ELSEVIER

0006-3207(95)00108-5

*Biological Conservation* **76** (1996) 113-122

0006-3207/96 $15.00+.00

# LARGE SNAKES IN A MOSAIC RURAL LANDSCAPE: THE ECOLOGY OF CARPET PYTHONS *Morelia spilota* (SERPENTES: PYTHONIDAE) IN COASTAL EASTERN AUSTRALIA

R. Shine & M. Fitzgerald

*School of Biological Sciences A08 and Institute of Wildlife Research, University of Sydney, NSW 2006, Australia*

(Received 8 May 1995; accepted 19 July 1995)

**Abstract**

*How can large pythons coexist with human beings in highly modified habitats throughout the eastern coastal region of Australia, when the same species has undergone rapid declines in other parts of the country? To investigate this question, we surgically implanted miniature temperature-sensitive radiotransmitters into 19 adult carpet pythons* Morelia spilota *(body lengths 1·3–2·8 m; 1·4–7·0 kg) from two study sites near Bangalow and Mullumbimby, NSW. We located the snakes every few days for the next 32–567 days (mean = 308 days), to obtain data on their movements, habitat use, postures, thermal biology, and food habits. Radio-tracked snakes were primarily arboreal (45% of locations), and generally selected trees with a dense covering of vines. Arboreality was more common in males than females, and more common in winter than in other seasons. The snakes generally avoided open areas, but frequently used artificial shelter (e.g. roof spaces in buildings; thickets of non-native tree species). Distances moved were generally small (mean <15 m/day; mean home range = 22·5 ha), and larger in males than in females. Population densities were high, especially in small forested areas that penetrated orchards (>6 snakes/ha; >20 kg/ha).*

*The success of carpet pythons in these areas reflects their inconspicuousness (due to their selection of densely vegetated arboreal habitats, their sedentary nature, and their cryptic coloration), and their preparedness to utilise 'artificial' habitats (such as roof spaces) and non-native prey species (mainly, commensal mammals). Prolonged immobility is possible because of the snakes' reliance on ambush predation, and their large body size facilitates thermoregulation without overt shuttling behavior. Pythons are vulnerable to predators (especially canids) when they move across large open areas, but generally avoid such habitats.* Morelia spilota *have declined in regions of Australia where agricultural practices have left no thickly vegetated habitats. Patches of such habitat (even if small, and composed of introduced plant species) appear to be vital for the continued presence of large pythons in the agricultural landscape. Copyright © 1996 Elsevier Science Limited.*

Correspondence to: R. Shine
Fax: 61-2-351-5609; e-mail: rics@bio.usyd.edu.au

*Keywords*: agriculture, feeding, habitat, home range, radiotelemetry, reptile, snake, thermoregulation.

## INTRODUCTION

Long-term coexistence of humans and large wild animals is rarely possible, and snakes are no exception in this respect. The encroachment of urban development or intensive agriculture generally results in a rapid decline in numbers of snakes, especially large species (e.g. Dodd, 1993). Within Australia, rapid human-induced habitat modifications over the last two centuries have caused the disappearance of many native vertebrates over large areas (e.g. Morton & Baynes, 1985). Nonetheless, some taxa of native fauna have been able to deal with such disturbance, and may have actually increased in numbers since the European invasion of Australia. Notable mammalian examples include grey kangaroos *Macropus giganteus* and brushtail possums *Trichosurus vulpecula* (Dickman, 1994). Among the snakes, some taxa with specialised habitat requirements have declined in numbers considerably (e.g. *Hoplocephalus bungaroides*–Shine, 1990), whereas some other species have fared much better. Perhaps the most surprising 'success story' is the continued presence of large pythons in intensively farmed regions along the northern and eastern Australian coast. The carpet python *Morelia spilota* remains abundant even in outlying suburbs of cities such as Brisbane (Covacevich, 1970; Wilson & Knowles, 1988), Darwin (Gow, 1976) and Sydney (Slip & Shine, 1988*a*), and is by far the largest snake to persist under these circumstances. The situation is even more remarkable in view of the apparently precipitous decline of the same species in other parts of Australia, including inland New South Wales and Victoria (Shine, 1994) and Western Australia (Smith, 1981; Pearson, 1993).

Why do some species withstand man-caused habitat modifications, or actually benefit from them, whereas closely related taxa (or, as in *M. spilota*, other populations of the same species) decline rapidly? Studies of the biology of successful commensal taxa may elucidate the reasons for their persistence, and hence clarify reasons for the decline of other taxa. Also, if such studies can identify the critical ecological features that enable a species to utilise modified habitats, then it may be possible to manage such areas to ensure that the species is retained. Such considerations are especially important for a species like *Morelia spilota*, that may confer a significant economic benefit to farmers through its predation on rodents (Cann, 1986). Thus, we carried out a two-year radiotelemetry study of free-ranging carpet pythons in coastal northeastern New South Wales, to examine how these large snakes are able to persist in the face of extreme habitat modification and human activities.

## MATERIALS AND METHODS

### Study areas

We radio-tracked pythons in two areas in near-coastal northeastern New South Wales, as follows.

(i) A 100-ha area comprising four farms near Bangalow (153°31; 28°41), all devoted to intensive tree-cropping (stone fruits, Macadamia nuts and sub-tropical fruits). The orchards consist of regularly-spaced trees surrounded by short grass, but these open areas are penetrated by corridors of relictual and regenerating forest (to 20 m width), particularly along watercourses and drainage lines. There are few buildings, and these are generally surrounded by manicured lawns.

