

THE REPRODUCTIVE BIOLOGY AND MATING SYSTEM OF DIAMOND PYTHON, *MORELIA SPILOTA* (SERPENTES: BOIDAE)

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Zoology A08, The University of Sydney, NSW 2006, Australia

ABSTRACT: Observations of 18 radio-tracked snakes in the field, combined with dissection of museum specimens, provided data on reproductive biology of eastern Australian diamond pythons (*Morelia spilota*). Both sexes mature at about 150 cm snout-vent length (SVL). Pelvic spurs are longer and thicker in males than in females and are used by males to manipulate the female's tail prior to copulation. Reproductive activities occurred in spring (late September to early November), when testes were at their maximal size. Two to six males aggregated around a single female. Male combat was not observed, and more than one male was seen to copulate with the same female, in the presence of other males. Mating aggregations lasted from 4-6 wk. Females oviposited in late December or early January inside "nests" of leaf litter and coiled around the eggs to incubate them.

Clutch size of diamond pythons varied between 9 and 54 eggs per clutch, and was positively correlated with maternal SVL. During reproduction, females lost approximately 44% of their initial body weight, about two-thirds of which was attributed to oviposition and the other one-third to metabolic costs and reduced feeding opportunities associated with incubation. Probably because of this high metabolic cost and the low energy intake associated with "ambush" foraging, females did not breed every year.

Key words: Boidae; Python; Reproduction; Mating; Parental care; Behavior; Reproductive frequency; *Morelia spilota*; Australia

IT is evident from recent reviews of the reproductive biology of snakes (Seigel and Ford, 1987) that, although there have been many significant advances, major gaps remain in our knowledge. Two particular problems are the scarcity of research on snakes other than North American and European colubrids and viperids, and the scarcity of detailed field studies of reproductive behavior. The phylogenetic and geographic biases are likely to obscure any overall understanding of the topic, because many facets of ecology and reproductive biology may vary among major lineages (Dunham and Miles, 1985) and among continents (Dodson and Westoby, 1985). One example of this phenomenon is the prevalence of maternal brooding behavior in pythons (Boidae), compared to its rarity in most other reptilian lineages (Shine, 1988). Boids are also unusual in that most species attain large body sizes and are a significant component of the snake fauna

in most tropical and subtropical parts of the world.

Snakes of the family Boidae are divided into two subfamilies: the viviparous Boinae (true boas) and the oviparous Pythoninae (Minton and Minton, 1973; Pope, 1961). These snakes are popular with reptile keepers throughout the world, and as boids have become more difficult to obtain, either because of declining natural populations or restrictive import-export regulations, much emphasis has been placed on the breeding of these snakes in captivity. Consequently, breeding behavior in captivity has been well documented for a number of pythonine species. However, there have been very few published observations on the reproductive behavior of pythons in natural habitats, and available data are restricted to a few observations of brooding females (e.g., Charles et al., 1985). The most complete description of reproductive behavior in any species of python is that given by Barker et al. (1979) on social organization and reproductive behavior in captive Indian pythons (*Python molurus*). Although other studies (reviewed by Slip,

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1986) provide considerable information on fecundity, egg and hatchling sizes, and incubation periods, they usually say little about courtship and mating. Indeed there are few detailed observations on courtship and mating behavior amongst any snakes, especially in the field. This dearth of information is probably due to difficulties of observation, which result from the generally secretive nature of snakes. In this paper, we describe reproductive biology of the diamond python, *Morelia s. spilota*, a large (to 3 m) snake of coastal eastern Australia. Our data come mainly from observations of free-ranging pythons followed by radiotelemetry, but this information is supplemented by examination of museum specimens.

MATERIALS AND METHODS

Dissection of preserved specimens in the Australian Museum provided information on several aspects of reproductive biology. Snakes were first measured [snout-vent length (SVL)] using a plastic tape measure. Length of the pelvic spurs and width at the base of the spur were measured using vernier calipers. A mid-ventral incision was made to determine sex, maturity, and reproductive condition. Females were considered mature if they contained thickened oviducts, ovarian follicles >5 mm, or oviductal eggs. Males were considered mature if they contained enlarged testes, or if the efferent ducts were thickened, opaque, and convoluted. Males were considered to be in breeding condition if the testes were turgid. Clutch size was estimated in females by counting the number of enlarged ovarian follicles or oviductal eggs.

