Breeding biology of *Python molurus molurus* in Keoladeo National Park, Bharatpur, India

Chinnasamy Ramesh & Subramanian Bhupathy

Sálim Ali Centre for Ornithology and Natural History, Anaikatty, India

We describe aspects of the breeding biology of free ranging *Python molurus molurus* based on observations during May–August 2008 in Keoladeo National Park, Bharatpur, India. For two females, the incubation period was 74 days, with a hatching success of 95%. All neonates dispersed on the fifth night from the date of first pipping. Incubating females did not feed, and abandoned the nests after 61 days, leaving them unattended for 11–13 days before hatching of eggs. Female pythons maintained a body temperature of 32.5±0.78 ˚C during incubation despite atmospheric temperatures varying between 9.7 ˚C above and 6.1 ˚C below this value. It appears that this was achieved by shivering thermogenesis, and changes in the coiling posture around the eggs; our data thus provide field-based evidence of facultative endothermy in this species. It is hypothesized that females leave the nest in order to facilitate the increased oxygen demand by embryos at late stages.

Key words: ectothermy, incubation, Indian rock python, nest temperature, reproduction

INTRODUCTION

The life history of reptiles has long remained relatively unknown compared to other vertebrates (Fitch, 1949). Parental care is a widespread adaptation, although it may entail both costs and benefits for developing offspring (Stahlschmidt & De Nardo, 2008; Stahlschmidt et al., 2008). Among reptiles, about 140 species show some degree of parental care such as egg attendance, egg brooding, egg guarding and complex active defence behaviour (Huang, 2006). Females of pythonid snakes are known to exhibit parental care by incubating their clutch through coiling around their eggs (Harlow & Grigg, 1984; Shine, 1988), which has been hypothesized to reduce the risk of desiccation and predation on eggs (Madsen & Shine, 1999; Stahlschmidt et al., 2008).

Several species of python maintain a narrow range of body temperatures during incubation (Hutchison et al., 1966; Harlow & Grigg, 1984; Shine, 1988). The nest temperature could vary little due to either maternal heat supplementation (intrinsic or extrinsic) or optimal nest site selection (e.g. a warm, well-insulated burrow). Shivering, winding and unwinding of body coils (muscular contractions) and frequent basking by females leaving the nest unattended would help to achieve this (Brattstrom, 1965; Harlow & Grigg, 1984; Shine, 1988; Kirschner & Seufer, 2003), but the role of muscular contractions in incubating pythons with respect to heat production is not clear (Brattstrom, 1965). In captivity, variation in brooding postures (tight and loose coils around eggs) by incubating Children's pythons *Antaresia childreni* maintain the water balance and metabolism of developing embryos (Stahlschmidt & DeNardo, 2008; Stahlschmidt et al., 2008).

Python molurus (Indian rock python) is listed in Schedule I of the Indian Wildlife Protection Act 1972, and has a widespread distribution in most parts of India (Whitaker, 1993; Bhupathy, 1995). However, information on the ecology of free-ranging *P. molurus* is scanty (Bhupathy & Vijayan, 1989; Bhupathy, 1993). Notes on the general ecology of this species are available in Smith (1943), Daniel (2002) and Whitaker & Captain (2004), whereas data on its breeding biology are largely based on observations in captivity (Hutchison et al., 1966; Vinegar, 1973; Mierop & Barnard, 1976, 1978; Dattatri, 1990; Vyas, 1996; Walsh & Murphy, 2003), and an introduced population of *P. m. bivittatus* in southern Florida (Snow et al., 2007; Krysko et al., 2008; Reed & Rodda, 2009). We here provide data on the breeding biology of free-ranging female *P. m. molurus* based on observations in Keoladeo National Park (KNP), Bharatpur, India.