(ii) A narrow ~300 ha valley at Mullumbimby Creek (153°26; 28°32) in the foothills of the Koonyum Range, enclosed to the west and south by rhyolite cliffs and to the north by a lower forested ridge. Elevations range from 350 to 70 m asl. North-facing slopes include a mosaic of active banana plantations, shrublands and regenerating forests, whereas south-facing slopes are covered by regenerating forests and relictual native forests on steeper scree slopes. Domestic residences are clustered by a road along the valley floor, beside a permanent stream, and are closely surrounded by trees.

The two sites are < 25 km apart and experience similar climatic regimes. Winters are mild (July means: minimum to maximum temperatures = 12–19°C Bangalow, 6–15°C Mullumbimby) and dry (mean precipitation June–August = 360 mm Bangalow, 425 mm Mullumbimby), with wet warm summers (January means: minimum to maximum = 21–27°C Bangalow, 17–26°C Mullumbimby; December–February precipitation = 520 mm Bangalow, 600 mm Mullumbimby: all data from CMA topographic maps).

### Study species

Carpet pythons *Morelia spilota* are large (up to 4 m) heavy-bodied (up to 10 kg) non-venomous constricting snakes that are widely distributed over the Australian mainland (Cogger, 1992). Dorsal coloration is variable, but usually involves irregular blotches of various shades of brown and grey. In the Mullumbimby area, adult pythons average approximately 2 m snout–vent length, and 3 kg (see Table 1 for body sizes of radio-tracked pythons). Males grow slightly larger than females in this population, but the size difference is small (Shine & Fitzgerald, 1995).

### Radiotelemetry

Pythons collected at both sites were implanted with miniature radiotransmitters before being released at the point of capture. To increase sample sizes, we also captured pythons in adjacent areas and released them at apparently suitable sites within the study areas. At the Bangalow site, we obtained seven resident snakes (four male, three female) and introduced three others (one male, two female). At Mullumbimby Creek we used four residents (three male, one female) and four non-residents (one male, three females). Temperature-sensitive radiotransmitters (Holohil Systems, Woodlawn, Ontario SI-2T, 45 × 15 mm, 35 g, with a 30 cm whip antenna) were calibrated in 2°C steps against a certified thermometer, over the range 5–40°C. The units were enclosed in flowable silicone and implanted into the peritoneal cavity via an incision in the lateral edge of ventral scales under inhalation anaesthesia (halo-thane). After surgery, pythons were held in captivity for 3–7 days before release. Telemetry signals were monitored with a Regal 2000 receiver and hand-held directional antenna (Titley Electronics, Ballina). Pythons were located two to three times per week. On each occasion, we took detailed notes on weather conditions and the telemetered snake's location, posture, and habitat use. Pulse interval of the telemetry signal was recorded, so that the snake's body temperature could be estimated. All locations were mapped so that distances moved by the snakes could be determined. Home ranges were estimated from these maps, using the minimum convex polygon technique (Jennrich & Turner, 1969).

Macrohabitats were classified into the following categories: (i) *building* — any house, shed, or similar structure; (ii) *forest* — any stand of trees forming a canopy which suppresses the growth of understorey plants. This category includes tree stands varying from original closed-canopy rainforests to narrow shelter belts dominated by introduced species such as camphor laurel *Cinnamomum camphora*; (iii) *thicket* — dense stands of saplings (< 3 m high), shrubs or other vegetation characterised by interlinkage and complexity; (iv) *open* — pasture, closely mown grass or other bare surface.

Microhabitats were categorised as follows: (i) *tree* — any woody perennial plant > 3 m high; (ii) *thicket* — complex dense vegetative structures, other than tree canopies. This category includes shrub growth to 3 m as well as gardens, low matted waterweeds, reeds and grasses; (iii) *heavy cover* — pythons located underground, or beneath logs, rocks, abandoned cars, or rubbish piles; (iv) *water* — submerged in a dam or creek; (v) *open* — pasture, closely mown grass or other bare surface; (vi) *roof* — in the ceiling space of a building.

If the telemetered snake was visible, we scored its posture as: (i) *compact coil* — more than a single layer of coiling, so that body surface exposure is reduced; (ii) *open coil* — any coiled posture where there is little or no contact between different parts of the python's body; (iii) *pancake coil* — flat with no stacking, or overlapping of the body, and in which there is virtually complete contact between adjacent coils; (iv) *outstretched* — linear posture, as when the python is moving.

In addition to the data on radio-tracked snakes, we also obtained information from other pythons collected in the Mullumbimby and Bangalow areas (either by us, or by local residents). These animals provided information on morphology, feeding habits (through regurgitation, scat analysis, or direct observation) and sources of mortality. All faeces produced by freshly captured snakes were examined microscopically to identify the prey species consumed. Mammalian fur was identified using the field guide by Brunner and Coman (1974).

## RESULTS

Nineteen radio-tracked adult pythons, ranging from 1·3 to 2·8 m snout–vent length (1·4–7·0 kg) were monitored for an average of 308 days (range 32–567 days: Table 1). Transmitters weighed < 4% of the snake's body mass (mean = 1·9%) and we noted no ill effects from the insertion or presence of the transmitters. All but one of the radiotracked snakes were recorded to have fed, and many reproduced during the study (Shine & Fitzgerald, 1995). Pythons captured elsewhere, and released on the study sites, generally behaved similarly to resident animals in terms of postures, habitat selection, and distances moved (unpaired two-tailed $t$-tests, $p > 0·05$ for all variables).

### Overall patterns in habitat use

The radiotracked snakes spent much of their time in the trees (mean = 45% of all locations), and were rarely visible from the ground because the animals consistently selected trees that were covered by a dense growth of vines and creepers. Thus, it was virtually impossible for the observer to see the snake even when its location was pinpointed by the telemetry signal. Similarly, terrestrial snakes were usually hidden deep within thickets (47% of all locations) or under heavy cover (7%). Snakes were rarely found in open areas, even though these constituted a high proportion of the available habitat in both study sites. As a result of this bias towards forested areas, the pythons on the Bangalow site were concentrated in the relatively small area covered by thick vegetation, and rarely encountered in the open areas (including the orchard itself: Fig. 1).

