

## Feeding Habits of the Diamond Python, *Morelia s. spilota*: Ambush Predation by a Boid Snake

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**ABSTRACT**—Diamond pythons (*Morelia s. spilota*) are large (to 3 m) snakes of temperate-zone coastal eastern Australia. Foraging behavior was studied by observation of telemetered snakes, and diets determined by dissection of museum specimens and collection of fecal samples from wild-caught snakes. Five adult snakes monitored in the field by radiotelemetry were found to be ambush foragers. In summer, telemetered snakes spent more than 80% of their time coiled, usually in a distinctive ambush posture near mammal trails. Telemetered snakes found feeding had occupied the site for at least a day beforehand. The diet of adult diamond pythons consisted almost entirely of mammals (91% of 44 records), mainly *Rattus rattus* and *R. fuscipes* (52%). Birds (9%) were taken infrequently. Juveniles ate mainly mammals (69%) and reptiles (23%). Larger snakes consumed larger prey. Hatchlings in captivity showed a preference for copper-tailed skinks, *Ctenotus taeniolatus*, but would also take newborn mice. Feeding occurred mainly in late spring, summer and early autumn. In terms of feeding biology, diamond pythons may be more similar to viperid snakes of other continents than to the elapids or colubrids with which they are sympatric.

The food that an animal eats, and the way it obtains that food, are central aspects of a species' ecology. Trophic interactions may influence the distribution and abundance of a predator (and perhaps its prey), and certainly will directly affect daily activity patterns and habitat use. Foraging behavior may determine rates of energy intake and survivorship, and hence may have wide-ranging effects on life-history variables, either as direct phenotypic effects, or as a basis for the evolution of modified morphology, physiology, behavior or reproductive biology (e.g. Vitt and Congdon, 1978; Ballinger, 1983). Feeding habits of snakes are of particular interest, as they show remarkable adaptations for locating, capturing, subduing and ingesting very large prey items (see Pough, 1983). Available published data on snake foraging are concerned primarily with active searching predators belonging to the families Colubridae and Elapidae (e.g. Godley, 1980; Greene, 1984). Sit-and-wait (ambush) predation also is common in snakes, but has been described in detail only for viperids (e.g. Reinert et al., 1984; Duvall et al., 1985).

Boid snakes are widely distributed in tropical and subtropical areas throughout the world, but have attracted little scientific study under field conditions. These snakes are of interest from several points

of view, including their large size, constricting behavior, and ability to consume extremely large prey items (e.g. Fitzsimons, 1930). In the present paper, we describe food habits and foraging behavior of diamond pythons (*Morelia s. spilota*) in southeastern Australia. This subspecies occupies a relatively small range in coastal New South Wales, whereas the related *M. s. variegata* occurs over most of the rest of the Australian continent. Adult diamond pythons average approximately 170 cm snout-vent length (Slip, 1986), and are black dorsally with yellow flecks. Neonates are mottled brown, and the ontogenetic shift in color is gradual (pers. obs.). We obtained data from observation of free-ranging radiotracked snakes, combined with dissection of museum specimens and analysis of fecal and stomach content samples from field-collected snakes. Because juvenile pythons are rarely encountered in the field, we examined dietary preferences of neonates in the laboratory. This work is part of a larger study on the ecology of diamond pythons (Slip, 1986; Slip and Shine, 1988a, b).

### MATERIALS AND METHODS

*Diet.*—Feeding records came from two sources: preserved specimens from the collection at the Australian Museum, and

snakes collected in the field. Museum specimens were dissected and the contents of the stomach and intestine were removed. Often the only gut contents were a few mammalian hairs in the lower intestine. Feeding records from freshly-captured animals in the field were obtained by palpation. If a bolus was detected in the stomach, the snake was forced to regurgitate, and the prey item was identified, measured and forced back into the stomach (Fitch, 1960). If fecal pellets were detected in the hind gut they were removed by palpation and collected. If no gut contents were obtained, snakes were held in isolation for up to two weeks at 26 to 28°C to allow passage of feces. If no fecal samples were found after this period the snake was assumed to be in unfed condition. Mammal hairs were identified by microscopic analysis (Brunner and Coman, 1974), and by use of a reference collection of fur samples. Prey length usually could be estimated from skeletal remains in fecal and gut samples, or mean lengths of mammalian prey were taken from Strahan (1983). Dates of capture of snakes were obtained from museum and field records and grouped according to season for analysis of the seasonality of feeding.

