

THERMAL AND REPRODUCTIVE ECOLOGY OF THE SNAKE *PSAMMOPHIS PHILLIPSI* FROM THE RAINFOREST REGION OF SOUTHERN NIGERIA

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Aspects of the thermal and reproductive ecology were studied in the colubrid snake *Psammophis phillipsi* from south-eastern Nigeria. The annual reproductive cycle was well synchronized and seasonal: females were gravid in the middle part of the dry season, and oviposition occurred in the second half of the dry season (February-March), whereas egg hatching occurred by the onset of the rainy season (mid April to early June). The mean number of eggs was 9.2 ± 0.9 ($n = 23$), and was related to maternal size. Gravid and non-gravid specimens did not differ significantly in terms of mean SVL, mean T_b , or T_s . Mean T_b tended to increase regularly from 0600 to 1200 hrs, attained the higher values in the middle of the day (1200-1500 hrs), and tended to decrease after 1800 hrs. Gravid individuals differed from non-gravid individuals in that their variances of T_b were notably lower both in the early morning and in the middle of the day, but higher at other times of day. Multiple regressions showed that the interaction of T_b and T_s had a significant effect on T_b , whereas T_b was not influenced by the number of eggs produced in gravid animals.

Key words: body temperatures, Colubridae, Psammophiinae, reproductive biology, tropical Africa

INTRODUCTION

The notion that thermoregulation is a central factor of reptilian biology is at the forefront of modern herpetology (e.g. see Avery, 1979; Huey & Slatkin, 1976; Peterson *et al.*, 1993) and has stimulated very sophisticated approaches and analyses (e.g. see Hertz, 1992; Hertz *et al.*, 1993, 1999; Christian & Weavers, 1996; Webb & Shine, 1998; but see Alexander & Currin, 1999; Currin & Alexander, 1999; Hertz *et al.*, 1999, for diverging opinions on the theoretical framework). In recent years, however, whether thermoregulation is indeed important for most reptiles has been called into question (Shine & Madsen, 1996). After studying the thermal ecology of Australian pythons, Shine & Madsen (1996) concluded that thermoregulation is of very limited relevance to the biology of these tropical reptiles. They also suggested that as thermal challenges to reptilian life should be trivial in the tropical environment, it is likely that thermoregulatory biology is of only minor relevance for most reptiles. Indeed, the majority of reptile species occur in the tropics and not in temperate regions where the majority of previous studies on reptilian thermoregulation is concentrated. Based on these contrasting views, it is obvious that, if we are to place the thermoregulatory biology of reptiles in its proper perspective, we need more information on the thermal ecology (and its links with the reproductive biology) of a wide variety of tropical reptiles, especially snakes, which have been neglected

until now in this respect (but see Luiselli & Akani, 2002a). Although tropical environments may not present the same problems associated with low temperatures as temperate regions, there may be problems of excessively high temperature, whose avoidance is a form of thermoregulation. Thus, studies of thermoregulation in temperate climates may not be of great relevance to species in the tropics, but it would be wrong to suggest that thermoregulation is unimportant in the tropics (Luiselli & Akani, 2002a).

The scope of the present paper is, therefore, to convey detailed field data on the body and environmental temperatures – and on their links with the reproductive biology – of a diurnal, fast-moving, mid-sized Afrotropical snake (*Psammophis phillipsi* Hallowell, 1844: Colubridae, Psammophiini), which has been totally unstudied in the past with regard to these aspects of biology. This species was selected as study model because of (1) its ecological characteristics (diurnality and fast-moving) which are entirely different from those exhibited by the pythons studied by Shine & Madsen (1996) or by the semi-aquatic species studied by Luiselli & Akani (2002a), and (2) its abundance in our study area (southern Nigeria) (e.g. see Akani, Barieenee, Capizzi & Luiselli, 1999), thus allowing easy accumulation of field data even within short time-spans of research.

