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THERMOREGULATION AND ACTIVITY PATTERNS IN CAPTIVE WATER DRAGONS, *PHYSIGNATHUS COCINCINUS*, IN A NATURALISTIC ENVIRONMENT

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Observations were made on the thermoregulatory behaviour and activity patterns of *Physignathus cocincinus* in a simulated tropical environment. *P. cocincinus* is a sit-and-wait predator with movement restricted to a maximum of 9 or 10 bursts of activity per day. Both terrestrial and aquatic activity were temperature dependent, and were greatest in hot, sunny weather. When the weather was overcast, the lizards spent most of their time in open areas and at higher levels in the canopy; increased sunshine induced movement to lower levels, with more time spent in shade. Regression analysis of the relationship between lizard and model temperatures was used to determine thermoregulation. *P. cocincinus* is basically a thermoconformer, but needs to thermoregulate on sunny days to avoid excessive heat loads. Control of body temperature during hot and intermittent sunshine was principally achieved by seeking shade and partial basking. On cloudy days the animals were thermoconformers, as environmental temperatures were sufficiently high to enable locomotory activity and feeding to take place, but not so high that excessive heat loads became a problem.

Key words: Physignathus cocincinus, thermoregulation, activity patterns

INTRODUCTION

Much of the early work on reptile thermoregulation concerned lizards from temperate or desert habitats (see Avery, 1979, 1982; Bradshaw, 1986 for reviews). These studies have given rise to a model of lizards as active sunbaskers, usually with precise body temperatures controlled by an elaborate series of shuttling or posturing behaviours. However, later research on lizards from forests and other densely vegetated environments described species with much broader activity temperatures, and with only occasional basking behaviour or none at all (e.g. Huey & Slatkin, 1976; Huey, 1982; Avery, 1982). Most of these studies have dealt with small lizards (<50 g); relatively few works have examined the thermal biology of the larger reptiles, including those from tropical forests. This paper is concerned with the thermal biology and activity patterns of a medium-sized, tropical forest lizard, the green water dragon, Physignathus cocincinus. Very little is currently known about the thermal ecology of P. cocincinus, despite its popularity as a zoological exhibit and presence in the pet trade. The only thermal studies are from Australian Physignathus, with field and laboratory body temperatures being recorded from P. longirostris (Licht et al., 1966) and P. lesueurii (Grigg et al., 1979).

The green water dragon, *P. cocincinus*, is a sit-andwait predator feeding on small vertebrates and insects. The species has an extensive distribution over southeast Asia and Indochina, where it lives in and around dense vegetation alongside rivers and other aquatic areas. Such environments are generally thermally stable, deviating only slightly from an annual mean of 25°C, with a wet season that lasts for several months each year. In this type of habitat, accurately measuring body temperature and continuously observing behaviour, including the habit of *P. cocincinus* of diving into water at the approach of danger, are problematical. However, in a spacious, simulated natural environment, captive animals may provide ideal subjects for detailed, continuous observation.

There has been some debate about how thermoregulatory data in reptiles should be interpreted. Early studies used the criterion of body temperatures being elevated above air temperatures as evidence of thermoregulation (Cowles & Bogert, 1944), but subsequent demonstration of the flaws of this method (Heath, 1964) prompted the use of more elaborate statistical methods. Regression analysis of body temperatures and environmental temperatures (Huey & Slatkin, 1976) provided a standard theoretical and statistical approach, although it has been suggested more recently that a reptile may not necessarily be thermoconforming when its body temperature is in agreement with environmental temperature (Hertz, 1992). The real comparison is between the actual body temperature of the reptile and the body temperature that it would have if it did not thermoregulate. This can be determined by placing models of the lizards in their environment (Bakken & Gates, 1975) and by comparing their temperatures with those of the reptiles. The temperatures of the models are therefore indicators of the consequences of non-thermoregulation in the lizards.