Regression analyses were performed on spur length against SVL and spur width against SVL, separately for males and females. The regression coefficients for each sex were compared using analysis of covariance. Data were log-transformed to homogenize variances.

Additional data were taken from 18 adult pythons radio-tracked in natural habitats over the period 1982-1985. Two study areas were used: Belrose and Cowan

valleys near Sydney, New South Wales. Both sites are steep and rocky and are covered in dry sclerophyll forest. Miniature 152 MHz temperature-sensitive transmitters (TT-IU-1000 from J. Stuart Enterprises, Grass Valley, California) with an operational life of 10-13 mo were surgically inserted in the peritoneal cavities of snakes while under halothane anesthesia. Transmitters were encapsulated in a paraffin-Elvax mixture and measured approximately 90 × 20 × 20 mm (mass 40 g, or 0.9-3.9% of snake body mass). Telemetered snakes were located with a Telonics receiver (TR-2E) and H-frame antenna. Reception range varied with topography but averaged approximately 400 m (extremes 50-1500 m). Reproductive behavior in telemetered snakes in the field was observed on four occasions, and detailed notes were taken in order to prepare a description of courtship and mating.

Reproductive females were weighed in the field 1-2 mo before oviposition, as any handling of the snakes closer to the time of egg-laying may have caused undue disturbance and provoked aberrant behavior. Females were weighed again after the eggs hatched. Clutch size was determined from recovery of empty egg shells. Neither the eggs nor the female were measured immediately after oviposition, because such a disturbance may cause the female to abandon the eggs (as has been reported in captivity: Boos, 1979; Charles et al., 1985; Ross, 1978). To determine the extent of loss in maternal mass resulting from oviposition, the recorded clutch size for that female was multiplied by mean egg mass. An estimate of mean egg mass of 36.8 g was derived from published data: Harlow and Grigg (1984) reported a mean egg mass of 33.4 g for *Morelia s. spilota* while Charles et al. (1985) gave mean egg masses of 39.1 g, 36 g, and 38.5 g for wild brooding *M. s. variegata*. In the present study, hatchlings were found to be of similar size ($\bar{x} \pm SD = 41.2 \pm 0.9$ cm SVL, 20.3 ± 1.6 g) to those measured by Harlow and Grigg (1984: 17.7 g) and Charles et al. (1985: 39-47 cm SVL, 22-30 g). Some of the clutches contained smaller deformed eggs which, when opened, were found to be infertile.

TABLE 1.—Time-table of reproductive activity of telemetered female diamond pythons. "Arrival of male snakes" refers to when males were first observed in proximity to the female. "Dispersal" refers to the first date when the female was observed alone.

	Order of arrival of male snakes					Dispersal	Female at site of oviposition	Oviposition
	First male	Second male	Third male	Fourth male	Fifth male			
1982	5 Sept.	23 Sept.	24 Sept.	20 Oct.	20 Oct.	7 Nov.	10 Nov.	20–22 Dec.
1983	22 Oct.					18 Nov.*	11 Jan.	16 Jan.
1984	6 Oct.	6 Oct.				22 Oct.*	14 Nov.	18–20 Dec.
1984	17 Oct.	17 Oct.	13 Nov.	14 Nov.	21 Nov.	7 Dec.	15 Dec.	27–30 Dec.

* Snakes were captured in aggregations on these dates and when released the males had dispersed.

These were weighed and found to have a mean mass of 10.0 ± 2.1 g.

RESULTS

Reproductive Cycles

Male pythons with turgid testes were found from June–November (10 of 12 individuals examined). Two snakes captured in November had semi-turgid testes. Snakes with regressed, flaccid testes were found from January–April ($n = 5$). No snakes were available from December or May. The smallest mature male had an SVL of 149 cm and the largest immature male had an SVL of 120 cm. All males that were followed by telemetry and had been in the wild the preceding winter (nine individuals on 12 occasions) exhibited reproductive behavior (i.e., were located in mating aggregations). Three males that had been held in captivity for 10–16 mo before being released in mid-August 1983 showed no signs of reproductive behavior the following spring, remaining relatively sedentary (unlike reproductive males that moved extensively: Slip and Shine, 1988a).

