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Evidence that humidity influences snake activity patterns: a field study of the Malayan pit viper *Calloselasma rhodostoma*

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Multivariate statistical methods were used to elucidate which environmental factors influence the activity patterns of free-living Malayan pit vipers, *Calloselasma rhodostoma*. Fourteen adult snakes were implanted with miniature radiotransmitters and located a total of 887 times in 5 months. The pit vipers usually remained coiled on the ground for several consecutive days before moving at night to a new site. Partial correlation tests revealed that the frequency and distance of movements to new sites by tagged snakes were highly positively correlated with ambient relative humidity, but not with rainfall, ambient temperature or the lunar cycle. This finding was corroborated by the frequency with which active non-tagged *C. rhodostoma* were encountered at night. In each site, the proportion of the snakes' bodies exposed to view was positively correlated with ambient humidity, and the snakes retreated to areas with deeper undergrowth when ambient humidity was low. Overt thermoregulatory behaviour was not observed, and implanted thermosensitive transmitters revealed that the snakes were passive thermoconformers.
These findings seem to contradict much of the current literature which shows temperature to be the dominant abiotic factor affecting reptilian activity, but most herpetologists have considered only temperate forms. Ambient temperature in our tropical study site was warm and relatively constant throughout the year (mean daily range = 24–33°C), so the pit vipers could passively maintain body temperature within a fairly narrow range, with a daytime mean of 29.4°C. Ambient relative humidity, on the other hand, was very variable, and confining exposure and activity to periods of high ambient humidity may be necessary to avoid dehydration.

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The factors which govern the activity patterns of snakes are only just starting to be clarified (reviewed by Gibbons and Semlitsch 1987, Gregory et al. 1987). Several recent studies examined the association between snake activity and the lunar cycle (Madsen and Osterkamp 1982, Houston and Shine 1994, Clarke et al. 1996), but most workers have focused solely on the role of environmental temperature. Numerous publications attest to the ability of snakes to regulate body temperature by moving to warmer or cooler microhabitats as and when appropriate (reviewed by Avery 1982, Lillywhite 1987, Peterson et al. 1993), and the use of implanted thermosensors to monitor core body temperature has become a popular refinement of ophidian telemetry studies (e.g. Sanders and Jacob 1981, Shine and Lambeck 1985, Graves and Duvall 1993).

The potential influence of humidity on snake behaviour, on the other hand, has largely been ignored by

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the scientific community. This variable is rarely monitored in laboratory or field investigations, and historically has been overshadowed by the assumption that the thermal environment is much more important. Repeated observations of a snake retreating under a rock at midday, for instance, would commonly be interpreted in thermoregulatory terms without considering, as an alternative hypothesis, whether it is seeking more hygric conditions (e.g. Huey et al. 1989). However, herpetoculturalists recognise the importance of maintaining certain levels of humidity for the successful husbandry of many species (Obst et al. 1988, Coborn 1991, Cox 1991). Further to this, many experienced field biologists suspect that snakes become more active under more hygric conditions (e.g. Fitch 1960, Klauber 1972, Shine 1991), but this conjecture has not been rigorously tested.

The aim of our investigation is to elucidate some of the abiotic factors which govern the activity patterns of the Malayan pit viper (*Calloselasma rhodostoma* [Boie]) with the aid of radiotelemetry and multivariate numerical methods. *Calloselasma rhodostoma* is a small (usually <1 m total length) crotaline snake which inhabits lowland forests, scrubland, plantations, and gardens in southern Vietnam, Laos, Cambodia, Thailand, west Malaysia and Java (Gloyd and Conant 1990). It typically lies coiled and motionless on the ground, relying upon crypsis to avoid detection by predators and to ambush prey. *Calloselasma rhodostoma* is nocturnal and tropical, and thus provides a novel contrast with most previous field studies of snakes, which examine the behaviour of diurnal, higher-latitude species. Furthermore, a better understanding of the behavioural ecology of this dangerous snake may help humans avoid being bitten, for *C. rhodostoma* is the leading cause of venomous snakebite in southeast Asia (Warrell 1986).

Our field-based study will adopt a largely multivariate approach to elucidate which environmental variable or variables are significantly associated with activity patterns exhibited by *C. rhodostoma*. A wide range of climatic and structural variables will be measured and tested simultaneously, including temperature, rainfall, and the lunar cycle. Unlike most ethological studies of reptiles, we will explicitly test whether snake behaviour is associated with temporal variation in humidity.

