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Graham J. Alexander & Catherine L. Marshall

Ecophysiological Studies Research Programme, Department of Zoology, University of the Witwatersrand, Johannesburg, 2050, South Africa

E-mail:

Short communication

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**GRAHAM J. ALEXANDER AND CATHERINE L. MARSHALL**

Ecophysiological Studies Research Programme, Department of Zoology,
University of the Witwatersrand, Johannesburg, 2050, South Africa
email: graham@gecko.biol.wits.ac.za

**Key words.**—Activity pattern; endogenous rhythm; photoperiod; temperature; elapid; snake; *Hemachatus haemachatus*.

**PHOTOPERIOD,** temperature, lunar phase and humidity have all been implicated in the regulation of activity in reptiles (Mangeldorff & Hauty 1972; Madsen & Osterkamp 1982; Underwood 1992; Daltry *et al.* 1998). Of all these variables, photoperiod is considered the most reliable cue for regulating or entraining the rhythmicity of an activity cycle, as it is not greatly affected by the vagrancy of daily climatic variability. However, because temperature has an obvious and direct effect on the physiology of reptiles, it is often assumed to dictate the activity schedules of these animals (Daltry *et al.* 1998) because the thermal environment is the primary determinant of body temperature ($T_b$) and thus, the reptile’s performance (Peterson *et al.* 1993).

Since snakes are secretive animals, relatively few detailed studies have been conducted on their activity patterns (Peterson *et al.* 1993). In field studies, activity often has to be inferred indirectly by trapping success (Whiting *et al.* 1996) unless the snakes are radiotelemetered (Daltry *et al.* 1998). Field studies have revealed the apparent ability of snakes to phase change their diel rhythm of activity according to season, becoming nocturnal in summer and diurnal in winter, or switching between unimodal or bimodal patterns (Seigel 1986; Gibbons & Semlitsch 1987; Underwood 1992). However, although field studies are ideal for measuring various attributes of activity such as the length of time spent active or when activity occurs under natural conditions, they are not well suited for elucidating what is responsible for controlling the pattern. Laboratory studies have the advantage of being more easily regulated, so that possible causal factors can be controlled for or altered, or their influence removed during measurements.

*Hemachatus haemachatus* is a cobra-like elapid that is endemic to the southern and eastern parts of southern Africa. In the northern parts of its range, *H. haemachatus* is restricted to higher altitudes occurring in montane grasslands and the highveld (Branch 1988). Many parts of its range are temperate, being highly seasonal with low temperatures during winter. Since circadian rhythms are especially likely to be adaptive to organisms in temperate areas (Tu & Hutchison 1995), we expected *H. haemachatus* to show clear diel rhythm in activity.

We tested for the presence of diel activity patterns in *H. haemachatus* maintained in the absence of thermal cues. Our snakes were maintained at a constant temperature of 25°C, with no diel fluctuation, for several years prior to our activity measures. If daily activity pattern were modulated only by temperature in *H. haemachatus*, we would expect our captive animals to show no significant patterns under the constant thermal conditions of our study.
Alternatively, if we found that a 24 h cycle in activity patterns persisted, with individual snakes remaining in phase with respect to each other, we could be sure that temperature is not the only cue for activity in this species.

Our study sample of snakes consisted of 20 *H. haemachatus* (11♂ 9♀), that were collected from their natural habitat close to Johannesburg, South Africa (26°28′S, altitude >1600 m). At the time of our study, the snake’s average mass (g) was 557 ± 271 (1 SD) (51.2-1093.5). Snakes were housed individually in wooden cages (750 x 450 x 450 mm) and acclimated to a constant temperature (25°C; this is the selected T_b of *H. haemachatus* during normothermia; Alexander 1996) and lighting regime (12:12 h light:dark cycle; local dawn at 06:00) in a windowless room. All the snakes used in our study had been in captivity under these constant conditions for at least five years prior to our study.

We used scan-sampling to measure activity patterns. Observations were made every second hour for two days every month, from March to August. This data collection regime resulted in observations for every hour of the day (24 h) for each of the six months included in our study, but at the same time maintained some degree of independence between data points, as recordings were made at least two hours apart. We classified snakes as either active or inactive. Active snakes were either moving around the cage or were clearly attentive and alert, with their heads held off the substrate. Inactive snakes were usually sequestered in their retreats or appeared to be asleep in an exposed position in the cage. We classified snakes to be sleeping if their heads rested on the substrate and they did not react to our presence. During the dark phase, we minimised disturbance by using a light of low luminescence.

The number of snakes recorded as active in the colony for each hour was converted to a percentage. We arcsine transformed these data and, since our activity measures were normally distributed (Lilliefors’ test for normality; NS), we used a repeated measures one-way ANOVA and post hoc pairwise Tukey tests to test for significant differences in the percentage of active snakes between hours of the day. Sequential adjustments for multiple paired comparisons (Rice 1989) were applied where appropriate, in order to control for Type I errors.