METHODS AND MATERIALS

ANIMALS AND ENCLOSURE

Five *Physignathus cocincinus* (two males, three females) were observed for a total of 173.7 hours on selected days from autumn 1996 to summer 1998 dur-

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ing periods of cloudy weather, intermittent sunshine and hot sunshine. The lizards used in the study were adults (one male and one female) and subadults (one male and two females), with body masses ranging from 220 to 540 g. One subadult male lizard was mostly used for behaviour observations because of its timid nature. All others could be readily approached.

The observations were carried out in a tropical enclosure at the Taylor Hill Annexe of Huddersfield Technical College. This enclosure is subject to natural sunlight through glass, measures approximately 6 m by 5.5 m at ground level, and is 4 m high. The unit was divided horizontally into 20 equally-sized areas and vertically into four levels (i.e. ground + heights 1, 2 and 3). The main shade plant was Cyperus involucratus, although several other tall species (e.g. Ficus, Dracaena & Monstera) were also present. Enclosure diversity was enhanced by the use of tree branches and a small pond (2 x 1.5 m), including a waterfall. Artificial rainfall was also in operation. On cool, cloudy days the lizards were given the opportunity to elevate their body temperatures through the use of two 275 W spot lamps. One of these was placed above a tree branch at height 2, the other focused on a ground area. Both lamps were placed in areas frequented by the lizards.

BEHAVIOURAL OBSERVATIONS

The locations of lizards were recorded, together with their positions in relation to sunlight. Behavioural definitions are similar to those in Meek (1984, 1988a): basking, inactive and exposed to the sun's rays; shade, inactive in an area where no sunlight penetrated. Locomotory activity is self explanatory, but a further apparently important behaviour is partial basking. Here the animal sits with a mosaic of sunlit and shaded patches on its body. Behavioural observations were continuous and defined as the total number of minutes that each animal was involved in a particular activity. Entry into the water was also recorded

BODY TEMPERATURES

A total of 608 body temperatures were recorded, although these were actually measurements of skin surface temperatures recorded with an infrared detector (Digitron 232-3305 Pyrometer). This device is a noninvasive temperature indicator that can measure the infrared radiation emitted by reptiles (emissivity = 0.95, Tracy, 1982). Infrared energy is focused onto a thermophile via a germanium filter. The equipment has a resolution of 0.1° C, and the error is 1%, although the larger the lizard and the closer to the animal that the readings can be taken, the more accurate the measurement. Most animals used in the study allowed approach to within a few centimetres of skin surface without any apparent disturbance of behaviour patterns.

Estimates of the differences between skin surface temperature and cloacal temperature have been made for *Cyclura nubila* by Alberts & Grant (1997). For animals of 500 g body mass they found a relationship of the form:

$$(T_{b}-T_{ss}) = 0.776 (T_{ss}-T_{a})+T_{a}$$

where the estimated difference between cloacal temperature T_b and skin surface temperature T_{ss} is derived from air temperature T_a and a regression coefficient of 0.776. Examination of the data from Table 1 of their paper using least squares regression (including an additional measurement of a 6.65 kg *C. nubila* mentioned in their text) indicates that the observed differences were mass-based with the general error estimated as:

$$(T_{b}-T_{c})=0.00114x+1.1195, (R^{2}=0.7)$$

where body mass (x) is in kg. This equation predicts an overestimate of cloacal temperature of between 1.3 and 1.7°C in 200-500 g animals, equivalent to the size range of the lizards used in this study.

For comparison, measurements of the differences between skin surface and cloacal temperature were made on a 540 g adult male *P. cocincinus*. Cloacal temperatures were measured with a Yellow Springs Instruments Telethermometer (model 441A) and calibrated thermistor probe. The results indicated an increasing difference between skin surface and cloacal temperature with increasing temperature. The highest overestimate (n = 9) was 3.5°C (mean=2.2, SE=0.8). Mean underestimate (n=5) was 1.2°C±1.1 but in one instance reached 3°C. Generally the Alberts & Grant (1997) model for *Cyclura* would predict smaller errors.