The small sample size of mature females in museum collections made a detailed analysis of female reproductive cycles difficult. Three females with ovarian follicles larger than 10 mm had been collected in May and June. Based on these animals and on clutches produced by telemetered snakes or previously reported in the literature, clutch size was found to increase with SVL ($n = 10$, $r = 0.90$, $Y = 0.47X - 65.0$ where $Y =$ clutch size, $X =$ SVL (cm); $P < 0.01$). The smallest mature female that we examined measured 150 cm SVL and the largest immature female was 130 cm SVL.

Based on direct observation, mating occurred in spring (September–November), with each female generally attended by several males (Table 1). When a male located a female, he remained with her for up to 8 wk and was often joined by more males (see below). By late November or early December, the snakes dispersed from the mating aggregations. Males began moving towards their summer ranges, presumably to feed, and females moved to oviposition sites. Three of the telemetered females were located at their subsequent oviposition sites, 4–6 wk before oviposition occurred (Table 1).

Sexual Dimorphism

Adult females attained larger average body sizes than did males, at least among the radiotracked pythons (\bar{x} female SVL = 194.2 cm, range = 182–230 cm, $n = 6$; \bar{x} male SVL = 167.0 cm, range = 143–182 cm, $n = 12$). Sexual dimorphism was also detected in spur size, with males having larger spurs than females at an equivalent SVL (Fig. 1). The slopes of the regression did not differ significantly between the sexes (ANCOVA $F_{1,65} = 0.462$, $P > 0.05$) but the elevations did ($F_{1,66} = 45.15$, $P < 0.001$). Similarly, the regression between spur width and SVL did not differ significantly between males and females in slope ($F_{1,65} = 1.41$, $P > 0.05$) but did differ in elevation ($F_{1,66} = 24.91$, $P < 0.001$; Fig. 1).

Costs of Reproduction

Females lost between 37% and 48% of their pre-ovipositional body mass by the time brooding had ceased. Approximately two-thirds of this mass loss was attributed to egg production and one-third due to

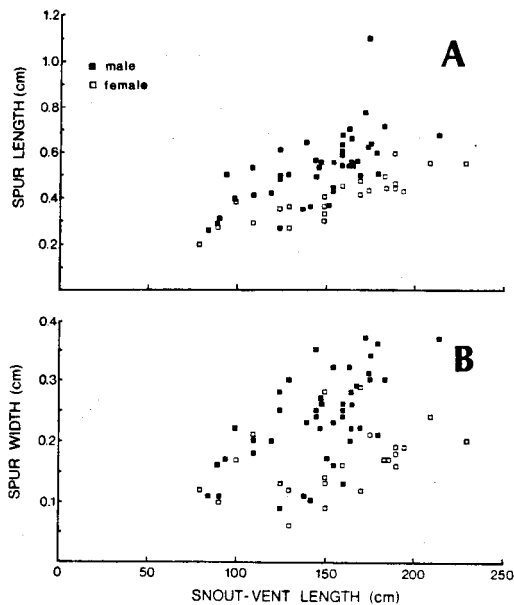


FIG. 1.—The relationship between (A) spur length and (B) spur width versus SVL of male (solid box) and female (open box) diamond pythons. Correlation coefficients (r) with SVL are: males, spur length (0.59), width (0.62); females, spur length (0.82), width (0.49). All regressions are significant ($P < 0.05$).

unknown causes, presumably the female's metabolic expenditure during incubation (Table 2). Females do not reproduce every year, because they are unable to replace this mass loss before the following reproductive season. Telemetered females regained mass slowly in the years following reproduction. One female that weighed 3.25 kg when she reproduced, weighed 2.95 and 3.20 kg in the following 2 yr, and she did not reproduce again during this period. Combining all available data from museum specimens and from pythons observed during our study (and counting each year separately for radio-tracked snakes),

only seven of 22 adult-size females (32%) were in reproductive condition in summer. A triennial female reproductive cycle may be the most common in our area.