At the Mullumbimby site, several snakes spent much of their time inside the roofs of buildings (domestic residences), and often remained there for long periods. For example, one female python remained inside a roof for 92 days. Habitat selection was not significantly related to body size in our analyses (Spearman Rank correlations of snake body size with % habitat use in each category: $p > 0·05$ in all comparisons).

### Individual differences in habitat use

Comparisons among the telemetered snakes showed that individuals differed significantly from each other in terms of their relative frequencies of use of macrohabitat categories (Bangalow, d.f. = 16, $\chi^2 = 114·1$, $p < 0·001$; Mullumbimby, d.f. = 21, $\chi^2 = 456·9$, $p < 0·001$) and microhabitat categories (Bangalow, d.f. = 32, $\chi^2 = 258·9$, $p < 0·001$; Mullumbimby, d.f. = 28, $\chi^2 = 480·4$, $p < 0·001$).

**Table 1. Carpet pythons *Morelia spilota variegata* studied radiotelemetrically in this project**

| Collection locality | Telemetry Locality | SVL (m) | Tail (m) | Mass (kg) | Sex | Date collected | Date released | Final date monitored | Duration of tracking (days) |
|---|---|---|---|---|---|---|---|---|---|
| Edenbridge | Bangalow | 1·80 | 0·25 | 2·98 | F | 2-Oct-93 | 6-Oct-93 | 17-Apr-94 | 193 |
| Belongil | Bangalow | 1·70 | 0·27 | 1·82 | F | 20-Feb-93 | 25-Apr-93 | 14-Oct-93 | 172 |
| Bangalow | Bangalow | 2·13 | 0·29 | 5·00 | M | 11-Oct-92 | 20-Oct-92 | 27-Mar-94 | 523 |
| Bangal | Bangalow | 1·91 | 0·34 | 4·10 | F | 11-Oct-92 | 20-Oct-92 | 17-Apr-94 | 544 |
| Belongil | Bangalow | 1·58 | 0·28 | 1·90 | F | 25-Feb-93 | 27-Apr-93 | 17-Feb-94 | 296 |
| Possum Ck | Bangalow | 2·08 | 0·26 | 4·04 | M | 12-Sep-92 | 26-Sep-92 | 10-Jan-93 | 106 |
| Bangalow site | Bangalow | 2·08 | 0·33 | 3·90 | M | 11-Aug-92 | 20-Sep-92 | 10-Apr-94 | 567 |
| Bangalow site | Bangalow | 1·75 | 0·28 | 4·35 | M | 12-Sep-92 | 22-Sep-92 | 18-Jan-94 | 483 |
| Bangalow site | Bangalow | 2·33 | 0·30 | 4·00 | M | 11-Oct-92 | 20-Oct-92 | 30-Aug-93 | 314 |
| Bangalow | Bangalow | 2·05 | 0·18 | 2·88 | F | 28-Nov-93 | 16-Jan-94 | 11-Mar-94 | 54 |
| Mullum. Ck | Alstonville | 1·85 | 0·28 | 3·10 | M | 3-Sep-93 | 10-Sep-92 | 12-Oct-92 | 32 |
| Mullum. Ck | Mullum Ck | 1·79 | 0·33 | 1·80 | M | 25-Sep-92 | 9-Oct-92 | 29-Nov-93 | 416 |
| Macleans Ridges | Mullum Ck | 2·83 | 0·40 | 7·00 | M | 1-Sep-92 | 15-Sep-92 | 25-Mar-94 | 556 |
| Mullum. Ck | Mullum. Ck | 1·69 | 0·26 | 1·63 | F | 9-Sep-92 | 16-Sep-92 | 21-Jan-93 | 127 |
| Mullum. Ck | Mullum Ck | 1·33 | 0·32 | 2·13 | M | 12-May-92 | 21-Sep-92 | 6-Mar-94 | 531 |
| Mullum. district | Mullum Ck | 1·77 | 0·26 | 1·83 | F | 15-May-93 | 1-Jul-93 | 11-Mar-94 | 253 |
| Mullum. Ck | Mullum Ck | 1·62 | 0·30 | 1·40 | M | 8-Sep-92 | 21-Sep-92 | 6-Jan-93 | 107 |
| Alstonville | Bangalow | 1·66 | 0·29 | 2·80 | F | 13-Oct-92 | 31-Oct-92 | 27-Jan-94 | 453 |
| Mullum. district | Mullum Ck | 2·26 | 0·37 | 4·15 | F | 19-Feb-93 | 2-Apr-93 | 10-Aug-93 | 130 |

[a]SVL, snout–vent length.
[b]Mullum, Mullumbimby.