LIZARD MODELS

To gather evidence of thermoregulation, models of P. cocincinus were constructed and placed in selected areas in the enclosure, usually in locations where the lizards had vantage points, but with one model placed in areas which they did not usually frequent (see Fig 1). The changes in temperature of the lizards and the models were compared using regression analysis, with the temperatures of the models treated as the independent variable and the temperatures of the lizards the dependent variable. The regression coefficients were then tested against the expected coefficients of a hypothetical thermoregulator (Bailey, 1981) which have expected values of 1.0 for thermoconformity and 0 for thermoregulation. This assumes a null hypothesis of no thermoregulation in the models (Bakken & Gates, 1975).

Lizard models were constructed of modelling clay with a light metal substructure. The models had similar mass and colour to the real lizards. A simple heating rate test comparing a 0.540 kg lizard and a 0.5 kg lizard model over a temperature range of 22.8 to 29.8°C showed that the lizard heated slightly more quickly than the model. The relationship is described by:

$$T_{h}=1.1T_{m}-1.17, (R^{2}=0.83)$$



FIG. 1. A series of histograms on a three dimensional plot showing the areas of the enclosure occupied by the lizards. The plots for individual lizards are: m_1 , a large adult male; m_2 , a subadult male; f_1 , a mature female; and f_2 and f_3 , subadult females.

where T_b is the temperature of the lizard, T_m model temperature and R^2 the coefficient of determination. This equation suggests that the models gave a reasonable estimate of potential lizard temperatures.

Lizard temperatures, model temperatures, air and substrate temperatures were recorded simultaneously. Air temperatures were taken 10 cm above the ground and substrate temperatures by directing the infrared pyrometer at the soil. Model temperatures were measured in a similar way to real lizard body temperatures, by pointing the pyrometer at the central area of either the animal's or model's mass. All body temperatures are shown with standard errors, and statistical tests are set at the 95% level using the F, t and Q-distributions (Parker, 1973; Bailey, 1981).

RESULTS

HORIZONTAL MOVEMENT

Fig. 1 is a series of histograms on a three dimensional plot showing the areas occupied by each lizard in the enclosure. The results are derived from the time the lizards occupied each grid square after the data were converted into percentages. No lizard during the observation periods was seen to move through all the grids (n=20), indicating a limited movement lifestyle. The large male (M_1) had been in the enclosure for the longest period (>2 years), but was not seen in five (25%) of the grids. The subadult male (M_2) had the most restricted movement, occupying only five grids and then mostly at higher areas in the canopy. The graphs show that each lizard occupied distinct areas with only small areas of overlap.



FIG. 2. Time spent by adults (left) and subadults (right) at different heights in the canopy. a, cloudy weather in winter; b, cloudy weather in summer; c, intermittent sunshine; d, hot sunshine. The data are shown as percentage frequencies from the highest (3) to lowest level (G).

TABLE 1. Summary statistics of the frequency of locomotor activity, the daily distances moved (in metres) during activity, and the frequency of entry into water (per hour) in *P.cocincinus* during different weather conditions. Data for *Activity* and *Entry into water* are shown as mean rates per hour; for distances travelled in each activity burst, the number of observations are shown. *n*=no. of days for *Activity* and *Entry into water*; *n*=no. of observations for *Distances travelled*.

	Range	Mean	SE	n
Activity:	-			
sunny weather	0.38-3.5	1.85	1.08	8
intermittent sunshine	0.32-3.8	1.25	0.99	10
cloudy weather	0-1.5	0.72	0.47	11
Distances travelled:				
sunny weather	0.1-5.0	1.02	1.01	73
intermittent sunshine	0.1-5.0	0.97	0.93	64
cloudy weather	0.1-4.5	1.05	0.96	56
Entry into water:				
sunny weather	0.43-0.87	0.58	0.17	4
intermittent sunshine	0.19-0.75	0.4	0.24	5
cloudy weather	0-0.45	0.17	0.15	6

VERTICAL MOVEMENT

Fig. 2 is a series of histograms showing the time different heights in the canopy were occupied by adult and subadult lizards during different seasons. On days with cool cloudy weather, either in summer or winter the lizards occupied higher levels of the canopy but responded to increasing amounts of sunshine by retreating to lower levels. However, subadults spent significantly more time at either height 3 (χ^2 =6367, df=3, P<0.001) or height 2 (χ^2 =14.82, df=3, P<0.01) than adults during any type of weather.