*Hatchling Food Preferences.*—Food preferences in hatchlings were investigated by presenting captive hatchlings with potential prey items. Eleven hatchlings were housed in individual glass and wire tanks 40 × 30 × 20 cm, heated with 60 watt bulbs and positioned near a window to provide natural light. The tanks were maintained at 25–30°C and water was provided.

When the hatchlings were 21 days old, they were presented with the following potential prey items: the skinks *Ctenotus taeniolatus*, *Lampropholis guichenoti*, *Leiopisma entrecasteauxii* and *Nannoscincus maccoyi*; hatchling dragons *Amphibolurus barbatus* and *Physignathus lesueurii*; the terrestrial tree frog *Litoria lesueurii*; the bush cockroach *Calolampra* sp., unfurred nestling laboratory mice and recently furred nestling laboratory mice (*Mus domesticus*). These species were chosen as representatives of naturally-occurring potential prey types within the range of *Morelia s. spilota*.

The order of presentation of prey was randomized. Each snake was presented with one prey item, which was left in the tank with the snake for 24 hours. If the prey remained after this time it was removed and another prey item presented. If the prey was consumed, one week was allowed before the next trial. When each hatchling had been exposed to all prey items they were fed (some force-fed) an unfurred nestling laboratory mouse. After one week the experiment was repeated.

*Foraging Behavior.*—Eighteen adult diamond pythons were monitored by radio-telemetry to provide information on thermoregulation, movements and habitat use (Slip, 1986); the present paper provides data on general behavior of five of these snakes (those for which most detailed data were available), and on feeding by another three. The two study sites used are valleys near Sydney, N.S.W. (Belrose and Cowan). Both sites are steep and rocky, and covered in dry sclerophyll forest. Miniature 152 mHz temperature-sensitive radiotransmitters (model TT-IU-1000, J. Stuart Enterprises, Grass Valley, California) were surgically inserted in the peritoneal cavities of snakes under halothane anesthesia. Single three-volt lithium cell batteries (National BR-2/3A) provided an operational life of 10–13 months. The transmitters were sealed with a waterproof coating of paraffin (80%) and elvax. The assembled unit measured approximately 90 × 20 × 20 mm with a mean mass of 40.2 ± 3.65 g, representing 0.9 to 3.9% of snake body mass. Most locations of telemetered snakes were made on foot, but continuous records of snake temperatures (pulse interval) and activity (signal intensity) were obtained by an automatic recording system consisting of a TR-2E receiver, H-frame antenna, TDP-2 digital processor (Telonics Telemetry Consultants, Mesa, Arizona) and a Rustrak dual level recorder. For further details on methodology see Slip (1986).

To investigate foraging mode, three male and two female snakes were monitored continuously by telemetry, each over a 72-hour period during summer. In addition to this continuous record of the amplitude and period of the telemetry signal, snakes

TABLE 1. Prey items identified from gut and fecal contents of adult and juvenile *Morelia s. spilota* (adult = SVL >150 cm, criteria for sexual maturity are given in Slip and Shine 1987a).

Prey	Snakes	
	Juveniles	Adults
<b>Mammals</b>		
<i>Potorous tridactylus</i>		1
<i>Trichosurus vulpecula</i>		3
<i>Pseudocheirus peregrinus</i>		6
<i>Petaurus breviceps</i>	1	1
<i>Perameles nasuta</i>		1
<i>Rattus fuscipes</i>	2	12
<i>Rattus rattus</i>	1	8
<i>Mus domesticus</i>	4	3
<i>Pseudomys novaehollandiae</i>	1	
<i>Oryctolagus cuniculus</i>		5
<b>Birds</b>		
<i>Manorina melanocephala</i>		1
<i>Melopsittacus undulatus</i>	1	
Unidentified birds		3
<b>Reptiles</b>		
<i>Amphibolurus barbatus</i>	1	
<i>Ctenotus taeniolatus</i>	1	
Unidentified skink	1	

