

**Habitat Use, Movements and Activity
Patterns of Free-Ranging Diamond Pythons,
Morelia spilota spilota (Serpentes : Boidae):
a Radiotelemetric Study**

David J. Slip and Richard Shine

Zoology Department A08, The University of Sydney, N.S.W. 2006, Australia.

Abstract

Miniature radio transmitters were surgically implanted in 15 adult diamond pythons from two areas near Sydney, N.S.W., in south-eastern Australia, and the snakes monitored for intervals of 4-32 months. We document patterns of habitat use and movements, and interpret these in terms of the feeding habits and reproductive biology of the pythons. These snakes were usually sedentary in summer and autumn, with occasional long movements to new sites. During spring (the mating season), males moved long distances, often daily. Telemetered pythons were generally diurnal and terrestrial rather than arboreal. Snakes were most commonly recorded coiled under vegetation which provided filtering cover (34% of locations). The relative use of different habitats by diamond pythons changed with season. In summer and autumn, snakes were most frequently in disturbed habitats (such as areas around houses), where prey are relatively common. In winter the snakes used rocky habitats, especially sandstone crevices. No winter aggregations were observed. The radio-tracked snakes had large (up to 124 ha), well-defined but overlapping home ranges, and these varied significantly between sexes and among seasons. Detailed analysis of python movements shows that at least two assumptions of many home-range analyses (normally distributed data and adequacy of small sample sizes) are invalid for our study.

Introduction

Detailed studies of activity patterns, habitat use and movements have rarely been carried out on snakes, primarily because of methodological difficulties. Mark-recapture techniques (e.g. Blanchard and Finster 1933; Stickel and Cope 1947; Fitch 1958, 1960) rely upon consistent relocation of individuals, and hence have often produced scant and inconclusive results. Systematic search and capture methods to identify habitat preferences (e.g. Carpenter 1952; Hebrard and Mushinsky 1978) introduce major biases because of variation in observability of snakes in different habitats (Reinert and Kodrich 1982; Weatherhead and Charland 1985). Both methods contain a bias towards active snakes as these may be more easily located. Radiotelemetry alleviates these problems and has been used to study activity patterns and/or habitat use in colubrids (Parker and Brown 1980; Weatherhead and Charland 1985), crotalids (Reinert and Kodrich 1982; Reinert 1984), acrochordids (Shine and Lambeck 1985) and elapids (Shine 1979, 1987). To our knowledge, ours is the first detailed study of habitat use or activity patterns for any species of python.

The present paper presents such data for the diamond python, *Morelia spilota spilota*, a medium-sized (to 3 m) boid snake of coastal south-eastern Australia, focusing on two aspects:

- 1 What habitats are used by the snakes, and how does this usage shift in response to seasonal variation in reproductive behaviour, prey availability, and opportunities for thermoregulation? All of these factors may be expected to influence patterns of space use by snakes, but have rarely been determined.
- 2 How large is the home range, how often and how far does a python move within it, and how are these variables influenced by sex and season?

We need a method for determining the size of the home range. We adopt the definition of home range used by Barbour *et al.* (1969): 'that area traversed by an animal in its normal activities of feeding, reproduction, and other facets of its daily life'. Many different methods have been used to assess home ranges, but all have difficulties (reviewed by Jennrich and Turner 1969; Waldschmidt 1979; Gregory *et al.* 1987). Procedures based on capture radii (Hayne 1949; Fitch 1958, 1960, 1963) equate a home range of any shape with a circle of similar area and therefore convey little information about the actual pattern of use of space if home ranges are long and narrow. Other methods for calculating home range area (Jennrich and Turner 1969; Koepl *et al.* 1975; Schoener 1978; Ford and Krumme 1979; Anderson 1982) describe home range as the probability, arbitrarily set usually at 50, 95 or 99%, of an animal's use of a particular part of its habitat, and assumptions are often made as to the shape, skewness or distribution of the data. Most statistical methods yield unrealistically inflated estimates of home range (Waldschmidt 1979; Rose 1982; Christian and Waldschmidt 1984), and the choice of probability level has a great effect on the size of the calculated area of home range (Schoener 1981).

A simpler and more popular method of calculating home range size involves drawing the smallest convex polygon that encloses all the location points (Southwood 1978), referred to as the minimum convex polygon (MCP). This method makes no assumptions about the shape of the home range, but can underestimate the area used if sample size is too small (Jennrich and Turner 1969; Ford and Myers 1981; Anderson 1982). The MCP method can also result in an overestimation of the space used by including an area where the animal is never found such as a lake or a highway. Although MCP home range estimates should grow arbitrarily close to the true home range as sample size increases, the problem remains to determine when sufficient samples have been collected. In the present paper, we use our extensive data set on python movements to evaluate some of the assumptions and limitations of the use of the MCP method for assessing home ranges of snakes.

Materials and Methods

Study Areas

Two study sites in the outer northern suburbs of Sydney, N.S.W., were used. Site 1 is at Belrose (33°44'S., 151°13'E., 50–197 m above sea level), and is a Hawkesbury sandstone valley covered in dry sclerophyll forest. A shallow creek runs through the steep-sided gully, with many areas dominated by sandstone cliffs. The head of the valley is surrounded by residential buildings, and the western and southern borders of the Belrose site are bordered by busy roads. A severe bushfire went through the valley late in 1981, but considerable regrowth had occurred prior to our study in March 1982. Site 2 is at Cowan (33°35'S., 151°09'E., 0–210 m above sea level), and is similar to site 1 in topography and vegetation. The two sites are 15 km apart.

Radiotelemetry

Snakes were captured by hand at the study sites, and released as close as possible to their capture points after transmitters had been implanted (see below). Each snake was equipped with a temperature-sensitive radiotransmitter (model TT-IU-1000, J. Stuart Enterprises, Grass Valley, California, U.S.A.), powered by a single 3-volt lithium cell battery (National BR-2/3A) which provided an operational life of 10–13 months. Transmitters were sealed with a waterproof coating of paraffin (80%) and elvax

(Du Pont Inc.). The assembled unit was about 90 by 20 mm in diameter, and had a mean mass of 40.2 ± 3.65 g (representing 0.9–3.9% of snake body mass).

