NOTES ON THE REPRODUCTIVE BIOLOGY OF AUSTRALIAN PYTHON, GENERA ASPIDITES, LIASIS AND MORELIA

Snakes of the family Boidae (pythons and boas) are among the largest and most spectacular reptiles, and consequently are often maintained in captivity. Hence, despite the scarcity of studies on natural populations (e.g. Hoyer 1974), considerable information is available on the reproductive biology of captive specimens (e.g. Ross 1978). One finding of great interest is that female pythons do not desert the eggs after oviposition (as is the general rule in reptiles), but instead coil around the clutch and defend the eggs against potential predators. In some, and perhaps all species, the female warms the clutch by metabolic heat production through muscular contractions of her body ("shivering thermogenesis") (see Shine 1985, for a review). Although about half of the world's python species are restricted to Australia, these forms have attracted less study than the Asian or African species. The present paper (i) provides information on reproduction of captive Aspidites melanocephalus, Liasis luscus, Morelia amethistina, M. oenpelliensis and M. spilota; (ii) describes natural nest sites and thermal regimes of four M. spilota clutches; and (iii) reviews published literature on reproductive biology of these species.

BLACK-HEADED PYTHON, Aspidites melanocephalus

This species is found over a wide area of northern Australia, and was studied by us near Townsville in coastal Queensland. In this region it is primarily nocturnal (20 of 24 specimens seen in the field were active at night) and feeds on a variety of vertebrate species. Captive specimens often refuse to feed on rats or mice, but readily accept other snakes as food.

Four A. melanocephalus were maintained in captivity in Townsville. The two males measured 1.9 and 2.1 m in total length (TL), and the females 1.5 and 2.0 m. The snakes were housed separately in cages measuring 1.1 x 0.5 m, with artificial heating. Based on experience with other locally-occurring pythons (Morelia spilota, Liasis luscus), we judged that mating in A. melanocephalus should occur in late winter or early spring (July-September). Hence, the snakes were placed together on 20 June 1981.

Mating occurred immediately with both pairs (Fig. 1). The males moved constantly about the cages, pressing their tails beside and under the females' tails. In the initial matings, the males persistently raked their "spurs" into the sides of the females' bodies near the cloaca. The spurs were raked rapidly (approximately two to three strokes per second) and vigorously. Spur use was seen only at the initial matings. Copulation was observed at all times of the day and night, but most frequently in early mornings (0800 h).

Duration of copulation was difficult to determine, but on at least one occasion exceeded 150 minutes. When the two males were introduced to the same cage (without females), the larger male immediately began biting and constricting the smaller male vigorously. The snakes were forcibly separated and the smaller male removed and replaced by a female. The large male showed no signs of aggression towards this female. However, removal of the female and reintroduction of the other male instantly resulted in attack by the large male. This procedure was repeated once more with the same results.

Both females were noted to show slight swelling of the posterior half of the body in early September. The females at this time were observed to lie with their ventral surfaces facing outward or upward for long periods. The smaller female had returned to her usual proportions (i.e. no swelling) by early October and began accepting food. The swelling in the larger female gradually increased in size, and this snake did not feed.

Eight eggs were laid by the larger female on 12 November, between 1100 and 1730 h. The eggs were laid in a loose group before being drawn together by the female and encircled by her coils. The eggs were supported off the floor by the female's body. Spasmodic "shivering" bouts, each of less than 20 seconds duration were observed (Fig. 1).

The eggs were removed in a single adherent mass, and incubated in moist vermiculite at 30°C (range 29.5 to 31°C). Egg dimensions averaged 9.2 (s.d. = 0.6) x 5.2 (s.d. = 0.2) cm. A "window" was cut in one egg after 55 days incubation, revealing an embryo which was fully-formed but only lightly pigmented. Hatching occurred on 16, 17 and 18 January (one, two and five eggs, respectively). The neonates emerged 24 to 30 hours after initial slitting of the shells. The hatching pythons...
The northern Australian water python has recently been moved from Liasis to Bothrochilus (Cogger et al. 1983). However the ICZN is currently considering an application that would cause fuscus to revert to Liasis (H. Cogger, pers. comm.). There is disagreement over whether the Australian form should be placed in the species mackloti (McDowell 1975) or fuscus (Cogger 1975).

