of evolutionary change of thermal physiology in ectotherms. Two conflicting opinions have been identified by Hertz et al. (1983). The "labile" view states that when environmental conditions induce a shift in activity body temperatures, parallel changes in thermal optima should readily evolve. Partial coadaptation between activity body temperatures and thermal optima has indeed been documented through interspecific studies of anoline (van Berkum 1986) and scincid lizards (Huey and Bennett 1987). The antagonistic "static" view claims that thermal physiology is evolutionary inert and resistant to directional selection. Support has been provided by Hertz et al. (1983) and Crowley (1985), who found no differences in the thermal sensitivity of locomotor performance among conspecific lizard populations inhabiting thermally distinct habitats.

We have shown that, in our mountainous population, the maintenance of T_b 's near the optimal range is temporarily impossible and costly during most of the day. Assuming

that running speed influences foraging success (Greenwald 1974; Avery et al. 1982) and/or probabilities to evade predation (Christian and Tracy 1981), the estimated impairment of running abilities in our mountainous lizards seems large enough to have important ecological consequences. In fact, the reduction in relative speed experienced by high altitude *P. tiliguerta* is larger than that estimated for other high elevation lizard populations (Hertz et al. 1983; Crowley 1985; van Berkum 1986). Still, we found no geographic differences in sprint performance curves. Hence, physiological adaptation to different thermal regimes, at least with reference to running abilities, is absent in *P. tiliguerta*.

This result supports the static view of thermal physiology, but at the same time it does not falsify the labile hypothesis. Rejection of the latter view requires actual demonstration of an adverse effect of locomotor impairment on fitness or, in other words, that differences in running performance constitute a "fitness gradient" (Arnold 1983). Our data do not address this issue, but we may consider why there could be no direct connection between performance and fitness.

First, high altitude *P. tiliguerta* were predicted to exhibit a serious locomotion handicap during only a portion of the day, at least during May. This daily interval may be extended at the onset of the activity season (April), but is probably more restricted during summer. The total annual duration of this period could be too short to induce a significant decrease in fitness.

Second, physiological performance (running speed) and ecological performance (foraging and escape success) probably do not scale directly (Huey and Stevenson 1979). Consequences of differential velocities would be levelled when large decrements in speed would be associated with only small changes in ecological performance. This assumption, however, seems counter-intuitive and examination of the few existing data (Huey and Stevenson 1979; Christian and Tracy 1981) suggests that the opposite is true: foraging and escape success scale positively to speed.

A complementary hypothesis is that the consequences of low speed are offset by compensatory behaviours, such as increased wariness (Rand 1964) or a shift in escape behaviours (Bauwens and Thoen 1981; Hertz et al. 1982; Crowley and Pietruzka 1983). We did not observe such behaviours, at least not in response to human predators. In contrast, lizards at the high altitude site were far less wary and easier to catch than the lowland lizards. Crowley (1985) describes remarkably similar experiences, in an identical context, with a phylogenetically distant lizard.

Third, the ecological relevance of high speed may vary between populations because of differences in selection pressures. If predation pressure at high altitudes is reduced and/or prey is more abundant or more easy to catch, maintaining high speeds might be less important there than at sea level (Crowley 1985). The observation that our mountainous lizards had reduced absolute velocities, accentuating the locomotor impairment induced by activity at suboptimal T_b 's, might indicate that selection on sprint speed is actually relaxed at high elevations. Also, in intraspecific studies of several lizard species have revealed considerable geographic variation in demographic parameters, reflecting proximate or adaptive responses to differential selection regimes (e.g. Tinkle and Ballinger 1972; Ballinger 1979; Dunham 1982; Ferguson et al. 1980).

The existence of physiological adaptation to environ-

mental conditions in a single lizard species still awaits demonstration. Success might depend upon the choice of performance traits that are subject to operative selective pressures at different localities (see also Hertz et al. 1983; van Berkum 1986). Selection and adaptation will only be fully understood when we estimate both the effects of physiological on ecological performance and of ecological performance on fitness (Bock 1980; Arnold 1983).