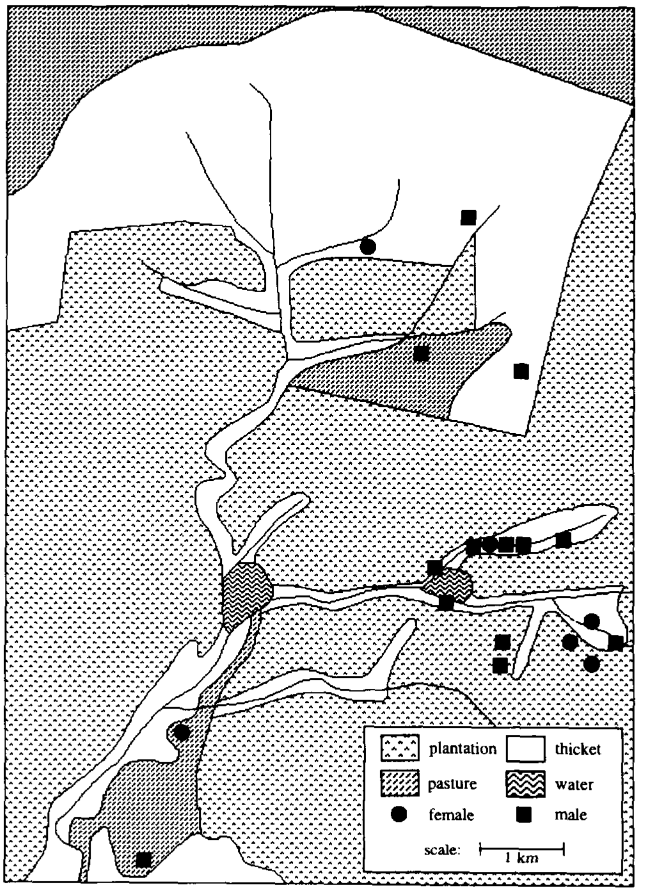


**Fig. 1.** A map of the study area at Bangalow, showing vegetation types and locations of first capture of carpet pythons. Thus, each point represents a different snake. Although most of the site consists of open orchards and pastures, the snakes were usually encountered very close to thick vegetation: typically, thickets in small gullies that extended into the open agricultural land.

**Sex differences in habitat use**

At both of the study sites, males were consistently more arboreal than were females (Bangalow, males 39% vs females 28% of locations; Mullumbimby, males 56% vs females 6%), and an unpaired *t*-test showed that these sex differences were statistically significant ($n$ = 9 males, 8 females, d.f. = 15, $t$ = 2·52, $p<0·025$). However, when using arboreal perches, the sexes did not differ significantly in the height of their perches above the ground (means = 8·1 m males, 11·1 m females, $F_{1,14}$ = 0·03, $p$ = 0·86).

**Differences in habitat use between the two study sites**

Given the differences in habitat types between our two sites, it is not surprising to find significant differences between the two areas in habitat usage by radio-tracked snakes. The primary differences were that Mullumbimby snakes spent more of their time inside buildings (36% vs 0%), and hence were less often recorded in thickets (30% vs 65%). Combining data from all snakes in each area, the proportional use of habitats differed significantly between the two sites, in terms of microhabitat (d.f. = 6, $\chi^2$ = 265·4, $p<0·0001$) as well as macrohabitat (d.f. = 3, $\chi^2$ = 330·9, $p<0·0001$).

**Seasonal shifts in habitat use**

The habitats selected by our radio-tracked pythons varied significantly among seasons. For analysis, we divided the year into four seasons: summer (December–February), autumn (March–May), winter (June–August) and spring (September–November). Contingency-table analysis revealed significant seasonal variation in the relative usage of different macrohabitats (d.f. = 9, $\chi^2$ = 124·6, $p<0·0001$), microhabitats (d.f. = 12, $\chi^2$ = 141·2, $p<0·0001$) and the frequencies of different postures (d.f. = 9, $\chi^2$ = 21·2, $p<0·02$). The habitat shifts (both macro- and micro-) reflected the greater use of arboreal perches in winter (58% vs 20% in summer, 48% in autumn, 42% in spring), whereas the postural changes were due to a greater tendency of snakes to be active (outstretched) in summer (16%) and spring (19%) than in autumn (8%) or winter (2%). Snakes monitored in winter were usually tightly coiled when located (63%, vs 41% in summer, 55% in autumn, 46% in spring).

The significant association of snakes with trees during winter was also reflected in a tendency for terrestrial snakes to be closer to trees in winter than in other seasons. The mean distance to the nearest tree for terrestrial snakes averaged 6·91 m (SD = 6·22) in summer, 6·76 m (SD = 4·67) in autumn, 4·52 m (SD = 1·50) in winter, and 4·87 m (SD = 4·42) in spring. A one-factor analysis of variance, with season as the factor, shows that these differences were highly significant ($F_{3,429}$ = 5·90, $p<0·0006$). However, the height above ground of arboreal snakes did not differ seasonally (means from 7·8 to 10·7 m; $F_{3,144}$ = 1·10, $p$ = 0·35).

**Reproduction and habitat use**

Reproductive activities apparently had little effect on habitat use. Courtship and mating were recorded both in trees and on the ground (Shine & Fitzgerald, 1995). One radio-tracked female deposited her eggs in a shallow hole in earth beneath a large hummock of molasses grass *Melinus minutiflora*, on a hillside at least 80 m from the nearest water supply (a creek). Another radio-tracked female oviposited under a thick clump of dead grass approximately 2 m from a small creek, among a dense stand of grasses, sedges and lantana. A third (non-telemetered) female was discovered coiled around a clutch of 16 eggs in a suburban backyard in Mullumbimby. Her eggs were deposited close to the edge of a large pile of banana stems and leaves, which wilted over the course of summer so that the female and her eggs were progressively exposed. Nonetheless, she incubated the clutch successfully through to hatching. A fourth clutch (old eggshells from a previous year) was located in an extensive stand of 1·5-m-high crofton weed *Eupatorium riparium* on a slope at Ewingsdale. Two gravid females collected < 10 days prior to oviposition were both found sheltering under clumps of mown grass. From these data, the edges of streamside thickets appear to be choice oviposition sites.

