

Field body temperatures, activity levels and opportunities for thermoregulation in an extreme microhabitat specialist, the girdled lizard (*Cordylus macropholis*)

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Abstract

The girdled lizard *Cordylus macropholis* inhabits semi-desert areas along the west coast of South Africa. Unlike many other small diurnal lizards living in open habitats, it exhibits extreme low levels of above-ground activity and does not show overt thermoregulatory behaviours, such as basking or shuttling. It has an extreme low movement rate and confines routine activity to the microhabitat of the succulent *Euphorbia caput-medusae*. We document this restriction of activity in time and space in relation to aspects of this lizard's thermal biology. Throughout the day, a majority of the lizards was found sheltering ('covered') among the branches of *E. caput-medusae* plants, and surface-active ('exposed') individuals were seen during only a restricted time period (i.e. 1100-1700 h). Mean body temperatures (T_b s) of both 'exposed' (29.4 °C) and 'covered' (28.4 °C) individuals were surprisingly low for a lizard inhabiting a hot and dry climate zone. This similarity of the T_b s of both groups, as well as the correspondence between the ambient temperatures in the plant microhabitat and the T_b s of 'exposed' lizards indicate that, for a considerable part of day, thermal conditions under plant cover allow achievement of T_b s at a similar level as that maintained by the 'exposed' lizards. Moreover, the absence of sightings of overtly basking lizards supports the view that *C. macropholis* warm up by adopting the ambient temperature in their shelters thereby reducing the time spent in surface activity. All lizards observed were within the periphery of *E. caput-medusae* plants, indicating that *C. macropholis* is an extreme microhabitat specialist. The succulent provides more and safer hiding places than other common shrubs in the environment. In addition, estimates of ambient temperatures indicate that these plants offer superior opportunities for thermoregulation compared with other available shrub microhabitats.

Key words: lizard, *Cordylus macropholis*, thermoregulation, behaviour

INTRODUCTION

Temperature regulation, a central paradigm of biophysical and physiological ecology (Bartholomew, 1964; Gates, 1980), is of paramount importance to many aspects of reptilian ecology and behaviour (Huey, 1982). Many species of diurnal reptiles maintain high and relatively constant body temperatures (T_b s) despite wide fluctuations in environmental heat loads (Avery, 1982; Huey, 1982). They achieve these mainly by adjustments of their behaviour, in particular, restriction of activity times, shuttling between hot and cool microhabitats, and postural modifications that alter the rates of

heating and cooling (Huey, Pianka & Hoffman, 1977; Hertz & Huey, 1981; Huey, 1982; Stevenson, 1985; Bauwens, Hertz & Castilla, 1996). However, not all reptiles maintain constant T_b s or spend considerable time and energy in thermoregulatory behaviours. For instance, some lizards that inhabit tropical forests exhibit few regulatory adjustments and their T_b s fluctuate with ambient conditions (Ruibal, 1961; Huey & Webster, 1975; Hertz, 1992). Other species live in habitats where ambient conditions enable them to be active at T_b s near the selected range (the range of T_b s maintained in the absence of physical restrictions) without overt thermoregulatory adjustments (Hertz, Huey & Stevenson, 1993; Shine & Madsen, 1996). Nevertheless, the maintenance of high and stable T_b s during activity and the extensive and overt usage of regulatory