Materials and methods

Study site

The study was based in Ladang Sungai Dingin, a 100 km^2 plantation estate in Kedah State, West Malaysia (5°22′N, 100°35′E: altitude 100 m). The climate in this region is seasonal, with low rainfall during January (94 mm) and February (79 mm): all other months have 140–430 mm on average. The temperature regime scarcely varies throughout the year, with monthly mean minimum air temperatures of 23–24°C and mean maximum air temperatures of 31–33°C (Pearce and Smith 1993).

The estate was partitioned into stands of rubber trees *Hevea brasiliensis* and oil palms *Elaeis guineensis* interspersed with numerous streams and drainage ditches. Trees were planted in rows at 4–5 m intervals, accessed by narrow footpaths cut through the undergrowth. The floor was heavily shaded by the tree canopy and largely covered by leaflitter and low (<1.5 m) native vegetation, predominantly the genera *Mimosa*, *Ipomoea*, *Blechnum* and *Pteridium*. Prey of *C. rhodostoma* were abundant, including frogs, small snakes and lizards, rats and centipedes. Predators of snakes within the estate included feral cats and dogs, mongooses, raptors and monitor lizards.

Study animals and radiotelemetry equipment

Epoxy-coated radiotransmitters with transmission frequencies of 173.20–173.35 MHz were used. Twelve were locational only and two were thermosensitive to monitor body temperature. Each complete package was 3.2–3.5 g mass (<5% snake body mass). Receiving equipment comprised an M-57 Mariner radar receiver with a 3-element Yagi antenna. The reception distance rarely exceeded 100 m.

Nine adult male (total length 596–693 mm; mass 70–175 g) and five female *C. rhodostoma* (total length 627–773 mm; mass 100–255 g) were found in January 1994 by driving through the estate after dusk. Under methoxyflurane anaesthesia, each transmitter package was intraperitoneally implanted posterior of the gall bladder via a 10 mm incision, and the 150 mm flexible whip antenna was implanted subcutaneously using the method of Reinert and Cundall (1982). Incisions were closed with chromic catgut (size 3.5). The pit vipers were left undisturbed for 48 h after surgery, then released at night to within 10 m of their capture sites.

The first tagged pit viper was released in January and the last data recordings were taken in late May 1994. This period included the start of the rainy season (late February), which marks the start of the mating season. Most adult female *C. rhodostoma* in west Malaysia are perceptibly gravid by May (Daltry 1995).

Data recording

Each snake was relocated at least once per 24 h during the day or night. Because post-surgical trauma may affect the behaviour of a snake for several days (Weatherhead and Anderka 1984, Lutterschmidt and Rayburn 1993), no data were collected until the tenth day after release. The following details were subsequently recorded: a) date and time of location; b) percentage of the snake's body visible from above (estimated to the nearest 5%); c) maximum height of undergrowth in the 25 × 25 cm site occupied by the snake; d) direct distance between the present site and the snake's previous location; e) ambient temperature 1.5 m above the snake (T_{site}); f) ambient relative humidity 1.5 m above the snake (RH_{site}). Relative humidity (expressed as a percentage) and temperature were measured using a high-precision hand-held probe.

For the two snakes (one male, one female) containing thermosensitive transmitters, we also measured the interval between signals to the nearest 0.01 s with a stop-watch and estimated body temperature (T_{body}) from calibration graphs provided by the manufacturer.

To supplement the activity data from radio-tagged snakes, we recorded the number of non-tagged *C. rhodostoma* observed crossing the 10 km asphalt road which passes through the Ladang Sungai Dingin estate. These searches were conducted for 18 consecutive nights in April by driving back and forth along the road from 1900 h to 0300 h at a constant velocity of 50 km h^{-1} (sunset was at 1800 h). This road can be regarded as a kind of line transect (Shaffer and Juterbock 1994). When a snake was seen, it was caught, sexed and released a few metres from the road.

To determine whether climate influences activity, we monitored daily rainfall (mm), ambient relative humidity (%) and ambient temperature (°C) from a weather station in the centre of the estate throughout the study. Mean ambient temperature and mean ambient relative humidity between 1900 h and 0700 h will be termed T_{night} and RH_{night} respectively. Wind speed below the tree canopy in the plantations was negligible, and was not considered. The lunar cycle was recorded as the proportion of the moon visible each night (e.g. new moon = 0, quarter moon = 0.25, full moon = 1). All data recorded as percentage values were arcsine transformed before being entered into statistical tests.