Observations of Courtship and Mating

1982 reproduction (Belrose).—A telemetered adult female python inhabiting a large rock crevice was joined by a male on 5 September, and the two snakes emerged and basked together daily until the departure of the male on 9 September. Two other males joined the female on 23 and 24 September, and one of them mated with her on 1 October. The male used his spurs as well as his tail to manipulate the female's tail into position for copulation. The other male departed the area a few days later, but two additional males arrived, one of which mated with the female on 20 October, in the presence of the previously successful male. No aggressive behavior between males was observed. On 22 October, the female emerged from the crevice before the males and travelled 100 m to a new location. The two males currently occupying the same crevice emerged 60 and 100 min later; each, after briefly basking, moved off along the same route as taken by the female. The three snakes spent that night loosely coiled together, and the males followed the female when she continued moving the next day. Two other males, which had been captured at the original crevice on 20 October and had subsequently had transmitters implanted, were released at the now unoccupied crevice on 24 October. Both males tongue-flicked extensively and zig-zagged across the path taken by the female, reaching the other snakes (and coiling up with them) within a few hours. All five snakes re-

TABLE 2.—Female mass loss during reproduction in telemetered diamond pythons. Egg mass was estimated, not directly measured.

Snake no.	SVL (cm)	Pre-oviposition mass (kg)	Post-hatching mass (kg)	% mass loss	% original mass loss due to egg production	% original mass loss due to brooding	Clutch size
1	195	3.25	1.80	45	31.2	13.8	27
2	184	2.50	1.58	37	24.7	12.3	16
3	182	2.90	1.50	48	31.7	16.3	25
4	190	3.44	1.88	45	29.9	15.1	28

mained within an area of 10×10 m until 7 November. The female copulated with one of the males (one of the two released on 24 October) on 27 October, and with another (the same male with which she had mated on 1 October) on 29 October. Occasionally another male would approach or crawl over the copulating snakes, but there was no obvious aggression. The males began dispersing on 3 November, and the female reached her eventual oviposition site on 10 November.

1983 reproduction (Belrose).—One adult male and a female (which produced eggs later that season) were found together on 18 November. The male had been solitary when last located on 22 October. Two other nonreproductive adult females were monitored over this time period, but they were not approached by males, even though telemetered males passed within 50 m of each of them during spring.

1984 reproduction (Belrose).—Two adult males and a reproductive female were located together in the bole of a dead tree (*Eucalyptus* sp.) about 10 m above the ground. They were first sighted on 6 October and were collected on 22 October.

1984 reproduction (Cowan).—Two adult males and a female (which later produced eggs) were together on a sandstone ledge area from 17–29 October, when the snakes were captured for transmitter insertion. Soon after release, the female was joined by one of the original males and a newcomer; the latter snake copulated with the female for 40 min on 13 November, after using his spurs to manipulate the female's tail. The other male basked 5 m from the copulating pair and did not interact with them; however, he was found in copulo with the female the next day. Two other adult males (one of them the snake that had copulated the previous day) lay loosely coiled over the midbody region of the copulating pair. The female was still accompanied by three males on 21 November but was solitary when next located (7 December). She had been in contact with at least five males during the mating period and had copulated with at least two of these.

DISCUSSION

Reproductive Cycles

Reproductive cycles in male snakes are less well known than those of females (Saint Girons, 1982), and nothing has been reported for the Boidae. Our limited data suggest that *M. s. spilota* shows "prenuptial spermatogenesis" (Saint Girons, 1982) with testicular enlargement occurring in winter and the testes regressing after mating occurs in spring. Cycles of this type have been found in some species of Australian elapids including two (*Pseudechis porphyriacus* and *Acanthophis antarcticus*) that are sympatric with *M. s. spilota* (Shine, 1977). The relationship between female SVL and clutch size shows that larger snakes produce more offspring, and this is consistent with data on many other species of snakes [see Pope (1961) for *Python*, Fitch (1970) for other taxa].