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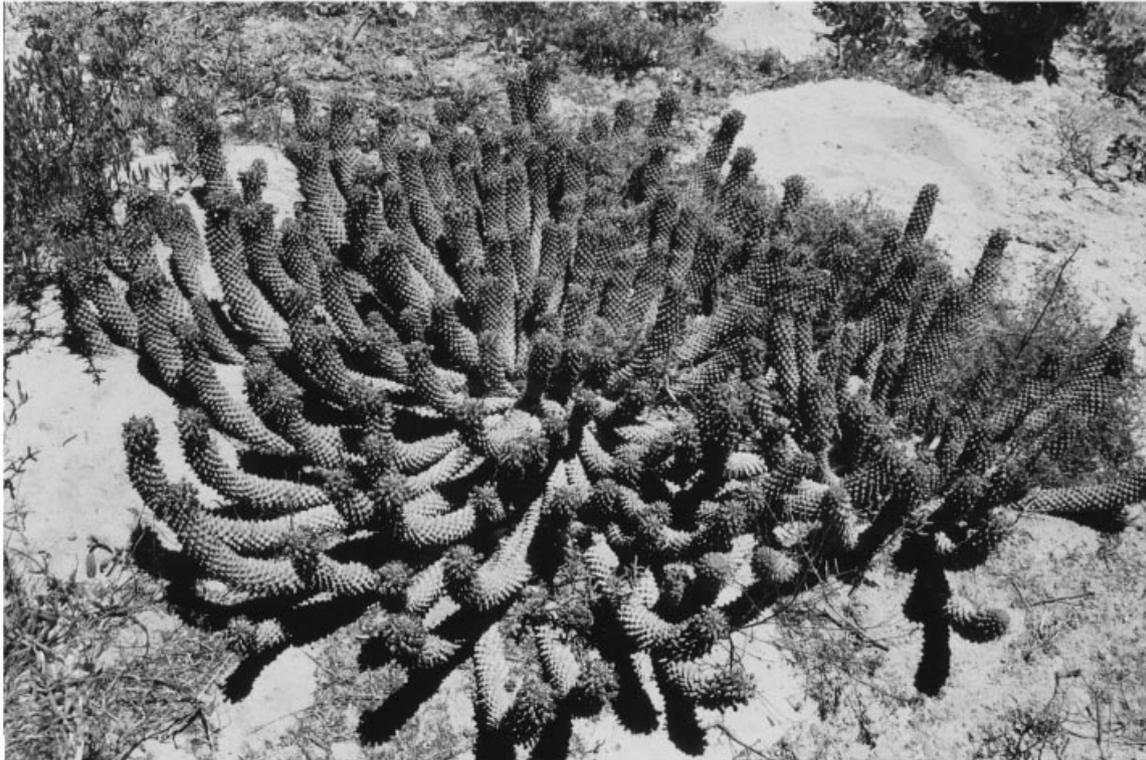


Fig. 1. Photograph of a full-grown *Euphorbia caput-medusae* plant.

behaviours are characteristic of small diurnal lizards that inhabit climates characterized by wide diurnal fluctuations of ambient temperatures.

We here report on a study of the activity patterns and field body temperatures in a population of the girdled lizard *Cordylus macropholis*. Cordylid lizards constitute a remarkable but poorly studied component of the fauna of Southern Africa. In fact, to the best of our knowledge, this is the first field study of body temperatures and thermoregulatory behaviour in this lizard family. In addition, several aspects of the ecology of *C. macropholis*, which inhabits open habitats in semi-desert areas, are peculiar for lizards. It is an extreme microhabitat specialist that often confines its activities to a single plant species, the succulent *Euphorbia caput-medusae*. Moreover, these lizards exhibit extreme low levels of above-ground activity, they are primarily found sheltering under plant cover, and they do not show overt thermoregulatory behaviours. We explore the consequences of this extreme restriction of activity in space and time on the T_{bs} of this lizard. Our aims are threefold. First, we document the T_{bs} maintained by lizards at different times of day. Second, we compare T_{bs} and opportunities for thermoregulation of lizards that were active on the surface to those that were found under plant cover and examine aspects of the species' thermoregulatory behaviour. Third, we use estimates of ambient heat loads in different microhabitats to examine the consequences of restricted microhabitat usage on opportunities for temperature regulation.

MATERIALS AND METHODS

Genera) procedures

Cordylus macropholis is a small-sized (snout-vent length of adults, 55-77 mm), terrestrial and diurnal lizard that is endemic to a narrow area along the west coast of South Africa (Branch, 1994). Fieldwork was carried out from 13 to 18 December 1997 near the village of Lambert's Bay (32°07'S, 18°19'E; Western Cape Province, South Africa). Weather conditions were fairly uniform during the study period, with continuous sunshine throughout the day, but with some differences in wind intensity among the days, especially during the afternoons. The study area was located immediately south of the village, between the coastal dunes and the road to Leipoldtville. The general area falls within the western arid zone of South Africa, characterized by a dry and hot desert-like climate. The habitat is composed of patches of bare sandy soil, interspersed among vegetation dominated by low shrubs (e.g. *Euphorbia mauritanica*, *Prenia pallens*); trees are absent. The vegetation is described as 'Strandveld Succulent Karoo' (Low & Rebelo, 1996). *Cordylus macropholis* shares this habitat with the skinks (Squamata: Scincidae) *Mabuya variegata* and *M. capensis*, and the lacertids (Squamata: Lacertidae) *Meroles knoxii* and *Pedioplanis lineoocellata*.

