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JOURNAL OF THE EAST AFRICA NATURAL HISTORY SOCIETY AND NATIONAL MUSEUM

3rd SEPTEMBER 1982

No. 176



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CONSTRAINTS OF HETEROTHERMY IN AN ALPINE HABITAT**

J. J. Hebrard

*Dept. of Zoology, University of Nairobi
P.O. Box 30197, Nairobi*

S.M. Reilly

P.O. Box 30261, Nairobi

M. Guppy

*Dept. of Biochemistry, University of Nairobi,
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INTRODUCTION

Lizards are termed heterothermic because their body temperatures vary by up to 30°C during a diel cycle, reaching a minimum at night and a maximum during the daylight hours. Body enzymes that must function over a wide range of temperatures are less efficient than those that operate at a set temperature (Low and Somero 1976, Fersht 1977, Holbrook *et al.* 1975), and most lizards that have been studied are able to maintain their body temperatures within a 3-5°C range when they are fully active during the day. This is accomplished by the animals' shuttling between sun and shade as ambient temperatures vary (see Cloudsley-Thompson 1971, Heatwole 1970).

Reptiles that make no attempt to thermoregulate during the day are apparently exceptional, but this may be because most studies of lizard thermoregulation have been done in desert environments where there is no lack of intense solar radiation. Thermal passivity has been reported in three species of the New World genus *Anolis* (Fitch 1972, Huey 1974, Hertz 1974); two from lowland tropical forest and one from high elevation cloud forest. In all three cases, the criterion for thermal passivity was high variability in cloacal temperatures, but in only one case were comparative data used convincingly.

Chamaeleo höhnelii Steindachner and *Mabuya varia* (Peters) are found in the moorlands of the Aberdare range above 3000 m. Skinks of the genus *Mabuya* are surface-active lizards whose thermoregulatory behaviour generally conforms with that noted in other such lizards (e.g. Withers 1981). Chameleons, as arboreal forms, may be expected to exhibit different thermal patterns from terrestrial forms. In what follows we will examine daily temperature cycles in relation to how each species is thermally adapted to life in their particular microenvironments within the moorlands.

STUDY AREA AND METHODS

The study was conducted in the course of two visits to the Fishing Camp in Aberdare National Park, from 31 January-2 February and 20-22 February 1981. The camp is situated in ericoid bushland where *Cliffortia nitidula* and *Stoebe kilimanjarica* are dominant shrubs. Between stands of shrubs are grassy meadows consisting of dense tussocks of *Eleusine jaegeri*, *Agrostis producta*, and *Festuca abyssinica*. Directly in front of the visitors' cabins is an area of about 2 ha which is about evenly divided between stands of *Cliffortia* and grassy patches (Plate 1). *Chamaeleo höhnelii* were found exclusively in the shrubs while *Mabuya varia* occurred only in the grass tussocks. Air temperatures during the study period varied over a range of 22.6°C, from a low of -2.1°C to a high of 20.5°C, both extremes occurring on 22 February (Fig. 1). Weather patterns were similar on all days of the study, with clear, sunny mornings followed by a build up of cumulus clouds in the afternoon. The only rain was a brief shower on the afternoon of 31 January.

Cloacal temperatures of both species of lizards were taken at intervals throughout the 24 hour cycle with a quick-reading thermometer. Chameleons were easily located on their sleeping perches within the shrubs, and once located, individuals were followed during their limited arboreal movements during the day. Skinks spent the night deep within grass tussocks, and could only be caught during the day when they were active on the surface. To facilitate measurement of nocturnal cloacal temperatures, five skinks were placed in a cardboard box containing an isolated grass tussock. The captive animals appeared to show normal sleeping and rousing behaviour which coincided with the behaviours of free-living skinks.



Study area at Fishing Camp in Aberdare N.P. *Mabuya varia* are found exclusively among the grass tussocks in the foreground, while *Chamaeleo höhnelii* are confined to the shrubs (*Cliffortia nitidula*) at the rear.

RESULTS

Chameleons descended into the interiors of *Cliffortia* shrubs at night where they slept at a mean height of 2.3 m above the ground. This movement apparently gained them little thermal advantage, though they were protected from direct frost. They were observed to supercool when the air temperature dropped below freezing (Figs. 1,2). The skinks burrowed into the cores of grass tussocks where ambient temperatures remained several degrees warmer than outside air temperature (Fig. 1). Both animals adopted sleeping postures that reduced their surface area-to-volume ratio, the chameleons with their tails tightly coiled and limbs appressed against the body, and the skinks in a tight coil with the tail wrapped around the body. Though mean body temperatures of sleeping chameleons and skinks did not differ significantly in this study (Fig. 3), the latter might gain an advantage in more severe freezes. Moderate supercooling is widespread among cold blooded vertebrates, however, and complete recovery has been reported in reptiles cooled to as low as -8°C (Lowe *et al.* 1976).