Statistical analysis

Environmental variables are often highly intercorrelated and this phenomenon can easily lead to erroneous conclusions in studies of animal behaviour. For example, if greater activity is stimulated by rainfall, activity levels might misleadingly appear to also be significantly correlated with temperature, because a drop in temperature is often associated with the start of a rainstorm. Therefore, we elected to use the partial correlation test (program 2R, BMDP, Dixon 1990) to assess the relationship between snake activity and each environmental variable. Correlations were first calculated among the independent variables (environmental factors) then, in a stepwise manner, the residuals were sequentially regressed against the dependent variable (snake activity). Thus, a correlation was computed between the dependent variable and each independent variable, with the other independent variables held constant.

The activity of the pit vipers was divided into two main components; namely the frequency of activity (the number of individuals which moved each night) and the magnitude of activity (the mean distance travelled each night). A partial correlation test was used to simultaneously compare 1) the total number of tagged males which moved each night between 12 February and 23 April with the following: i) day number (1–70); ii) mean ambient temperature each night (T_{night}); iii) mean ambient relative humidity each night (RH_{night}); iv) proportion of the moon visible each night; v) total daily rainfall (mm). This 70-day period covers the main part of the study, when most individuals were being monitored simultaneously (we failed to find two of the males on 24 April, and several more shortly after. By the end of May, only four individuals could be found with functioning transmitters).

This was repeated for the same 70 d using the following dependent variables in turn: 2) total number of tagged females which moved to a new site each night; 3) mean distance moved by tagged males each night; and 4) mean distance moved by tagged females each night.

To determine which, if any, of the environmental variables influenced the height of vegetation occupied by the snakes during the same 70-d period, the same test was repeated using the following dependent variables: 5) mean maximum height of vegetation in sites occupied by tagged males; 6) mean maximum height of vegetation in sites occupied by tagged females.

A similar approach was adopted to analyse the data from the 18 nights of controlled searches for pit vipers crossing the estate road between 1900 and 0300 h. A partial correlation test was used to compare the mean number of male *C. rhodostoma* seen per hour each night with i) day number (1–18); ii) mean ambient temperature each night (T_{night}); iii) mean relative humidity each night (RH_{night}); iv) proportion of the moon visible each night; v) total daily rainfall (mm).

Data from males and females were treated separately because snakes often exhibit sexual differences in activity (Gibbons and Semlitsch 1987). To explicitly test whether male *C. rhodostoma* move more or less frequently than females, the mean number of days that individual tagged pit vipers remained in each site were compared using a Mann-Whitney U-test (program 3S, BMDP). To determine whether males travel greater or lesser distances than females on average, a second Mann-Whitney U-test was conducted on the mean distance travelled per 24 h by each tagged snake. This test was repeated to ascertain whether males occupied significantly taller or shorter undergrowth than females, by comparing the mean maximum height of vegetation in sites occupied by each individual.

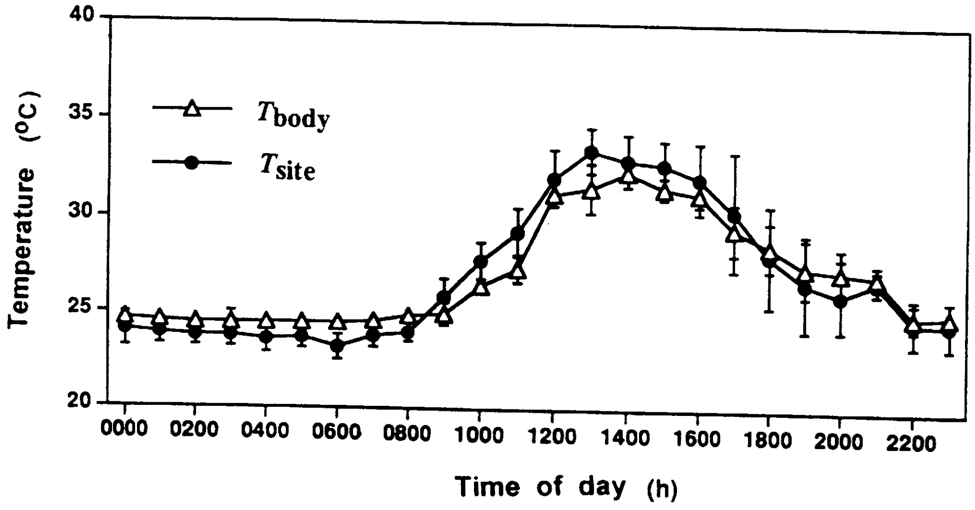

Fig. 1. Mean daily variation in the ambient temperature of sites occupied by a female pit viper (T_{site}) and its simultaneously recorded body temperature (T_{body}). Mean hourly temperatures (± 1 SD) were obtained by pooling data from 134 telemetric fixes taken during February through May, each rounded up to the nearest hour.