A previous study by P. le F. N. Mouton in the same area demonstrated that *C. macropholis* confines its activities to a single plant species, the succulent *Euphorbia caput-medusae*. This dwarf shrub has

cylindrical branches (2-6 cm diameter), covered with tubercles, that radiate from a low, central stem. The branches of young plants are short (*c.* 10-20 cm) and remain in an upright position. In older plants, the branches spread, attain lengths of up to *c.* 150 cm and lie on the ground and on top of each other in irregular piles (Fig. 1). The undermost branches often die and their colour changes from uniformly green to greyish brown. Lizards shelter within older plants, in spaces between layers of branches and between the central stem and the branches.

We systematically searched an area of *c.* 200 × 70 m, paying special attention to *E. caput-medusae* plants, but avoiding examination of individual plants more than once. We slowly walked towards an *E. caput-medusae* plant to locate lizards that perched on or near the branches. The lizards that we observed invariably retreated quickly to shelter between the branches; we hand-caught them by searching between the branches at the spot where they disappeared. We subsequently searched for other sheltering lizards in the rest of the plant, by lifting up the branches and carefully examining the spaces among branches and near the central stem. We also thoroughly searched for lizards in plants on which no perching lizards were observed. For all lizards seen we recorded date, time of day, age class (immature: SVL < 55 mm, adult: SVL > 55 mm), sex and whether the lizard was 'exposed' (= perching on or near a plant with at least part of the body exposed to solar radiation) or 'covered' (= sheltering between the branches) upon first sighting. When the lizard was caught, we immediately measured its body temperature (cloacal = T_b) and the shaded air temperature at the place of first sighting (shaded bulb = T_a) to the nearest 0.1 °C with a quick-reading Miller-Weber thermometer.

Estimates of ambient heat loads

To estimate ambient heat loads (T_{ams}) in different microhabitats, we measured the temperature of an unshaded thermocouple bulb connected to an electronic thermometer (DGT-Therma 3; to nearest 0.1 °C). These can be considered as crude estimates of 'operative temperatures'. Measurements using hollow copper lizard models (e.g. Bakken, 1992; Hertz, 1992; Bauwens *et al.*, 1996) would give more accurate estimates, because these models mimic the size, shape and radiative properties of lizards and better integrate the effect of various biophysical factors (e.g. air temperature, solar radiation, wind). Nevertheless, our primary aim was to estimate heat loads at the base of structurally different shrub-microhabitats, which are most often shaded and where air temperature is probably the most important biophysical factor that influences a lizard's heat balance. We assume that our measurements provide, at the very least, relative estimates of the heat loads that lizards encounter in distinct microhabitats.

We measured T_{ams} at 15 fixed sites, distributed over 3

structurally different microhabitats, at 30 min intervals from 08:30 to 19:00 on 15 December 1997. We sampled the *E. caput-medusae* microhabitat at 6 sites, 3 near the centre of the plant and 3 between branches at *c.* 50 cm of the centre. Ambient heat loads in shrub microhabitats were measured at 3 sites located near the base of *Euphorbia mauritanica* bushes and at 3 sites at the base of *Prenia pallens* bushes. The latter grow to a height of *c.* 200 cm, have a typical shrub structure, and are representative of the majority of the bush microhabitats in the area. We also sampled open microhabitats by measuring T_{ams} (2 cm above ground) in the centre of 3 patches of bare sandy soil.

The frequency distributions of the T_{ams} estimate the body temperatures that lizards can potentially achieve in different microhabitats. By comparing these T_{am} distributions to the target T_{bs} that thermoregulating lizards attempt to achieve (often indexed by the T_{bs} selected in a laboratory thermogradient), one can estimate the suitability for thermoregulation of the different microhabitats (Huey, 1991; Hertz *et al.*, 1993; Bauwens *et al.*, 1996). Microhabitats wherein T_{ams} are equal to or close to the target T_{bs} have high thermal suitability, because their thermal characteristics pose few physical constraints on the achievement of the target T_{bs} (Hertz *et al.*, 1993). Here we used a similar approach and evaluated the T_{ams} , measured at different times of day in the different microhabitats, with reference to the T_{bs} of 'exposed' lizards. Hence, we examined to what extent ambient heat loads in different microhabitats allowed lizards to achieve T_{bs} similar to those measured in the 'exposed' lizards. In other words, we evaluated the suitability of microhabitats for achieving the T_{bs} maintained by 'exposed' lizards, not for attaining the selected temperatures (as in Hertz *et al.*, 1993). The target range (T_{exp}) was estimated by the central 50% of the T_{bs} measured in 'exposed' individuals. We used 2 indices to determine how well a distribution of T_{ams} conformed to T_{exp} . First, we determined the percentage of T_{ams} readings that fell within T_{exp} . Second, we calculate d_{am} , that is the absolute value of each deviation of T_{am} from T_{exp} . When T_{am} is within T_{exp} , the corresponding d_{am} equals 0. Mean d_{am} estimates the thermal suitability of a microhabitat, that is, how close the heat loads are to the T_{bs} maintained by the 'exposed' lizards.

