THERMOREGULATION AND ACTIVITY PATTERNS IN CAPTIVE GROUND IGUANAS *(CTENOSAURA SIMILIS)*

KYLIE GREENWOOD, STEPHEN CRANSTON, HELEN DARLINGTON
AND LAUREN GOMERSALL

The Herpetological Unit, Huddersfield Technical College, Huddersfield, U.K.
[correspondence to R. Meek at same address]

THE iguanas of the genus *Ctenosaura* are a conspicuous element of the Central American herpetofauna. Herpetologists have studied certain aspects of the biology and ecology of several species including one of the larger forms *Ctenosaura similis* (e.g. Henderson, 1973; Fitch, 1973; Fitch & Henderson, 1978; van Devender, 1979; Janzen & Brodie, 1995). The results have indicated that *C. similis* is associated with dry open woodland and savannah (Fitch, 1973, van Devender, 1979; Fitch & Hackforth-Jones, 1983), and is both terrestrial and arboreal using hollows in tree trunks, tree roots, old buildings or rock piles as retreat sites (Fitch, 1973; Burger & Gochfield, 1991). The juveniles are mainly insectivorous, but as growth proceeds shift to a mainly herbivorous diet, although when resources are scarce, may consume small vertebrates and large insects (Fitch, 1973; van Devender, 1979). Under certain circumstances they are known to travel distances to feed (Fitch & Henderson, 1978; Fitch & Hackforth - Jones, 1983).

Field workers have commented on the difficulties of studying this species under natural

conditions, pointing out that they are wary and difficult to capture as a result of their close location to retreat sites. Under captive conditions, on the other hand, certain individuals quickly become accustomed to human presence and in large naturalistic enclosures make ideal subjects for detailed continuous observation. There is little information on the behaviour and biology of captive *C. similis* - most texts are confined to a few paragraphs (e.g. Rogner, 1997), despite its presence in herpetological collections including those of zoological gardens. In this paper we have attempted to provide baseline observations on activity, behaviour and thermal biology in captive *C. similis* in the hope that the information will contribute to improving the design of appropriate naturalistic housing (see Warwick & Steedman, 1995). The results are based on a second year BTEC National Diploma Animal Behaviour Assignment at Huddersfield Technical College in which two adult *C. similis* were studied in a large naturalistic enclosure. Our assignment brief was to compare the behaviour of captive *C. similis* with what is known in the literature of the field biology of this species.

METHODS

Our observations were made at the Herpetological Unit of Huddersfield Technical College between September 1999 and May 2000. We also employed data recorded between February 1998 and June 1999 on the same lizards by two previous second year BTEC National Diploma students. A male with a body mass of 1.6 kg (Plate 1) and a female of 1.2 kg were observed for a total of 47 hours over 17 days. The enclosure layout measured 4m by 5m in ground area with a height of 4m at the apex. Natural light through glass was supplemented with four 275w spot lamps and five UV *Desert Lights* with additional heating supplied by pipes underneath the rockwork around the enclosure periphery. A major visual barrier for the lizards were two 1.5m high walls which partially

divided the unit in addition to a series of rocky outcrops and tunnels that served as retreat areas. The unit was planted with dry adapted succulent plants including two trees (*Ficus benjamina & Dracaena* sp.). These features served to enhance both the physical and thermal complexity of the enclosure (see Avery, 1985).

The amount of time (in minutes) the lizards spent in each behaviour was recorded. Behaviours were defined as 1) *basking*; either under a heat lamp or sitting in sunshine 2) *partial basking*; where part of the body was under a lamp or in sunshine 3) *shade*; no part of the body was under a heat lamp or in sunshine and 4) *hiding*; the animals were in tunnels. *Active* or *feeding* is self-explanatory. The number of activity bursts and the distances travelled were recorded.

Body temperatures were obtained by measuring skin surface temperature every 10 minutes or so using an Omega OS204 infrared detector directed at the central area of the body a few cm from skin surface. This instrument has a residual error of $\pm 1°C$ but in practice the closer the instrument to the skin surface the more accurate the reading. Generally skin surface temperature exceeds cloacal temperature in lizards and is usually dependent on body mass. For example, the difference between skin surface and core temperature was measured in a series of *Cyclura nubila* of different body masses (Alberts & Grant, 1997). Meek (1999) quantified these measurements and defined the relationship between core temperature (T_b) and skin surface temperature (T_{ss}) as:

$$(T_b - T_{ss}) = 0.00114x + 1.1195 \ (r^2 = 0.7)$$

where x is body mass in g and r^2 is the coefficient of determination. When this equation was applied to our *C. similis*, it predicted a general overestimate of core temperature from skin surface temperature of 2.9°C in our 1600g male and 2.5°C in our 1200g female. Measuring skin surface temperatures has two important benefits 1) skin surface temperature appears to be the principle input for thermoregulation in lizards