Although the proportion of body exposed to view partly reflected the height of ground vegetation in its 25 × 25 cm site (i.e. the shorter the vegetation, the more likely the snake will be visible), the pit vipers could adjust the position of their coils amongst the foliage and leaflitter and thereby become more or less exposed to view without actually leaving the site. Since previous studies have recorded various species of snakes thermoregulating by basking or seeking shelter as appropriate, we predicted there would be an association between body exposure and ambient temperature. The Spearman's rank correlation (program 3S, BMDP) was used to test whether the proportion of body exposed when viewed from directly above during daylight was significantly associated with ambient temperature (T_{site}) or relative humidity (RH_{site}). Treating both genders separately, a partial correlation test was used to simultaneously compare the percentage of body visible when viewed from above: i) day number (1–70); ii) ambient temperature (mean T_{site}): iii) ambient relative humidity (mean RH_{site}).

Results

General observations

The miniature transmitters did not seem to cause any obvious distress and the tagged specimens appeared able to move, feed, and copulate normally. The small surgical incisions healed rapidly with no evidence of tissue irritation. Provided that nothing touched them, the pit vipers appeared unperturbed by being periodically approached, as indicated by their relaxed musculature and respiration rate.

Tagged snakes were located on 887 occasions. Each snake typically remained coiled in one place on the ground for several days before moving to a new site. Individuals seen in one spot on consecutive days were invariably found in precisely the same site throughout the intervening nights. Once a snake had left a particular site, however, it did not return during the course of this study.

The maximum direct distance travelled between rest sites in one night was 129 m, but most movements were of <5 m. Most activity occurred at night; diurnal movements were extremely rare and short (<1 m direct distance). By recording the linear distance between successive rest sites we have probably underestimated the actual distance travelled, but our occasional sightings of the snakes moving at night found that their course was remarkably direct.

Only four snakes were recaptured at the end of the study period, and were all found to have increased in weight (N = 4, mean mass in February = 139.0 g, mean mass in May = 172.5 g).

Daily pattern of body temperature

Over 130 body temperature recordings were taken from the female implanted with a thermosensitive transmitter (total length 773 mm). Like the other tagged females, this specimen was very sedentary, moving to a new site only once every 9.1 days on average. The female's mean body temperature (T_{body}) for each hour of the day is plotted in Fig. 1. Mean T_{body} at each hour rose and fell in accordance with the mean hourly ambient temperature recorded 1.5 m above the snake (T_{site}) (paired t-test comparing mean hourly T_{body} temperature with mean hourly T_{site} over 24 h; $t = 0.16$, $DF = 23$, $p > 0.8$). Mean maximum T_{body} was attained at 1400 h (mean = 32.4°C) and mean minimum T_{body} was recorded during the second half of the night (mean = 24.5°C). Grand mean T_{body} over 24 h was 26.97°C (SD = 2.8), whilst grand mean T_{site} for sites occupied by this female was 27.01°C (SD = 3.1).

Table 1. Partial correlation coefficients between five environmental variables and the behaviour of radio-tagged male ($N = 9$) and female ($N = 5$) pit vipers between 12 February and 23 April. Number of nights = 70, degrees of freedom = 68. The total number of males and females which moved and the mean distance moved on each night were strongly associated with mean ambient humidity (RH_{night}). Male pit vipers also exhibited a significant decline in activity through the study period (Day number). Mean maximum height of undergrowth in sites occupied by pit vipers was significantly associated with day number and, especially, with mean ambient humidity.

		Environmental variables				
		Day number	T_{night}	RH_{night}	Moon	Rainfall
Number of tagged pit vipers that moved each night	Males	−0.3462*	−0.1147	0.3506*	0.1285	−0.0704
	Females	−0.2040	−0.0144	0.4621*	0.0977	−0.1631
Mean distance moved by tagged pit vipers each night	Males	−0.1880	−0.0913	0.3263*	−0.0371	−0.0502
	Females	−0.1691	0.0535	0.3094*	0.0156	−0.0359
Height of vegetation in sites occupied by tagged pit vipers	Males	−0.2723	−0.0105	−0.5760*	−0.0645	−0.0428
	Females	−0.2972	0.1947	−0.4816*	0.0431	−0.0015

* $p < 0.05$ after applying a sequential Bonferroni correction to each test (Rice 1989).