RESULTS

Activity patterns

All *C. macropholis* observed were within the periphery of *E. caput-medusae* plants and the majority of them (72%, $n = 170$) were hidden among the branches when first seen. Lizards that perched on or between branches were very shy, quickly withdrawing to shelter on approach, often from distances > 5 m. Hence, it is not unlikely that some of the lizards that were found hidden, had been perching immediately before but

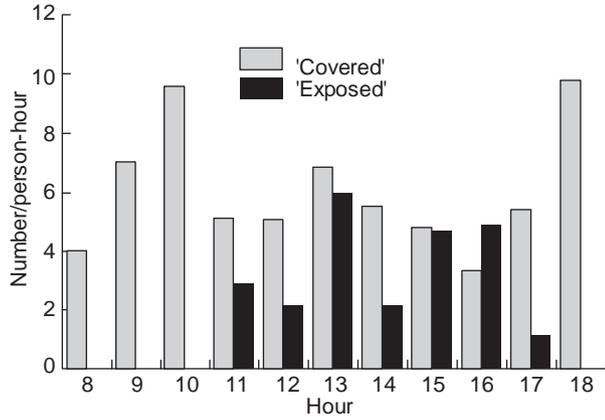


Fig. 2. Number of lizards that were 'covered' or 'exposed' upon first sighting, observed per person hour at different times of day.

retreated unnoticed when we approached them. A fraction of the 'exposed' lizards sat motionless on top of the cylindrical branches or on the sand, adjacent to a branch, and could be observed from a distance. Others lay among the branches, with part of their body exposed to the sun; they could only be seen from within close range. Casual observations (5 min duration, repeated at 30 min intervals) of undisturbed 'exposed' lizards revealed that they retained the same position on the same spot for periods up to 2 h. We never saw a lizard moving, except when induced by human contact.

The numbers of 'covered' individuals found at different hours did not differ from those expected on basis of the number of person hours spent searching in each hourly interval ($\chi^2 = 9.87$, 10 d.f., $P > 0.40$). Hence, the numbers of 'covered' lizards seen per person hour can be considered as approximately constant through the day (Fig. 2). In contrast, the number of 'exposed' lizards was not proportional to searching-time ($\chi^2 = 22.88$, 10 d.f., $P = 0.01$). We saw fewer 'exposed' lizards than expected before 11:00 and after 17:00, and more than expected during the interval 13:00-17:00 (Fig. 2).

Table 1. Summary statistics (mean \pm SD) of body (T_b) and air (T_a) temperatures, and of the difference between both for 'covered' and 'exposed' lizards of three age-sex groups. n = number of temperature measurements

	T_b	T_a	$T_b - T_a$	n
'Covered'				
Immature	26.62 \pm 3.57	24.10 \pm 3.60	2.53 \pm 2.48	20
Adult males	28.62 \pm 3.84	26.48 \pm 3.18	2.14 \pm 1.58	24
Adult females	28.97 \pm 3.64	25.60 \pm 2.99	3.37 \pm 2.10	61
Total	28.44 \pm 3.75	25.51 \pm 3.22	2.93 \pm 2.12	105
'Exposed'				
Immature	27.50 \pm 1.80	19.82 \pm 1.06	7.68 \pm 2.81	6
Adult males	29.46 \pm 2.05	21.72 \pm 3.54	7.74 \pm 3.60	5
Adult females	30.06 \pm 2.26	22.82 \pm 3.47	7.24 \pm 3.81	16
Total	29.38 \pm 2.31	21.95 \pm 3.26	7.43 \pm 3.46	27