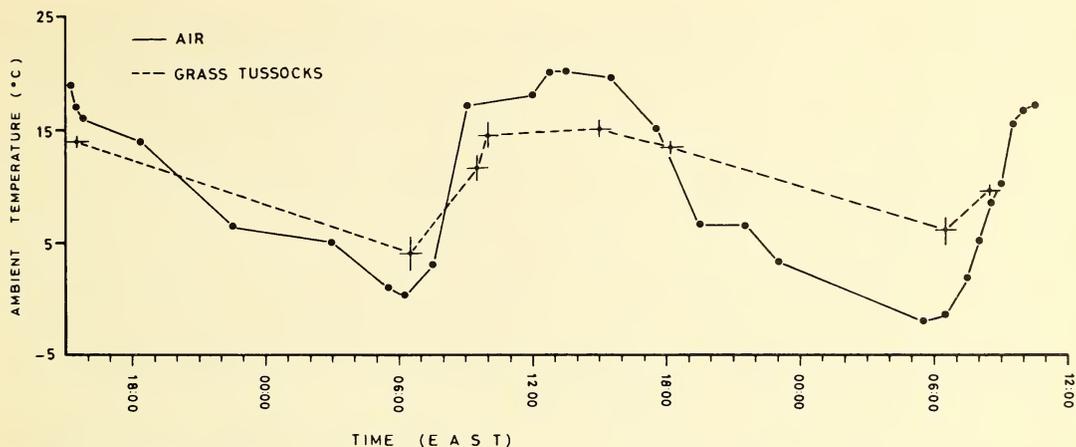


Fig. 1 Air temperatures (solid line) and core temperatures of grass tussocks (dashed line) for the period 20-22 February 1981. Tussock temperatures are expressed as means (horizontal line) \pm critical distance (c.d. = $s.d. \sqrt{2/N}$).

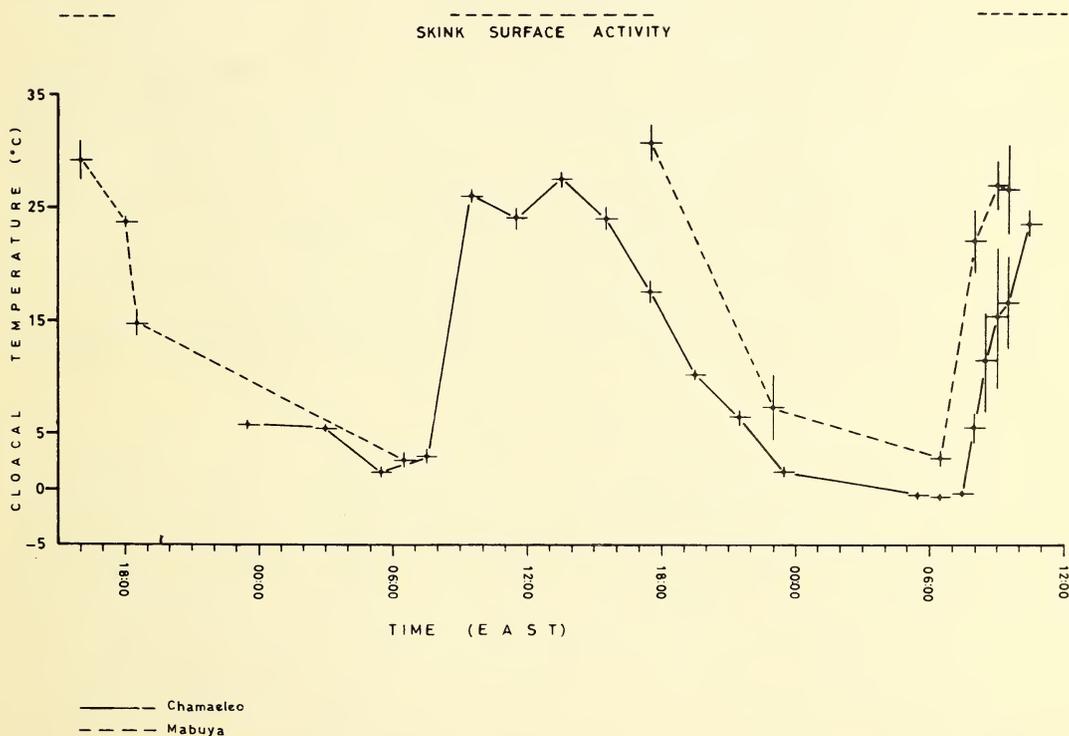


Fig. 2. Cloacal temperatures of *Chamaeleo höhnelii* (solid line) and *Mabuya varia* (dashed line) over the period 20-22 February 1981. Temperatures are expressed as means (horizontal bar) \pm critical distance. When critical distances do not overlap, means are significantly different at $P .05$. Horizontal dashed lines indicate the interval between the first sighting of wild skins in the morning and the last in the afternoon.