Only 38 body temperature recordings were taken from the male (total length 612 mm) which carried the second thermosensitive transmitter, but a similar pattern of variation over each 24-h period was exhibited, giving a grand mean T_{body} of 27.15°C (SD = 3.3).

Because many previous studies have revealed a stronger thermophilic response by snakes which have recently fed, are gravid, or due to slough (Lutterschmidt and Reinert 1990, Schwaner 1991, Peterson et al. 1993 and references therein), a shift to warmer microhabitats by *C. rhodostoma* under such circumstances was expected, but not observed. The daily temperature regimes (both internal and external) were fairly consistent from one day to the next throughout this study, as indicated by the small standard deviations in Fig. 1.

Activity each night

Throughout the 5-month study, males were active more frequently than females; in other words they occupied each site for a significantly shorter period (males: $N = 9$, mean = 3.4 days in each site; females: $N = 5$, mean = 9.4 days in each site; Mann-Whitney $U = 7$, $p < 0.05$).

As shown in Table 1, the number of tagged males and females which moved each night showed a highly significant association with the nightly mean ambient relative humidity (RH_{night}): fewer snakes were active when relative humidity was low. Male activity was also significantly correlated with day number with a general decline in activity through the study period. There was no association between activity and rainfall, the lunar cycle or temperature. The mean distance moved each night by both genders was also highly significantly associated with RH_{night} (Table 1). Males travelled significantly further between consecutive sites than females (males: $N = 9$, mean = 21.0 m; females: $N = 5$, mean = 6.5 m; Mann-Whitney $U = 5$, $p < 0.05$).

These findings were supported by the controlled searches by car for non-tagged pit vipers on 18 consecutive nights in April. Up to 0.75 h^{-1} pit vipers were seen each night, of which the majority were male. The partial correlation test revealed a strong positive correlation between the mean number of male *C. rhodostoma* seen each night and mean ambient relative humidity (RH_{night}) (Table 2). (Too few females were seen for statistical analysis).

Note that although the females were larger on average than the males, the difference in activity was much more strongly associated with gender per se than body size. Not even the two smallest females, which fell well within the males' size range, moved as far or frequently as any male. Even within each gender, there was no sign of a relationship between body size and activity.

Height of ground vegetation occupied

Although ground vegetation grew rapidly during the rainy season the estate workforce regularly cut it back, so there was no net change in the height of undergrowth available to the snakes throughout the study period. Nonetheless, there was a general decrease in the height of vegetation cover occupied by tagged pit vipers during the study period. In February, for example, the mean maximum height of vegetation in sites occupied by pit vipers (both genders combined) was 0.82 m, but in April it was only 0.61 m. As shown in Table 1, the mean height of vegetation selected by both genders each day was significantly associated with day number and especially ambient relative humidity (RH_{night}): the lower the humidity, the taller the vegetation in sites occupied by pit vipers.

Body exposure during daylight

Although the pit vipers were cryptically coloured and typically settled in areas with tall undergrowth, they were seen on 262 occasions during daylight. Despite being generally smaller, males tended to be more

Table 2. Partial correlation coefficients between five environmental variables and the mean number of non-tagged male pit vipers seen per hour crossing the estate road each night from 10 and 28 April. Number of nights = 18, degrees of freedom = 16. The number of pit vipers seen was strongly associated with mean ambient humidity (RH_{night}) only.

	Environmental variables				
	Day number	T_{night}	RH_{night}	Moon	Rainfall
Number of non-tagged pit vipers seen each night	−0.0042	−0.0155	0.6881*	−0.4533	0.0301

* $p < 0.05$ after applying a sequential Bonferroni correction (Rice 1989).

greatly exposed to view than females (N = 262; Mann-Whitney U = 10122, $p < 0.01$): mean body exposure 32.1% and 21.8% by males (N = 152) and females (N = 110) respectively.

As shown in Figs 2 and 3, there was a decrease in the mean proportion of body visible at extreme ambient temperatures, T_{site} (both genders combined: $r_s = -0.75$, N = 262; $p < 0.05$), but the association between body exposure and ambient relative humidity (RH_{site}) was more strongly defined ($r_s = 1.0$, N = 262; $p < 0.001$). When RH_{site} was low, the snakes tended to be fully concealed by foliage and leaflitter. Partial correlation tests of percentage body exposed versus day number, T_{site} and RH_{site} found body exposure to be significantly associated with humidity alone (Table 3).