Body temperatures

The 'covered' and 'exposed' lizards were subject to different ambient conditions, particularly the intensity of solar radiation and wind. Hence, we incorporated exposure state as a factor in all analyses of T_b and the relations between T_b and T_a . Immature lizards maintained lower T_b s than both adult males and females (Table 1; two-way ANOVA, age-sex: $F_{(2,126)} = 4.75$, $P = 0.01$, exposure state: $F_{(2,126)} = 1.82$, $P > 0.10$; interaction: $F_{(2,126)} = 0.01$, $P > 0.90$). However, the difference between age/sex groups vanished when we accounted for variation in T_a (two-way ANOVA with T_a as a covariate, age-sex: $F_{(2,125)} = 2.19$, $P > 0.10$, exposure state: $F_{(2,125)} = 44.79$, $P < 0.001$; interaction: $F_{(2,125)} = 0.62$, $P > 0.50$). Because of the similarity among the relations between T_b and T_a , we combined data for all age/sex groups in further analyses.

Body temperatures of 'covered' lizards were more variable than were those of 'exposed' individuals (Table 1; Levene's test: $F = 5.35$, $P = 0.02$), but the mean T_b s did not differ between these two groups (t -test for unequal variances: $t_{66} = 1.64$, $P > 0.10$). The regression line of T_b on T_a for 'covered' lizards is highly significant ($r^2 = 0.83$, $P < 0.001$) and its slope does not differ from unity ($b = 0.961$, $SE = 0.065$; $t_{103} = 0.60$, $P > 0.50$; Fig. 3). In contrast, T_b s of 'exposed' lizards were largely independent of T_a (Fig. 3); the regression slope was low ($b = 0.187$, $SE = 0.137$) and not different from zero ($r^2 = 0.26$, $P > 0.10$). The difference between T_b and T_a was more variable (Table 1; Levene's test: $F = 18.95$, $P < 0.001$) and on average higher (t -test for unequal variances: $t_{31} = 6.47$, $P < 0.001$) in the 'exposed' individuals. Hence, the T_b s of exposed lizards were more elevated above T_a than those of hidden lizards, especially at $T_a < 24$ °C (Fig. 3). The difference between the T_b to T_a relationships presumably reflects exposition to different sets of external heat loads. The 'exposed' lizards are subject to the effects of solar radiation, wind and air and substrate temperatures, whereas 'covered' individuals are mainly affected by the air and substrate temperatures in their shelters. Hence, the closer match

Table 2. Summary statistics (mean \pm SE) of body temperatures of 'covered' and 'exposed' lizards at different times of day. n , number of temperature measurements

Hour	'Covered'		'Exposed'	
	$x \pm SE$	n	$x \pm SE$	n
08:00	18.8 \pm 0.7	2	-	-
09:00	19.8 \pm 0.5	6	-	-
10:00	25.2 \pm 0.9	7	-	-
11:00	28.7 \pm 0.8	9	28.4 \pm 0.6	3
12:00	29.5 \pm 0.4	15	28.8 \pm 0.4	5
13:00	29.6 \pm 0.6	10	29.1 \pm 1.2	6
14:00	32.0 \pm 0.6	14	31.2	1
15:00	30.4 \pm 0.6	12	30.2 \pm 0.6	7
16:00	29.4 \pm 0.9	10	30.5 \pm 1.7	4
17:00	27.5 \pm 0.8	14	25.3	1
18:00	27.1 \pm 0.8	6	-	-