Telemetry signals were received with a TR-2E miniature telemetry receiver (Telonics Telemetry Consultants, Mesa, Arizona, U.S.A.), and a hand-held H-frame directional antenna (Telonics RA-2AK). Signals were monitored continuously with the TR-2E receiver interfaced with a programmable scanner, a Telonics TDP-2 digital processor linked to a dual level Rustrak recorder which provided data on both the period and amplitude of the signal, and an omnidirectional whip antenna.

Snakes were anaesthetised with inhaled halothane via a Fluotec-3 anaesthetic machine with an open circuit T-piece system. Transmitters were implanted into the peritoneal cavity by aseptic surgical technique through a 25 mm incision in the lateral scales adjoining the ventrals. Wound-healing was good and there was no abnormal swelling around the transmitter. The behaviour of snakes captured in the mating season seemed to be unaltered by capture and transmitter implantation. One male was observed copulating less than 24 h after having a transmitter implanted. All animals captured during mating (three females and ten males) remained in mating aggregations subsequent to having transmitters implanted and the females all produced fertile clutches. Telemetered snakes fed and gained weight even after long periods of tracking. No animal lost weight which could not be accounted for by some specific activity such as reproduction or overwintering.

Habitat Selection

All regions within the study areas were classified into four broad habitat types: 1 rock outcrops (dominated by sandstone cliffs and outcrops—vegetation sparse, consisting of low shrubs and grasses); 2 woodland—dominated by an overstorey of eucalypts and an understorey of shrubs and grasses less than 1 m high; 3 scrub—dominated by *Banksia* spp. but including other small shrubs and grasses; and 4 disturbed areas—cleared for settlement, grazing or cultivation, and including the areas surrounding houses. 'Scrub' included small pockets (less than 1 ha) of woodland and scrub surrounded by cleared land, or had been cleared or partly cleared and had regrown.

All recorded locations of telemetered snakes were classified according to these four habitat types, and assigned to one of six broad categories of micro-habitat use: in trees, in buildings; under or in logs; under rocks; under scrub which provided filtering cover; or on open ground. To increase independence of samples, snakes which were continuously monitored were included only once per day (at the first location). Data on brooding females are not included in the present analysis: they have been described in another paper (Slip and Shine 1989). Seasonal differences in habitat selection were compared using a four-by-four contingency table (Zar 1974). Relative habitat used was compared between sexes using a two-by-four contingency table.

Relative Prey Density

To determine the relative prey density in each of the four habitat types, small mammals were trapped with Elliott traps at both study areas. Small mammals are the most important component of the diet of adult *M. s. spilota* (Slip and Shine 1988). A five-by-five, 1-ha trap grid was used in each habitat on each site. Trapping was conducted on four consecutive nights in early autumn (March).

Activity Patterns

Snakes were classified according to activity using the following categories: 1 under heavy cover, including rocks, logs, etc.; 2 coiled under filtering cover, usually vegetation, such that direct sunlight shining toward the snake would be filtered by the cover; 3 tightly coiled in the open; 4 basking, when the snake was outstretched or loosely coiled in the open; or 5 moving, including only animals which travelled at least 10 m in the move. Where animals were monitored continuously, activity could be inferred from chart recordings: an animal was assumed to remain in one category if no movement was detected from analysis of signal amplitude. Nocturnal activities were inferred in this way.

Home Range

The area of home range was determined using three methods: two based on the minimum convex polygon (MCP) method (total home range and combined home range), and the third based on the probabilistic method of Jennrich and Turner (1969), 'corrected' home range. The positions of relocated snakes were plotted on a 1:2000 map of each study site, a convex polygon was drawn through the outermost location points, and the area of this polygon was determined mathematically. The area enclosing all location points for an individual snake was termed the total home range. The areas used

in autumn (Mar.–May), winter (June–Aug.), spring (Sept.–Nov.) and summer (Dec.–Feb.) were also determined in this way. These areas are termed the seasonal home ranges. An area termed the combined home range was determined by combining the seasonal home ranges, less any overlap. The combined home range will be equal to or smaller than the total home range as it will not include some large areas where the animals were never located. A 'corrected' home range was determined by applying the correction factor of Jennrich and Turner (1969) to total home range.

The sizes of total home ranges were compared between sexes by means of a Mann–Whitney test (Zar 1974). The sizes of seasonal home ranges were compared among seasons and between sexes by analysis of variance. Male home ranges for spring were only included in this analysis if they included the pre-mating period (see Slip and Shine 1989). Regression analysis was performed to investigate the relationships: 1 between snout–vent length (SVL) and total home range for each sex; and 2 between SVL and spring home range for male snakes.