(Crawshaw, 1980) and 2) it is non - invasive and hence minimises the disturbance of behaviour patterns. Therefore although the measurements were made by placing the IR detector within a few centimeters of the skin surface of the lizards, this did not appear to disturb them in any way. A mercury bulb thermometer was used to measure shaded air temperatures 0.5m above the ground
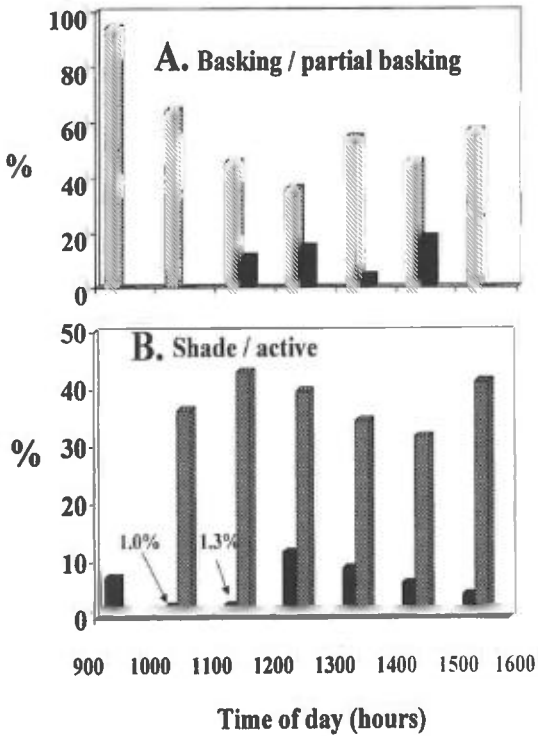
Fig. 1. Graphs showing behaviour changes as percentage frequencies of total behaviour within each hourly time period. In graph A basking is represented as cross-hatched bars and partial basking as solid bars. Graph B shows shade as cross hatching and locomotory activity as solid bars.

We recorded a total of 342 body temperatures in addition to corresponding air and substrate temperatures (Σn = 684). A further 87 records of body temperature and associated air and substrate temperatures were employed from a previous student assignment on *C. similis* giving an overall
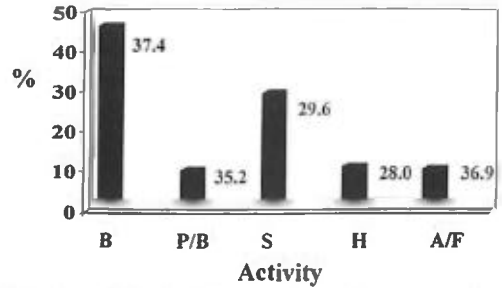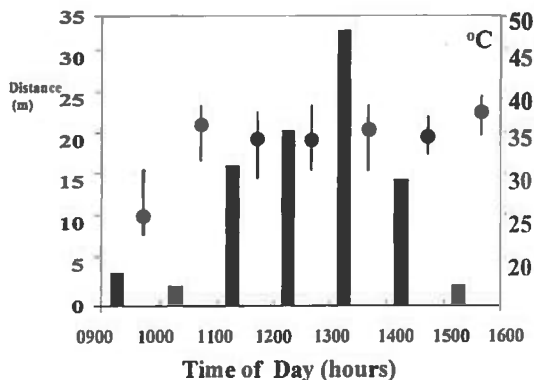

total of 429 body and 858 air and substrate temperatures.

Fig. 2. Proportional differences in behaviours (shown as percentages of total observations) observed during the study period alongside the mean body temperatures recorded during each behaviour for comparison.

RESULTS

Behaviour and Activity - Figure 1 shows the behaviour patterns of both *C. similis* over hourly periods from 0900 - 1600hrs. Basking was the dominant activity during the early part of the day but gradually declined as the morning progressed and was lowest between 1200 - 1300hrs. In the afternoon basking gradually increased again as did time spent in the shade, which was greatest during midday and late afternoon. Figure 2 shows these behaviours when the data sets from the time periods are pooled. The majority of time was spent either basking (44.8%) or inactive in shaded areas (27.9%). Smaller amounts of time were spent partially basking (8.7%) in retreat areas (9.6%) or in locomotory activity and feeding (9%).