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References

- Arnold SJ (1983) Morphology, performance and fitness. *Am Zool* 23:347-361
- Avry RA (1982) Field studies of body temperatures and thermoregulation. In: Gans C, Pough FH (eds) *Biology of the Reptilia*. Vol. 12. Academic Press, London, pp 93-146
- Avry RA (1984) Physiological aspects of lizard growth: the role of thermoregulation. *Symp Zool Soc Lond* 52:407-424
- Avry RA, Bedford JD, Newcombe CP (1982) The role of thermoregulation in lizard biology: predatory efficiency in a temperate diurnal basker. *Behav Ecol Sociobiol* 11:261-267
- Ballinger RE (1979) Intraspecific variation in demography and life history of the lizard, *Sceloporus jarrovi*, along an altitudinal gradient in southeastern Arizona. *Ecology* 60:901-909
- Barber BJ, Crawford EC (1977) A stochastic dual-limit hypothesis for behavioral thermoregulation in lizards. *Physiol Zool* 50:53-60
- Bauwens D, Thoen C (1981) Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta viripara*. *J Anim Ecol* 50:733-743
- Bennett AF (1980) The thermal dependence of lizard behaviour. *Anim Behav* 28:752-762
- Berk ML, Heath JE (1975) An analysis of behavioral thermoregulation in the lizard *Dipsosaurus dorsalis*. *J Therm Biol* 1:15-22
- Berkum FH van (1986) Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution* 40:594-604
- Berkum FH van (1988) Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *Am Nat* 132:327-343
- Bock WJ (1980) The definition and recognition of biological adaptation. *Am Zool* 20:217-227
- Brattstrom BH (1971) Critical thermal maxima of some Australian skinks. *Copeia* 1971:554-557
- Burns TA (1970) Temperature of Yarrow's spiny lizard *Sceloporus jarrovi* at high altitudes. *Herpetologica* 26:9-16
- Campbell GS (1977) *An Introduction to Environmental Biophysics*. Springer, Berlin Heidelberg New York
- Christian KA, Tracy CR (1981) The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia* 49:218-223
- Christian K, Tracy CR, Porter WP (1983) Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (*Conolophus pallidus*). *Ecology* 64:463-468
- Clark DR, Kroll JC (1974) Thermal ecology of anoline lizards: temperate versus tropical strategies. *Southwest. Nat* 19:9-19
- Crowley SR (1985) Thermal sensitivity of spring-running in the lizard *Sceloporus umululatus*: support for a conservative view or thermal physiology. *Oecologia (Berl.)* 66:219-225
- Crowley SR, Pictruszk R D (1983) Aggressiveness and vocalization in the leopard lizard (*Gambelia 11isli=en11ii*): the influence of temperature. *Anim Behav* 31:1055-1060
- Dunham AE (1982) Demographic and life-history variation among populations of the iguanid lizard *Urosaurus omatus*: implications for the study of life-history phenomena in lizards. *Herpetologica* 38:208-221
- Ferguson GW, Bohlen CH, Woolley HP (1980) *Sceloporus 1111dula-111s*: comparative life history and regulation of a Kansas population. *Ecology* 61:313-322
- Greenwald OE (1974) Thermal dependence of striking and prey capture by gopher snakes. *Copeia* 1974:141-148
- Harlow HJ, Hillman SS, Hoffman M (1976) The effects of temperature on digestive efficiency in the herbivorous lizard, *Dipsosaurus dorsalis*. *J Comp Physiol* 111:1-6
- Harwood RH (1979) The effect of temperature on the digestive efficiency of three species of lizards, *Cnemidophorus tigris*, *Gerrhonotus multicarinatus* and *Sceloporus occidionalis*. *Comp Biochem Physiol* 63A:417-433
- Hertz PE (1981) Adaptation to altitude in two West Indian anoles (Reptilia: Iguanidae): field thermal biology and physiological ecology. *J Zool* 195:25-37
- Hertz PE, Huey RB (1981) Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. *Ecology* 62:515-521
- Hertz PE, Nevo E (1981) Thermal biology of four Israeli agamid lizards in early summer. *Isr J Zool* 30:190-210
- Hertz PE, Huey RB, Nevo E (1982) Fight versus flight: body temperature influences defensive responses of lizards. *Anim Behav* 30:676-679
- Hertz PE, Huey RB, Nevo E (1983) Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. *Evolution* 37:1075-1084
- Huey RB (1974) Behavioural thermoregulation in lizards: importance of associated costs. *Science* 184:1001-1003
- Huey RB (1982) Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough FH (eds) *Biology of the Reptilia*. Vol. 12. Academic Press, London, pp 25-91
- Huey RB, Bennett AF (1987) Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41:1098-1115
- Huey RB, Pianka ER (1977) Seasonal variation in thermoregulatory behavior and body temperature of diurnal *Chalcidophorus* lizards. *Ecology* 58:1066-1075
- Huey RB, Slatkin M (1976) Cost and benefits of lizard thermoregulation. *Quart 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
- Huey RB, Webster TP (1976) Thermal biology of *Anolis* lizards in a complex fauna: the *Cristate/1111* group on Puerto Rico. *Ecology* 57:985-994
- Huey RB, Schneider W, Eric GL, Stevenson RD (1981) A field-portable racetrack and timer for measuring acceleration and speed of small cursorial animals. *Experientia* 37:1356-1357
- Knötig H (1964) Energie-Bilanz eines Poikilothermen (*Lacerta nana*). *Helgol. wiss. Meeresunters* 9:261-273
- Licht P, Dawson WR, Shocmakr V H, Main AR (1966) Observations on the thermal relations of western Australian lizards. *Copeia* 1966:97-111
- Licht P, Hoyer HE, van Oordt PGWJ (1969) Influence of photoperiod and temperature on testicular recrudescence and body growth in the lizards *Lacerta sicula* and *Lacerta 11111ralis*. *J Zool* 157:469-501
- McCullough EC, Porter WP (1971) Computing clear day solar radiation spectra for the terrestrial ecological environment. *Ecology* 52:1008-1015
- Montei th J L (1973) *Principles of Environmental Biophysics*. E. Arnold Publ. London