MATERIALS AND METHODS

The field study was carried out at a site in south-eastern Nigeria (vicinity of Eket, Akwa-Ibom State, $04^{\circ}50' N$, $07^{\circ}59' E$), characterized by a moist rainforest patch

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growing along the banks of the River Quo-Ibo (= Kwa-Ibo), partially inundated during the wet season, and surrounded by areas of subsistence cultivation (pineapple, banana, plantain, cassava, yam, etc). The study area –which is located within the Guinea-Congolian rainforest block (White, 1983) and has a typical tropical climate (wet season: April-September; dry season: October-March) – was already well explored because it was previously used for other ecological studies on both snakes (Luiselli *et al.*, 1998) and other reptiles (Luiselli *et al.*, 1999).

Field data on the thermal ecology of the snakes were collected, both on sunny and on rainy days, during the dry seasons of 2000 (March) and 2001 (January-February-March), and during the wet season of 2000 (April to June) and 2001 (April and May), whereas field data on the reproduction of snakes were collected in the period September 1996 to July 2001.

Snakes were searched for along standardized routes within the various microhabitats frequented by them at the study area (see Luiselli & Akani, 1999, 2002b). Each snake eventually captured was measured for snout-vent length (SVL, to the nearest 0.1 cm), and individually marked by ventral scale clipping for future identification. For females, eventual pregnancy status and numbers of eggs were determined by abdominal palpation (precision: ± 1 egg). In addition, specimens found already dead during our surveys (e.g. snakes killed by farmers, squashed by cars, etc.) were dissected to determine their eventual numbers of eggs. Because determination of sex is often problematic in *P. phillipsi* even in adults (if not using invasive techniques) and may lead to misidentifications (Akani *et al.*, unpublished), we subdivided our specimens into two categories: gravid (GR) and non-gravid (NGR). GR were all females obviously carrying eggs, and NGR were all adults which were obviously not pregnant (i.e. males plus non-gravid females). To discriminate between juveniles and adults, we followed Butler (1993), who found that the smallest mature *phillipsi* female was 650 mm SVL, and that females were significantly smaller than males. Thus, we assumed that all specimens shorter than 650 mm were immatures, and these were excluded from the analyses.

Body (cloacal) temperature of each captured snake was measured within 60 seconds from capture, by a rapid-recording Schultheis thermometer (range: 0/50°C, manufactured by Miller & Weber Inc., New York). At each capture spot, air temperature and substratum temperature were also measured. Air temperature was measured at approximately 100 cm above the ground, and substratum temperature was measured at soil level at the site of the snake. Both air and substratum temperatures were always taken in the shade, as all specimens used for body temperature recording were captured in total or partial shade. In addition, the hour of the day (Lagos standard time), substratum type, and the activity type exhibited by the snakes at the time of capture were recorded. To avoid statistical problems caused by

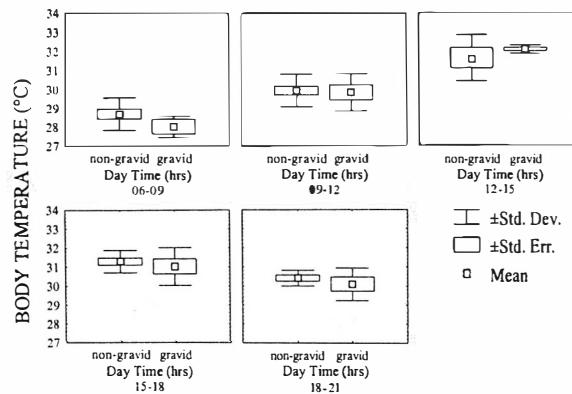
pseudo-replication of the data (cf. Hurlbert, 1984; Licht *et al.*, 1966; Mathur & Silver, 1980), we took body temperature only once from each snake, i.e. the recaptured individuals were never used again for body temperature recording. This procedure was applied in consideration of the abundance of *P. phillipsi* at the study area (where it is the most common snake species, cf. Luiselli *et al.*, 1998; Luiselli & Akani, 1999), thus making the above procedure feasible.

All statistical tests were two-tailed, with alpha set at 5%. In the text, the means are followed by \pm LSD. Body temperatures are indicated by T_b , air temperatures by T_a , and substratum temperatures by T_s . All tests were done using STATISTICA (version 5.0 for Windows) computer package (Statsoft, 1996). When the effects of the interaction of reproductive status (gravid versus non-gravid) and hour of the day on T_b were analysed, it was done after having verified that the interaction effect explained more of the T_b than a simple additive model (one-way ANOVA) based on the two factors taken separately.