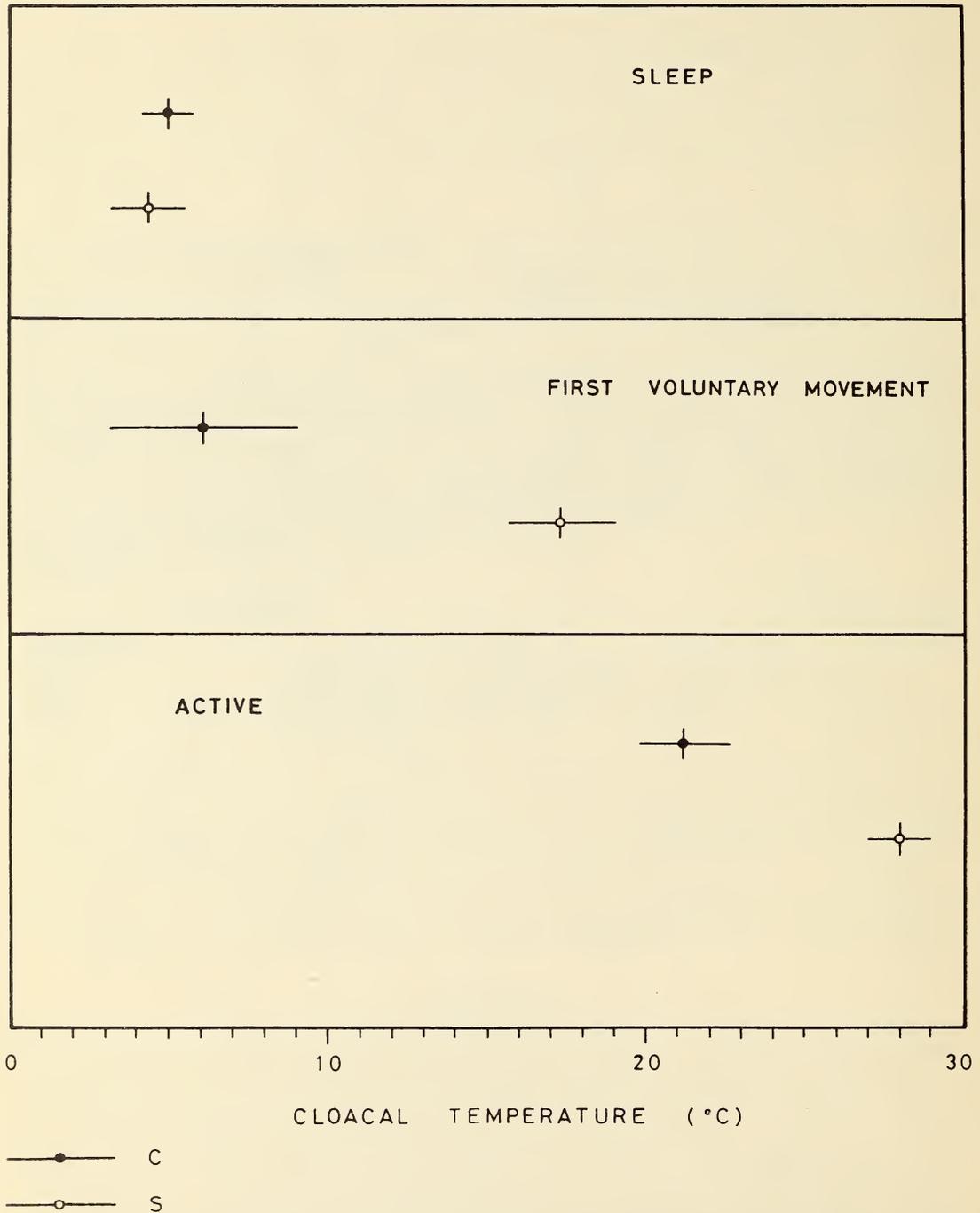


Fig. 3 Mean cloacal temperatures (vertical bar) \pm critical distance (horizontal bar) for sleeping, rousing, and active *Mabuya varia* and *Chamaeleo höhnelii*. Sample sizes are as follows: Sleeping, *Chamaeleo* (73), *Mabuya* (9); First Movement, *Chamaeleo* (4), *Mabuya* (5); Active, *Chamaeleo* (34) *Mabuya* (20).