LOCOMOTOR ACTIVITY AND ENTRY INTO WATER

Table 1 shows the levels of activity and frequency of entry into the water. The data from all five lizards are pooled. Entry into the water is shown in both series of data as the mean rate of entry per hour. Activity and entry into the water increased proportionately with increasing levels of sunshine, being most frequent during hot sunny weather. During cloudy weather locomotor activity and entry into water did not occur at all on certain days. The attached standard errors show some variation within, and overlap between, the data sets. However, analysis of variance indicated that they were not homogenous; *activity*, $F_{2, 26}$ =3.50, P< 0.05; *swimming*, $F_{2, 12}$ = 4.32, P< 0.05 (*n*-2 days). Further analysis using a multiple range test with the Q-distribution (Parker, 1973) showed that the frequencies of activity and swimming observed under cloudy weather were significantly lower than recorded during the other weather periods (P < 0.05).

Distances travelled during bursts of activity during sunny weather, intermittent sunshine and cloudy weather, winter or summer, are shown in Table 1. Comparison of these data using analysis of variance showed that there were no significant differences between the data sets ($F_{2,191}=0.11$, P>0.05). Although activity there-



FIG. 3. Comparative behavioural patterns in *P. cocincinus* during: a, sunny weather; b, intermittent sunshine; c, cloudy weather in summer; d, cloudy weather in winter. The data are expressed as percentage frequencies of time in shade (S), partial basking (P/B), basking (B) and basking under a heat lamp (BL).

fore increased with increasing levels of sunshine, the actual distances travelled during each burst of activity did not.

THERMOREGULATORY BEHAVIOUR PATTERNS

Fig. 3 shows behaviour patterns for all five lizards during different weather and at different times of the year. The graph clearly shows major adjustments with different environmental conditions. For example, basking was only a major activity when the weather was cloudy. Shade seeking increased in proportion to the amount of solar energy available, being lowest through the winter period (7.5%), progressively increasing through cloudy weather in summer (17.1%) and intermittent sunshine (32.1%), and reaching a peak in hot sunny weather (54.5%). Partial basking was an important behavioural mechanism for controlling body temperature when the sun was shining or if there was intermittent sunshine (37% and 43.6% of observations respectively). In summer, when the weather was overcast, 76.4% of observations were of lizards situated in a full basking position and only 2.1% basking under a heat lamp. On overcast days in winter, 69.8% of lizard behaviour was spent in a full basking position, with a significant increase in basking under heat lamps (22.8%; χ^2 =19.7, P<0.001, using Yates' correction factor).

Although subadults spend more time at higher levels in the canopy than adults, the differences in time that either group spent in shade during hot sunshine (adults 56.4%, subadults 58.6%) or intermittent sunshine (adults 45%, subadults 41%) were not significant. There was also no significant difference in the amount of time that either group spent partially basking during hot sunshine (adults 37.1%; subadults 36.9%) or intermittent sunshine (adults 28%; subadults 30.5%). All χ^2 tests, *P*>0.05.

BODY TEMPERATURES

Fig. 4 shows the distribution of P. cocincinus body temperatures during different weather conditions, with the corresponding values for skewness and kurtosis; Table 2 shows the summary statistics. Body temperatures (data for all five lizards pooled) were higher when there was hot (mean=28.7±2.9°C, n=153) or intermittent sunshine (mean= 28.7 ± 2.3 °C, n=240) than on days (winter or summer) when the weather was overcast (mean=26.1±2.9°C, n=146). Comparison of these data using analysis of variance revealed a significant difference ($F_{2,537}$ =0.2, P<0.0001). Analysis with a multiple range test showed that cloudy weather data were significantly lower (P < 0.05). Body temperature distributions were negatively skewed during sunny weather and when the lizards used the basking lamps during overcast weather; under other conditions they showed positive skewness. The kurtosis value (k=3.9) exceeded that expected in a normal distribution (k=3.0) only during hot sunny weather. A rather low value (k=2.0) was found for data from overcast days when the lizards used basking lamps.