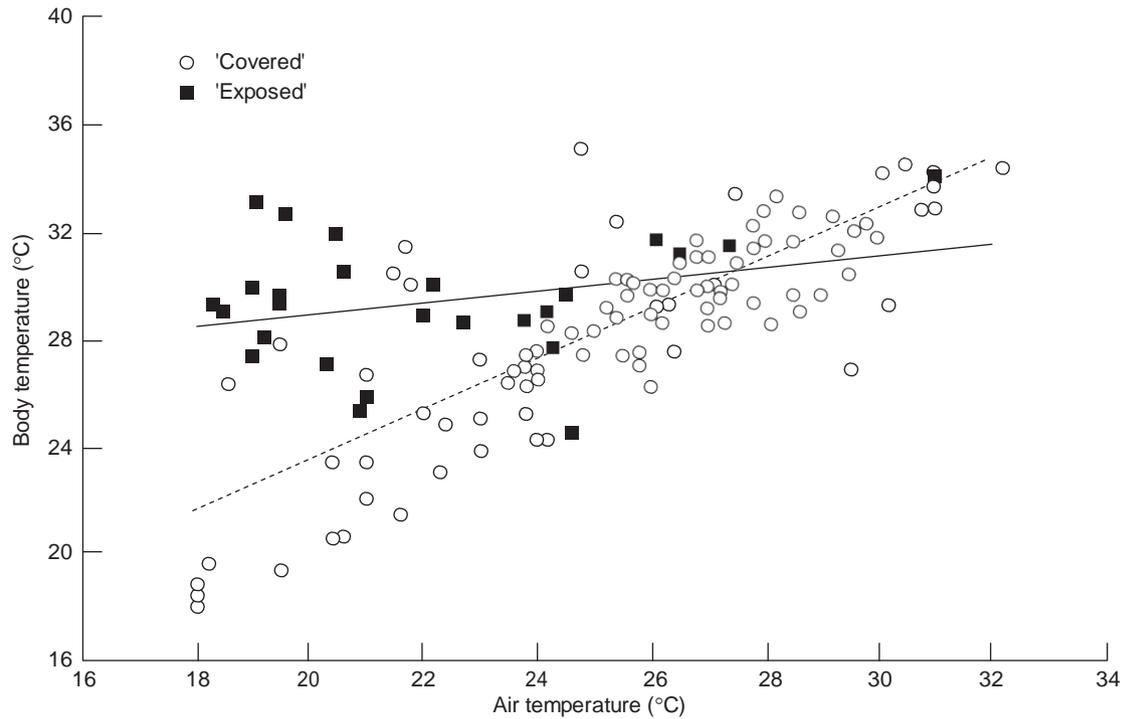


Fig. 3. Relationships between body temperature and air temperature for 'covered' (circles; dashed line) and 'exposed' (squares; full line) lizards.

between T_b and T_a in the 'covered' lizards presumably reflects, at least in part, that T_a is a better estimator of the overall heat loads experienced by these lizards.

Body temperatures did not exhibit significant diel variation in 'exposed' lizards (Table 2; one-way ANOVA: $F_{(6,20)} = 1.05$, $P > 0.30$). However, the T_b s of the 'covered' lizards differed among hours (one-way ANOVA: $F_{(10,94)} = 20.15$, $P < 0.001$). This variation was mainly induced by the lower T_b s recorded before 1100 h and after 1700 h (Duncan's New Multiple Range test; Table 2) and presumably induces the higher overall variance of the T_b s of the 'covered' lizards.

Therma) properties of microhabitats

The central 50% of the T_b s measured in 'exposed' individuals (i.e. T_{exp}) occurred between 28.0 and 31.2 °C. We use this range as a reference with which we compare the T_{ams} measured in different microhabitats at different times of day.

We used repeated measurements ANOVA to assess the effects of microhabitat type and measurement site, nested within microhabitat type, on variation in T_{am} and d_{am} , with measurement period as the within-subject factor. We detected no significant effect of site and of the interaction between site and period (all $P > 0.90$). Both T_{am} and d_{am} differed among microhabitats (T_{am} [mean \pm SE]: *E. caput-medusae*: 26.9 \pm 0.4 °C, shrub: 25.1 \pm 0.3 °C, open: 29.8 \pm 0.5 °C, $F_{(2,12)} = 37.96$, $P < 0.001$; d_{am} : *E. caput-medusae*: 2.3 \pm 0.2 °C, shrub: 3.1 \pm 0.2 °C, open: 2.1 \pm 0.3 °C, $F_{(2,12)} = 5.22$, $P < 0.05$). Moreover, the variation in both T_{am} and d_{am} was

significantly influenced by the interaction between microhabitat type and period (T_{am} : $F_{(40,240)} = 9.14$, $P < 0.001$; d_{am} : $F_{(40,240)} = 12.10$, $P < 0.001$), indicating that the pattern of diel variation in ambient heat loads differed among the three microhabitats. An identical result was obtained when the analysis was restricted to the comparison between the *E. caput-medusae* and shrub microhabitats (T_{am} : $F_{(20,200)} = 5.39$, $P < 0.001$; d_{am} : $F_{(20,200)} = 4.75$, $P < 0.001$).