Morning arousal in chameleons, as indicated by the first limb movement, occurred at body temperatures not significantly higher than their sleeping temperatures (Fig. 3). Animals were completely immobilized when their body temperatures dropped below freezing, and they appeared dead; some even dropped from their perches. The first sign of life was when the eyes opened and visible breathing began. In some individuals the first movement adjusted the position of the animal on its perch so that one side of the body was perpendicular to the sun's rays; other individuals made no discernable attempt to bask. In basking animals, the side exposed to the sun was darkened while no colour change occurred on the shaded side. Non-basking individuals began climbing immediately, though very slowly at first. On the morning of 2 February, two animals were each 70 cm above their sleeping perches at 08:50 hrs when the air temperature was 9.3°C, and two others were 10 and 15 cm above their nocturnal perches. This ascent undoubtedly takes them into more direct sunlight where they quickly reach their active temperature (Figs. 2, 3). Because of the lack of a consistent basking period, chameleons were considered active after their first voluntary movement. Thus, body temperatures of active animals were both lower and more variable than those of *Mabuya varia*. One *Chamaeleo höhnelii* was observed to capture an insect when its cloacal temperature was only 7°C, suggesting that the tongue muscles are able to function efficiently even when the body musculature is capable of only very slow movement. Even when their body temperatures were at a peak, the chameleons did not move around much, but rather appeared to rely on concealment to ambush prey that approached them.

The following arousal sequence for skinks is based on a combination of data from animals kept in a box overnight and from free-living individuals captured when they were active on the surface of the grass tussocks. Skinks within a tussock in early morning exhibited no movements until their cloacal temperatures were above 17°C (Fig. 3). Depending on the rate of warming, first movements occurred as early as 07:55 hrs and as late as 09:46 hrs. In each of the five captive animals, the first movements took them from the interior of the grass tussock to a position in full sunlight. In all cases, the first basking site was near the base of the tussock, where the animals were not fully exposed to view. Initiation of the heating cycle while still under cover has been reported in desert iguanas by McGinnis and Dickson (1967), and is believed to function in shielding the animals from predators before full activity temperature is attained. At a mean cloacal temperature of 26.3°C (s.d. = 0.8), skinks left the grass tussock at a time coinciding with the first appearance of free-living skinks on the surface. Temperatures of active skinks during the warm part of the day averaged just over 28°C, significantly higher than those of chameleons (Fig. 3). In addition, the variation about the mean was significantly smaller than that for active chameleons ($F = 3.74, P < .01$), suggesting more efficient thermoregulation. The interiors of grass tussocks, which may have provided thermal refuges for skinks at night, became thermal traps during the day, as their temperatures never reached the levels required for full skink activity (Fig. 1).

DISCUSSION

Because of the lack of clearly defined basking, the greater variability in body temperatures of active animals, and the lower maximum body temperatures, *Chamaeleo höhnelii* can be said to be thermally passive relative to *Mabuya varia* on the moorlands of the Aberdares. Their respective microhabitats offer different thermal environments which are exploited by the two species in accordance with their behavioural and physiological limitations. The open grassland inhabited by the skinks receives maximum solar radiation, allowing the animals to rapidly attain a high, and, more importantly, a relatively constant body temperature. Skinks of the genus *Mabuya* pursue prey actively, and are capable of very rapid movement over short distances. Thus, it is to their advantage to maintain their body temperatures within a narrow range to maximize biochemical efficiency. The dense, shady shrubs inhabited by *C. höhnelii* afford fewer suitable basking perches (see Huey 1974), with the result that body temperatures of active animals fluctuate over a wide range. According to our initial hypothesis, this should result in lowered biochemical efficiency, and this is borne out by the animals' lethargic behaviour and their ambush method of prey capture. The chameleon's tongue-shooting ability at 7°C (see Results) may seem contrary to expectation, but the muscular involvement in this mechanism is akin to a slow pumping up, and does not necessitate a high rate of metabolism (Bellairs 1969).

The retreat of skinks to the interiors of grass tussocks and of chameleons into the interiors of shrubs may serve the dual function of protecting the animals from formation of frost on the body surface, and protection from predators while they are immobilized by low body temperatures. Unfortunately, no long term records of temperature are kept above inhabited levels on the Aberdares, so we cannot discuss extreme minimum temperatures experienced by the lizards. The study was conducted during the southern hemisphere summer, thus it is unlikely that the low temperatures recorded were annual minima. Depending on the extremes in the area, the chameleons might have to seek greater protection during colder periods or perhaps suffer local extinction.

ACKNOWLEDGEMENTS

This study was supported by a grant from the National Geographic Society (U.S.). A number of people helped with the work as follows: Sarah Guppy, Thomas Madsen, and Monika Osterkamp provided expert assistance in the field, Alex Duff-Mackay and Gary Ferguson criticised the manuscript, and George Kinoti gave advice and encouragement.

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Revision received 25 November 1981

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