A specimen from Townsville, Qld., deposited 19 eggs (four infertile) on 15 November 1982. The eggs were laid at intervals of approximately 10 minutes, with the first at 0610 h and the last before 1030 h. Although the female had been observed to have courtship in early August, no copulation had been observed. The 15 fertile eggs varied in mass from 1.0 to 44.5 g (s.d. = 4.2, range 42.4 to 52.3). Hence, they were significantly larger in all these respects than were the previous clutch from the same female. Data are also available on eggs laid on 28 October 1984 by a captive L. fuscus in Townsville. The clutch of 16 eggs had a mass of 999 g, with the female having a mass of 2200 g after oviposition (Relative Clutch Mass (RCM) = 0.46). The eggs were measured 174 g (s.d. = 1.4, range 160 to 184) and 748 g (s.d. = 1.8, range 425 to 1080).

Another female A. melanocephalus from Weipa, Qld., laid 10 eggs on 13 October, but none hatched. Previous records of A. melanocephalus reproduction reveal considerable variation in egg size, hatching size, and incubation period. Whereas we recorded hatchlings of 69 cm (94 gm), hatching after 66 days, Boos (1979) recorded hatchlings of 50 cm (69 gm), hatching after 28 days, 'Boos (1979) incubated the eggs. Hatchlings recorded by Murphy et al. (1981) were intermediate in size (60 cm, 81 gm) and incubation period (83 days) between the above values. Clutch sizes of A. melanocephalus range from five to twelve eggs, with specific records of 5, 6, 7, 8, 10, 11 and 12 (Gow 1976; Boos 1979; Murphy et al. 1981; P. Harvey, pers. comm.; present study).

WATER PYTHON, Liasis fuscus

This species is one of the most common and widespread Australian pythons. Two broods of female M. x variegata were discovered in suburban Brisbane in January 1982, and one in January 1985. The first snake (total length 215 cm) was under a pile of iron bane and housed together in a cage 2 m x 1 m x 1 m made of sheet metal, glass and natural (Brisbane) photoperiod.

The snakes were found in copula at 2300 h on 24 September 1981. Their tails were intertwined and the rest of their bodies stretched out loosely side-by-side. Copulation continued for 15 min and was repeated on the next night. The female bled from the cloaca at each mating. From the time of mating, the female refused to feed and spent long periods basking. She often lay with her ventral surface facing outwards or upwards.

Seven eggs were deposited on 26 December 1981, and the female coiled tightly around them. No "shivering" was observed, but temperature readings from within the coils revealed a constant 30°C over 16 measurements during 8 days and nights. (Measurements taken daily at 0630 and 1900 h.) Cage temperature ranged from 28° to 30°C over this time. The eggs were removed on 5 January. They were tightly adherent and the seven eggs had a mass of 20.4 to 22.4 g (s.d. = 1.6). The female began to feed normally after the eggs were removed.

The eggs were incubated at 29 to 30°C on moist vermiculite (50% water by weight), and one egg hatched on 10 April, 105 days after laying. Another egg was slit on 11 April, three on 12 April, and one on 13 April. The last egg was opened artificially on 13 April, revealing a live neonate which then emerged successfully. Most neonates remained inside the eggs for 48 h before the time of first sitting the shell, and final emergence. All neonates were light brown in colour, and were not as distinctly reticulated as the adults. The hatchlings comprised four females and three males, with a mean SVL of 54.1 cm (s.d. = 1.3, range 52.0 to 56.0), mean TL 63.9 cm (s.d. = 1.6, range 61.0 to 66.0), and mean mass 60 g (s.d. = 1.0, range 58 to 61).

There are few published reports of reproduction in Morelia amethistina with which to compare our data. Shivering thermogenesis has been noted in M. amethistina. Egg incubation has been estimated at 19° (Pope 1969), McPhee 1979) and 10 to 20 (Gow 1976), whereas Boos (1979) provides data on two clutches of 7 and 12 eggs. The incubation period reported by Boos (on a maternally-incubated clutch) was shorter than that observed by us (76 versus 106 days), but the hatchlings were of similar size (64 cm, 50 to 60 g).