Discussion

Snake activity and temperature

Echoing a view held by many herpetologists, Heatwole (1976) stated that temperature is "almost certainly the most important single physical factor in the ecology of reptiles and a great portion of the daily activity of many species is devoted to responding to the thermal environment". Indeed, numerous studies of habitat use or activity patterns of these ectothermic animals have highlighted the importance of behavioural thermoregulation. For example, snakes are often observed spending long periods basking or exploiting cool microhabitats with the effect of controlling their body temperature within narrow limits (e.g. Fukada 1985. Shine 1987, Schwaner 1989).

It may therefore seem surprising that we observed that *C. rhodostoma* passively allowed its body temperature to conform to that of its immediate environment. Pit vipers seen in one site for several successive days were invariably found in precisely the same place during the intervening nights, irrespective of fluctuations in ambient temperature – one individual in this study did not leave a 25 × 25 cm site for 20 successive days. The gradual changes in body temperature throughout each diel period (Fig. 1) concorded with Peterson's (1987) "smooth pattern" indicative of thermoconformity. The pit vipers did not actively seek cooler locations at midday, did not bask, and nor were there any marked postural changes during the day which could readily be interpreted in thermoregulatory terms (see Avery 1982). A thigmothermic response to warm surfaces, such as asphalt roads at night, has been reported in other nocturnal crotalines (Klauber 1972),

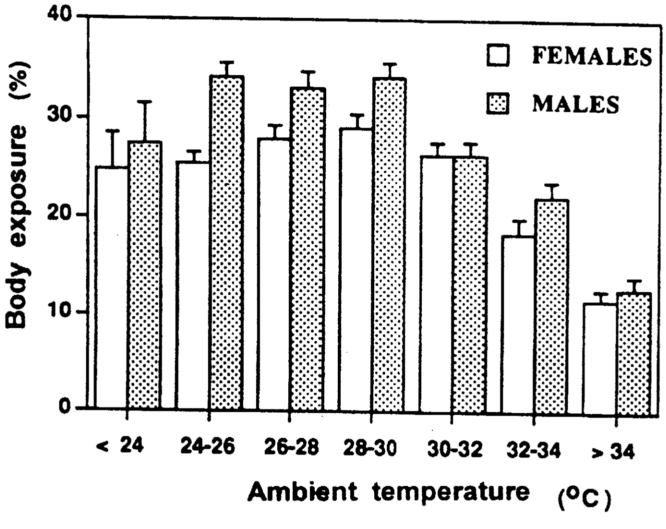

Fig. 2. The relationship between ambient temperature (T_{site}) and the mean percentage of body exposed to view (+1 SE) by tagged pit vipers when seen from above; based on all cases where male and female pit vipers were visible (152 and 110 sightings respectively).

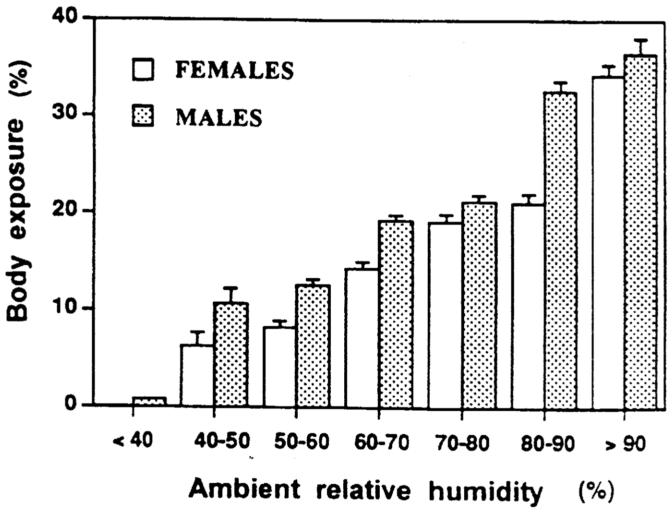

Fig. 3. The relationship between ambient relative humidity (RH_{site}) and the mean percentage of body exposed to view (+1 SE) by tagged pit vipers when seen from above: based on all cases where male and female pit vipers were visible (152 and 110 sightings respectively).

Table 3. Partial correlation coefficients between environmental variables and the percentage of body visible when seen from directly above. Tagged male pit vipers were visible on 152 occasions (degrees of freedom = 150) and tagged females were visible on 110 occasions (degrees of freedom = 109). Body exposure was significantly associated with ambient humidity in sites occupied by the snakes (RH_{site}).