FIG. 4. Frequency distributions of body temperature of P. cocincinus at 2°C intervals during: a, sunny weather; b, intermittent sunshine; c, cloudy weather; d, cloudy weather when the lizards used heat lamps for basking. The data are shown as percentage frequencies, with the degrees of skewness (S) and kurtosis (K) for each histogram.

The data in Table 2 show that the interquartile ranges were narrower during hot sunny weather or intermittent sunshine than when the weather was overcast, both when the lizards used the heat lamps and when they did not. Statistical tests for differences between the body temperatures of adults and subadults were made in consideration of subadults spending more time at higher levels in the canopy. The differences (Table 2) were not significant. Presumably, subtle behavioural adjustments - e.g. postural changes or variations in the ratio of shaded areas to non-shaded areas on the body during partial basking - were employed to cancel out different thermal loads at different canopy heights.

Body temperature levels were significantly higher when the lizards used the basking lamps on cloudy days in winter (mean=31.0±4.0°C) than during cloudy days, either in summer (mean=26.9±2.9°C) or in winter (mean=25.7±2.6°C) when they did not; $F_{2, 213}$ =22.9, P<0.0001 and multiple range test (P<0.05).

TABLE 2. Summary statistics of body temperatures of *P. cocincinus* recorded under different environmental conditions. Q_1 and Q_3 represent the lower and upper quartiles. The mean values are given with one standard error, number of observation *n*, and minimum and maximum ranges. Statistical comparison of subadult and adult body temperatures, by analysis of variance, are also shown when appropriate.

	Mean	SE	п	Q ₁	Median	Q ₃	Max.	Min.		
Sunny weather (sum	ner)									
Adults	28.4	3.01	90	26.7	28.3	30.7	34.7	19.0		
Subadults	29.1	3.07	63	28.4	29.8	30.9	35.8	20.0		
	$F_{1,151} =$	0.26, <i>P</i> >0	0.05							
Intermittent sunshine										
Adults	27.8	2.2	112	26.7	27.8	29.2	34.0	22.8		
Subadults	28.4	2.4	128	27.0	28.2	30.7	34.8	22.2		
	$F_{1,238} =$	3.096, <i>P</i> >	0.05							
Overcast (winter and	summer whe	n heat lan	nps were	not used)						
Adults	26.2	3.1	98	23.8	25.8	28.8	33.4	20.0		
Subadults	27.0	3.8	48	23.0	28.3	30.8	32.1	20.8		
	F _{1,144} =	1.88, <i>P</i> >0	.05							
Overcast winter (heat lamps used).										
Adults	31.0	4.0	69	27.8	31.9	34.3	36.4	23.1		

COMPARISON OF BODY TEMPERATURES WITH MODEL TEMPERATURES

During cloudy weather, regression analysis of the relationship between lizard body temperatures (T_b) and temperatures of the models (T_m) situated where the animals spent most of their time $(T_{m1}$ was taken at high elevations between levels 1 and 2, and T_{m2} was for ground areas) gave:

> $T_b = 0.72T_{m1} + 7.02, R^2 = 0.57, and$ $T_b = 0.91T_{m2} + 4.35, R^2 = 0.23.$

Data gathered during intermittent sunshine gave regression coefficients close to 0, but with very low coefficients of determination $(T_{m1}=0.18, R^2=0.11; T_{m2}=0.31, R^2=0.10)$ as did those for sunny weather $(T_{m1}=-0.04, R^2=0.08; T_{m2}=-0.03, R^2=0.07)$. These results indicated a number of trends. During

These results indicated a number of trends. During cloudy weather *P.cocincinus* thermoconformed with regression coefficients of 0.72 and 0.91 against the (non-thermoregulating) models. A series of *t*-tests (Bailey, 1981) confirm a significant departure from thermoregulation: $(T_{m1}) t=15.2$, P<0.001, df=179; $(T_{m2}) t=6.54$, P<0.001, df=179. Intermittent sunshine gave regression coefficients closer to those of a hypothetical perfect thermoregulator, but still significantly different values for *t*; $(T_{m1}) t=4.72$, $(T_{m2}) t=4.38$ - both P<0.001; df=174. The regressions differ significantly from thermoconformity (*t*-values 8.83 and 9.94, both P<0.001). Although just outside theoretical predictions, during hot, sunny weather with clear skies the

regression coefficients (-0.04, -0.03) were in agreement with thermoregulation (*t*-values -0.99 and -0.93, both P>0.05).

