BODY TEMPERATURES OF CAPTIVE TORTOISES AT HIGH ALTITUDE IN ZIMBABWE, WITH COMMENTS ON THE USE OF "LIVING MODELS"

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It is difficult to devise physical models which precisely mimic the body temperatures (T_b's) of large reptiles in the field. Studies of large reptiles have the compensating advantage that individuals can be followed for long periods, so that translocated individuals can be used as 'living models'. We compare T_b's of two tortoise species in an enclosure in Harare (altitude 1500 m) with those in the field at Sengwa (900 m), where mean air temperatures were about 5°C higher. *Kinixys spekii*, which occurs naturally near Harare, had similar T_b's at the two sites (means 27.6 and 27.0°C, respectively). *Geochelone pardalis* had significantly lower T_b's in Harare (29.1°C) than at Sengwa (32.6°C), even though activity was shifted towards midday in Harare. The inability to reach high T_b during activity may explain the absence of *G. pardalis* near Harare, and the distribution of this species in southern Africa.

INTRODUCTION

Physical models of reptiles can be used to estimate body temperatures (T_b's) in different locations and thus to describe the thermal environment available to an animal (Beaupre, 1995). The use of models to estimate T_b's is difficult in species of large body size, in which thermal inertia and physiological thermoregulation become important factors. Hollow metal models painted to match the absorptivity of the live animal have been used to measure the operative temperatures (T_e's) of chelonians (Crawford, Spotila & Standora, 1983; Ellner & Karasov, 1993). The time constants of such models are, however, much lower than those of living animals; models of *Pseudemys scripta* had time constants of 1-2 mins (Crawford *et al.*, 1983), compared to 100-200 mins for living chelonians of comparable size (Hailey & Loveridge, 1997). Even the solid metal models used by Zimmerman *et al.* (1994) showed much faster temperature responses than tortoises. The T_e of a metal model is essentially an instantaneous measure of the potential heat load on an animal, and will only be equal to T_b in equilibrium conditions (Bakken, 1992), which are probably infrequent in active reptiles.

Models incorporating thermal inertia are required to estimate T_b's of large reptiles, but the physiological thermoregulation of these animals (Bartholomew, 1982) presents another difficulty. The water-filled carapaces of *K. spekii* used by Hailey & Coulson (1996a) only heated at half the rate of living animals, even though they had the same surface characteristics. The difference in heating rates was probably due to physiological thermoregulation, which enables live tortoises to heat faster than they cool (Voigt & Johnson, 1977; Els, Erasmus & Winter, 1988). The bottle models of Hailey & Coulson (1996b) heated at the same rate as tortoises in hot radiant conditions, but are likely to have reached higher equilibrium temperatures due to the high absorptivity of black paint (Crawford *et al.*, 1983). These models would not give good estimates of T_b's on cool days, when equilibrium temperatures are important (Hailey & Coulson, 1996a). A particular model can therefore be designed to simulate T_b's only in some conditions, which complicates comparisons between different environments.

Although it is difficult, perhaps impossible, to estimate T_b's of large reptiles accurately using passive physical models, large body size has the advantage that individuals can be followed for long periods by radio tracking or thread trailing, and their T_b's measured by telemetry. This gives the possibility of using translocated animals as 'living models' to assess thermal constraints in different environments, in particular whether T_b can be maintained at the original level by a change in activity period, and if so whether the time available for activity is reduced. As an example, we compare body temperatures of two species of tortoise at an altitude of 1500 m, where only one occurs naturally, with those measured in the wild at a lower altitude.

METHODS

This study used 35 adult *Kinixys spekii* (mean mass 0.7 kg) of both sexes and nine adult female *Geochelone pardalis* (4 kg), each of which was given a unique mark by sawing the edges of the marginal scutes. Tortoises were kept in a large enclosure (100 m²) at the University of Zimbabwe, containing both tall and short grass and some small trees, and provided brassica leaves as additional food. Both *K. spekii* and *G. pardalis* occupy a variety of vegetation types at Sengwa (Hailey & Coulson, 1995), and the habitat in the enclosure was within the range of those occupied in the field (it was structurally similar to bushed grassland, vegetation types h-k of Hailey & Coulson, 1995). Body temperatures were measured with a Yellow Springs Instrument

Co. thermistor with a plastic-covered general purpose probe calibrated against a mercury thermometer. The probe was inserted 2-4 cm into the cloaca (depending on tortoise size) of active tortoises seen between 8.30 and 16.30 hr. Body temperatures were measured on nine days between 8 January and 18 February 1992; all active tortoises which could be located were measured at intervals of 1 hr or more. Body temperatures recorded in Harare (altitude 1500 m) are compared with those measured in the field at Sengwa (900 m) by Hailey & Coulson (1996a). Most (60/63) of the T_b's of *G. pardalis* from Sengwa were measured in January and February 1992, that is at the same time as observations in Harare. Means are shown ±1 standard deviation.