were located soon after sunrise and observed continuously for four hours. Their positions and behaviors were then checked three or four times at approximately two-hour intervals, and the snakes were observed continuously for about two hours immediately before sunset. Nocturnal activity was determined from changes in the amplitude of the radio signal. Movement of the transmitter relative to the receiver results in a change in amplitude, and a crude calibration of movement was obtained by noting amplitude response on a chart recorder while simultaneously observing the telemetered snake. For example, it was possible to distinguish postural readjustments (such as moving from a tight coil to a loose coil) from continuous movement, and periods of no movement. Three categories of behavior were used for the analysis: (1) moving, determined from direct observation or telemetry data; (2) basking, determined from direct observation (it was assumed no basking took place at night), defined as when a snake was lying loosely coiled or uncoiled in direct or filtered sunlight; and (3) coiled (not moving),

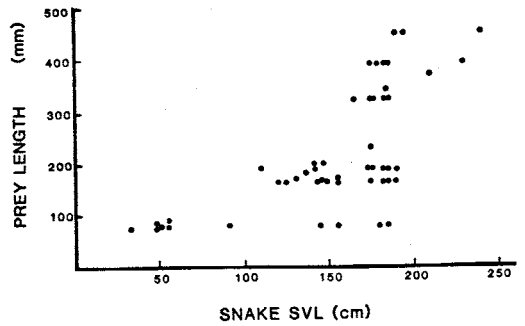


FIG. 1. The relationship between snout-vent length (SVL) of diamond pythons and the lengths of prey taken.

determined from direct observation and telemetry data.

RESULTS

**Diet.**—Of the 108 *M. s. spilota* examined, 49 (45%) contained prey items in the stomach (8) or produced fecal samples (41). Single prey items were identified from most snakes, but six snakes contained two items each and one contained three. The food types recorded were mammals (49 records, 86%), birds (5 records, 9%) and reptiles (3 records, 5%). The mammals most commonly recorded were rats (two *Rattus* species, 40% of all records) and possums (three species, 19%; Table 1). The three reptilian prey items came from juvenile snakes.

A comparison of snake body length to estimated prey length (Fig. 1) shows that small snakes took only small prey such as reptiles, mice and sugar gliders (*Petaurus breviceps*). Larger snakes also took small prey, but in addition they consumed large animals such as brushtail possums (*Trichosurus vulpecula*) and rabbits (*Oryctolagus cuniculus*). Some prey items were very large: for example, a brushtail possum consumed by a 3.2 kg snake was estimated to weigh approximately 2 kg.

*Morelia s. spilota* show distinct seasonal differences in frequency of feeding (Table 2) with a higher proportion of recently-fed snakes captured in summer (73.9%) than in other seasons (0-42%). No snakes captured during winter showed evidence of recent feeding. These seasonal differences are significant ( $R \times C$  chi-square from Zar, 1974;  $\chi^2 = 28.610$ ,  $v = 3$ ,  $P < 0.001$ ). No adult

TABLE 2. Monthly variation in the numbers of *Morelia s. spilota* containing food items in the digestive tract (letters indicate months of the year, and asterisk indicates gravid females).

		S	O	N	D	J	F	M	A	M	Winter
Adult males (>150 cm)	Fed	0	0	0	3	14	2	2	1	0	0
	Not fed	4	8	1	2	3	1	3	2	4	6
Adult females (>150 cm)	Fed	0	1	0	0	8	5	5	0	0	0
	Not fed	0	2	4*	1	0	3	1	0	2	4
Juveniles (<150 cm)	Fed	1	1	6	1	0	1	1	2	0	0
	Not fed	0	2	0	1	1	0	0	1	2	3

males were found with prey items during spring (N = 13) and no prey items were recorded from gravid females (N = 4, Table 2).

*Hatchling Food Preferences.*—Three of the 11 hatchling pythons used showed no interest in any of the food items. The remaining eight hatchlings all took *Ctenotus taeniolatus* when offered, and furred laboratory mice on at least one occasion. Six also took unfurred mice, and two hatchlings took *Leiolopisma entrecasteauxii*. None showed interest in any of the other prey items offered (Table 3).