The animals did not, however, display rigid behaviour patterns. Time in hide areas could be high on certain days, either as a result of late emergence or early retreat. For example, on 9/2/99 most observations (78%) showed that the female was in retreat until 1415hrs, and on two other days (19/10/99 & 2/11/99) the male spent 70.6% and 31% of the day in retreat. The two former instances relate to late emergence, the latter to early afternoon retreat. Environmental temperatures were not particularly low on these days, although the weather was overcast. On other days with overcast weather, the lizards were

Fig. 3. Hourly changes in body temperatures defined as medians and interquartile ranges (solid circles and attached bars) in comparison to the absolute distances travelled within any given hourly period.

abroad throughout the daily period and emerged early.

In general, locomotory activity involved shuttling between basking and shaded areas, foraging for food or to defecation sites. Early morning locomotory activity mainly concerned movement from retreat to basking sites. Figure 3 shows the total distances travelled in metres at different times of the day, indicating that locomotory activity was greatest during midday and early afternoon particularly between 1300 - 1400hrs. In general the male covered 2.1 metres per hour and the female 0.55 metres per hour. Figure 4 shows the frequency of the distances travelled during bursts of locomotory activity. These results show that most movement involved distances of less than 1 metre, although distances up to 5 - 6 metres were recorded.

Body temperatures - Table 1 gives details of the body temperature levels recorded during the study periods. The mean body temperatures (with standard errors) of the male (33.9 ±5.8°C) and female (34.5 ± 5.7°C) were not significantly different (ANOVA, $p > 0.05$) and therefore the data sets have been pooled. Mean shaded air temperatures and standard errors were 22.5±3.7, range =15 - 34.2°C, and substrate temperatures 29.1±4.9, range = 21 - 45°C. Body temperatures

ranged from 23 - 44.2°C with a general mean of 34.4°C and were significantly higher than either air ($F_{(1,856)} = 1203.2$, $p < 0.0001$) or substrate ($F_{(1,856)} = 190.6$, $p < 0.0001$) temperatures.

Regression analysis has been applied to body temperatures and associated air and substrate temperatures as a test for thermoregulation. Here a regression coefficient of 0 indicates thermoregulation and 1 thermoconformity (Huey & Slatkin, 1979). A coefficient of determination (r^2) was then applied to the data to determine the amount of variation in body temperature that could be accounted for by variation in air or substrate temperatures. Values of r^2 range from 0 - no relationship, to 1 - all variation in y (body temperature) can be accounted for by variation in x (air or substrate temperatures). The results gave regression coefficients close to, but significantly different from 0 ; air temperature = 0.27, ($t = 3.7$, $p < 0.001$), substrate temperatures = 0.22, ($t = 4.05$, $p < 0.001$). The coefficients of determination were low (air temperature, $r^2 = 0.04$; substrate temperatures, $r^2 = 0.05$). These results indicate active thermoregulation in the lizards.

Body temperatures, behaviour and time of day – Behaviour related body temperature levels are shown in Fig. 2. The highest body temperatures were recorded when the animals were in open areas (basking or partial basking) or when they were active. Comparison of these 'open area body temperatures' by analysis of variance indicated a significant difference ($F_{(2,268)} = 8.35$, $p < 0.001$). Further analysis using a multiple range test showed that partial basking body temperatures were significantly lower ($p < 0.05$). There was a significant difference between body temperatures of the lizards when they were abroad but in the shade, and when they were in hide areas in the afternoon or morning ($F_{(2,155)} = 10.2$, $p < 0.0001$). Morning retreat area body temperatures were significantly lower (multiple range test, $p < 0.05$).

In general body temperatures in excess of 30°C were attained between 1000 - 1100hrs, just before the initiation of major locomotory activity. Body temperatures were relatively stable throughout the daily period from 1000hrs
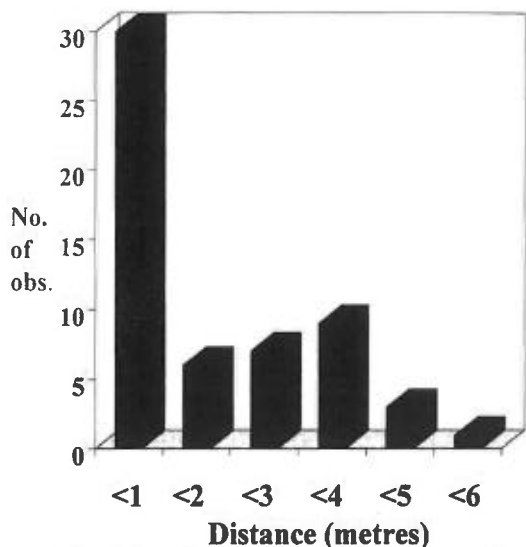
onwards although the interquartile ranges were narrower during the afternoon (1400 - 1600hrs).