Data on the annual variation of air temperature (T_a) at different sites were obtained from meteorological stations at Sengwa and Harare, and from Fullard & Darby (1977), as the mean daily maximum T_a and mean daily minimum T_a in each month. The mean T_a in each month was calculated as the average of these two variables (Meteorological Office, 1996, p viii). Distribution of tortoises is considered in relation to the effective temperature (ET) of different sites, which has been found to be useful in analysing the distribution of snake species in southern Africa (Stuckenberg, 1969).

Effective temperature was calculated as $(8T+14R)/(R+8)$, where T is the mean T_a for the year (averaged across all months) and R is the difference between the mean T_a's of the warmest and coldest months, all in °C (Stuckenberg, 1969).

RESULTS AND DISCUSSION

BODY TEMPERATURE

Frequency distributions of T_b of both species in Harare and at Sengwa are shown in Fig. 1. Body temperatures of active *K. spekii* in Harare had a mean of 27.6±3.0°C (n=160), not significantly different from the mean of 27.0±3.1°C found at Sengwa ($F_{1,383}$=3.62, P=0.058). Body temperatures of active *G. pardalis* in Harare had a mean of 29.1±3.1°C (n=174), significantly higher than T_b's of *K. spekii* in Harare ($F_{1,332}$=19.2, P<0.001), but significantly lower than the mean of 32.6±3.6°C for *G. pardalis* at Sengwa ($F_{1,235}$=55.6, P<0.001). There was no significant difference between T_b's of female, male, and unsexable juvenile *G. pardalis* at Sengwa ($F_{2,60}$=0.26, P=0.775). The mean T_b of females at Sengwa (33.0±3.8°C, n=15) was slightly higher than that of other animals, so that the low T_b of the *G. pardalis* in Harare was not due to their sex. Analysis of variance showed no significant differences between individual *G. pardalis* in Harare ($F_{8,165}$=1.76, P=0.088) or at Sengwa ($F_{42,20}$=1.29, P=0.271). Mean T_bs of the individual tortoises had a mean of 29.0°C in Harare and 32.7°C at Sengwa, very similar to the means of the separate T_b's given above. The variability of mean T_b between individuals was lower in Harare (SD=1.0, n=9) than at Sengwa (SD=3.1, n=43) because there were more T_b measurements for each individual in Harare. The mean T_bs of the individual *G. pardalis* were therefore compared non-parametrically; these differ significantly between
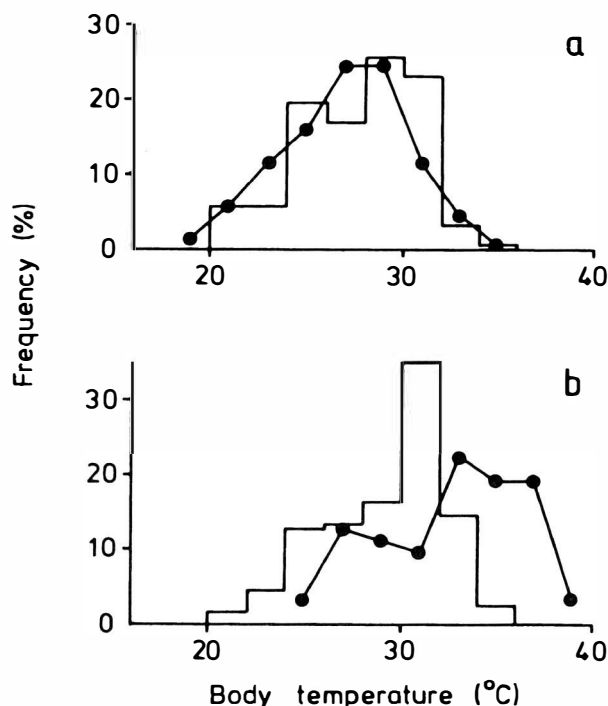