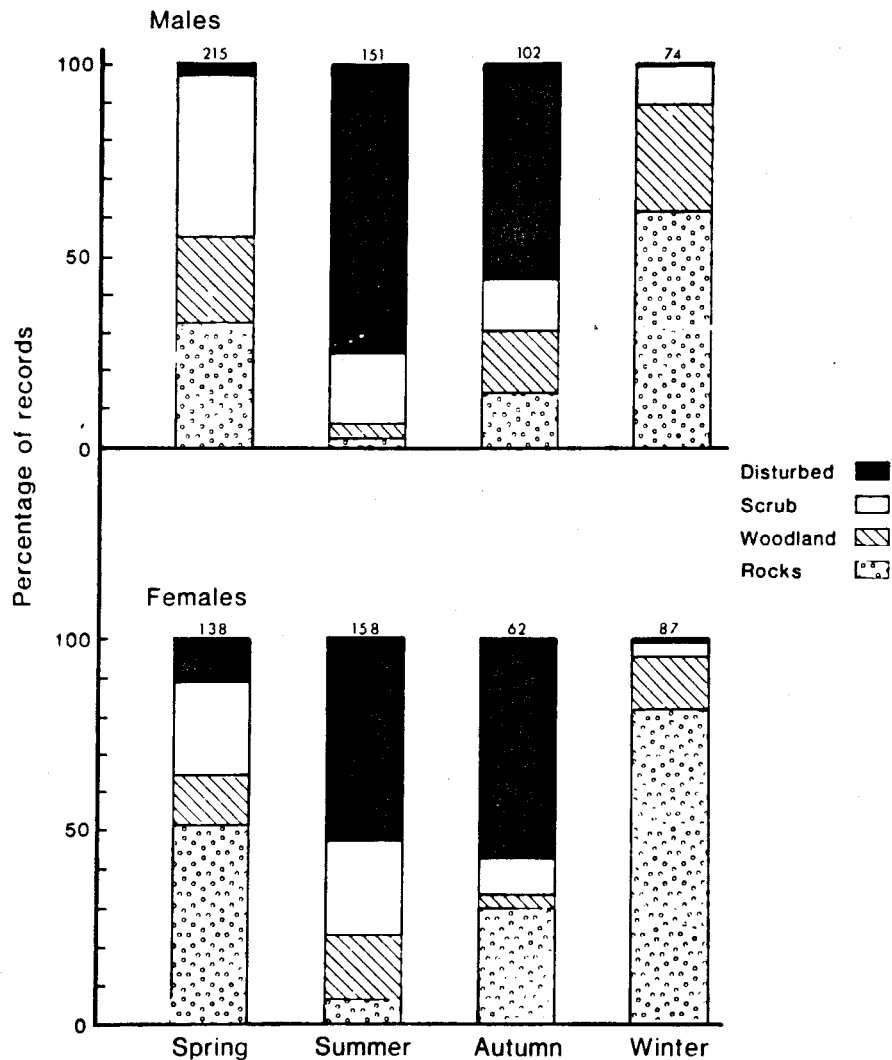


Fig. 1. Frequency of habitat use by male and female diamond pythons in each season. Numbers above bars indicate sample sizes. See Materials and Methods (p. 517) for definitions of habitats.

Results

Information on habitat use and movement patterns were obtained from 15 adult pythons (nine from Belrose, six from Cowan) which were radio-tracked for intervals of 4–32 months (12.7 ± 9.9 , mean \pm SD). These included six females (SVL 182–230 cm, mass 2.3–3.7 kg) and nine males (SVL 143–182 cm, mass 1.0–2.1 kg).

Habitat Selection

The frequencies with which snakes were located in each habitat are shown in Fig. 1. There were significant interseasonal differences in habitat use both for males ($\chi^2 = 334.10$, $\nu = 9$, $P < 0.001$) and for females ($\chi^2 = 198.76$, $\nu = 6$, $P < 0.001$). Both males and females were mainly located in disturbed habitats in summer and autumn, and in rocky habitats in winter.

Despite this general similarity, there were significant differences in habitat use between males and females in each season. In spring ($\chi^2 = 25.76$, $\nu = 3$, $P < 0.001$), females were found mostly in rocky areas (51%) whereas males were found almost equally in rocky habitats (34%) and scrub (43%) and less frequently in woodland (23%). Habitat use by males and females was also significantly different in summer ($\chi^2 = 29.71$, $\nu = 3$, $P < 0.001$): males were found mostly in disturbed habitats (76%) and scrub (20%), whereas females were found in disturbed habitats (52%), scrub (24%) and woodland (18%). The differences between the sexes in habitat use in autumn ($\chi^2 = 9.94$, $\nu = 3$, $P < 0.025$) reflected the greater use of rocky habitats by females (29%) than by males (15%), whereas males were found more often in woodland (15%) than were females (3%). Both sexes were mostly in disturbed habitats (52% males, 55% females). Sex differences in habitat use in winter ($\chi^2 = 90.02$, $\nu = 3$, $P < 0.05$) were due to greater use of rocky habitats by females (82%) than males (62%), whereas males were found more often in woodland (27%) than were females (16%).

Table 1. Frequency of microhabitat use by radio-tracked diamond pythons

See Materials and Methods for definitions of microhabitats

Season	Trees	Buildings	Logs	Rocks	Filtering cover	Open ground	Total
Spring	41	10	19	104	79	100	353
Summer	17	36	28	6	179	43	309
Autumn	24	17	7	23	58	45	164
Winter	17	0	17	88	24	15	161
Total	99	53	71	221	340	203	987
Total %	10	6	7	22	34	20	100

Table 1 shows microhabitat use by male and female diamond pythons in each season. When snakes were located in buildings they were always in the roof. Thus, by combining the locations from trees and buildings, 16% of locations were from 'arboreal' habitats.

Relative Prey Density

The results of small-mammal trapping at the two study sites are presented in Table 2. At Belrose, the highest densities of *Rattus* were found in disturbed habitat. High densities of *Antechinus stuartii* were found in rocky habitat, but these do not feature in the diet of *M. s. spilota* (Slip and Shine 1988). At Cowan, more mammals were captured in scrub habitat than in other habitats. The low trapping success in disturbed habitat at Cowan is surprising because many scats, and the obvious presence of *Rattus rattus* (personal observation, DJS) suggested a high density of rats.

Table 2. Numbers of small mammals captured in Elliot traps from 100 trap nights in each habitat at each of the two study sites

See Materials and Methods for habitat descriptions

Species	Rocky		Woodland		Scrub		Disturbed	
	Belrose	Cowan	Belrose	Cowan	Belrose	Cowan	Belrose	Cowan
<i>Rattus rattus</i>	0	0	0	2	0	2	9	0
<i>Rattus fuscipes</i>	9	1	1	1	4	7	18	1
<i>Antechinus stuartii</i>	10	2	0	0	0	1	0	0
<i>Perameles nasuta</i>	1	0	0	0	0	0	0	0
<i>Mus domesticus</i>	0	0	0	0	0	0	1	0

Activity Patterns

The highest frequency of movements was by males in spring (Fig. 2). A typical early spring day for males consisted of emergence from under cover (generally rocks) or filtering cover between about 0800 and 1000 hours, followed by basking (30–60 min). Males would then move extensively until about 1400–1600 hours before retiring under filtering or heavy cover. This pattern occurred on both clear (> 1 h of sunshine) and cloudy days provided air temperature reached about 20°C. Emergence was generally later on cloudy days, and if air temperatures remained below about 20°C males would remain under cover. This pattern continued until the male located a reproductive female, after which males would remain with the female and engage in reproductive activity (Slip and Shine 1989).