REGRESSIONS FOR NON-TERRITORIAL LOCATIONS

The regressions for body temperatures in relation to the temperatures of a model (T_{m3}) situated in areas which the lizards only rarely frequented gave similar results. For cloudy weather (not including data when the lizards used basking lamps) the results indicate thermoconformity, since:

$$T_{b}=1.02T_{m3}+0.93, R^{2}=0.51$$

with the regression coefficient not significantly different from 1.0 (P>0.05). There was no agreement between lizard body temperatures and model temperatures during hot or intermittent sunshine. The regressions were 0.08 (sunny weather, R^2 =0.008) and -0.08 (intermittent sunshine, R^2 =0.008).

BODY TEMPERATURES DURING CLOUDY WEATHER IN WINTER

Data gathered in the winter months was confined to days when the weather was overcast. On the days when *P. cocincinus* basked under the lamps, the regressions $(T_{m1}=0.05, R^2=0.11; T_{m2}=-0.06, R^2=0.05)$ showed very little association between body temperatures and model temperatures. The regressions do not differ significantly from 0 (*t*=0.21 and -0.15 respectively, both *P*>0.05).



FIG. 5. Thermal history of adult male (>500 g) *P. cocincinus* (solid squares), high-level model (T_{m1} , solid circles) and low-level model (T_{m2} , open circles) during a day of cloudy weather and occasional hazy sunshine. At the bottom of the graph are shown: the number of bursts of activity (solid triangles); time spent by the lizard in open areas (unhatched), partial shade (hatched), and in shade (solid); weather conditions as hatched areas for hazy sunshine and solid areas for cloudy weather.



FIG. 6. Thermal history of the lizard and models described in Fig. 5, but during a day with hot sunshine and continuously clear skies. The symbols on the main graph are those for Fig. 5. At the bottom of the graph are shown:the time the models spent in full sun (unhatched); filtered sun (hatched) and shade (solid). The circled points on the main graph indicate the readings of body temperature prior to entry into water.

BODY TEMPERATURES, MODEL TEMPERATURES, WEATHER AND TIME OF DAY

Fig. 5 shows an example of the thermal history of a large (alpha) male in relation to corresponding temperature changes of the models during cloudy weather with occasional hazy sunshine. In the lower part of the graph, the number of bursts of activity and the time the lizard spent in the sunshine, shade and partial shade are shown, in addition to weather conditions on the day (10 June). Mean lizard body temperature and SE for the period was $27.2\pm1.6^{\circ}$ C; compared to T_{ml} at $27.3\pm1.8^{\circ}$ C and T_{m2} , at $23.5\pm1.2^{\circ}$ C. The lizard spent 61% and 39% of its time at levels 1 and 2 respectively.

Models were placed at the junction of levels 1 and 2 (T_{m1}) and on the ground (T_{m2}) . Regressions of lizard body temperatures against model temperatures, with ttests against thermoconformity gave coefficients of 0.7 for T_{m1} (R²=0.70; t=0.19, P>0.05) and 0.76 for T_{m2} $(R^2=0.26; t=2.76, P<0.02)$. These results suggest that the lizard essentially thermoconformed. However, the behaviour of the lizard appears to show subtle thermoregulation using minimum activity. From 0800-1100 hrs the animal spent its time at height 2 in an open area close to the position of T_{mi}. During most of this period there was hazy sunshine, with about 45 mins of cloud when the lizard elevated its body temperature from 22-31°C. Two short bursts of activity at 1100 hrs (the only movement recorded throughout the observation period) taking it to a shaded area, resulted in stable body temperatures for the rest of the period. The brief period in hazy sunshine from 1215-1235 hrs was the result of the movement of the sun in relation to the stationary lizard.