Ambient heat loads in the *E. caput-medusae* and shrub microhabitats increased in a similar way during the morning hours (Fig. 4). However, T_{ams} in the *E. caput-medusae* microhabitats were higher during midday and decreased more slowly in the afternoon compared with those in the shrub sites. The interval

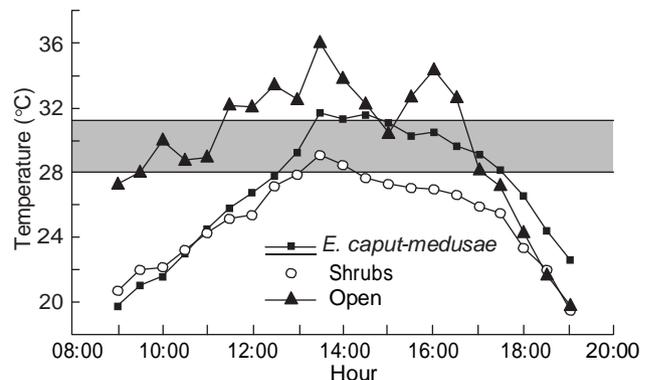


Fig. 4. Diel variation of the average ambient heat loads (T_{am}) in the *E. caput-medusae*, shrub and open microhabitats. The hatched area identifies the central 50% of the T_b s measured in 'exposed' individuals (i.e. T_{exp}).

during which at least one of the T_{ams} fell within T_{exp} (i.e. $d_{\text{am}} = 0$) in each sampling period, was considerably longer in the *E. caput-medusae* (11:30-18:00) than in the shrub microhabitat (12:30-16:30).

The open microhabitats were the hottest and experienced extremely variable T_{ams} during of the day (Fig. 4). In the morning hours (09:00-12:00) a considerable fraction of the T_{ams} were within T_{exp} , whereas during the interval 12:30-14:00 all of the T_{ams} exceeded the reference zone. A windy spell (14:30-15:30) induced T_{ams} to drop within T_{exp} ; they again exceeded T_{exp} in the subsequent two sampling periods. From 17:30 onwards, all T_{ams} in the open microhabitat were below the reference zone.

DISCUSSION

Cordylus macropholis does not correspond to the typical diurnal temperate-zone lizard that regulates its T_b by shuttling between microhabitats and overtly exposing itself to solar radiation. We discuss three noticeable aspects of the thermal biology of *C. macropholis*. First, the T_b s maintained during activity are rather low relative to those of other species inhabiting similar environments. Second, it exhibits no overt thermoregulatory behaviours, and seems to adopt T_b s close to the temperatures encountered in its shelters. Third, it restricts microhabitat usage to a single plant species that offers more suitable thermal conditions than do other shrub microhabitats.

This study provides the first published data on field T_b s in cordylid lizards. The T_b s of both 'exposed' (mean = 29.4 °C) and 'covered' (mean = 28.4 °C) *C. macropholis* were surprisingly low for a lizard inhabiting a hot and dry climate zone. For instance, T_b s of species of Lacertidae, Agamidae and Scincidae that inhabit African desert-like habitats are usually within the range 34-39 °C (Huey *et al.*, 1977; Pianka, 1986). As there is no published information on T_b s for other cordylids, we cannot determine whether the relatively low T_b s recorded for *C. macropholis* are peculiar for this species or rather represent a general characteristic of the Cordylidae. However, the following data seem to favour the latter interpretation. The selected body temperatures, maintained in laboratory thermogradients, of two *Cordylus* species are relatively low (*C. vittifer*: 32.1 °C [Skinner, 1991]; *C. jonesi*: 33.5 °C [Wheeler, 1986]). In addition, casual records of field T_b s of *C. cataphractus*, *C. niger*, *C. polyzonus* and *Pseudocordylus capensis* indicate that they are within the range 29-32 °C (J. B. Losos, P. le F. N. Mouton, D. Bauwens and A. M. Castilla, pers. obs.).

A remarkable aspect of the biology of *C. macropholis* is the low level of surface activity that we observed. Throughout the day, a majority of the lizards was found sheltering among the branches of *E. caput-medusae* plants, and surface-active individuals were seen during only a restricted time period. Most studies of field T_b s and behavioural thermoregulation of reptiles concen-

trate on exposed, active animals, although some notable exceptions have dealt with thermoregulation in retreat sites (e.g. Stebbins & Barwick, 1968; Christian, Tracy & Porter, 1984; Peterson, 1987; Huey *et al.*, 1989). The simultaneous presence of 'exposed' and 'covered' *C. macropholis* enables us to compare their T_b s and opportunities for thermoregulation. The T_b s of 'exposed' and 'covered' lizards were highly similar, especially during the interval 11:00-17:00, when individuals of both groups were caught. Such similarity of the T_b s suggests that during this period, thermal conditions encountered within the *E. caput-medusae* plants are conducive to the T_b s maintained by the 'exposed' lizards. The suggestion is supported by the correspondence between the T_{ams} within the plants and the T_b s of 'exposed' lizards. In other words, by exploiting the thermal conditions encountered under plant cover, lizards can and do maintain their T_b at levels identical to those of individuals active at the surface. Hence, based on thermoregulatory considerations alone, it is not surprising that large numbers of lizards remain under plant cover between 11:00 and 17:00.