Little is known of the frequency of female reproduction in natural populations of pythons. In captivity, *M. s. spilota* breeds only every second year (Harlow and Grigg, 1984; A. Walters, personal communication; P. Whittaker, personal communication) as does *Python reticulatus* (Fitch, 1970) and several boine species (Huff, 1980). Female *Python molurus* can produce a clutch every year in captivity (Fitch, 1970) and *Epicrates cenchria* may do so in the wild (Vitt and Vangilder, 1983). Crotalid and viperid snakes generally have low reproductive frequencies with females reproducing, most commonly, every second year (Gibbons, 1972; Klauber, 1972; Seigel and Ford, 1987). In natural habitats, female *M. s. spilota* are reproductive at best every second year, but data from the only female tracked over three reproductive seasons suggest that a longer cycle may exist. Bull and Shine (1979) found a correlation between the occurrence of a low frequency of reproduction (LFR) and the existence of an accessory reproductive activity (such as brooding or a long migration). They suggested that the low reproductive frequency was favored because of the fecundity-independent nature of the "costs" of such activities. The loss in mass

attributed to brooding by female *M. s. spilota* appears to be a fecundity-independent cost in that the costs of brooding probably depend relatively little on the number of eggs to be brooded, and this may be one reason for the low reproductive frequency of females.

Because the present study is the first to provide detailed information on field reproductive biology of any python, it is of interest to see how *M. s. spilota* compares, in broad terms, with previously studied snakes of other families. The life history of *M. s. spilota* appears more similar to that of crotalids and viperids than to that of elapids and colubrids. Many viperids are characterized by high adult survivorship, low fecundity, and high age at maturity (Parker and Plummer, 1987). As female diamond pythons do not reproduce every year, mean annual fecundity is low. Assuming a 3-yr reproductive cycle, mean annual fecundity of diamond pythons (based on reproductive records of free-ranging snakes) is 7.1 offspring per female per year (range 3.7–9.3). This is similar to the mean fecundity of late maturing viperids (\bar{x} = 6.0, range 4.6–7.9), and lower than that recorded for most colubrid snakes (\bar{x} = 12.2, range 6.1–22.3) (Parker and Plummer, 1987). Also, reproductive frequencies generally are lower in viperids than in elapids (Shine, 1980). A further similarity between *M. s. spilota* and many viperids is their ambush foraging behavior (Slip and Shine, 1988b). Ambush foraging generally results in a lower rate of food intake than does active foraging (Fitch, 1960; Shine, 1980). Thus, the low mean annual fecundity of *M. s. spilota* may be due to the low rate of energy intake which results from ambush foraging, as well as to the high "costs" of brooding.

Sexual Dimorphism

The use of spurs during courtship by captive boids has been described for several species including *Aspidites melanocephalus* (Charles et al., 1985), *Python curtus* (Davis, 1936), *Python molurus* (Gillingham and Chambers, 1982), *Moria boeleni*, *Candoia bibroni*, *Corallus*

canina (Murphy et al., 1978), *Lichanura roseofusca* (Kurfess, 1967), *Acrantophis madagascariensis*, and *Liasis boa* (Murphy et al., 1981). However, *Liasis childreni* and *L. mackloti* apparently do not use their spurs in this way (McLain, 1980; Murphy et al., 1981). In all cases where spurs were used in courtship, their use was by males and involved erection of the spurs and some form of contact of the spurs with the lower part of the female, generally around the region of the cloaca. These actions generally have been interpreted as stimulatory and appear to induce receptivity on the part of the female. However, our observations suggest that males can use their spurs in conjunction with the tail, to manipulate the female into position. There is no evidence that female spurs are functional. Thus there may be some selective advantage for large spur size in males but not in females. The use of spurs by males has also been observed during combat bouts in some boid species (Barker et al., 1979; Carpenter et al., 1978).

Mating Behavior

Telemetered male pythons increased their activity in early spring and began to make large daily movements, presumably in the search for mates (Slip and Shine, 1988a). Trail-following has been demonstrated in some colubrid, typhlopoid, and leptotyphlopoid snakes (Ford, 1981, 1987; Ford and Low, 1984; Gehlbach et al., 1971) and has been observed in association with mating in *Coluber constrictor* in the wild (Lillywhite, 1985). Observations of accurate trail-following by males in the present study suggest that this may be the mechanism by which females are located, and that the increase in frequency of movements and distance moved would increase the likelihood of males encountering the trail of a female.