RESULTS

REPRODUCTIVE CYCLE

Heavily gravid specimens of *P. phillipsi* were found in the field only during the dry season: 17 specimens were collected in November, 14 in December, 11 in January, and 9 in February. No gravid specimens were seen in any other month, but newborn specimens (i.e. specimens with highly visible umbilical scars; SVL: 23.7 ± 2.1 cm, $n=18$) were collected at the end of April ($n=2$), March ($n=11$) and early June ($n=5$). This suggests that the annual reproductive cycle of *P. phillipsi* is well synchronized and strongly seasonal in southern Nigeria: females are gravid in the middle part of the dry season, and likely to oviposit in the second half (February-March), whereas egg hatching probably occurs by the



REPRODUCTIVE STATUS

FIG. 1. Hourly variations of means (and dispersion measures) of body temperatures of gravid and non-gravid *Psammophis phillipsi*, throughout five time intervals. Numbers of specimens: 06-09 hrs – gravid $n=5$, non-gravid $n=8$; 09-12 hrs – gravid $n=6$, non-gravid $n=11$; 12-15 hrs – gravid $n=5$, non-gravid, $n=6$; 15-18 hrs – gravid $n=6$, non-gravid $n=9$; 18-21 hrs – gravid $n=5$, non-gravid $n=9$. For statistical details see the text.

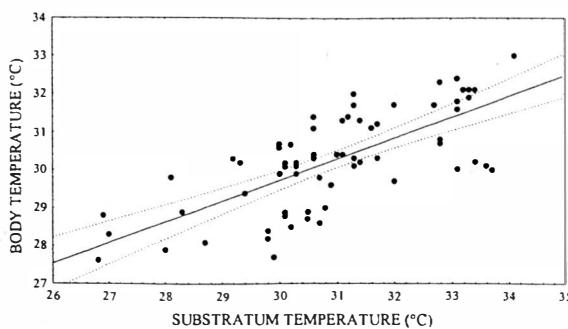


FIG. 2. Relationships between body temperature and substratum temperature in *Psammophis phillipsi*. For statistical details, see the text.

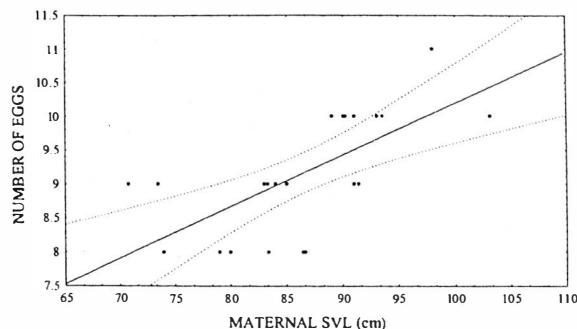


FIG. 3. Relationships between body temperature and number of eggs in gravid female *Psammophis phillipsi*. For statistical details, see the text.

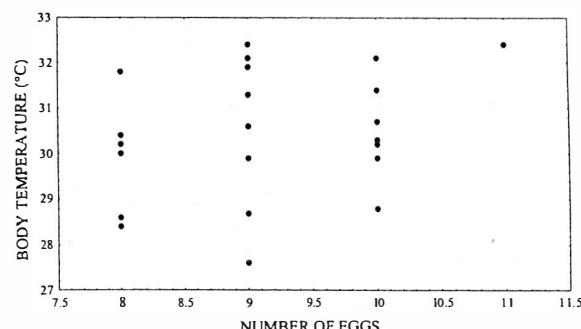


FIG. 4. Relationships between maternal SVL and number of eggs in gravid female *Psammophis phillipsi*. For statistical details, see the text.

onset of the rainy season (i.e. mid April to early June). The mean number of eggs was 9.2 ± 0.9 ($n=23$).