MATERIALS AND METHODS

Study site

KNP (27˚7.6'N, 77˚33.2'E, Fig. 1) is located in the Indian state of Rajasthan, and is a World Heritage Site (Vijayan, 1991). The area of the park covers 29 km^2, including 8.5 km^2 of wetlands. The vegetation is dominated by a mixture of xerophytic and semi-xerophytic species such as *Acacia nilotica*, *Prosopis juliflora*, *Salvadora persica, S. oleoides*, *Capparis decidua* and *C. sepiaria* (Prasad et al., 1996). The climate is sub-humid to semi-arid with monthly mean temperature and relative humidity varying from 0.5 ˚C to 50 ˚C and 15% to 90% respectively. The annual rainfall is about 655 mm and is largely received during the southwest monsoon (July– September).

Field methods

At fortnightly intervals we monitored python burrows in KNP (Fig. 1). Burrows were identified on the basis of body marks, shed skins, or direct sighting of snakes. The activity of pythons was restricted to a 1–5 m radius of the ground burrows during the colder months (November–

Correspondence: Subramanian Bhupathy, Sálim Ali Centre for Ornithology and Natural History, Anaikatty (PO), Coimbatore – 641 108, India. *E-mail:* bhupathy.s@gmail.com

Fig. 1. Keoladeo National Park, Bharatpur, India, showing the location of burrows used by *Python molurus* during winter and nests studied.

March; Ramesh & Bhupathy, unpublished data). During surveys in the first fortnight of May 2008, we observed the movement of two female snakes away from their respective burrows (Fig. 1). Subsequently, these burrows and surroundings were monitored from 16 May onward. On the morning of 20 May, we observed both snakes in coiled postures. Muscle twitching was observed at regular intervals, and we suspected egg brooding. A patch of ground layer between three and five metres radius from the nest was cleared and monitored for tracks of snakes in the morning (0600) and evening (1700) until the dispersal of hatchlings to document potential movements.

The thermistor probe of a digital thermometer (EUROLAB, 288 ATH, accuracy $\pm$1 ˚C) was inserted (approximately 60 mm) between the skin folds of the brooding female to record the body temperature as a proxy for clutch temperature. The body and ambient (one metre above ground from nest) temperatures were also recorded every 15 minutes from 1800 for 24 hours on 8–9 June 2008. Body movements of the incubating snake, if any, during this period were also noted. Incidences of body shivering were recorded visually for one minute every 15 minutes. As the incubating pythons maintained a narrow range of nest temperatures (mean 32.98 SD$\pm$0.25 ˚C; range 32.40–33.90 ˚C) throughout period 1 (Fig. 2), subsequent observations during 27 June and 15 July 2008 (periods 2 and 3) were restricted to daylight hours (0600–1800). All observations were made at nest 1 (Fig. 1).

The length of incubating snakes was visually estimated after they abandoned the nest. From the date of first pipping of eggs and until the dispersal of hatchlings, we monitored both nests (nests 1 and 2, Fig. 1) continuously from morning (0600) to evening (2000), without disturbing the hatchlings. The number of eggs found in the nests and their hatching or non-hatching status was recorded. Dispersal of hatchlings occurred during the night (after 2000), and a thorough search was conducted over a 25 m radius around the nests on the following morning (between 0600 and 0700). Snout–vent length (SVL) and tail length (TL) of neonates were measured using a twine and metal ruler (accuracy 1 mm) and hatchlings were weighed using a Pesola spring balance (300 g, accuracy $\pm$0.3%). Ventral and sub-caudal scales were counted for a subset of individuals. Dorsal blotch structure of hatchlings was noted following Bhupathy (1990) to confirm the usefulness of body patterns in individual identification.