FIG. 1. Body temperatures of *Kinixys spekii* (a) and *Geochelone pardalis* (b) in an outdoor enclosure in Harare (histograms), compared to field measurements at Sengwa (points). Field T_b data are from Hailey & Coulson (1996a).
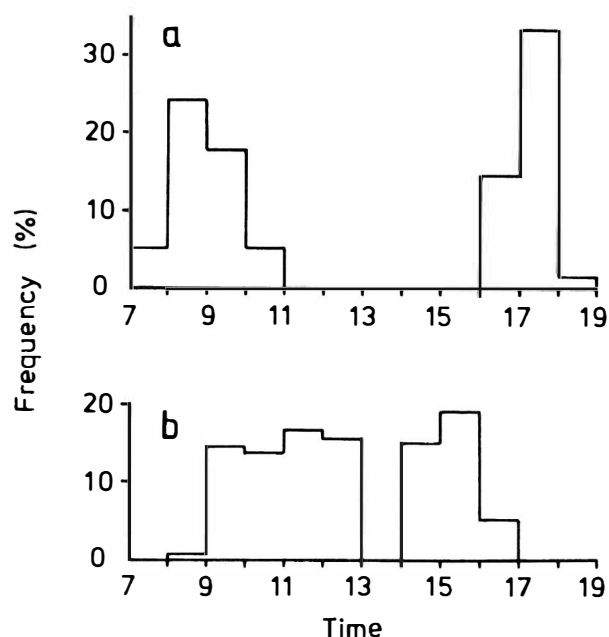
FIG. 2. The times at which body temperatures of *G. pardalis* were measured at Sengwa (a) and in Harare (b). (The gap from 13-14.00 hr in (b) is an artifact of sampling times, not a result of tortoise inactivity.)

Harare and Sengwa (Mann-Whitney test, $P=0.0012$). The identity of individual $K.$ $spekii$ was not recorded in Harare, but there were no significant differences between individuals at Sengwa ($F_{31,193}=0.45$, $P=0.995$). Many of these data were from five thread-trailed individuals (Hailey & Coulson, 1996a), which had similar T_b's: 26.0 ± 2.9, 26.7 ± 2.9, 27.0 ± 3.4, 27.1 ± 3.3 and $27.5\pm3.7°C$, respectively.

One major mechanism of thermoregulation in tortoises is to vary the period of daily activity, towards midday in cooler environments (Hailey, Pulford & Stubbs, 1984). Body temperatures of $G.$ $pardalis$ in the field were measured in the morning or late afternoon, which was the only time that they were active, while captive animals were measured around midday (Fig. 2). Thus $G.$ $pardalis$ had low T_b's in Harare even though measured at the warmest time of day. There was no evidence that the cooler climate of Harare reduced the time available for activity; the daily activity period was longer there (7-8 hr) than at Sengwa (5-6 hr).

BODY TEMPERATURE AND DISTRIBUTION

$Kinixys$ $spekii$ achieved similar T_b's in Harare and at Sengwa, despite mean T_a at Harare being about $5°C$ cooler throughout the year (Fig. 3). This result is not surprising as $K.$ $spekii$ has a particularly low T_b for a tortoise (Hailey & Coulson, 1996a), this species occurs naturally around Harare, and its activity at Sengwa was limited on hot days (Hailey & Coulson, 1996a). $Geochelone$ $pardalis$ had lower T_b's in Harare than at Sengwa, despite being active at the hottest time of day. It is possible that the failure to achieve high T_b's during activity is responsible for the absence of this species around Harare, and in other parts of southern Africa. Fig. 4 shows the similarity between the distribution of $G.$ $pardalis$ in this region, and the $16°C$ isotherm of effective temperature. Fig. 4b shows the cooler area to the east of Harare, from which $G.$ $pardalis$ is absent (as shown by the detailed point-location distribution map given by Broadley, 1989).