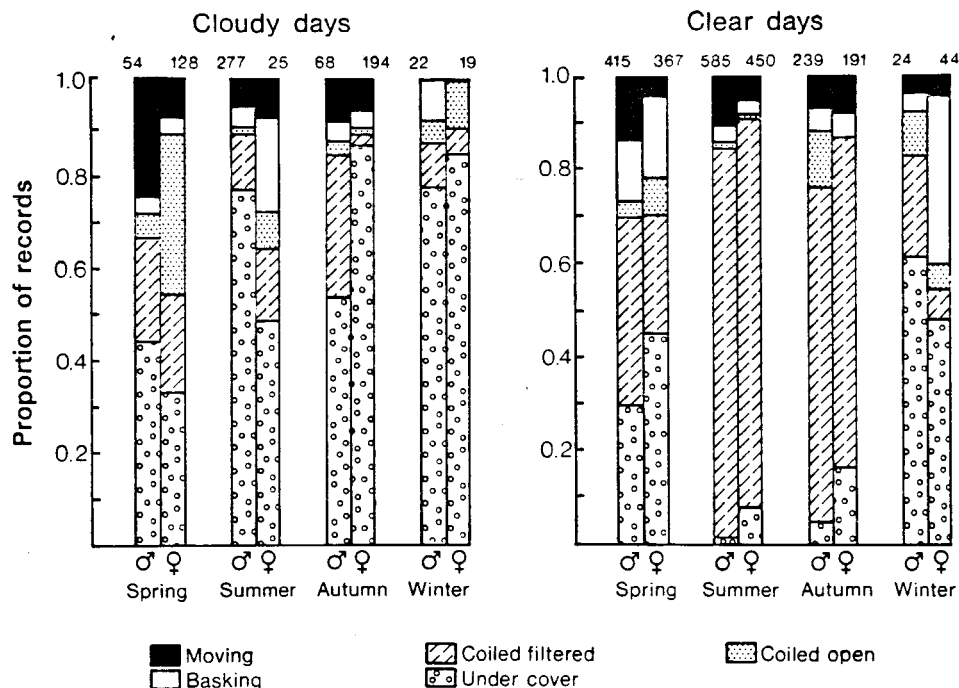


Fig. 2. Activity patterns of male and female diamond pythons on clear and cloudy days in each season. Numbers above bars indicate sample sizes. See Materials and Methods (p. 517) for definitions of activities.

A typical early spring day for females consisted of emergence from under cover (generally rocks) between about 1000 and 1200 hours, followed by basking (30–60 min), after which the female would retire under cover. Females made relatively few movements in spring. Reproductive females made a few short movements (less than 200 m) before mating. Non-reproductive females began moving away from rocky habitats from mid to late October and began to use woodland, scrub and disturbed habitats. Reproductive females made longer (400–600 m) movements to their oviposition sites in late November. Both male and female *M. s. spilota* were diurnal in spring with the highest frequency of movements between 1000 and 1400 hours (Fig. 3).

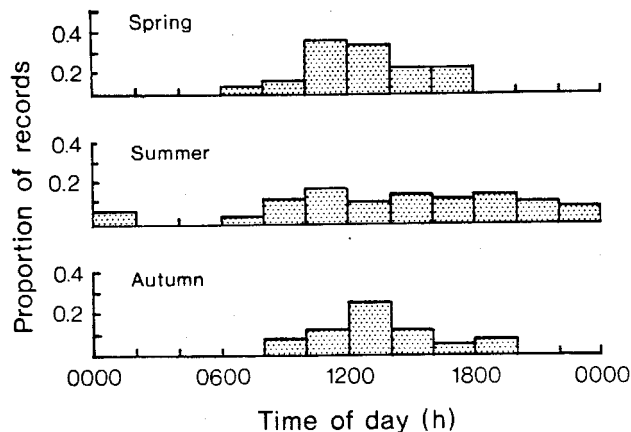


Fig. 3. Frequency distributions of movements by diamond pythons relative to time of day for clear days in spring, summer and autumn.

Summer activity patterns were generally similar in males and females on clear days although males made a higher proportion of movements. The most common activity in both sexes was coiling under filtering cover and following clear days snakes remained under filtering cover at night. In summer, snakes were found under cover more frequently on cloudy days than on clear days (Fig. 2). Although activity patterns on cloudy days appear to differ between males and females (Fig. 2), the small sample size for females may contribute to this difference. A typical summer day consisted of emergence from under filtering cover between about 0700 and 0900 hours, followed by basking (30–60 min), after which snakes would generally retire under filtering cover. On very hot days snakes would seek shelter under heavy cover in the middle of the day. A relatively low proportion of time was spent moving (11% males, 6% females). Movements occurred between 0600 and 0200 hours on clear days, with the highest frequency of movement between 1000 and 1200 hours (Fig. 3).

On clear days in autumn males and females were most often located under filtering cover (71% males, 70% females) while on cloudy days both sexes were most often found under full cover (54% males, 86% females). Activity patterns in early autumn were similar to those in summer. Movements were between 0800 and 2000 hours in autumn (Fig. 3).

In winter males and females most often stayed under cover on both clear and cloudy days (Fig. 2). On clear days in winter, snakes emerged between about 1100 and 1300 h, after which they would bask for about 30–90 min then retire under cover. Females were observed basking more frequently than males on clear days. There were very few movements in winter. On cloudy days snakes generally remained under cover. All activity records in winter were collected during daylight hours and this, together with the small sample size (Fig. 2), may have resulted in the proportion of time spent under cover being underestimated.

Movement Patterns

To determine whether diamond pythons move about a home range or wander randomly, we plotted the distance from the original release point against days since release, using only locations that were 10 weeks apart, to increase independence of data points. If an individual is restricted to a home range, the distance between where it was first seen and where it is seen subsequently tends first to rise then remains constant with time. If an animal wanders at random there is a tendency for it to be located, on average, farther and farther away from where it was first seen, as time goes on. For each pair of locations, the distance moved between sightings was determined. Movements within a 10-m diameter circle around the animal's previous location, such as daily emergence to a basking site, were not considered as movements. There was no significant relationship between the distance a snake was located from its point of release and the number of days since release ($F_{1,98} = 0.088$, $P > 0.05$, $r^2 = 0.001$, Fig. 4), suggesting that diamond pythons restrict their movements to a home range. Some individual snakes returned to specific sites after 11–644 days. These sites consisted of logs, trees, rock crevices and buildings, and snakes were located from 50 to 1100 m away from a site in the intervening period. Some sites were revisited up to four times.