CARPET PYTHON, Morelia spilota

This species is one of the most common and widespread Australian pythons. Two broods of female M. x variegata were discovered in suburban Brisbane in January 1982, and one in January 1985. The first snake (total length 215 cm) was under a pile of iron and "fibro" building materials (Fig. 2), and had been observed by workers to emerge and bask in the sun each morning for the preceding week. When the material covering the python was lifted, she was seen to be tightly coiled around a mass of eggs (Fig. 2). She was very aggressive, striking vigorously and repeatedly. The probe from an electronic thermometer was rejected. The male was tightly coiled around several coils, and three readings were taken over the next
The snake and eggs were collected on 9 January. The adherent mass of 23 eggs (two of which were discoloured and clearly dead) was 900 gm. As soon as she was placed in a cage, the female coiled around the eggs. Again, temperatures taken four to six times per day within the python’s coils remained at 30°C, except for one reading. At this time, air temperature in the cage fell to 26°C (rather than the usual 28°C) and egg temperature was 34°C. "Shivering" behaviour was not observed.

At 0830 h on 14 February, the python was seen to be draped only loosely around the eggs. Eleven of the eggs were slit, with seven of these eggs of almost completely dried grass clippings. She was very aggressive when disturbed. Temperatures within the coils at this time varied between the snake’s coils, and 29°C in the surrounding air. The python abandoned this clutch following a heavy hail storm on 19 January, so the clutch (total mass 540 gm) was moved and artificially incubated at 25 to 29°C. Hatching occurred on 21 to 24 February 1985, with neonate masses of 22 to 25 gm, and approximately 40 cm total length (R. Drans, pers. comm.).

A fourth brooding carpet python was discovered on 15 January 1985 in Townsville. As in the previous case, the clutch was laid at ground level in long dried grass clippings of unknown origin. Readings at 1300 h revealed a air temperature of 31°C, and a clutch temperature of 32°C. The female returned to the clutch after disturbance on two occasions. The clutch of ten eggs had a mass of 388 gm, and the female 680 gm (145 cm SVL). Following removal to the laboratory at 31°C, the eggs hatched on 11 February 1985. Neonate averaged 29.7 g (s.d. = 1.5, range 27 to 33); 40.1 cm SVL (s.d. = 1.2, range 37.3 to 41.5), and 47.2 cm TL (s.d. = 1.2, range 44.4 to 48.7).

Two captive Morelia s. variegata maintained in Townsville, northern Queensland, were observed to mate several times in August, always in the early morning. Mating was first recorded on 4 August 1982, and last recorded on 26 August 1982. The female laid twelve fertile eggs, beginning at 1500 h on 23 November 1982 and finishing at 0630 h the following morning. She coiled around ten of the eggs, but all developed fungal infestations and failed to hatch. The twelve eggs averaged 50.5 gm (s.d. = 1.6, range 48.7 to 54.3), and measured approximately 55 x 38 mm (in lengths 51.7 to 71.5; range in width 30.2 to 40.8).

Data were obtained on another Townsville pair of M. spilota in the following year. The male (255 cm) and female (230 cm) mated on 11 August, beginning at 1730 h (duration of mating at least 90 minutes). From mid-September the female was often seen bask- ing with the ventral surface turned upward or outward. Twenty-nine eggs were laid on 16 November 1985 (30). Of the 29 eggs, 25 had normally calcified shells, and most of the abnormal eggs failed to develop. The female coiled around the eggs, with spasmodic "shivering" bouts persisting for several days after the eggs were removed on the day of oviposition. The clutch had a mass of 1699 gm, and the female 3700 gm after oviposition. Three infertile eggs were smaller (approx. 52 x 34 mm, 46 gm) than the other 26 fertile eggs (length: X = 63.1 mm, s.d. = 3.1, range 57 to 68; width: X = 31.7 mm, s.d. = 1.9, range 39 to 45; mass: X = 65.5 gm, s.d. = 2.1, range 60 to 65). Only six of these eggs, incubated at 30°C, hatched: on 17 January (one), 18 January (four), and 20 January (one). The hatchlings averaged 37 cm SVL (s.d. = 1.8, range 34 to 39), and 26 gm mass (s.d. = 2.0, range 25 to 29).