**Body temperature regimes**

Pythons were observed basking only rarely, and were able to maintain high and relatively constant body temperatures by subtle postural shifts in a sun–shade mosaic. In a few cases where we were able to observe pythons high in trees, from even higher vantage points in adjacent trees, we observed the snakes basking in direct sunlight on branches or 'platforms' of dense vegetation, or (more commonly) basking while positioned just below the surface of dense vegetation (such that most of the body was not exposed to direct solar radiation). Basking in direct sunlight was seen infrequently, and was recorded mostly for brooding females. Mean body temperatures of the radio-tracked pythons showed no significant seasonal variation, with all seasonal means within a range of < 1°C (27·5–28·1°C: $F_{3,1436} = 1·70$, $p = 0·17$). We thus combined data from throughout the year to examine the effects of time of day and reproductive activity on thermal levels. The snakes were divided into three groups: males, non-reproductive females and reproductive females. A two-factor ANOVA, with hour of day and reproductive category as the factors, showed that body temperatures varied with time of day ($F_{15,169} = 10·29$, $p < 0·001$: see Fig. 2) as well as among categories ($F_{2,169} = 5·91$, $p < 0·004$), with no interaction between the two effects ($F_{24,169} = 0·72$, $p = 0·83$). The effect of reproduction is due to a tendency for reproductive females to maintain higher and less variable body temperatures than do snakes in the other categories (mean = 29·3°C, vs 26·8 for males, 27·2 for non-reproductive females: see Fig. 2).

**Distances moved**

Most movements by telemetered snakes occurred in the late afternoon or evening, or at night (i.e. successive locations within the same day rarely revealed displacement, except when the second location was late in the evening). The proportion of snakes that were moving about when located was highest in the morning (for all hourly means 07·00–10·00 h, > 10% of records were of crawling snakes), low during the day (hourly means < 06%, 11·00–18·00 h), and rose again in the evening (> 10%, 18·00–19·00 h). Contingency-table analysis falsified the null hypothesis of constant proportions of snakes in each posture category throughout the day (d.f. = 36, $\chi^2 = 61·2$, $p < 0·006$). Posture categories also differed between the sexes (d.f. = 3, $\chi^2 = 37·8$, $p < 0·0001$): males were more often found moving or in compact coils, whereas females tended to be coiled more loosely (in 'open' or 'pancake' postures). The mean daily displacements of radio-tracked snakes varied among seasons, being higher in spring (12·3 m, SD = 38·1) and summer (11·4 m, SD = 21·1) than in autumn (6·3 m, SD = 17·4), and with little movement in winter (1·4 m, SD = 3·4) ($F_{3,1348} = 6·14$, $p < 0·0005$). Males tended to move further than females (means of 12·6 m per day, SD = 31·1 vs 6·7 m, SD = 28·6: $F_{1,17} = 4·99$, $p < 0·04$).

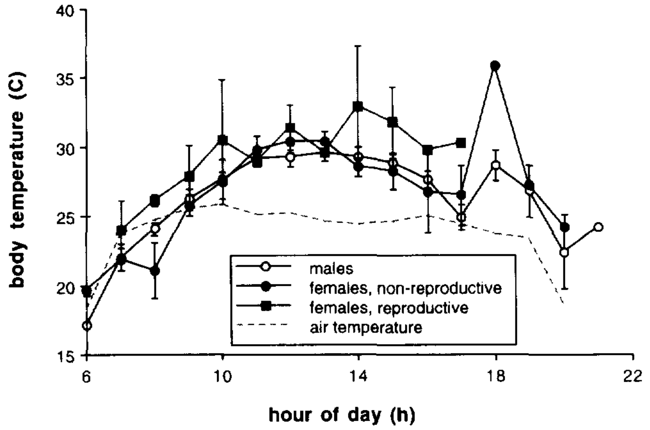


**Fig. 2.** Body temperatures of radio-tracked carpet pythons in summer (December–February). The graph shows mean hourly body temperatures of males, non-reproductive females and reproductive females, plus standard deviations for each. Air temperatures were taken at the same time as body-temperature data. See text for statistical tests.

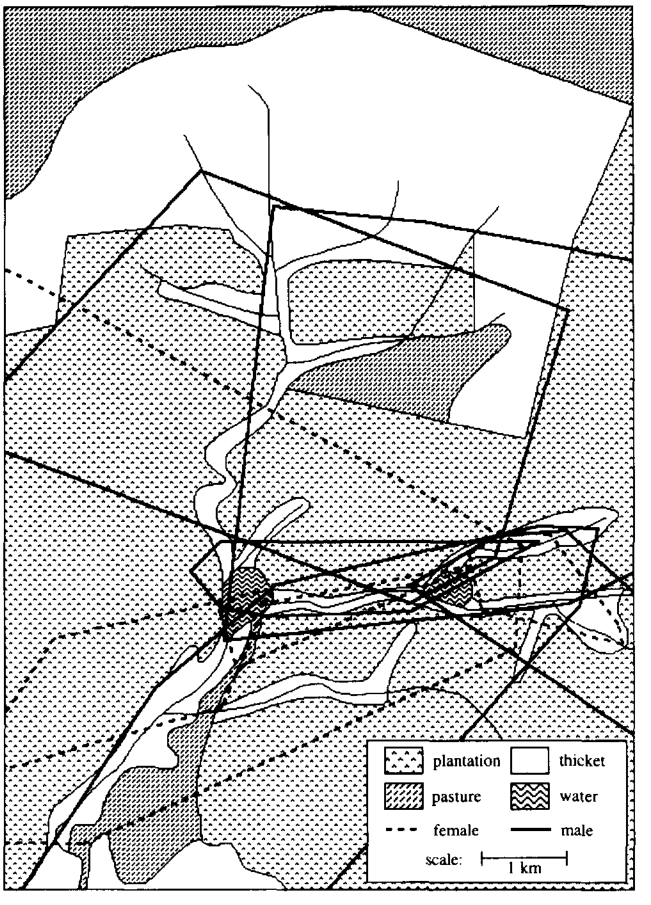


**Fig. 3.** A map of the Bangalow study area showing home ranges of radio-tracked carpet pythons. The outlines of the home ranges are shown as calculated by the minimum convex polygon technique, and undoubtedly incorporate some areas rarely (or never) used by the snakes. Note the considerable overlap in home ranges, and the highly variable home range sizes.