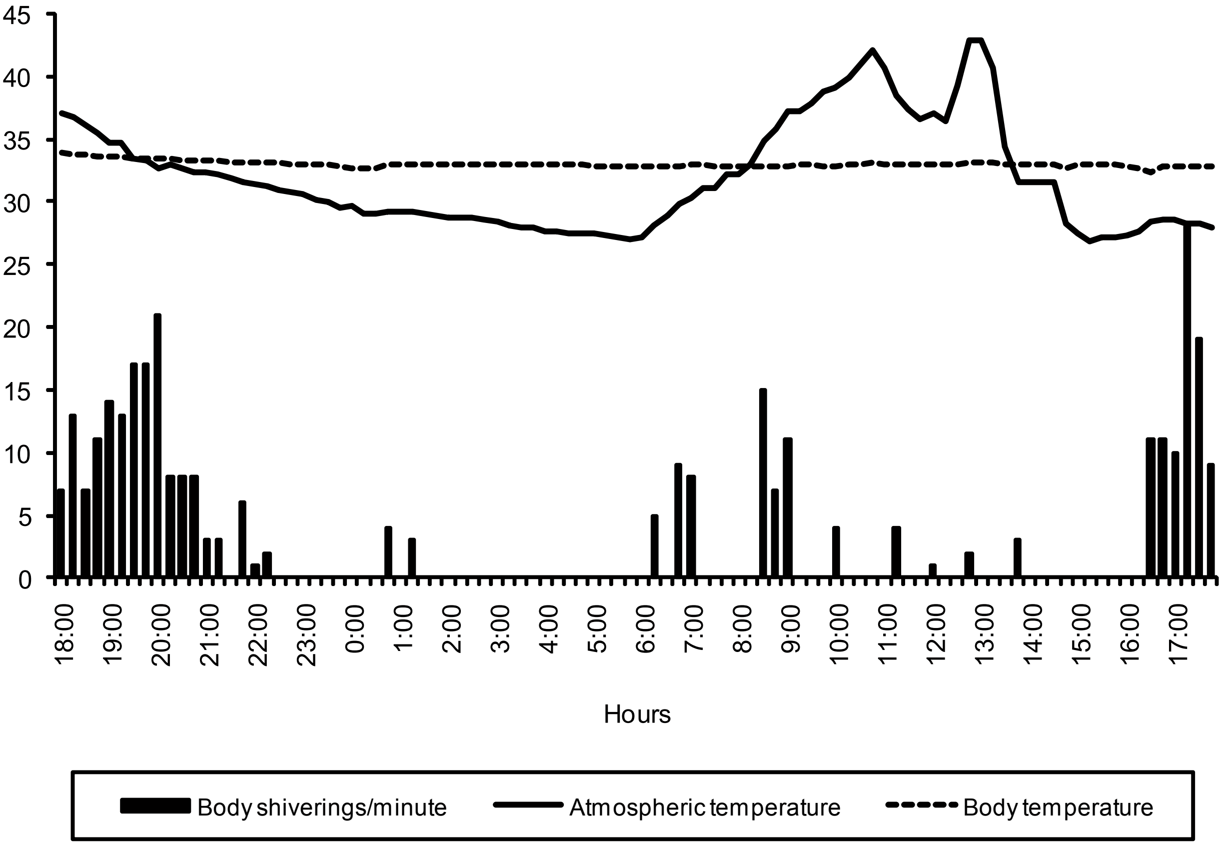

Fig. 2. Ambient temperature, body temperature and frequency of body shivering by incubating *Python molurus* over a 24-hour cycle (1800 on 8 June to 1800 on 9 June 2008). Bars: shivering frequency; dashed line: body temperature; solid line: atmospheric temperature.

Analysis of variance (ANOVA) was applied to test for differences in ambient and body temperatures of incubating snakes among various periods.

RESULTS

Sloughed skins and black, gel-like cloacal excretions were found approximately 100 m from the nesting sites two weeks prior to oviposition. Based on tracks and direct observations, it was found that snakes moved from one bush to another. Nests 1 and 2 were found 5 m and 250 m away from the females' wintering locations. Nest 1 was found in a depression in a termite hill (depth of cavity = 86 cm, average diameter = 28 cm) surrounded by thickets of *Acacia nilotica*, *Zyziphus* sp. and *S. persica*. Nest 2 was located in an unused jackal (*Canis aureus*) burrow on a wetland embankment, which had a gentle slope (depth = 163 cm, diameter = 26 cm), and the nest was located at the lower end.