		Environmental variables		
		Day number	T_{site}	RH_{site}
% body visible when seen from above	Males	0.1396	0.0342	0.3857*
	Females	0.2928	−0.1060	0.4675*

* $p < 0.05$ after applying a sequential Bonferroni correction (Rice 1989).

but is unknown in *C. rhodostoma*: we observed that this species pauses while crossing a road only if startled by a vehicle. At most, there was a slight tendency for the pit vipers to become more greatly concealed by foliage and leaflitter within their rest sites when the ambient temperature was <26°C or >32°C (Fig. 2).

Although these findings appear to differ from most previous studies of reptiles, it should be noted that work on ophidian behaviour has traditionally been conducted in areas with greater extremes of temperature, where behavioural thermoregulation may be important. The biology of snakes in thermally more stable environments, such as warm water bodies or the humid tropics, has rarely been investigated. Two notable exceptions, both conducted in tropical northern Australia, were firstly a study which revealed that the aquatic filesnake *Acrochordus arafurae* maintained a mean body temperature of 26–30°C by passively thermoconforming (Shine and Lambeck 1985); and secondly a radio-telemetry study of *Liasis fuscus* which concluded that these pythons maintained body temperatures of around 30°C, again without overt thermoregulatory behaviour (Shine and Madsen 1996). The temperature regime of northern Malaysia is similarly warm and fairly constant, with a mean daily temperature range of 23–33°C throughout the year. The mean body temperature of *C. rhodostoma* in our study site between dawn and dusk was 29.4°C, which is well within the 28–32°C range commonly preferred by actively thermoregulating snakes in less benign climates (Lillywhite 1987). Shine and Madsen (1996) rightly pointed out that the vast majority of species inhabit the tropics, and further studies in this region may ultimately topple the common assumption that thermoregulation is of paramount importance in the daily life of most reptiles.

Nonetheless, even though the daily mean ambient and body temperatures in our study site were almost constant from one day to the next, body temperature fluctuated by an average of 10°C within each diel period (see Fig. 1). Since *C. rhodostoma* is provenly capable of sensing subtle variation in environmental temperature (de Cock Bunting 1983), one might wonder why it does not behaviourally thermoregulate to reduce this fluctuation. After all, body temperature is known to affect many important facets of a reptile's development and behaviour, such as its digestive efficiency, growth, resistance to disease and locomotory ability, and these processes can be optimized through precise control of body temperature (Osgood 1978, Stevenson et al. 1985, Lillywhite 1987, Seigel and Ford 1987). Yet stenothermicity is not without its costs (Huey 1982). Posture adjustments or shuttling between different thermal environments, such as patches of sun and shade on the plantation floor, would expend additional energy and might attract the attention of other animals (*C. rhodostoma* largely depends upon effective crypsis to ambush prey and evade predators). Further studies will be necessary to determine whether this species can be induced to behaviourally thermoregulate through exposure to more extreme thermal conditions than are normally experienced in Malaysia.

Snake activity and the lunar cycle

Increased activity on dark nights was observed during studies of the nocturnal snakes *Lycodonomorphus bicolor* (Madsen and Osterkamp 1982), *Acrochordus arafurae* (Houston and Shine 1994) and *Crotalus viridis* (Clarke et al. 1996). The authors suggested that moonlight deters activity because the moving snakes become more visible to their prey or predators.

No such lunar cyclicity in the frequency or magnitude of activity of tagged snakes was detected in the present study. Perhaps this is because much of the ground in tropical forests and plantations is heavily shaded by the canopy, allowing the snakes to remain in shadow even during full moon. Roads tend to be brightly illuminated on cloudless nights when the moon is full, however, and during extensive fieldwork throughout southeast Asia, we found markedly fewer pit vipers crossing roads under such conditions. (Note that the lunar influence on the number of pit vipers found on the estate road only marginally failed to be significant after applying a sequential Bonferroni correction: see Table 2). Bouskila (1993) similarly concluded that the pit viper *Crotalus cerastes* avoids open areas on moonlit nights.

Snake activity and humidity

Unexpectedly, the activity patterns of *C. rhodostoma* in west Malaysia were more strongly correlated with variation in relative humidity than with any other variable tested, including temperature. (Note that although relative humidity is by definition partly dependent on temperature, the thermal component was partialled out in our statistical tests). More snakes were active, and greater distances were covered, on more humid nights. There was also a general decline in the activity of males towards the end of the study period, however, which probably reflected a decrease in mate-seeking behaviour towards the end of the mating season (see also Madsen 1984, Shine 1987).