**Table 2. Use of different macrohabitats and microhabitats by radio-tracked carpet pythons *Morelia spilota variegata* in northeastern New South Wales. N, number of observations. See text for definitions of macrohabitats and microhabitats**

| Locality | Snake No. | *N* | Sex | Macrohabitat use: propn. of observations in | | | | Microhabitat use: propn. of observations in | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Building | Forest | Thicket | Open | Tree | Thicket | Heavy | Water | Open | Roof |
| Bangalow | 819 | 45 | m | 0·00 | 0·04 | 0·96 | 0·00 | 0·00 | 0·96 | 0·00 | 0·00 | 0·04 | 0·00 |
| Bangalow | 750 | 77 | f | 0·00 | 0·09 | 0·89 | 0·01 | 0·18 | 0·82 | 0·00 | 0·00 | 0·00 | 0·00 |
| Bangalow | 482 | 38 | f | 0·00 | 0·34 | 0·66 | 0·00 | 0·37 | 0·61 | 0·00 | 0·03 | 0·00 | 0·00 |
| Bangalow | 950 | 66 | m | 0·00 | 0·32 | 0·62 | 0·06 | 0·30 | 0·62 | 0·00 | 0·00 | 0·08 | 0·00 |
| Bangalow | 928 | 133 | m | 0·00 | 0·54 | 0·45 | 0·01 | 0·54 | 0·44 | 0·01 | 0·00 | 0·02 | 0·00 |
| Bangalow | 650 | 133 | f | 0·00 | 0·41 | 0·59 | 0·00 | 0·39 | 0·57 | 0·04 | 0·00 | 0·00 | 0·00 |
| Bangalow | 230 | 54 | f | 0·00 | 0·28 | 0·72 | 0·00 | 0·37 | 0·31 | 0·31 | 0·00 | 0·00 | 0·00 |
| Bangalow | 608 | 135 | m | 0·00 | 0·47 | 0·52 | 0·01 | 0·44 | 0·36 | 0·20 | 0·00 | 0·00 | 0·00 |
| Bangalow | 860 | 136 | m | 0·00 | 0·57 | 0·43 | 0·00 | 0·57 | 0·40 | 0·02 | 0·01 | 0·00 | 0·00 |
| Bangalow | 692 | 274 | f | 0·37 | 0·04 | 0·52 | 0·07 | 0·02 | 0·57 | 0·13 | 0·00 | 0·01 | 0·27 |
| Mullumbimby | 906 | 106 | m | 0·69 | 0·00 | 0·31 | 0·00 | 0·02 | 0·27 | 0·04 | 0·00 | 0·00 | 0·64 |
| Mullumbimby | 819 | 49 | f | 0·00 | 0·19 | 0·81 | 0·00 | 0·00 | 1·00 | 0·00 | 0·00 | 0·00 | 0·00 |
| Mullumbimby | 786 | 113 | f | 0·90 | 0·00 | 0·10 | 0·00 | 0·02 | 0·10 | 0·08 | 0·00 | 0·00 | 0·80 |
| Mullumbimby | 879 | 321 | m | 0·05 | 0·72 | 0·22 | 0·01 | 0·69 | 0·24 | 0·01 | 0·00 | 0·00 | 0·06 |
| Mullumbimby | 971 | 203 | m | 0·17 | 0·71 | 0·11 | 0·00 | 0·46 | 0·16 | 0·27 | 0·00 | 0·00 | 0·09 |
| Mullumbimby | 458 | 134 | f | 0·71 | 0·03 | 0·17 | 0·09 | 0·02 | 0·24 | 0·03 | 0·00 | 0·00 | 0·71 |
| Mullumbimby | 842 | 366 | m | 0·00 | 00·81 | 0·19 | 0·00 | 0·72 | 0·26 | 0·02 | 0·00 | 0·00 | 0·00 |

**Home ranges**

Because we found no evidence of any seasonal shifts in the locations of home ranges (as in diamond pythons– Slip & Shine, 1988*a*), we calculated single estimates based on all data for each individual. We did not correct these estimates for differing sample sizes (numbers of observations per snake), because sample sizes were large for all specimens (mean = 126·1, SD = 80·9, range = 38–321) and were not correlated with our home range estimates ($r = 0{\cdot}14$, $p = 0{\cdot}60$). The areas used by different pythons showed considerable overlap (Fig. 3). Home ranges for 17 radio-tracked pythons averaged 22·5 ha (range = 10–198 ha, SD = 11·61), but this mean was strongly influenced by a single large male snake in the Mullumbimby Creek site. His home range (198 ha) was much larger than recorded for any of the other 16 snakes (maximum = 60 ha; mean = 12 ha, SD = 16). Mean home ranges did not differ significantly between our two study sites, whether or not the atypical animal was included in the analysis (unpaired $t$ = 1·04, 15 d.f., $p = 0{\cdot}32$ for all snakes, $t = 0{\cdot}09$, 14 d.f., $p = 0{\cdot}93$ without the large male). Excluding the single atypical animal, mean home ranges were similar in the two areas (Bangalow, mean = 11 ha, SD = 12, $n = 9$; Mullumbimby Creek, mean = 12 ha, SD = 22, $n = 7$). A two-factor ANOVA, with sex and residency status (resident versus introduced) as the independent variables, showed that neither of these factors explained a significant proportion of the observed variance in home range sizes (sex, $F_{1,13} = 0{\cdot}59$, $p = 0{\cdot}46$; residency, $F_{1,13} = 0{\cdot}46$, $p = 0{\cdot}51$).