Nest 1 (produced by a female with total length 3.9 m) comprised 37 eggs and nest 2 (produced by a female 3.3 m long) 19 eggs. The eggs were not visible until 14 July 2008. Although the nests were about 6.25 km apart from each other, we observed synchronized egg laying and dispersal of hatchlings. Emergence of hatchlings occurred from the night of 30 July to 1 August 2008, after 74 days. This included 61 days of active incubation by females and a period of 11 to 13 days when nests were left unattended. A few hatchlings emerged from the eggs (in both nests) on the 72nd night, but did not move out of the nest until 2000. The remainder left on the 74th night after egg laying. The pipping of the first egg was observed on 28 July (70th day) in both nests and partial emergence of a few hatchlings from eggs were observed on the 70th day, but all of them perhaps retreated into the shell for another two or three nights. Dispersal of hatchlings occurred at night when cloudy and rainy conditions prevailed.

Hatching success of *P. molurus* was 95% in both nests (35/37 and 18/19 eggs in nests 1 and 2, respectively). Three hatchlings left the yolk sac in the shell while emerging. Mean SVL and TL of 13 hatchlings (four from nest 1, nine from nest 2) were 531.53 ($\pm$37.64 SD) mm and 82.3 ($\pm$6.32) mm, respectively, with a mass of 111.15 ($\pm$9.16) g. The numbers of ventral and subcaudal scales of nine hatchlings were 243–251 (mean 247.22$\pm$2.38) and 60–68 (63.33$\pm$2.23), respectively. One hatchling found dead near nest 1 measured 640 mm in total length and weighed 200 g, and had no sign of deformity. During dis-

Table 1. Variation in body temperature of *Python molurus* in relation to ambient temperature during June–July 2008 in Keoladeo National Park, Bharatpur, India; numbers in parentheses are standard deviation and range.

Date	Mean body temperature of python	Mean ambient temperature
8 June	32.98 ˚C (±0.25, 32.40–33.90)	34.24 ˚C (±5.02, 26.9–42.8)
27 June	32.91 ˚C (±0.19, 32.10–33.10)	33.93 ˚C (±3.70, 28.5–40.5)
15 July	31.22 ˚C (±0.04. 31.10–31.30)	33.32 ˚C (±2.74, 29.0–37.0)

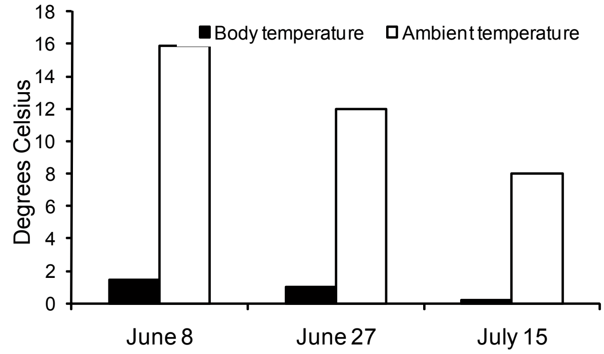

Fig. 3. Range of variation in ambient and body temperatures of *Python molurus* in Keoladeo National Park on 8 June, 27 June and 15 July 2008.

section, we found a mass of fat along the oesophagus and cloaca lying between the skin and alimentary canal. Each hatchling had a unique dorsal pattern with regards to the size and shape of the first five blotches posterior to the lancet mark on the head.

Neither female fed during the incubation period and incubating snakes abandoned the nest on the 61st day and subsequently sloughed their skin. A pool of rain water was available near nest 2, and the snake entered the water, wallowed for about an hour, and subsequently moved away. The other female strayed out for about 20 m and returned to the nest as revealed from tracks, and also was found nearby the nest for two days without coiling around the eggs. The eggs in both nests were exposed and unattended for 11–13 days until hatching and dispersal of the offspring. Ectoparasites (ticks) were common on incubating snakes and nearby nests, and their proliferation around the nest (3 m radius) was noted about 7–9 days prior to hatching.

Python molurus maintained their body temperature within a narrow range (31.1–33.9 ˚C) throughout the incubation period, irrespective of high variations in diurnal temperatures. During 24 hours of continuous monitoring, the ambient temperature was up to 6.1 ˚C lower than the body temperature of the snake between 0830 and 1430 (Fig. 2), whereas the body temperature was up to 9.7 ˚C lower than the ambient temperature during early afternoon (1245–1300). Variations in body temperature of the snake and ambient temperature were higher at the beginning of incubation compared to later periods (Table 1, Fig. 3). Diurnal ambient temperatures measured at 15-minute intervals did not vary significantly between the three periods, but the body temperature of the incubating female was significantly different (F=2536.57, df=2, P<0.001).