Fig. 6 shows the thermal history of the same lizard during hot, sunny weather with clear skies (17 June). The lower part of the graph represents the amount of locomotory activity and the time the lizard or models spent in sunshine, partial shade or shade. The models were placed in similar locations to 10 June and the amount of time they were situated in sunshine, partial sunshine or shade was entirely dependent on the movement of the sun.

Compared to the data in Fig. 5, several important differences are apparent. There was an increased level of locomotory activity (eight bursts) and more entries into water (two). A large part of the day was spent lower in the canopy, with 47% at ground level and 53% at height 1. Entry into the water resulted in major reductions in body temperature. The temperature of the models reached lethal levels for lizards ($T_{ml} = 54.4$ °C; T_{m2} =45.2°C) and were high for most of the day. Lizard body temperatures, however, were in good agreement with body temperatures shown in Fig. 5 (intermittent sunshine and cloud, mean=27.2±1.6°C; hot sunshine, mean=26.04 \pm 2.54°C, $F_{1,53}$ =3.46, P>0.05). For a brief period the lizard was in full sun (2.2% of observations), the rest being spent either partially basking (17.9%) or in the shade (79.9%). The regression coefficients indicated no association with the models and no significant departures from 0 (T_{ml} =-0.09, T_{m2} =0.16; *t*-values -1.34 and 2.03, both *P*>0.05). The coefficient of determination was 0.06 for T_{ml} and 0.27 for T_{m2} . This shift in association between the models may reflect changes in vertical movement of the lizard in the canopy during different types of weather.

DISCUSSION

Continuous observation of *P. cocincinus* showed that by thermoregulating carefully, this species is active (i.e. able to remain abroad and vigilant) throughout even the hottest weather. Excessive heat loads are dealt with by microhabitat selection (e.g. by moving within the canopy or by entering water) and behavioural adjustments; primarily, partial basking and shade seeking. Under natural conditions it might have been concluded that at such times the lizards were inactive, as a result of the difficulties of observation.

However, it is possible that in a captive environment there were factors influencing the ability to thermoregulate and display natural behaviour patterns;. For example, the observations on different individuals were not independent. Social behaviour is one possible influencing factor. There are good reasons for believing that the effect was minimal in this study. Intense levels of social interaction were not apparent in the study animals, and in the species generally, may be confined to rivalry between large adult males, only one of which was present in the enclosure. These large males appear to be tolerant of subadults and females, who interact with one another only at a very low level, if at all (nothing of any significance was observed during the study). It was not uncommon for lizards to be situated close to each other, and the subadult male was even observed in the close vicinity of the large male.

The data in Fig. 1 show not only limited home ranges, but also territory overlap between certain animals. It is likely that this limited movement lifestyle is based on energy costs rather than constraints on social behaviour - the greater range of the adult female possibly being related to exploratory behaviour for nest sites. The presence of subadults (Fig. 2) higher in the canopy may be an adaptation to avoiding terrestrial predators, larger animals finding it more difficult to perch on the thinner vegetation. The absence of statistical departures in body temperature levels between adults and subadults suggests a limited thermoregulatory cost in this behaviour, if any at all.

An open-mouthed posture - similar in appearance to gaping - was regularly observed in the adult male and female *P. cocincinus* during the study period. Simultaneous measurements of body temperatures (range 23-31°C, n=12) and observations of behaviour suggest that the function is probably (in conjunction with headbobbing and arm waving) for communication between individuals rather than a thermoregulation mechanism. This may have been a communication between the two

adults since they were in the vicinity of one another at such times - although the open-mouthed posture was never observed simultaneously in the two animals. Furthermore, there was no intense follow up, such as evidence of chasing, after it occurred.