Why should there be such a strong positive association between snake activity and humidity? One hypothesis might be that the snakes increase their feeding success by becoming more vagile when hygrophilic prey are active. Frogs, for example, are an important constituent of the diet of *C. rhodostoma* in Malaysia (Daltry et al. 1996, 1997) and were conspicuously more active under more humid conditions. This is unlikely to provide the full explanation, however, because *C. rhodostoma* is an ambush hunter rather than an active forager. Moreover, females of this species cease to feed during ovogenesis (Koch 1991), and even though at least two of the tagged females were perceptibly gravid by May, they continued to respond positively to ambient humidity.

An alternative explanation for the observed correlation between snake activity and humidity is that the snakes are susceptible to desiccation at low relative humidity, when the evaporative power of the air is heightened. Contrary to popular belief, reptiles can lose a substantial amount of water through the epidermis (Bentley and Schmidt-Nielsen 1966. Nagy 1982), especially taxa from humid habitats (Heatwole 1976). The elongate body of a snake further exacerbates the problem of water conservation by providing a large surface area for evaporation (Mautz 1982). In support of this hypothesis, captive Malayan pit vipers are highly prone to desiccation, and exhibit dysecdysis and aphagia when housed at <70% relative humidity, even when given unrestricted access to drinking water (York 1983, unpubl.). Because increased activity by a reptile accelerates its rate of evaporative water loss (Heatwole 1976), restricting long-distance movements to the most humid nights may lessen the risk of dehydration. The rate of cutaneous water loss may also increase during ecdysis (Lillywhite and Maderson 1982), but *C. rhodostoma* appears to counteract this problem by sloughing when ambient humidity is highest – all five cases of ecdysis witnessed during this study occurred at dawn, coinciding with a predictable daily peak in ambient relative humidity of over 90%.

During the day, the pit vipers typically remained motionless in areas with a dense cover of undergrowth. This supports our thesis that this species is hygrophilic, for even at midday the relative humidity amongst 0.75 m bracken was usually >70%, whereas the ambient humidity on bare ground commonly dropped <60%. Admittedly, *C. rhodostoma* might select tall undergrowth for reasons other than, or in addition to, its protection against desiccation, such as to avoid the attention of predators. However, it is noteworthy that the mean height of vegetation cover selected by the snakes gradually decreased in significant association with the seasonal rise in mean nightly ambient relative humidity (RH_{night}) (Table 1). Tagged snakes were rarely seen at the beginning of the year, but full exposure on the leaflitter and even on the bare soil of footpaths, became more frequent by late April/May, by which time the mean nightly ambient humidity was substantially higher. Because most bites are the result of accidentally treading on these snakes (Warrell 1986), this may suggest that the likelihood of a plantation worker being bitten is directly related to ambient relative humidity! Indeed, Reid et al. (1963) found that the incidence of snake bites in Malaysia rises dramatically during the rainy season, when ambient humidity peaks.

The mean daily range in ambient relative humidity in the study area was 53–92%, but there was also considerable seasonal variation, with values as low as 36% recorded during the brief dry season in January and February. Perhaps the association between *C. rhodostoma* activity and humidity becomes even stronger in the northerly parts of its distribution range where the dry season is more severe. The ambient relative humidity in dry forest in northeastern Thailand, for example, falls <40% every day during the four-month dry season (Inger and Colwell 1977) and local villagers assert that pit vipers "disappear" during this period (pers. comm.) Similarly, Saint-Girons and Pfeffer (1972) report that Cambodian *C. rhodostoma* exhibit a "latency period" during the long dry season.

This correlation between relative humidity and activity raises the question of whether the snakes directly respond to changes in relative humidity or to some other intercorrelated environmental factor that has not yet been tested. However, studies of captive specimens have provided strong evidence that *C. rhodostoma* can accurately perceive hygric change. Females of this species are known to remain with their eggs throughout incubation and consistently vary their posture in accordance with relative humidity; when humidity falls, the females coil more tightly and completely cover the eggs, whereas an increase in humidity prompts egg exposure. Changes in temperature alone, on the other hand, elicit no such response (York and Burghardt 1988).

Although our investigation is, to the best of our knowledge, the first to demonstrate a significant association between variation in humidity and the activity of snakes in the wild, it is not yet possible to determine whether *C. rhodostoma* is unusual in this respect. Little is known of the activity patterns of snakes outside of temperate zones and, more to the point, humidity is rarely monitored during investigations into reptile behaviour. We strongly urge that humidity be given much more serious attention in future behavioural and ecological studies of reptiles.

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