Winding and unwinding of the body coils was commonly observed during both day and night. The frequency of body shivering varied from 0 to 28/minute (mean = 3.36±5.75 SD, n=96), and was highest at 1700–2000 (4.31±6.03, n=13) followed by 0600–0900 (4.23±5.26 SD, n=13); low or no shivering was observed at other times (Fig. 2). A higher frequency of shivering was observed when there was a shift from day to night or vice versa (Fig. 2). The frequency of body shivering was significantly different among the three observation periods (F=12.905, df=2, P<0.001).

The relationship between the frequency of shivering in incubating python and both ambient and body temperatures is shown in Figure 4. Although no clear pattern was observed, it appears that relatively higher frequencies of shivering occurred when the ambient temperature was below 31 ˚C and above 35 ˚C (see also Table 1).

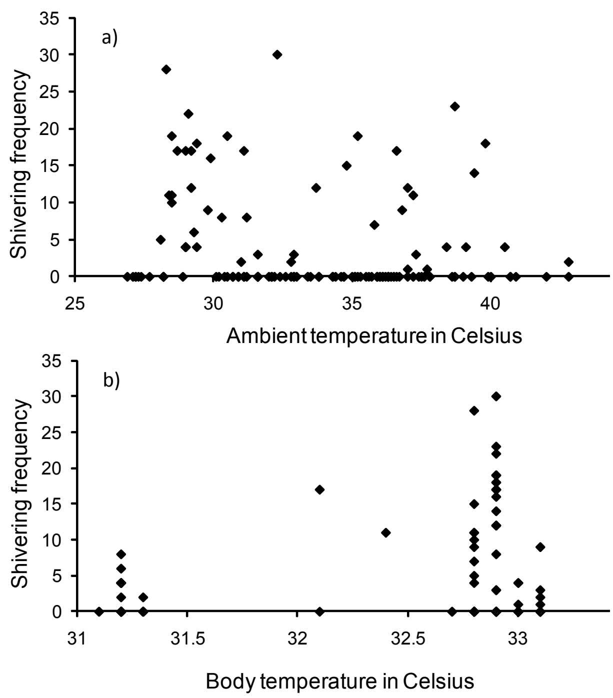

Fig. 4. Relationship between body shivering frequency in incubating *Python molurus* with respect to a) ambient and b) body temperatures in Keoladeo National Park, Bharatpur, India.

DISCUSSION

Data on the nesting habitat and behaviour of snakes are rare, and the excretion of cloacal matter by *P. molurus* in close vicinity to the nesting site, their movement around the burrows during winter and ecdysis upon termination of incubation has previously only been documented in captivity (Walsh & Murphy, 2003). The selection of oviposition sites by pythons has rarely been studied (Shine, 1985; Madsen & Shine, 1999). In the present study, incubating snakes did not feed and did not show any aggressive behaviour, which is similar to observations in captivity for *P. molurus* and *Morelia s. spilota* (Kalaiarasan & Rathinasabapathy, 1990; Slip & Shine, 1988).

The incubation period of *P. m. molurus* was 74 days, the final 11–13 days being unattended by females. Walsh & Murphy (2003) reported that a clutch with 22 eggs, artificially incubated with a temperature range from 27.2 to 32.2 ˚C, had an average incubation period of 72.5 (range 61–86) days. A wide variation of 57–93 days in incubation period for this species has been reported in captivity (Vinegar, 1973; Daniel, 1983; Kalaiarasan & Rathinasabapathy, 1990; Vyas, 1996; Walsh & Murphy, 2003), which may be attributed to varying temperatures. In most species of pythons, it is believed that the females remain with the clutch for the entire duration of incubation, and leave the nest only after the hatching of eggs (Shine, 1988). Hutchison et al. (1966) and Mierop & Barnard (1976) reported that *P. m. bivittatus* did not leave the nest even if an external heat source was available nearby. In the present study, the snakes abandoned the nest 11–13 days prior to the hatching of eggs, and in nest 1 the snake remained nearby but did not incubate the eggs for two days. Abandoning of the nest by incubating snakes may be influenced by a combination of thermal requirements and oxygen demands at late developmental stages. Kalaiarasan & Rathinasabapathy (1990) reported abandonment of nests by *P. molurus* in captivity and speculated that prolonged starvation was a probable reason. Incubating females of *Morelia spilota spilota*, *M. s. variegata*, *M. amesthystinus*, *Liasis fuscus* and *P. regius* may leave the nest for basking (Slip & Shine, 1988).