*Foraging Behavior.*—Telemetered snakes were often observed in a coiled or loosely coiled posture with the head positioned at the top of the coil and inclined at an angle of about 15° above horizontal. Generally this position was adopted partially under cover, with the head oriented toward open ground, and often on the edge of mammal runways such as those used by rats, rabbits and bandicoots. These runways could be identified by the presence of scats or scratchings.

Telemetered snakes were observed feeding in the field on three occasions. On 16

February 1982, at 1150 h, a female (SVL 195 cm) was observed swallowing an adult brushtail possum (*Trichosurus vulpecula*). The snake was in a fork of a 10 m *Eucalyptus oblonga*, about six m above the ground. When located on the previous two days, this snake had been coiled in the same fork. On 15 October 1983, at 1250 h, a female python (SVL 184 cm) was observed swallowing an adult rabbit. This snake had been previously located two m away on 13 October coiled tightly and partially concealed by long grass at the edge of a 30 cm wide trail, which was used as a runway by small mammals. The snake completed swallowing in 45 minutes. On 14 December 1983, at 1200 h, a male diamond python (SVL 165 cm) was observed swallowing an adult ringtail possum (*Pseudocheirus peregrinus*) with an estimated body length of 350 mm. The snake was lying on leaf litter at the base of a six m *Casuarina* sp. When located on the previous day, this snake had been coiled 10 m away at the base of a *Xanthorhea* sp.

Table 4 shows the amounts of time each of five snakes spent coiled, moving and basking over 72 hours. Heterogeneity chi-

TABLE 3. Feeding preferences of hatchling *Morelia s. spilota*.

Prey species	Approx. SVL (mm)	Approx. mass (g)	Eaten	Not eaten
<i>Amphibolurus barbatus</i>	44	4		22
<i>Physignathus lesueurii</i>	46	5		22
<i>Ctenotus taeniolatus</i>	80	10	16	6
<i>Lampropholis guichenoti</i>	40	3		22
<i>Leiolopisma entrecasteauxii</i>	50	5	4	18
<i>Nannoscincus maccoyi</i>	50	5		22
<i>Litoria lesueuri</i>	50	8		22
<i>Caloolampra</i> sp.	30	1		22
Unfurred neonate <i>Mus domesticus</i>	20	5	11	11
Furred neonate <i>Mus domesticus</i>	40	10	14	8

TABLE 4. Activity budget, in hours, for snakes monitored continuously over 72 hours.

Snake	Sex	SVL (cm)	Number of hours spent in each activity		
			Coiled	Moving	Basking
#1	F	195	57.5	10	4.5
#5	F	184	59.5	8.5	4
#12	M	149	51.5	16	4.5
#14	M	180	60.5	10	1.5
#18	M	175	59	9	4
Total hours			288	53.5	18.5
Mean $\pm$ SD			57.6 $\pm$ 3.58	10.7 $\pm$ 3.03	3.7 $\pm$ 1.25
Mean proportion of time			0.80	0.15	0.05

square analysis shows that individuals were similar in the proportions of time spent in each of the three activities ( $\chi^2 = 3.93$ ,  $v = 8$ ,  $0.75 < P < 0.90$ ). Snakes monitored continuously in summer spent most of their time (80%) in a coiled position.

#### DISCUSSION

*Diet.*—Published data on the diet of *Morelia s. spilota* are generally consistent with the results of our study, in that most authors consider birds and mammals to be the commonest food items (Table 5). Our data suggest clearly that mammals are the principal component of the diet of adult *M. s. spilota* (contra McPhee, 1979). The low incidence of birds in the diet may reflect the infrequency of arboreal activity (Slip and Shine, 1988b). No eggs, reptiles or frogs were recorded from the digestive tract of adult *M. s. spilota*. Published data on the diets of other species of pythonine snakes are primarily anecdotal, but mammals seem to be an important component of the diets

of the larger species such as *Python molurus*, *Python reticulatus* and *Python sebae*, with large individuals capable of taking very large prey (Pope, 1961; Branch and Hacke, 1980). Mammals are probably the most important component of the diets of most Australian pythons except *Aspidites melanocephalus*, which feeds mainly on reptiles (Shine and Slip, unpubl. obs.). The species of mammals eaten by *M. s. spilota* are mainly nocturnal (Watts and Aslin, 1981; Strahan, 1983) and as adult diamond pythons are predominantly ambush predators, most prey encounters would occur at night.