There are three areas where the distribution of $G.$ $pardalis$ does not correspond to the $16°C$ isotherm of ET. First, along the east coast, where temperatures are raised by the warm southward-flowing Agulhas/Mozambique current (Schulze & McGee, 1978). This discrepancy is common to the tropical herpetofauna assemblage of southern Africa (Poynton & Broadley, 1978). Second, the western region, around Windhoek; and third, south, around Graaff Reinet. Both of these locations have lower ET's than Harare (Fig. 4), but higher mean temperatures during the rainy season when tortoises are active. Mean T_a is higher at Graaff Reinet from December to March (Fig. 3), and at Windhoek from November to March, compared to Harare. (All these sites have peak rainfall during summer, lasting from about November to March, except for Cape Town which has peak rainfall during winter.) It is therefore
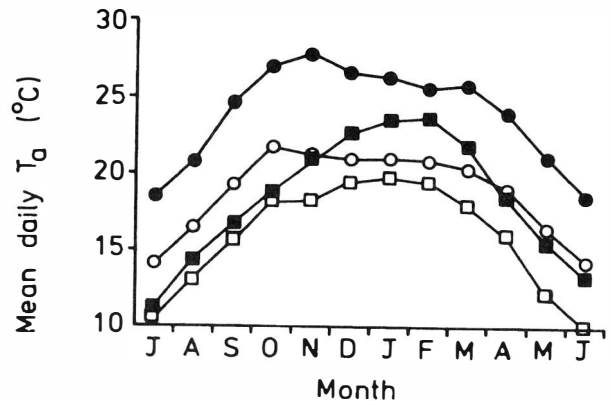

FIG. 3. Annual variation of mean daily air temperature at Sengwa (filled circles), Harare (open circles), Graaff Reinet (filled squares) and Johannesburg (open squares). Data are from Sengwa and Harare meteorological stations, and Fullard & Darby (1977).
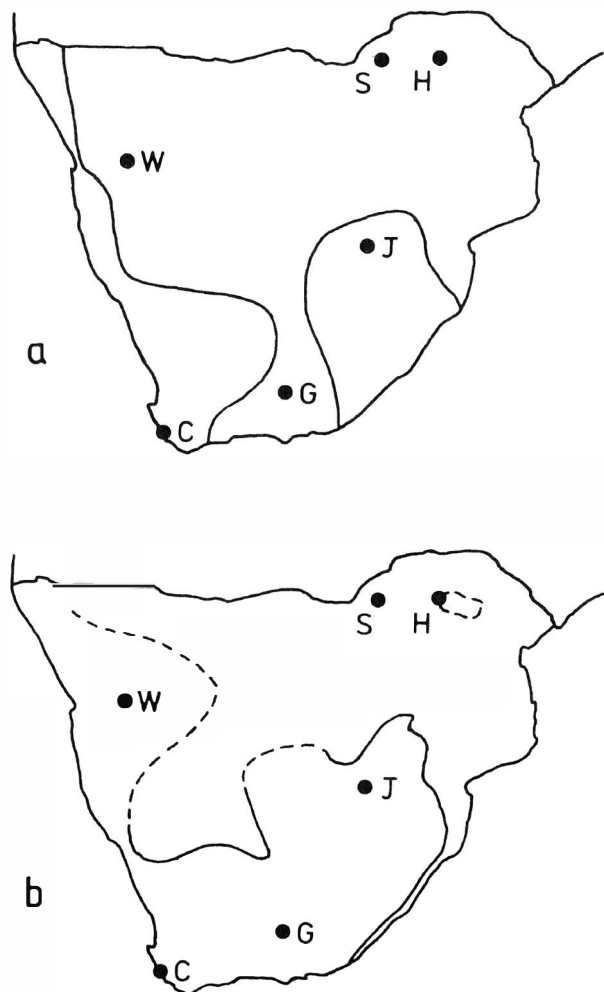

FIG. 4. Maps of southern Africa (south of the Cunene and Zambezi rivers). (a) The distribution of $G.$ $pardalis$, after Branch (1988). (b) The $16°C$ isotherm of effective temperature, after Stuckenberg (1969). Locations: S=Sengwa (ET=18.5°C), H=Harare (16.4°C), W=Windhoek (16.0°C), J=Johannesburg (14.9°C), G=Graaff Reinet (15.9°C), C=Cape Town (15.3°C).

possible that the need to achieve high T_b's during activity restricts the distribution of *G. pardalis* in southern Africa.