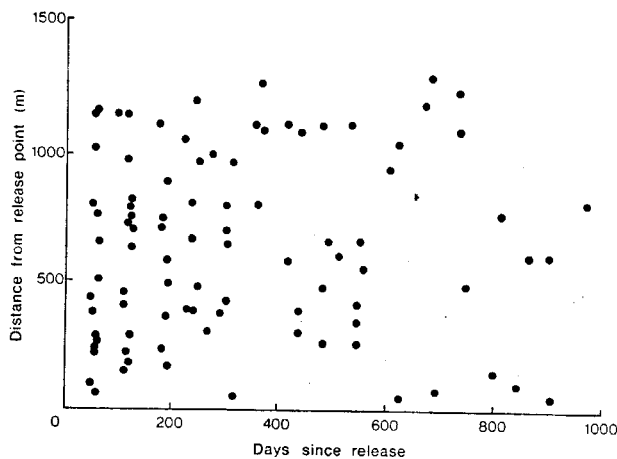


Fig. 4. The distances telemetered diamond pythons were located from their original release point relative to days since release.

Movement distances were grouped into 50-metre intervals and are presented as frequency distributions for each sex and in each season (Fig. 5). Male diamond pythons made a higher proportion of longer movements (greater than 500 m) between relocations in spring than at other times. Female snakes made relatively few movements of greater than 500 m and these were associated with movements to and from oviposition sites (in summer and autumn) or from overwintering sites to summer feeding areas (non-reproductive females in spring). The longest movement recorded in a single day was 550 m by a female snake after leaving the incubation site. The longest single-day movement by a male snake was 460 m in spring. Another male was recorded to have moved 1150 m in two days, also in spring.

The frequency distributions of the minimum duration between movements (> 10 m displacement) for males and females in each season are presented in Fig. 6. Durations of over 30 days between successive movements were recorded for females in all seasons, whereas males only remained sedentary for long periods in winter.

Home Range

The total home ranges for males and females at both study sites overlapped extensively

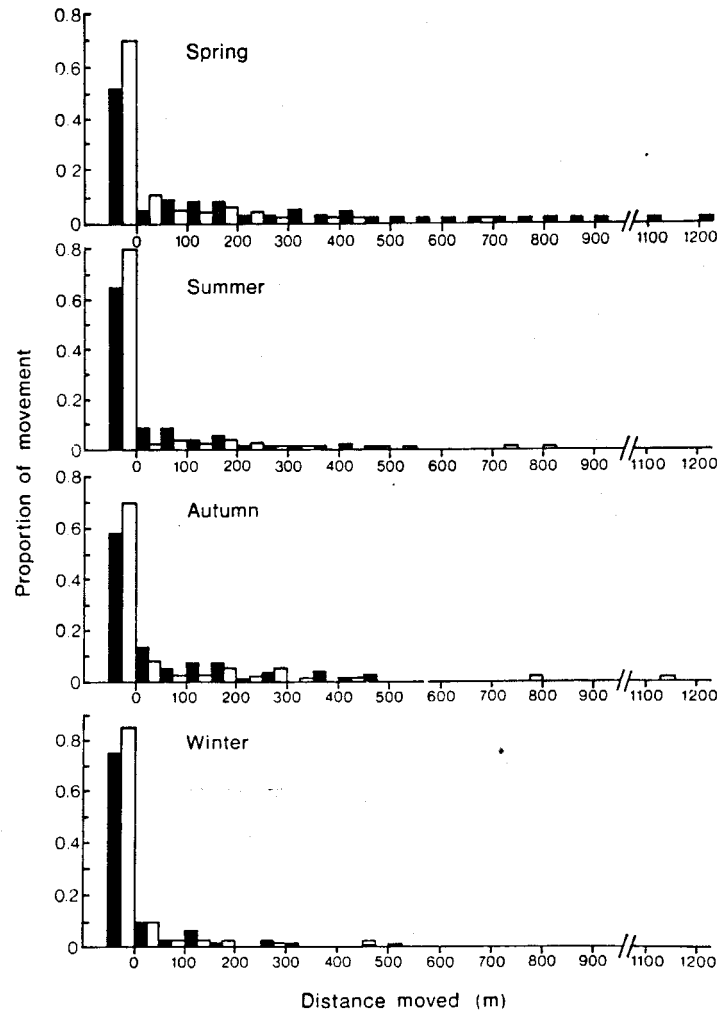


Fig. 5. Frequency distributions of distances moved by telemetered male and female diamond pythons in each season. Solid bars, males; open bars, females.

among individuals with no evidence of mutually exclusive home ranges between adjacent snakes of either sex. The areas of total home ranges, 'corrected' home ranges and combined home ranges are presented in Table 3. The mean total home range of male diamond pythons was significantly larger than that of females ($U=44$, $n_1=5$, $n_2=9$, $P<0.05$). The variances associated with mean total home range were homogeneous ($F_{9,6}=1.477$, $P>0.05$). Regression analysis revealed no significant relationship between SVL and total home range for males ($F_{1,7}=0.041$, $P>0.05$, $r^2=0.01$), or for females ($F_{1,4}=0.11$, $P>0.05$, $r^2=0.03$).

Home range size changed with season (Table 4). Analysis of variance showed a significant difference in the area used among seasons ($F_{3,53}=15.75$, $P<0.001$) and between sexes ($F_{1,53}=11.59$, $P<0.001$), with no significant interaction effect ($F_{3,53}=1.58$, n.s.). An *a posteriori* Newman-Keuls multiple range test revealed the following: 1 the mean areas used by male snakes in spring were significantly larger than those used by males or females in all other seasons; 2 there were no significant differences among the mean areas used by

Table 3. Size of home ranges of male and female diamond pythons, calculated by three methodsSee Materials and Methods for explanation of methods of determining the size of the home range; 'Snake No.', identification numbers of snakes; *N*, number of locations

Snake No.	<i>N</i>	Total (ha)	'Corrected' (ha)	Combined (ha)
<i>Males</i>				
11	59	41.02	61.88	40.92
12	113	96.90	115.20	77.20
13	63	60.54	87.24	49.37
14	205	124.16	125.78	103.24
15	40	23.80	40.60	20.40
16	29	25.90	53.20	15.25
18	28	42.30	88.80	35.20
19	10	37.80	283.70	37.80
20	18	22.80	64.20	7.90
Mean ± SD		52.80 ± 35.42	102.29 ± 73.76	43.03 ± 30.50
<i>Females</i>				
1	218	82.58	82.80	52.17
2	78	16.48	21.81	12.38
3	72	36.80	50.50	18.57
4	25	3.80	8.00	3.40
5	22	8.10	18.80	4.30
6	25	19.30	44.80	13.60
Mean ± SD		27.84 ± 29.14	37.79 ± 27.35	17.35 ± 18.03

males in summer, males in autumn, females in spring, females in summer or females in autumn; 3 there were no significant differences between the mean areas used by males and females in winter; and 4 the mean areas used by males and females in winter were significantly smaller than the areas used in all other seasons. Regression analysis revealed no significant relationship between male SVL and male spring home range ($F_{1,5} = 0.06$, $P > 0.05$, $r^2 = 0.01$).