The significant seasonal variations observed in feeding frequency could be due either to differences in prey availability (perhaps because of seasonal habitat shifts by the snakes) or to other behavioral shifts in the snakes or their prey. Thus, for example, the high frequency of feeding in summer may reflect fluctuations in prey density, as *Rattus fuscipes* occurs in highest densities at this time (Watts and Aslin,

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Reference	Diet
Kreff, 1869	Birds and small mammals. The young feed on insects, frogs or bird eggs.
Lucas and le Souef, 1909	One record of a 2.59 m snake eating a ringtail possum, one record of a 2.74 m snake eating a brushtail possum.
Waite, 1929	Rabbits, wallabies, possums, ducks, other birds, bird eggs, lizards, frogs and snakes.
McKay, 1948	Warm-blooded animals such as birds, rats, mice, rabbits, and small possums.
McPhee, 1979	Principally birds, also consume mammals such as rats, mice, marsupials, possums and bandicoots.
Worrell, 1963	Birds and mammals.
Kinghorn, 1964	Rabbits and mammals of similar size, rats and mice.
Rose, 1974	One record of <i>Pseudocheirus peregrinus</i> .
Gow, 1976	Birds and mammals, three records of lizards.
Cogger, 1983	A variety of terrestrial vertebrates.
Lunney and Barker, 1985	One record of <i>Hydromys chrysogaster</i> .
Weigel and Worrell, 1985	Adults feed on mammals and birds. Young feed exclusively on reptiles.

1981). Diamond pythons are sometimes active on warm nights and often remain coiled under light scrub in an ambush posture, only retiring under heavy cover on colder nights (Slip and Shine, 1988b). They also select habitats with higher prey densities in summer and autumn than at other times (as determined from mammal trapping: Slip and Shine, 1988b). Thus, with the exception of brooding females, snakes would have the highest likelihood of prey encounter in summer and part of autumn.

The cessation of feeding by adult males during the spring (mating season) is interesting in that the snakes are in habitats containing reasonably high prey densities at this time. We hypothesize a specific disinclination to feed, perhaps because (i) a large food item in the stomach would reduce mobility (Garland and Arnold, 1983; Ford and Shuttlesworth, 1986), and hence possibly reduce the likelihood of locating females; and (ii) as they are ambush predators, the time spent waiting for prey would reduce the time available to search for mates. A similar cessation of feeding by males during mating has been found in viperids (Prestit, 1971) and natricines (Aleksiuk and Gregory, 1974) but not elapids (Shine, 1975). Continued feeding in male elapids may be possible because elapids search actively for prey and must also search widely for mates: the two activities may be combined (Shine, 1975). Also, since most elapids take relatively smaller prey than do viperids or boids feeding would be less likely to reduce their mobility.

The absence of prey items from gravid females is consistent with the reduction in food intake widely recorded in gravid snakes (Fitch and Shirer, 1971; Prestit, 1971; Klauber, 1972; Shine, 1979, 1980a; Reinert et al., 1984). Foraging may cease because of reduced foraging efficiency, increased vulnerability to predation, or the difficulties of maintaining the thermal requirements for optimum embryonic development while foraging (Shine, 1980a). Gravid female *M. s. spilota* thermoregulate carefully and retire under cover on most nights, sometimes using the oviposition mound a few weeks before depositing the eggs (Slip, 1986). Increased time spent under cover may reduce encounters with prey. Since

pythons subdue prey by constriction, the act of capturing prey may involve some risk of damage to the eggs, as well as making the snake more obvious to potential predators (Shine, 1987).