Lizards were active at the surface for a limited time period. The absence of 'exposed' individuals during the morning (i.e. before 11:00) is especially noteworthy. This contrasts sharply to the situation in many other diurnal lizard species, where large numbers of individuals overtly expose themselves to solar radiation (i.e. 'bask') during the early-morning warm-up period (e.g. Avery, 1976; Huey *et al.*, 1977; Hertz & Nevo, 1981; Van Damme, Bauwens & Verheyen, 1987; Bauwens *et al.*, 1990, 1996). Through the adoption of basking postures, these lizards maximise their heating rate and acquire T_b s that are well above ambient temperatures (Pearson, 1954; Avery, 1976; Van Damme *et al.*, 1987; Bauwens *et al.*, 1990, 1996). In contrast, individuals of *C. macropholis* remain under cover during the morning period and seem to warm by adopting the slowly increasing ambient temperature in their shelters. They did not expose themselves until some of the T_{ams} within the *E. caput-medusae* plants, and the T_b s of the covered lizards, exceeded c. 28 °C.

These findings suggest that lizards warm up in their shelters and only initiate surface activity when their T_b exceeds some threshold value. The observation of large numbers of 'covered' lizards throughout the day indicates either that not all lizards initiate overt activity, or that they leave their shelters for only brief periods. Thus, *C. macropholis* seems to strongly reduce the time spent in surface activity. Lizards that remain under cover between 11:00 and 17:00 encounter thermal conditions enabling them to regulate their T_b at levels identical with the 'exposed' individuals. The piled-up branches of the *E. caput-medusae* plants also offer hiding sites inaccessible to most potential predators. Alas, most of the lizards' prey items have been encountered among the plants' branches, suggesting that lizards forage while they remain under cover (P. le F. N. Mouton, pers. obs.). All these factors presumably contribute to the advantages of staying under plant habitat. For instance, activity in the open microhabitats would enable lizards to lengthen the interval wherein T_b s can be maintained within the range 28-31 °C. We

cover. However, lizards that stay under cover cannot exploit the full range of thermal conditions in their

had observed that T_{ams} in the open microhabitats were often within this range during the morning hours. Moreover, individuals of *Mabuya variegata*, *Meroles knoxii* and *Pedioplanis lineocellata*, which maintain higher T_b s than *C. macropholis* (i.e. within the range 34–37 °C; Huey *et al.*, 1977; Pianka, 1986) and typically bask overtly on sand, were frequently observed from the first morning hours onwards.

In addition to the reduced number and the restricted time period during which surface-active lizards individuals were seen, *C. macropholis* shows an extremely low rate of visible movements. It is indeed remarkable that we did not observe moving lizards, apart from those that fled upon our approach. Casual observations of 'exposed' lizards showed that they retained their position for periods up to 2 h. The apparent low movement frequency of this terrestrial cordylid parallels the extremely low movement rates observed in five rock-dwelling *Cordylus* species (Cooper, Whiting & van Wyk, 1997). It contrasts clearly to the behaviour of the sympatric skink *Mabuya variegata*, which was frequently seen moving among different microhabitats.

Cordylus macropholis exhibits severely restricted microhabitat usage. All lizards observed, whether they were 'covered' or 'exposed', were within the periphery of *E. caput-medusae* plants. Although this plant is quite common in the study area, attaining densities of *c.* 1 plant per 10 m², it covers <5% of the surface. Hence, *C. macropholis* uses only a small fraction of the available space and microhabitats. What factors may favour the use of the *E. caput-medusae* microhabitat relative to that provided by other plants? With its peculiar form, this succulent provides more and safer hiding places than do more typical shrubs. The *E. caput-medusae* plants also house a large variety of invertebrate prey species (P. le F. N. Mouton, pers. obs.). In addition, our estimates of ambient heat loads indicate that thermal conditions in the *E. caput-medusae* microhabitat are conducive to the T_b s of exposed individuals for a longer daily period than in the microhabitats provided by other shrubs. The difference was most notable in the late afternoon. Hence, these plants offer superior opportunities for thermoregulation to other shrubs present in the habitat.

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