Discussion

Habitat Selection

Habitat use by *M. s. spilota* changed dramatically with season. Rocky areas dominated by sandstone cliffs and outcrops were preferred in winter, and disturbed habitats were preferred in summer and autumn. Scrub and woodland were used frequently by males in spring and less frequently by both sexes at other times.

What then are the likely benefits provided by each habitat? Rocky habitats generally included steep sandstone cliffs with a wide variety of subterranean retreats which may provide good insulation from low ambient temperatures. These areas were generally higher in elevation than other habitats and snakes used rocky areas with an aspect between east and south-west, avoiding slopes with southerly aspects. Thus, these habitats may have also provided good access to basking sites because they were not shaded by heavy vegetation.

The benefits of using scrub and woodland may be more subtle than those provided by rocky habitats. Some areas of scrub maintain moderate densities of small mammals (e.g. Cowan, see table 2). Snakes may be able to identify microhabitats within scrub where mammal densities are highest, such as mammal runways, dreys and burrows, and thus increase their likelihood of encountering prey. Scrub also provides areas of filtering cover which may have certain thermal benefits: snakes can maintain high body temperatures under

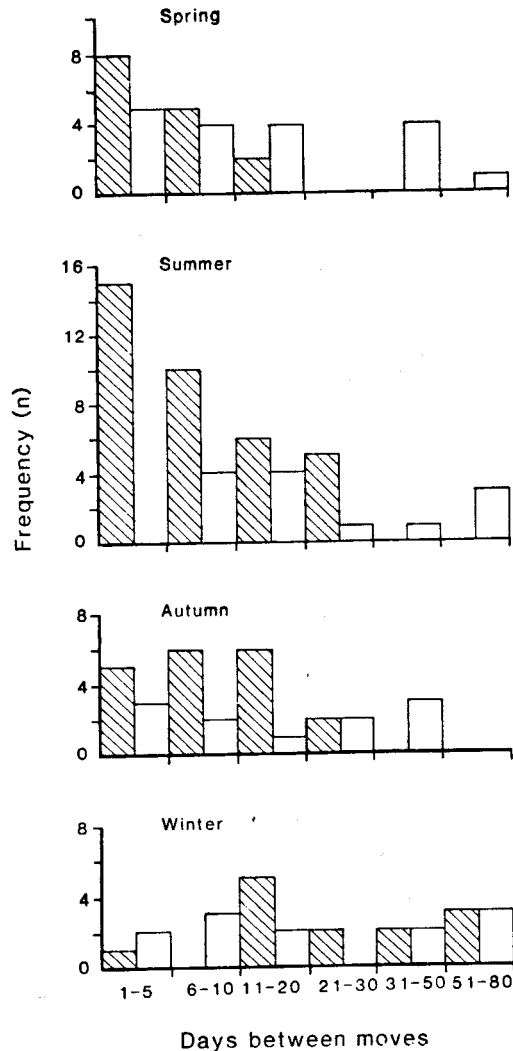


Fig. 6. Frequency distributions of the time between successive movements of male (hatched bars) and female (open bars) diamond pythons in each season.

filtering cover without the need for prolonged basking and this may reduce the likelihood of predation. However, filtering cover may not provide adequate insulation against cold. This interpretation is supported by the observation that on overcast days in summer, male diamond pythons spent more time under cover than under filtering cover (Fig. 2), probably as a response to lower air temperatures. Woodland habitats provide shelter in the form of hollows in trees. Trees also provide good basking sites. Mammal-trapping suggests relatively low densities of small mammals are found in woodland habitats, but woodland may provide a good source of other prey types, especially birds and larger mammals such as possums.

The increased use of disturbed habitat in summer and autumn may be a response to high prey density in these areas (as shown by mammal trapping, and our observations of rats and rabbits). Habitat selection as a response to prey densities has been suggested for the colubrid snakes *Natrix natrix* (Madsen 1984) and *Elaphe obsoleta* (Weatherhead and Charland 1985). Unlike *M. s. spilota*, these snakes are active foragers rather than ambush predators (see Slip and Shine 1988).

Male and female diamond pythons had different habitat preferences in spring, reflecting differences in reproductive behaviour. In spring males make large movements in search of

Table 4. The sizes of seasonal home ranges (ha) of diamond pythons

'Snake No.', snake identification number. Individual animals may appear more than once in the table: each home range estimate is based on data from a single year and some snakes were tracked over 2 or 3 years. Values in parentheses are the number of times snakes were located

Snake No.	Autumn	Winter	Spring	Summer
<i>Males</i>				
11	1.79 (29)	0.14 (12)	40.60 (18)	
12	3.70 (12)	1.80 (13)	15.59 ^A (24)	12.90 (21)
12	7.40 (12)	0.63 (13)	54.80 (15)	8.50 (9)
13	8.74 (14)	0.001 (9)	44.54 (22)	4.14 (18)
14	1.24 (16)	3.98 (16)	16.09 ^A (26)	7.46 (23)
14	5.40 (16)	0.47 (11)	95.75 (47)	3.59 (25)
14			41.55 (15)	1.40 (10)
15			8.60 ^A (20)	6.00 (20)
16			10.60 ^A (20)	4.30 (9)
18		3.10 (6)	32.20 (12)	0.40 (10)
19			37.80 (10)	
20	3.40 (4)		3.40 ^A (6)	1.20 (12)
<i>Females</i>				
1	3.79 (25)	0.001 (22)	5.29 ^B (41)	10.81 ^B (33)
1	4.84 (14)	1.39 (14)	31.86 (18)	3.84 (24)
1	1.25 (7)	0.005 (14)	3.89 (7)	
2		0.66 (12)	3.64 (17)	0.76 (17)
2			2.93 ^B (13)	4.74 ^B (19)
3			3.42 ^B (6)	5.35 ^B (18)
3	6.70 (13)	1.28 (9)	1.39 (12)	0.063 (14)
4			3.40 ^B (9)	0.04 ^B (16)
5		0.40 (6)	13.10 (9)	0.40 (10)
6			0.60 (13)	3.80 (9)

^A Areas based on locations of males after they had mated; other spring home ranges for males include both pre- and post-mating times.