**Population densities and biomass**

Because the carpet pythons were generally found in or near dense vegetation (see above), our estimates of population density depend heavily on whether calculations are based only on such habitat, or if open areas are also included. If the entire region is included, each of our two study sites contained at least 20 adult pythons within a region of approximately 50 $km^2$ (7 × 7 km), for a biomass of at least 1 $kg/km^2$. If the calculation is based only on areas of thick vegetation, the densities are much higher. For example, we captured six adult pythons within a single thicket < 1 $km^2$ in extent at Bangalow (Fig. 1), for a minimum biomass of 20 $kg/km^2$. Undoubtedly, many more pythons occurred in these areas but were not captured during our study.

**Mortality**

Carpet pythons are killed occasionally by motor vehicles, especially on the major highways, but local residents seldom deliberately run over *Morelia*, and nocturnal traffic activity is low on most roads. However, agricultural practices may kill many pythons. We found dead pythons on three occasions after grass-slashing by tractors at Bangalow, and two gravid *Morelia* coiled beneath clumps of cut grass at Bangalow in areas which were occasionally mown. Grass swards in orchards are kept too low to shelter *Morelia*, but thickets of tall grasses and weeds (1–2 m high) form in areas only mown a few times per year, and carpet pythons use this habitat. The only juvenile python found at the Bangalow site was discovered perched 1·5 m off the ground in a wild tobacco bush after being unintentionally struck (and seriously injured) by a worker manually brush-hooking overgrown terraces in a citrus orchard. An adult python was also killed by brushcutting activities during our study. The clearing of thickly vegetated areas (e.g. lantana, Barner grass *Pennisetum purpureum*) by tractor and excavator during our study would have threatened the lives of any pythons in these areas, and construction of a dam at Bangalow in January 1994 flooded an overgrown grassy paddock. Any brooding female python on eggs in this area would have been forced to abandon her clutch.

Parasites may also be important sources of mortality. Adult pythons often have large (cricket ball-sized) fibrous masses in the mid-gut, and occasional individuals with this feature are encountered in an emaciated condition. The masses may be related to long-term infestations of ascaridoid nematodes, eventually causing obstruction to the passage of prey items, either directly or by reduced elasticity of the gut. Ectoparasites may also be significant: for example, an adult python captured in March 1994 had >300 ticks attached to his head. The python's vision was totally obscured by the bodies of ticks, and his nasal passages and labial pits were blocked. Without our interference, this animal probably would have died.

The deaths of 10 radio-tracked snakes during our study provided additional evidence of high mortality rates. The cause of death was unknown for two snakes. In the other cases, the transmitters had characteristic bite marks when recovered: one from lace monitors *Varanus varius* and seven from canids. In at least two of the seven latter cases, it is clear that the snakes were killed by foxes when they left the shelter of forested gullies to cross open orchard areas. This is likely to have occurred in all seven cases. Also, one of our brooding female pythons was attacked by a large lace monitor that consumed 12 of her 18 eggs; the female deserted the remaining six eggs less than a day after this predation event.

### Feeding habits

Direct observations of feeding suggest that carpet pythons are ambush predators. For example, one of us (M.F.) saw a stationary, arboreal python seize and constrict an agamid lizard *Physignathus lesueurii* that fled from the observer's approach. Other situations where we have found pythons constricting prey also suggest that the immobile snake has encountered a mobile prey item. Nonetheless, the occurrence of stationary prey in the diet (e.g. eggs and nestling birds: Table 3) indicates that these snakes will also actively search for prey. The 84 prey items recorded from carpet pythons in the Mullumbimby district suggest that these snakes feed primarily on rodents, but are also prepared to take much larger mammalian prey (e.g. megachiropterans, bandicoots, dogs [beagles]), as well as birds and reptiles (Table 3). Most (75 of 84, = 89%) of the prey items we recorded were not native species. Instead, they were commensal taxa (e.g. *Rattus rattus*, *Mus domesticus*) or domestic pets and livestock (mice, poultry, cagebirds, and the dog).

**Table 3. Prey items of *Morelia spilotes variegata* in the Mullumbimby region, as determined from faecal examination, regurgitation and reports from local land-owners**

Non-native prey species indicated by asterisk.

| Prey type | | No. of records (No. of snakes) |
|---|---|---|
| Mammals | | |
| Rats | | |
| | *Rattus* sp.* | 15 (15) |
| | *Rattus rattus** | 24 (24) |
| Mice | *Mus domesticus** (feral) | 11 (11) |
| | Pet mice* | 7 (2) |
| Bandicoot | *Isoodon* sp. | 1 (1) |
| Bat | *Pteropus* sp. | 1 (1) |
| Dog | *Canis familiaris*[a]* | 1 (1) |
| Birds | | |
| Honeyeater | Meliphagidae | 1 (1) |
| Magpie | *Gymnorhina tibicen* | 1 (1) |
| Nestlings | spp. | 3 (3) |
| Pigeon | *Columba livia** | 1 (1) |
| Cagebirds | *Agapornis pullaria** | 4 (2) |
| Poultry | *Gallus domesticus** | 4 (4) |
| Goose eggs | *Anser anser** | 7 (1) |
| Reptiles | | |
| Agamidae | *Physignathus lesueurii* | 1 (1) |
| | *Pogona barbata* | 1 (1) |

[a]Python found constricting beagle; dog not swallowed.