Stahlschmidt & De Nardo (2008) reported for *Antaresia childreni* that coiling around the eggs helps maintain oxygen requirements, water balance and metabolism, and the tightly coiled brooding posture decreased intra-clutch oxygen pressure compared to the nest environment. Loose coiling increases oxygen intake, but also water loss, and parental care in pythons can balance the different physiological requirements of developing embryos. Intra-clutch hypoxia also increases with incubation progress as embryonic metabolism and respiratory gas exchange increases (Stahlschmidt & De Nardo, 2008). This suggests that the abandoning of nests would coincide with the completion of embryonic development before hatching, when coiling around the eggs would be detrimental or disadvantageous. Also, KNP receives about 70–90% of its annual rainfall during July–September (Vijayan, 1991), providing suitable water conditions when eggs are not incubated.

We hypothesize that female snakes left the nest to avoid further attack or infection by proliferating ticks in the nest during the later part of incubation. Sloughing and wallowing in water may be useful in reducing the pressure of ectoparasites. Congregations of ticks have also been observed around iguana nests (B. Reed, pers. comm.). The ectoparasites were not identified but probably represent two genera of ticks (*Amblyomma* and *Aponomma*) reported from *P. molurus* in the same area (Bhupathy & Vijayan, 1989).

Python molurus is one of the most common snakes in zoological gardens, and has been bred in captivity (Dattatri, 1990; Kalaiarasan & Rathinasabapathy, 1990; Whitaker, 1993; Vyas, 1996, Joshi et al., 2001). It was assumed that females leave their nest due to starvation, and eggs were regularly moved to incubators. At times, zoo keepers tend to open the eggs to see the status of the embryos. The present study shows that abandoning of nests by female pythons is a natural behaviour.

Vijayan (1991) reported the germination of seeds and sprouting of vegetation in KNP with the advent of rain during July, which coincides with the dispersal of hatchlings, and might be used by hatchlings for shelter. Dispersal of hatchlings during the night is advantageous for avoiding predators (Burger, 1998). The present record of 95% hatching success is the first for this species in the wild. In captivity and during artificial incubation, it varies between 28.57 and 73% (Vyas, 1996; Baskar et al., 1999; Joshi et al., 2001; Walsh & Murphy, 2003). Body size (SVL, TL and mass) of hatchlings was similar to that reported in Indian zoos (Dattatri, 1990; Kalaiarasan & Rathinasabapathy, 1990; Vyas, 1996, 1998), and elsewhere (Mierop & Barnard, 1976). Krysko et al. (2008) reported neonates of invasive *P. m. bivittatus* to have a total length of about 450 mm (n=4) during June in Everglades National Park. Each hatchling had a unique dorsal pattern, confirming observations by Dattatri (1990) and Bhupathy (1990).

Python molurus maintained their body temperature within a narrow range throughout incubation irrespective of high variations in ambient temperature. Reports of body temperatures above the ambient temperature exist for colder regions (Hutchison et al., 1966; Vinegar, 1973), and this may also be essential for faster development of embryos in warmer climates (this study). Brooding pythons require 9.3 times more oxygen compared to non-brooding females (Hutchison & Maness, 1979).

In KNP, it appears that *P. molurus* use both mechanical and physiological means to maintain their temperature. Body shivering was associated with higher ambient temperatures, and hence it is unlikely that this action was intended to generate heat. In homeotherms, shivering is an involuntary body action to increase body temperature, but the reasons for shivering in incubating female pythons at high ambient temperature are unclear. Although several open questions remain, our data provide the first field-based evidence of facultative endothermy in this python species.

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