^B Females which were reproductive.

females, and hence, must move through the large areas of woodland and scrub on the study sites. In contrast, females tend to be sedentary at this time of year. In three of the four instances where reproductive behaviour was observed, males located females in rocky habitats in similar sites to those used by females in winter. In the other instance, the female had overwintered in a tree hollow on a margin between woodland and rocky habitat and males located her in the tree. As females do not reproduce every year, there are many non-reproductive adult females in the population (Slip and Shine 1989). These non-reproductive animals may feed in spring, and the higher proportion of females than males using disturbed habitat at this time may be due to feeding behaviour.

The winter shift to rocky habitats is in some ways analogous to the seasonal migrations of many northern hemisphere snakes to communal overwintering hibernacula. Communal use of crevices in winter was never recorded in *M. s. spilota*, possibly because winter ambient temperatures are generally mild compared to winter in the northern temperate zone. This alleviates the need for deep hibernacula, so that there are many suitable rock crevices. Also, the densities of *M. s. spilota* seem relatively low compared to some of the species previously studied in this respect. Scarcity of suitable hibernacula is the main cause of communal denning in many cases (Gregory 1984).

We infer that habitat selection may be most influenced by reproductive behaviour in spring; by feeding behaviour in spring (for non-reproductive females), summer (except brooding females) and autumn; and by thermal requirements in winter.

Activity Patterns

Diamond pythons spend only a small proportion of time moving. The high proportion of time spent coiled under filtering cover appears to be important in ambushing prey (Slip and Shine 1989). This behaviour is most common in summer and autumn, at which time most feeding occurs. The extensive movements by males in spring are associated with reproductive activity (mate-searching). Summer movements appear to be movements from one hunting site to another. The summer increase in nocturnal activity, and in time spent under cover in the middle of the day, may be to avoid high temperatures. Similar shifts in activity have been reported in other snakes. *Agkistrodon contortrix* becomes exclusively nocturnal in summer to avoid high temperatures (Sanders and Jacob 1981), whereas *Pseudechis porphyriacus* becomes more crepuscular (Shine 1987). In the geographic range of *M. s. spilota*, ambient temperatures are not high enough to suppress all diurnal activity.

An Evaluation of the Minimum Convex Polygon Method

Most methods of calculating home range are sensitive to the absolute number of relocations or capture points. If an animal does restrict itself to a discrete area, the size of its home range should stabilise after a given number of sightings. Data on reptiles suggest that the MCP method is sensitive to sample sizes below about 10–20 observations (Rose 1982; Schoener and Schoener 1982; Waldschmidt 1983).

The probabilistic method most commonly used to determine the home range of reptiles is that of Jennrich and Turner (1969). This method assumes a bivariate normal distribution and calculates home range size based on the determinant of the covariance matrix of the capture points. By computing the expected ratio of minimum convex polygon area to the area calculated using this method, they are able to generate a set of correction factors to scale upwards an area calculated using the minimum convex polygon method. Many studies of reptile home ranges have applied the Jennrich and Turner correction factor without first checking the validity of the inherent assumptions (Brown and Parker 1976; Kjekorian 1976; Goddard 1981; Reinert and Kodrich 1982). This approach has been criticised as the Jennrich and Turner method produces an overestimate of home range size if the assumptions are violated (Waldschmidt 1979; Rose 1982; Christian and Waldschmidt 1984; Gregory *et al.* 1987).

To test the validity of these assumptions we examined the seasonal home ranges of 8 male snakes for skewness and kurtosis. Each of these ranges was based on a sample size of 18 or more observations (20.3 ± 5.50 , mean \pm SD). A line was drawn through the longest axis connecting two locations and this line was divided into five equal segments. The number of sightings in each segment was counted. Conformance to a bivariate normal distribution was tested by means of the G_1 and G_2 statistics (Sokal and Rohlf 1981). Four were found to be significantly platykurtic and six were significantly skewed. Waldschmidt (1979) and Rose (1982) similarly tested sightings of lizards for conformance to a bivariate normal distribution and, as in the present study, most did not conform to normal distribution.

Another assumption inherent in the Jennrich and Turner correction factor is that movements are random. This assumption seems unlikely to hold in real life as the physical attributes of the habitat, the density of food or the presence or absence of other individuals may influence the frequency of use of particular sites. Thus, the use of the Jennrich and Turner correction factor appears to be inappropriate in the present study and it is included only to serve as a comparison to previous studies where only 'corrected' values of home ranges are given (e.g. Reinert and Kodrich 1982).

Plotting home range as a function of the number of locations should reveal how many locations are required to reduce sample size bias (Rose 1982; Waldschmidt 1983). We have performed this analysis on 14 seasonal home ranges of male snakes. In each case more than 15 locations made up the maximum home range (20.8 ± 5.92 , mean \pm SD). Sightings were included chronologically. For some individuals home range size increased rapidly, reaching 100% of maximum with as few as eight locations. The movement pattern of these individuals constituted several large moves early in the season followed by a long period of relative inactivity (Fig. 7a). Other individuals showed a much slower increase, reaching 100% of maximum home range after about 20 locations (Fig. 7b). These snakes were relatively