THERMAL ECOLOGY AND ITS LINKS TO REPRODUCTIVE BIOLOGY

Gravid snakes averaged 86.6 ± 7.83 cm SVL ($n=23$), compared to 88.7 ± 14.62 cm SVL in non-gravid specimens ($n=44$). The two samples did not differ significantly in terms of mean SVL (one-way ANOVA: $F_{1,65} = 0.41$, $P=0.523$); mean T_b (non-gravid: $30.2 \pm 1.28^\circ$ C, $n=44$, gravid: $30.4 \pm 1.37^\circ$ C, $n=23$; one-way ANOVA: $F_{1,65} = 0.53$, $P=0.468$), and mean T_s (non-gravid: $30.9 \pm 1.69^\circ$ C, $n=44$, gravid: $31.1 \pm 1.77^\circ$ C, $n=23$; one-way ANOVA: $F_{1,65} = 0.28$, $P>0.65$).

The hourly variations in T_b (means and dispersion measures) for both gravid (total examined $n=27$) and

non-gravid specimens ($n=40$) are presented in Fig. 1. Data are grouped into five time intervals, each three-hours long. In general, it appears that mean T_b tended to increase regularly from 0600 to 1200 hrs, attained the higher values in the middle of the day (1200–1500 hrs), and tended to decrease after 1800 hrs. This daily pattern was evident in both gravid and non-gravid specimens (Fig. 1).

After pooling gravid and non-gravid specimens, the hourly variations in T_b were significant ($F_{4,62} = 27.3$, $P<0.001$), and a Levene test for heterogeneity of variances indicated no significant effect of the time of day on the variances ($F_{4,62} = 0.67$, $P=0.617$). The results of the analyses were not changed by log-transforming the T_b data. The interaction of reproductive status (gravid versus non-gravid) and hour of the day had a very significant effect on T_b (MS effect = 8.198, $F_{9,57} = 12.00$, $P<0.001$). Post-hoc comparisons (Tukey HSD test) showed that the variance of T_b of gravid and non-gravid specimens did not differ significantly at time intervals 0900–1200, 1500–1800 and 1800–2100 hrs, but the gravid specimens had significantly lower variances than non-gravid specimens at time intervals 0600–0900 hrs and 1200–1500 hrs. Also in this case, the results of the analyses were not changed by log-transforming the T_b data.

T_s had significant effect on T_b (T_s : $r=0.720$, $P<0.001$; equation: $T_b = 13.230 + 0.550 T_s$, see Fig. 2). Concerning gravid specimens, T_b was not influenced by the number of eggs produced ($r=0.276$, ANOVA: $F_{1,21} = 1.727$, $P=0.203$; equation: $T_b = 26.532 + 0.425$ number of eggs, see Fig. 3), which was in turn positively related to maternal SVL ($r=0.672$, $P<0.01$; equation: number of eggs = $2.578 + 0.076$ SVL, see Fig. 4).

DISCUSSION

REPRODUCTIVE CYCLE

Butler (1993) described the annual reproductive cycle of *P. phillipsi* captured from several localities north of the equator as a monoestrous dry season cycle (*sensu* Saint Girons, 1982; Saint Girons & Pfeffer, 1971), and observed that testicular recrudescence begins at the end of the rainy season, vitellogenesis by the end of the rainy season, oviposition by mid-dry season, and egg hatching at the onset of the rainy season. In addition, Senter (2001) confirmed the occurrence of dry season oviposition in *P. phillipsi* from Liberia. Our data agree completely with the observations by these authors, and indicate that the annual cycle of reproduction is nearly perfectly synchronized in all *P. phillipsi* populations from the west African rainforest block (Senter, 2001, and part of the data given in Butler, 1993) to the Nigeria-Cameroon rainforest block (present study, data in Butler & Reid, 1990, and part of the data given in Butler, 1993).