On encountering a reproductive female, males generally stayed with her despite the presence of other males. If reproductive females are in short supply (possibly because of the lower reproductive frequency of females than males), then the likelihood of a male encountering another reproduc-

tive female would be low. The high cost of additional searching, due to energy expenditure and possible increased exposure to predators, with the low chance of reproductive gains would make it advantageous to remain with the first female located and risk competing with other males for reproductive opportunities. Reproductive aggregations of snakes characterized by a single female attended by several or many males are typical of the natricine colubrids such as *Thamnophis* and *Nerodia* (Aleksiuk and Gregory, 1974; Fitch, 1965; Gibson and Falls, 1975) and have been reported in acrochordids (Shine, 1986) and typhlopids (personal observation). This type of mating behavior occurs in snakes with a variety of body forms, includes both temperate and tropical zone species, and may occur where males greatly outnumber females in the breeding population. This skew in the Operational Sex Ratio (Emlen and Oring, 1977) could result from a number of factors including differential mortality, delayed maturation in females, low frequencies of reproduction in females, or behavioral differences between the sexes (such as females dispersing singly from hibernation dens as in *Thamnophis*). In *M. s. spilota*, the most likely reason for these mating aggregations is the low percentage of reproductive females in the population each year.

Male combat associated with reproductive behavior has been recorded in many species of snakes (Carpenter, 1986), including the pythons *Aspidites melanocephalus* in captivity (Barker et al., 1979; Charles et al., 1985) and *Morelia spilota variegata* in the field (Covacevich, 1975). In the present study, there was no evidence of male-male aggression in *M. s. spilota* during reproduction. The apparent difference between the two subspecies of *M. spilota* is surprising. It may be that the large mating aggregations of *M. s. spilota* mean that there would be no advantage to a male in engaging in combat with other males; while fighting was occurring, other males could copulate with the female. The two taxa of pythons reported to show male combat (see above) are generally tropical. In these species, females may reproduce

more frequently than do females of *M. s. spilota*, due to a reduced cost of incubating eggs and perhaps a higher availability of food (i.e., longer activity season). This may lead to a lower ratio of males to reproductive females, and increase the advantage of male combat. Until more is known of the reproductive cycles in nature of these species, this possibility remains speculative.

Mating by one female with more than one male has been observed, or inferred to occur, in viperids (Schuett and Gillingham, 1986; Stille et al., 1986) and colubrids (Gibson and Falls, 1975; Hammerson, 1978). In the 1982 mating season, a female *M. s. spilota* was observed copulating five times, involving three different males, and in 1984, a female was observed copulating with two different males. Individual males will copulate with a female more than once. In terms of male fitness, this behavior is likely to be favored by natural selection because of sperm competition, or simply because it renders the female unavailable for mating with other partners.

The advantages of multiple matings to the female are less obvious. Multiple matings may be advantageous to females in ensuring that sufficient viable sperm are available to fertilize all of her eggs, or it may not be worthwhile for a female to reject courting males. In some snakes, mating involves some risk, such as the reduced ability to escape predation (Gibson and Falls, 1975). Multiple mating by females may be selected for if the energy expended by the female in avoiding multiple mating, and the risk she faces, would be high and the risks involved in mating are low. Mating does not involve vigorous movement, of the type liable to attract potential predators. On the other hand, courting males are very active and more likely to attract predators to themselves and hence their mates. Willingness to engage in multiple matings may thus decrease a female's exposure to predators.

Acknowledgments.—This paper comprises part of an M.Sc. Thesis by the senior author. We thank R. Williams and G. Swan for capture of pythons, C. James, R. Lambeck, P. Harlow, and T. Pople for technical assistance, J. Bennett for assistance with

surgery, G. Grigg for advice and the loan of equipment, and J. Jeffery for artwork. H. Cogger and A. Greer kindly allowed us to dissect Australian Museum specimens. The Peter Rankin Fund assisted with the purchase of transmitters, and the N.S.W. National Parks and Wildlife Service provided permits for the work.

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