Among the elapids sympatric with *M. s. spilota*, some cease feeding in winter, while a small number of individuals of other species contain prey (Shine, 1980b, c, 1981). Shine (1980c) suggested that in colder areas, only snakes of relatively small body size would have the ability to maintain body temperatures high enough to permit winter feeding. Low temperatures reduce both the digestive rate (Skoczylas, 1970; Greenwald and Kanter, 1979; Naulleau, 1983) and the efficiency of prey capture (Greenwald, 1974) in some reptiles. In winter, *M. s. spilota* will bask on sunny days and elevate its body temperature close to those reached at other times of year, although mean daily body temperatures are lower in winter than in other seasons (Slip, 1986). However, winter nights are generally spent deep under cover (Slip, 1986) which may reduce the likelihood of encountering nocturnal mammalian prey. Thus, although *M. s. spilota* may not actively avoid feeding in winter, fluctuations in prey density and changes in snake habitat use, while maximizing prey encounter rate in summer, may considerably reduce it in winter.

*Hatchling Food Preferences.*—Reptiles appear to be an important part of the diet of juvenile and hatchling *M. s. spilota*. Weigel and Worrell (1985) suggested that young diamond pythons feed exclusively on reptiles, but our data suggest that hatchlings and juveniles will eat mammals and birds as well as reptiles. Reptiles may become less important as snakes grow to a size at which they can subdue and swallow larger mammalian prey. The ontogenetic shift in diet away from reptiles may also reflect differences in foraging behavior between adults and juveniles. A similar dietary shift has been identified in death adders (*Acanthophis antarcticus*: Shine, 1980b), European vipers (*Vipera berus*: Prestit, 1971) and in some rattlesnakes (Klauber, 1972), all of which are predominantly ambush predators as adults.

*Foraging Behavior.*—Our data on behavior of radio-tracked pythons (Table 4) and ob-

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servations of feeding in the wild indicate that diamond pythons ambush their prey rather than actively search for it. Although we have no information from the field on diets or behavior of juvenile pythons, our laboratory studies suggest that coppertail skinks, *Ctenotus taeniolatus*, may be an important dietary component. These skinks are abundant and extremely fast-moving, and almost certainly could be captured only by ambush predation. Hence, diamond pythons of all ages are probably sit-and-wait predators. One major ontogenetic shift may be in the time of day at which feeding occurs: the skinks eaten by juvenile pythons are diurnal, whereas most of the mammals eaten by adult pythons are crepuscular or nocturnal. The predominance of diurnal rather than nocturnal movements by adult snakes (Slip and Shine, 1988b) may maximize their time available for nocturnal ambush predation.

Foraging mode is phylogenetically conservative in snakes. In general, viperids are ambush predators (e.g. Prestt, 1971; Klauber, 1972), whereas most colubrids, elapids and acrochordids may search actively for their prey (e.g. Shine, 1977; Godley, 1980; Greene, 1984; Shine and Lambeck, 1985). Thus, in terms of foraging behavior, diamond pythons are more similar to viperids than to the elapids or colubrids with which they are sympatric. Nonetheless, many authors have recognized that the apparent dichotomy between "sit-and-wait" and "active searching" is in reality a continuum, and closely-related species may differ in their position on this continuum. Such variation is evident within each of the major families of snakes. Although most elapids are active foragers, species of at least two genera (*Acanthophis* and *Denisonia*) rely on ambush predation (Shine, 1980, 1983). Most hydrophiids also search actively for prey, but *Pelamis* uses an unusual form of sit-and-wait foraging (Kropach, 1975; Burns, 1984). Viperid snakes vary in the importance of mobility in their foraging behavior (e.g. Reinert et al., 1984). Such variation can occur even within species, perhaps ontogenetically or seasonally. For example, the colubrid *Nerodia rhombifera* is usually an active searcher, but has been reported to use ambush predation in some

situations (Gillingham and Rush, 1974). *Acrochordus arafurae* does the same (pers. obs.). Hence, our data on *Morelia spilota* show only that this species feeds primarily by ambush; any attempts to generalize on foraging strategies of other pythons would be premature at this stage. Detailed studies of other pythons—especially tropical species—would be very interesting in this respect.

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