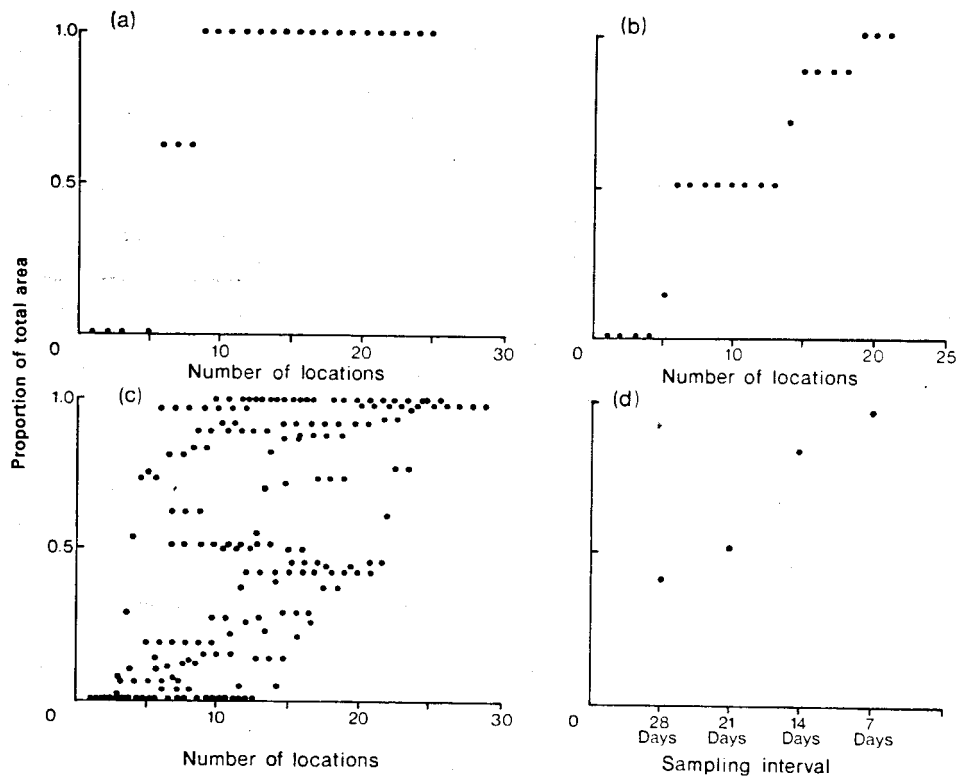


Fig. 7. (a) The relationship between number of locations and per cent of final seasonal home range size for an individual diamond python which moved early in the season then remained relatively sedentary; (b) the relationship between number of locations and per cent of final seasonal home range size for an individual diamond python which remained relatively sedentary early in the season and made longer movements late in the season; (c) the relationship between number of locations and per cent of final seasonal home range for fourteen male diamond pythons (final seasonal home range was determined from at least 15 locations for each individual); and (d) the effect of sampling interval on the estimate of home range size in diamond pythons. The graph shows the mean proportion of final seasonal home range as estimated by data from locations determined every 28 days, every 21 days, every 14 days, or every 7 days.

inactive in the early part of the season and made several large moves towards the end of the season. When all individuals are combined there is no obvious flattening of the curve (Fig. 7c). Thus the behaviour of the snakes makes it difficult to determine when enough locations have been made to provide an adequate basis for calculating home range.

Another approach is to plot cumulative home range against different sampling times. In our data on *M. s. spilota*, a sampling interval of 2 weeks (corresponding to seven

locations) accounts for 80% of the maximum home range, whereas an interval of 1 week (corresponding to 13 locations) accounts for about 97% of maximum home range (Fig. 7d). Thus, a sampling period of 1-2 weeks over a season reduces the sample size bias and provides an adequate basis for determining home range size by the MCP method. In the present study snakes were only rarely located at longer intervals, with no bias towards any one season or sex.

Python Home Ranges

Although early mark-recapture studies of snakes argued for random wandering rather than the maintenance of a discrete home range (Blanchard and Finster 1933; Hirth *et al.* 1969), subsequent work has generally identified discrete home ranges in snakes (e.g. Reinert and Kodrich 1982; Madsen 1984; Shine and Lambeck 1985). The movement patterns of *Morelia s. spilota* suggest that they do have a discrete home range (Fig. 4). The total home ranges of both male and female diamond pythons were larger than the home ranges reported for other snakes (reviewed by Parker and Brown 1980). However, comparisons among different studies must be made with caution, bearing in mind differences in the methods used in each study to define and calculate home range, and whether or not seasonal migrations were included, and the duration of each study.

Few generalisations have been drawn from the investigation of snake home ranges, probably because of the small number of long-term studies. Lizards have received more attention in this regard. Active foraging lizards generally have larger home ranges than 'sit-and-wait' predators (Rose 1982). Christian and Waldschmidt (1984) found a significant positive relationship between lizard body mass and home range size, and suggested that the energetic requirements of a lizard dictated the size of its home range. Some lizards shift their home range location in response to seasonal climatic changes (Christian *et al.* 1983), and social factors such as population densities and reproductive behaviour (Rose 1982). In many iguanids, home ranges are much larger for males than for females during the mating season (Stamps 1983).

The increase of home range size by male diamond pythons in spring results in their having larger total home ranges than do females. The large spring home ranges of males appear to be the result of mate-searching behaviour. Extensive and frequent movements by males relative to females during the reproductive season have been related to mate-searching activity in several species of snakes (Viitanen 1967; Prestt 1971; Parker and Brown 1980; Madsen 1984; Duvall *et al.* 1985; Shine 1987). However, an increase in the frequency and extent of movements does not necessarily result in an increase in home range size. In species that overwinter in hibernacula, reproductive behaviour generally takes place in the vicinity of the hibernaculum in either spring or autumn (Gregory 1984). Thus, males of these species may not need to cover large areas in search of mates. Female pythons made a few long moves to and from their oviposition sites, as has been reported in other species of snakes (Parker and Brown 1972; Madsen 1984). There appears to be no consistent trend for snakes of one sex to move more frequently or to have larger home ranges than the other sex: several studies have found no difference in movement patterns or home ranges between sexes (Clark 1970; Goddard 1981; Michot 1981; Reinert and Kodrich 1982; Gregory *et al.* 1987).

The smaller home ranges during winter of both male and female diamond pythons may be a response to thermal conditions, as ambient temperatures become too low to allow extensive movements. Thus, movements are restricted to a few short moves between sites which afford good cover. The size of summer and autumn home ranges may be determined by food availability, as diamond pythons show a high frequency of feeding at these times (Slip and Shine 1989). Because diamond pythons are ambush predators, movements while foraging are not extensive. Instead, they consist of a number of short moves from one ambush site to another.

We conclude that the size of the home range in *M. s. spilota*, and the frequency and extent of movements by this species, are influenced by a number of factors such as reproductive condition, presence of conspecifics in reproductive condition, food availability and the thermal requirements of the snake. The relative importance of these factors in determining movement patterns changes throughout the year.

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