Another captive M. spilota in Townsville laid 11 eggs on 25 November 1984 (mean egg mass 49.1 gm, s.d. = 4.0, range 44 to 59 gm; dimensions 48 x 39 mm to 65 x 39 mm). The clutch mass was 540 gm, and the female 2600 gm after oviposition (RCM = 0.21). Following incubation at 30 to 31°C, all eggs hatched on 2 February 1985. Hatchlings averaged 33.8 gm (s.d. = 1.3, range 32 to 35), 41.0 cm SVL (s.d. = 1.1, range 39.8 to 42.9) and 49.1 cm TL (s.d. = 1.1, range 48 to 51.2). Agonistic behaviour by male was noted by B. Barnett (pers. comm.). Incubation at 30°C was accomplished in Lantana scrub close to a stream. During a short period after capture and removal to a cage, the egg, and sparsely infested the eggs, and was aggressive when disturbed. She refused food until the eggs were removed, at which time she commenced feeding. Following a brief (6-day) period of artificial incubation, the eggs hatched to produce neonates 37.5 to 43 cm TL (L. Naylor, pers. comm.).

There have been few previous observations of female pythons brooding eggs in the wild. Published records of reproduction in Morelia spilota and M. s. variegata include clutch sizes of 12 to 47, with specific records of 12, 14, 15, 16, 26, 32, 34, 40, 47 (Fleay 1960; Covacevich 1970; Ross 1978; Boos 1979; Banks 1979; Gow 1976; McPhee 1979; Harlow and Grigg 1984). Clutch sizes of 14 and 16 eggs were recorded by R. Barnett (pers. comm.). Incubation periods apparently are variable, with extremes of 37 to 103 days (Boos 1979; Banks 1979). Hatching sizes reported by us (37 to 41 cm, 21 to 30 gm) are similar to those previously published (38 cm - Fleay 1960; 30-38 cm - Gow 1976, 1977, 30-45 cm - Banks 1979).

OENPELLI PYTHON, Morelia cenpelliniens

A female of this large and rare species, collected in the Arnhemland escarpment on 29 September 1984, laid a single egg with a mass of 184.9 gm (measuring 120 x 50 mm) on 20 October 1984. Nine remaining eggs were
removed surgically on 27 October 1984 and were of similar size of the first egg. All were apparently fertile but failed to develop. Egg mass averaged 185.6 g (s.d. = 8.8, range 176 to 203 g), and dimensions ranged from 90 x 60 mm to 105 x 60 mm. No previous data on M. oenpelliensis reproduction are available.

DISCUSSION

Data gathered in the present study generally are consistent with the results of previous studies. Maternal egg-brooding was seen in all four of the species in which reproduction in captivity was observed. Temperature measurements and/or observations of "shivering" suggest that females utilize metabolic thermogenesis to warm the eggs in all four forms. Our measurements of clutch temperature in M. spilota are, to our knowledge, the first made of brooding pythons in the field: although scanty, they are consistent with the prediction that maternal thermogenesis may enable a high and constant temperature to be maintained in the egg clutch (e.g. Harlow and Grigg 1984).

Our study also reveals interspecific similarities in some reproductive parameters (e.g. times of mating and oviposition) and differences in others (e.g. egg and offspring sizes; incubation periods). Many of these differences are surprising. For example, A. melanocephalus has a much larger egg and offspring, relative to adult body size, than the other species studied. Indeed, the hatchlings of A. melanocephalus are considerably larger than those of the amethystine python, M. amethystina. Nonetheless, the incubation period for these large offspring is very brief, similar to that for the much smaller offspring of L. fuscus and M. spilota. Additionally, the growth rates recorded for captive neonates of A. melanocephalus are surprisingly high. Any attempt to interpret the evolutionary and ecological significance of such differences would be premature at the moment: comparative data on the reproductive biology and natural history of other Australian pythons are needed for such a synthesis.

ACKNOWLEDGMENTS

We are grateful to several reptile keepers who provided data on their charges: J. Roberts, J. Devenish, P. Harvey, J. Bredl, B. Barnett and L. Naylor. We thank the Queensland National Parks and Wildlife Service for permission to conduct these studies, and the Northern Territory Conservation Commission for the gravid Oenpelli python. Valuable comments on the ms were provided by D. Slip and R. Lambeck. We thank also Terri Shine and Sylvia Warren for typing this paper.

LITERATURE CITED


NEIL CHARLES
8 Mahonia Street
Bellbowrie, Queensland 4020
Australia

RAY FIELD
1 Faraday Street
Wulugu, Queensland 4811
Australia

and

RICHARD SHINE
Zoology A08
University of Sydney, NSW 2006
Australia