- Muth A (1977) Thermoregulatory postures and orientation to the sun: a mechanistic evaluation for the zebra-tailed lizard, *Callisaurus draconoides*. *Copeia* 1977:710-720
- Porter WP, Mitchell JW, Beckman WA, DeWitt CB (1973) Behavioral implications of mechanistic ecology. Thermal and behavioral modeling of desert ectotherms and their microenvironment. *Oecologia* 13:1-54
- Rand AS (1964) Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology* 45:863-864
- Roughgarden J, Porter WP, Heckel D (1981) Resource partitioning of space and its relationship to body temperature in *Anolis* lizard populations. *Oecologia* 50:256-264
- Stevenson RD, Peterson CR, Tsuji JC (1985) The thermal dependence of locomotion, tongue-flicking, digestion, and oxygen consumption in the wandering garter snake. *Physiol Zool* 58:46-57
- Tinkle DW, Ballinger RE (1972) *Sceloporus undulatus*: a study of the intraspecific comparative demography of a lizard. *Ecology* 53:570-584
- Tracy CR (1982) Biophysical modeling in reptilian physiology and ecology. In: Gans C, Pough FH (eds) *Biology of the Reptilia*. Vol 12. Academic Press, London, pp 275-321
- Van Damme R, Bauwens D, Verheyen RF (1987) Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara*. *Herpetologica* 43:405-415