In addition, a remarkable similarity between the present study and that of Butler (1993) was found in other aspects of the reproductive biology, including the mean offspring SVL, which was very similar in the two

studied samples (between sample comparison: $t=1.92$, $df=26$, $P=0.661$). On the other hand, the number of eggs produced by females in our study was less than that of females studied by Butler (1993) (between sample comparison: $t=3.61$, $df=30$, $P=0.0011$), but our data are based on abdominal palpation, whereas those of Butler (1993) are based on dissection, which may have partially biased our estimates (i.e. lowering our egg counts). Moreover, Butler (1993) did not find any significant relationship between maternal size and the number of eggs produced, whereas our study did. In this case, it is likely that Butler's study was based on too small a number of gravid specimens ($n=9$) to find any significant correlation between these variables, and so the apparent differences between the two studies may be explained by sample sizes differences rather than actual ecological divergence.

THERMAL ECOLOGY AND ITS LINKS TO REPRODUCTIVE BIOLOGY

Our detailed data on field T_b , and its relationships with external temperatures suggest that thermoregulation is not very important for the fast moving, highly active *P. phillipsi*. In fact, T_b 's were very significantly correlated to T_s , which suggests a degree of thermo-conformity in this species (although far from ideal poikilothermy), in which the main requirement is to lose heat (due to the high external temperatures) rather than to accumulate heat. To lose heat, these snakes rest in the shade, and when basking, they always avoid resting fully exposed to the sun (Akani *et al.*, unpubl. obs.). Thus, the fact that snakes select shady spots is due to their avoidance of thermally stressful exposure to full solar radiation, and is certainly a form of behavioural thermoregulation. In addition, the fact that gravid specimens maintained the same T_b as non-gravid specimens at nearly all periods of the day is further evidence of the fact that during pregnancy, elevation of T_b by thermoregulation is not necessary (e.g. see Avery, 1979). However, gravid specimens tended to maintain higher T_b than non-gravid specimens during the middle of the day, which is quite difficult to interpret at present. In this regard, it is necessary to stress that many previous studies (e.g. Hertz, 1992; Hertz *et al.*, 1993, 1999) have suggested that gravid females differ from non-gravid animals not so much in the mean temperature selected, but in the degree of precision. This pattern, with variances notably lower for gravid animals, is also emerging in our study, but only in the middle of the day (see Fig. 1). Indeed, according to Fig. 1, it is the gravid females that have the more variable mean T_b (over the first three periods), which is contrary to the idea that gravid females keep their T_b within a narrower range. A possible interpretation of the significant interaction between time period and reproductive status is that T_b was higher in gravid than in non-gravid females at some times of day, but lower at other times. Thus, the lower variance of gravid females' T_b at some times of the day may be nothing to do with thermoregulation, but per-

haps a quirk of relatively small sample sizes. Mean T_b of *P. phillipsi* was quite constant throughout the day (but lower at night), and was also relatively similar to that exhibited by several other colubrids from temperate regions (e.g., Dmi'el & Borut, 1972; Mushinsky *et al.*, 1980). However, it was lower than the preferred T_b of other diurnally active, fast moving colubrids (Fitch, 1963; Hirth & King, 1969; Vitt, 1974).

Although based on a relatively small sample size, our study also showed that the numbers of eggs carried by a female does not have any influence on the female T_b , which supports the idea that thermoregulation plays a relatively minor role in some aspects of the life-history of this tropical colubrid. However, it is noteworthy that the reproductive females continue feeding even when heavily gravid (Akani *et al.*, 2003), and thus it would be of great interest to further investigate the interrelationships between feeding rates, reproductive condition and thermal ecology in this Afrotropical species. We suggest that *Psammophis phillipsi* is a potential model species for the study of these issues in the Afrotropics. Whereas almost nothing is known of the links between energy intake, thermal ecology and reproductive biology in snakes from this geographic region, *Psammophis phillipsi* is abundant and widespread, is relatively easy to study, and displays some life history characters of remarkable interest (e.g. dietary shift during pregnancy, feeding extended over the gestation period, etc.; see Akani *et al.*, 2003). Comparisons of *Psammophis phillipsi* with species from temperate regions – which are often regarded as model organisms for herpetological study (e.g. Bonnet *et al.*, 2001) – would be of interest.

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ERRATUM

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Figures 3 and 4: The caption for Fig. 3 relates to Fig. 4, and vice versa.

Page 64, Results, Reproductive Cycle, line 8: For "March ($n=11$)" read "May ($n=11$)".