Such a restriction assumes that the thermal physiology of *G. pardalis* is evolutionarily inert or static (Bogert, 1949), rather than easily modified or labile (Hertz, Huey & Nevo, 1983); otherwise, populations in cold regions could adapt to low T_b's. There is no fundamental constraint of moderately low T_b on tortoises, as some species are normally active with T_b's below 30°C (Hailey & Coulson, 1996a). The 'labile thermophysiology' hypothesis, which is necessary to any analysis of the coadaptation of T_b with performance (Hailey & Davies, 1988) or risk (Hailey & Coulson, 1996a), is gaining support (Diaz, Bauwens & Asensio, 1996). One of the best examples of labile thermophysiology is of a chelonian; Ellner & Karasov (1993) showed that northern box turtles had lower selected and field T_bs than southern populations. The apparent limitation of activity T_b's on distribution of *G. pardalis* is thus of interest; it suggests that T_b and thermal physiology are sufficiently resistant to change in this species to prevent its presence in otherwise suitable areas.

Data on the variation of T_b of *G. pardalis* throughout its range are important for the resolution of this question. It is unfortunate that although *G. pardalis* is perhaps the most-studied tortoise in Africa, work on T_b has concentrated on thermal selection in the laboratory (Perrin & Campbell 1981; Zurovsky *et al.*, 1987), rather than field T_b's.

ALTERNATIVE CONSTRAINTS ON DISTRIBUTION

A constraint on the distribution of *G. pardalis* from habitat or food requirements is unlikely as this species is a generalist in terms of both vegetation types occupied (Hailey & Coulson, 1995) and diet (Milton, 1992; Rall & Fairall, 1993). Alternative thermal factors (other than T_b's during activity) which should be considered are winter and nest temperatures. Tortoises in the seasonal tropics are inactive during unfavourable periods (Hailey & Coulson, 1996a), and show physiological adaptations to dormancy (Hailey & Loveridge, 1997). It is therefore unlikely that temperatures in winter will limit distribution in southern Africa, as they do not become lethally low (Poynton, 1964). In addition, the 0°C isotherm of July (midwinter) mean daily minimum temperature (Fig. 4b of Schulze & McGee, 1978) encloses an area inland between Cape Town and Johannesburg, cutting across the southern distribution of *G. pardalis*. Both general and specific arguments thus suggest that winter temperatures are not important in limiting the distribution of *G. pardalis*.

Temperatures of nests might also be important (Lambert, 1983), particularly as incubation times of *G. pardalis* are apparently shorter closer to the equator in Zambia (6-7 months; Wilson, 1968) than in Zimbabwe

and South Africa (13-14 months; Bennefield, 1982 and references therein). This explanation also assumes an evolutionarily static variable, in this case the temperature-sensitivity of development. The presence of *G. pardalis* in the south but not around Harare shows that temperatures in summer are more important than the overall annual temperature (as measured by ET). If nest temperature is the limiting factor, this distribution suggests that the long incubation period of over a year includes a pause during winter.

LIVING MODELS

The demonstration that activity T_b's of *G. pardalis* are limited at high altitude in Zimbabwe thus raises a number of interesting questions about the thermal biology of this species, and shows the potential of translocated animals used as 'living models'. Reciprocal translocations between areas where a species occurs naturally are possible as well as translocations out of the natural range as used here. Animals in the field could be followed by radio tracking or thread trailing, their T_b's measured directly or by telemetry, and behaviour recorded to show the method of thermoregulation (or its failure) in the new conditions.

Live animals are more difficult to use than physical models, but potentially provide much more information; observations on activity need to be made together with measurements of T_b. Body temperatures of *G. pardalis* in Harare were lower than those at Sengwa, even after the daily activity period had been shifted to midday, showing that tortoises could not compensate completely for the cooler climate. Physical models would show that temperatures were lower in Harare, but not whether changes in activity time could compensate for this. The 3°C difference between T_b's in Harare and Sengwa was significant; a similar difference between temperatures of models would not be as convincing, given the difficulty of estimating T_b's from physical models in different conditions.

The statistical analysis of data from such studies requires some attention. The first treatment above used T_b measurements as the unit of statistical analysis. This method assumes that variation between individuals is small compared to the variation between repeated measurements on the same individual. This assumption is valid for physical models measured at long intervals. It was also found to be valid for *G. pardalis*, there being no significant differences between individuals, and results using individual tortoises were similar to those using separate T_b measurements.

Nevertheless, the interchangeability of individuals cannot be assumed in all cases, and should be investigated in each study. Radiotelemetry in particular typically produces large volumes of data from a few individuals; an optimal study would use many individuals for short periods.

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