We also tested for observer-effects on our snakes. Since one of us had to enter the room to record which snakes were active, it is possible that our method of data collection caused some disturbance to the snakes. At night, this also involved switching the room light on for a short period of time (total time ± two min). In order to determine if observer activity influenced snake activity, we installed a video camera and recorded the behaviour of three individual snakes during the photophase of the photoperiod, between and during our observations. Video footage showed no evidence of an observer effect, at least during daylight hours. Also, five years of captivity has resulted in a colony habituated to nearby human activity.

Snakes in our colony showed clear rhythms in their daily activity (Fig. 1). ANOVA revealed significant differences in activity levels between hours (F_{23,115} = 8.28, P < 0.001). Out of a possible total of 276 pairwise comparisons, 53 were significant at the 0.05 level. Generally, significant differences were between hours in the middle of the night and hours during midday. The pattern in activity was simple, with the number of active snakes in the colony peaking at midday, at which time an average of approximately 40% of the snakes were active. Night-time levels of activity were much lower, with approximately 10% or less of the colony being active between 18:00 and 06:00. This unimodal pattern of activity was consistent throughout our study and we did not observe any shift in phase between diurnal and nocturnal patterns (snakes were primarily diurnal in all months of the study). On average, snakes spent 19.5% of their day (SD 3.8 between days) in an active state.

Our results clearly show that *H. haemachatus* maintains a diel activity pattern at constant temperature conditions of 25 °C. This finding demonstrates that temperature is not the sole
proximal cue for the modulation of activity in *H. haemachatus*. Since the snakes that we used in our study had been maintained under constant conditions for more than five years before our study commenced, we also conclude that the activity pattern that we measured was not a temperature-entrained endogenously controlled rhythm. If the activity pattern were temperature entrained, we would expect that individual snake’s activity patterns would be out of phase with each other. Our snakes’ activity patterns remained in phase, within a period of 24 h, over the entire six months of measurement.

Since our study was conducted on individuals that had been maintained in captivity under constant temperature and photoperiod for a long period of time, caution must be exercised in extrapolating any of our findings to free ranging *H. haemachatus* in natural conditions. It is possible, for example, that our snakes moved shorter distances than would usually be the case with *H. haemachatus*, since our snakes were confined to moving around within their cages. Thus, captivity may have caused our snakes to be less active than free-ranging *H. haemachatus*. However, our measures of total activity time for *H. haemachatus* appear to be comparable to measures made for other species of free-ranging snakes. Secor & Nagy (1994) recorded *Crotalus cerastes* spending 30% of the day in surface activity, and *Masticophis flagellum* spending 16%. Our measure of 19.5% is thus credible and may not underrepresent activity of free-ranging *H. haemachatus*.

The *H. haemachatus* in our study were primarily diurnal. This follows the trend highlighted by Shine (1979), who states that the majority of elapids studied thus far are diurnal. *Hemachatus haemachatus* also has circular pupils (Broadley 1983), a characteristic usually associated with diurnal activity (Greene 1997). However, Branch (1988) describes *H. haemachatus* as nocturnal, although it is unclear what he bases this conclusion on. Possibly, *H. haemachatus* shows geographic variation with regards to time of activity, since such variation has been found in other species of snakes, or it may phase-shift between being diurnal and nocturnal, which is also common in snakes (Gibbons & Semlitsch 1987).

We found no evidence of phase-shift between nocturnal and diurnal, or between unimodal and bimodal patterns in our snakes. Our study ran mainly over the austral winter (March to August) and it is possible that *H. haemachatus* becomes nocturnal during midsummer, when temperatures are higher during the night. Heckrotte (1975) demonstrated that *Thamnophis radix* is diurnal when maintained at 15 °C or 20 °C, but becomes nocturnal at temperatures above 30 °C. We maintained our snakes at a relatively low temperature of 25 °C. Alternatively, if photoperiod is the entraining agent or is responsible for modulating diel activity patter,
keeping photoperiod constant, as was the case in our study, could have inhibited a phase shift. Clearly, the seasonal effects on diel rhythm and the importance of photoperiod on *H. haemachatus* activity require further investigation before the issue of phase shift can be clearly resolved.

Gibbons & Semlitsch (1993) highlight the need for investigating ultimate causes leading to the evolution of particular activity patterns. Although it would be naive to suggest that temperature has no proximal effect on activity patterns in *H. haemachatus*, we believe that we have demonstrated that temperature is not the sole modulator or entraining agent for activity patterns in this species. Our study has also established a basis for designing and testing ideas regarding the ultimate and proximate factors leading to the activity patterns shown by *H. haemachatus*.

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