Activity patterns of reptiles in tropical environments are constrained by high heat loads (e.g. Hailey & Coulson, 1996) rather than by the primary requirement of basking to raise body temperature in temperate forms (e.g. Avery, 1976; Avery et al., 1982), particularly when body masses approach 1 kg (e.g. Meek, 1988a). The results of this study are in good agreement with those of Stevenson (1985), who estimated that habitat use and adjustments in activity were the most effective mechanisms for a 1 kg reptile to control body temperature, a view supported in subsequent studies of a tropical tortoise Kinixys spekii by Hailey & Coulson (1996). The behaviour of P. cocincinus fits theoretical predictions on the effects of high heat loads on sit-andwait predators, which should increase activity as a result of solar radiation falling on selected vantage points. Sit-and-wait predation is energetically economical, since four- to six-fold increases in locomotory activity increase energy costs by approximately 30-50% in reptiles (Huey & Pianka, 1981).

Sentinel behaviour and site location in sit-and-wait predators are crucial for detecting predators and prey, and in males for monitoring the movements of females and rival males. Thermoregulatory behaviour in an ecological context must be sensitive to these requirements if they are to be balanced optimally. *P. cocincinus* were present for long periods at regular perch sites, often with no major locomotory activity for several days. However, they were always alert and presumably scanning the surrounding area. Partial basking is a behavioural mechanism that contributes in an important way to balancing heat losses and gains. This permits the retention of scanning opportunities by avoiding a full retreat into dense shade.

In a tropical environment, the costs of basking and raising body temperature for P. cocincinus should be low, as movements between sunlit and shaded areas will be short. When conditions allow, thermoconformity saves energy by reducing shuttling, but any movement away from cover increases the costs of shade seeking (Asplund, 1974; Lee, 1980; Huey, 1982). Precise thermoregulation during hot sunshine, and thermoconformity during overcast weather, may reduce the energy costs of thermoregulation in tropical reptiles (e.g. Lee, 1980; van Marken Lichtenbelt et al., 1997). For example, in shaded forests Anolis lizards thermoconform, but they thermoregulate carefully in open habitats (Huey, 1974; Lister, 1976; Lee, 1980; Huey, 1982). Thermoregulatory costs may be reduced in semi-aquatic reptiles which thermoconform when water temperatures are high but bask when the weather is cooler or overcast (Edgren & Edgren, 1955; Meek, 1983). Increases in body mass further increase the costs of shuttling, although how important this is in *P. cocincinus* is not clear. It is interesting to note, however, that short term shuttling is not abandoned in *Crocodylus porosus* and *Crocodylus johnstoni* until body masses of 20 kg are exceeded (Grigg *et al.*, 1998).

The ability to feed at relatively low body temperatures (minimum observed, based on five cool days: 21.8°C, mean=22.6±0.53) and the occasional use of basking lamps during prolonged periods of overcast weather, could suggest an adaptation to cooler conditions during wet seasons. Why P. cocincinus should use basking lamps to raise body temperature only on certain days is not immediately obvious, although under natural conditions irregular basking has been observed in free-living reptiles, including temperate forms (e.g. Auth, 1975). The low kurtosis value shown in Fig. 2 may be relevant. It could, for example, indicate a reluctance to temporarily abandon sentinel locations; movement to the sites of the basking lamps may be energetically or ecologically costly and any benefits gained from raised body temperatures must be outweighed by the costs incurred. There was no evidence of daily shuttling between basking and perch sites, that is there was invariably only one visit to a heat lamp on such days.

Even allowing for the differences between skin surface temperature and core temperature, the body temperature ranges recorded in P. cocincinus were lower than the body temperatures recorded from the Australian form P. longirostris (Licht et al., 1966). P. longirostris (Licht et al., 1966) and P. lesueurii (personal observation) occupy more open and structurally simpler habitats than P. cocincinus, and may have greater thermoregulatory costs (Asplund, 1974; Huey, 1982). Relatively low body temperatures in P. cocincinus could also indicate a wide safety margin before critically high temperatures are experienced, as has been indicated in Kinixys spekii (Hailey & Coulson 1996). Even temperate reptiles of this size range are in danger of overheating during hot weather (Meek, 1984), particularly when involved in crucial activities (Meek, 1988b). Low body temperatures also reduce metabolic costs (Christian et al., 1984) and when inactivity and cryptic colouration are the main predatory/ anti-predator mechanisms, sprint speed - an ecologically important performance trait in lizards (Garland & Losos, 1994) - may not be so critical.

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