Fig. 4. Frequency (on the y-axis) of distances travelled during bursts of locomotory activity in *Ctenosaura similis.*

The results are shown in Figure 3 as the hourly changes in median and interquartile ranges in body temperatures and in relation to levels of locomotory activity during the daily period.

DISCUSSION
The results of this study, based on continuous observation, have shown that two *C. similis* spent most of their time inactive in shaded or basking areas with locomotory activity and feeding accounting for only a limited amount of the daily time budget. Thermoregulation was achieved by the selection of favourable microhabitats involving shuttling between sunlit, shaded and hide areas. Relatively high and constant body temperatures throughout the daily period (Fig.3) were mainly achieved through partial basking and also the low skin surface area-to-body mass ratio that accompanies large size. This resulted in slow rates of heating and cooling giving relative thermal stability, particularly once the target body temperature range had been achieved; this must ultimately

reduce the frequency and energy costs of shuttling. Other large iguanids maintain high

Male *Ctenosaura similis.* Photograph by J. Avison.

constant body temperatures, for example *C. hemilopha* (Soule, 1963) and *Iguana iguana* (McGinnis & Brown, 1966). Improved digestive efficiency may be one of the principle benefits here, since even small differences in body temperature are known to affect digestion in reptilian herbivores (Troyer, 1987).

Through the placement of carefully selected hot spots, walls, tunnels and vegetation, our study enclosure provided both thermal and environmental complexity. In general a test for the suitability of a captive enclosure could be the degree of departure of captive animals behaviour and physiology from free-living individuals - although it should be noted that unlike our observations, the field studies of *C. similis* have been based on spot sample records. However, a general comparison of our data with current field knowledge of *C. similis*, does suggest that our lizards maintained some degree of naturalistic behaviour. For example, the extensive basking observed in our animals is similar to the field observations of both Fitch (1973) and van Devender (1979). Fitch noted that Ctenosaurs 'spend much of their time basking in sunshine even when temperature is relatively high' and suggested that 'absorption of heat may be reduced by position and orientation'. He also described what appears to be partial basking in *C. similis*. Additionally, Burger & Gochfield

(1991) found the behaviour of free-living *C. similis* in Costa Rica to be largely a function of temperature, since in this region they bask early in the morning but seek shade as the temperatures rise. Our observations of behavioural thermoregulation in captive *C. similis* showed that after a period of high early morning basking intensity, body temperatures were relatively stable with hourly median temperatures ranging between 35.5 and 38.9°C (Fig.3). These body temperatures are generally in good agreement with the field study of Fitch (1973) who indicated a thermal preferendum of 36 - 37°C based on 54 measurements of juvenile *C. similis* body temperatures in Costa Rica, although it should be noted that these were cloacal measurements.

Low levels of activity are a feature of adult *C. similis* whether they are wild (van Devender, 1979) or captive. Burger & Gochfield (1991) found that activity in *C. similis* may be bimodal with a midday retreat to burrows to escape excessive heat loads before emerging later in the afternoon. Since our study was undertaken mainly during the winter months, the enclosure was not subjected to high solar intensity and heat loads. However, bimodal activity has been observed in our animals during the summer months when temperatures are particularly hot (R.Meek, personal communication). Under such conditions our captive and wild lizards emerged earlier in the day (0730 - 0800hrs).

In its natural environment *C. similis* apparently forages at distances of only a few metres from retreats sites. Our observations indicate that retreat sites were particularly important to *C. similis*, since movement at distances from hide areas was infrequent despite their familiarity with human observers. At the completion of our study, the male lizard had used the same burrow for over two years regardless of the availability of other borrows in the enclosure. In one field study nine wild *C. similis* occupied the same burrow over a two-year study period (Burger & Gochfield, 1991). Burrows that are wider than they are high with an entrance that is exposed are the preferred types. It has been suggested that this is to facilitate basking at the burrow entrance in the morning and to optimise predator detection (Burger & Gochfield, 1991).

Retreat sites are particularly important when introducing animals into a new environment. Our male lizard when first introduced into the enclosure spent nearly 3 weeks inactive in his burrow before finally emerging. This hypoactivity has been defined as shutdown behaviour and a response to an inadequate environment (Warwick, 1995). However it could also be a temporary stress reducing mechanism (he was left undisturbed during this period) and not necessarily a long-term condition. Moving into hide areas enabled our lizards to select body temperatures lower than normal 'activity' temperatures (see Table 1); movement into hide areas forms an important part of thermoregulatory repertoires in reptiles (Huey, 1982). Licht (1965) observed deleterious effects on the physiology of certain reptiles that were unable to cool to below normal activity temperatures.

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