## DISCUSSION

Previously published information on the ecology of a Sydney-area population of the southern subspecies, the diamond python *Morelia spilota spilota* (Slip & Shine, 1988*a*,*b*,*c*,*d*,*e*) provides an interesting comparison with the present study. The broad outlines of ecology are similar for both subspecies: both are large cryptic ambush predators, using disturbed habitats for feeding on commensal endotherms, but retreating to thickly vegetated areas for shelter. However, many differences are apparent, probably due in large part to the higher ambient temperatures of northeastern New South Wales. This climatic difference may be responsible for the trends to nocturnal activity, and the much more subtle nature of seasonal shifts in habitat types, in our carpet pythons. Unlike Slip and Shine's (1988*a*) diamond pythons, which travelled many hundreds of metres to exposed rocky outcrops for winter, our radio-tracked carpet pythons simply moved into more densely forested areas, and up into trees. Winter inactivity was less pronounced in our snakes than in the diamond pythons. Home ranges were much smaller than those reported by Slip and Shine (1988*a*), presumably because of higher prey availability (reducing the need for long-distance shifts to new ambush sites) and smaller mate-searching movements by reproductive males (probably because the higher population density increased encounter rates with reproductive females). In both subspecies, movements were more extensive in males than in females. However, in carpet pythons, the greater daily movements of males did not translate into larger home ranges, because the males tended to stay within relatively small areas.

Some of the minor sex differences that we documented in *M. s. variegata* are probably related to reproductive biology. For example, males moved about more than females during the mating season (as in many other snake species, e.g. Gregory *et al.*, 1987), and females maintained higher body temperatures during reproductive activity (see Grigg & Harlow, 1984). The trend for males to use arboreal habitats more than females is puzzling, but similar sex differences have been reported in other species of snakes (e.g. Houston & Shine, 1993; Zinner, 1985) and may relate to subtle differences in foraging biology (Shine, 1991).

Our data strongly support the idea that carpet pythons can maintain high numbers in areas that have been profoundly altered by human disturbance. The two sites we used differed in many respects, in landforms as well as patterns of human activities, but pythons were abundant in both areas. Indeed, the population densities of adult pythons in the small forested gullies that penetrate orchard areas at Bangalow were remarkably high relative to most previously reported estimates of population densities of large snakes (Parker & Plummer, 1987; Houston & Shine, 1994). How do these large animals persist in such highly modified habitats?

The persistence of *Morelia spilota* populations in close proximity to humans relies upon several aspects of the biology of this species, and the ways in which these characteristics are influenced by local climatic conditions, habitats and prey resources. The key feature appears to be the fact that, even when they are abundant, pythons are rarely seen by potential predators (humans, dogs, etc.). The low encounter rate between humans and pythons is due to the following characteristics of snake behavior: (a) the snakes actively select arboreal perches or dense thickets; (b) the trees they use are typically covered in vines and creepers, further reducing visibility; (c) daily movements are small, as are home ranges; (d) most activity occurs late in the evening or at night, when the snakes are less easily observed; and (e) the snakes rely on crypsis to avoid predation, and their dorsal colours provide excellent camouflage, so the animals are unlikely to be seen even if they are in relatively open areas. The high mortality rates of radio-tracked snakes that entered open areas during our study support the notion that snakes are most visible (and thus, vulnerable) when they are moving about (and see Andren, 1985; Madsen & Shine, 1993; Shine, 1993 for similar results on other taxa). Because male pythons moved about more than females (in terms of daily movements as well as overall home range size), mortality associated with movement by the snakes may be concentrated on males rather than females. Any such bias will tend to reduce the impact on population recruitment rates from a given level of adult mortality.

The sedentary nature of *M. s. variegata* is explicable in light of other aspects of this species' biology. First, carpet pythons rely mainly on ambush predation, which necessarily involves prolonged immobility. Second, the large body size of adult pythons confers a high degree of thermal inertia, so that these snakes do not need to engage in conspicuous thermoregulatory behaviors such as shuttling between sun and shade (Slip & Shine, 1988*a*). Thermoregulatory movements (on both a daily and a seasonal level) are further reduced by the relatively high and constant ambient temperatures experienced in the study area (Fig. 2). Arboreality offers the possibility for precise thermoregulation in an unseen three-dimensional habitat with minimal need for movement: the sun strikes the treetops earlier and remains later than in terrestrial locations, and shade of different densities is always nearby. Thus, pythons have little need to carry out any overt activity to maintain suitable body temperatures, and do not need to move long distances between thermally distinctive habitat types on a seasonal basis (as do more southern populations of this species—Slip & Shine, 1988*a*). The concentration of activity at night rather than by day presumably reflects the higher ambient temperatures as well: southern conspecifics are primarily diurnal, but become nocturnally active on exceptionally hot nights (Slip & Shine, 1988*a*).

The pythons' exploitation of commensal animals (including pets and domestic livestock) also contributes significantly to the success of this species in disturbed habitats. While native species may decline in abundance in such areas, overall prey biomass is probably increased substantially. The forested gullies used by carpet pythons also contain very high densities of feral rats *Rattus rattus*, that emerge at night to feed upon agricultural products (personal observations). Thus, human activities may have enhanced prey availability for the python — and the pythons may, in turn, contribute in economic terms by removing many rats. The pythons' willingness to feed upon non-native prey is a reflection of their general flexibility in ecological traits. Thus, for example, they are prepared to use 'artificial' shelters (such as dense stands of introduced camphor laurel trees, or roof spaces within buildings) if these habitats offer the same general characteristics (in terms of thermal biology and prey availability) as their 'natural' retreat sites such as thickets and vine-covered trees.

An additional factor that may contribute to the persistence of *M. spilota* in built-up areas is a widespread reluctance of local residents to kill this species. Because of their distinctive size, thickset build and colour pattern, adult carpet pythons cannot readily be confused with any of the sympatric venomous (elapid) snakes. The notion that 'a python in the feed shed helps to control rodent populations', and hence that such snakes should not be killed, is widely held in rural Australia

(Cann, 1986; Shine, 1994). Farmers and other local residents generally recognise pythons and do not attempt to kill them, as they would most other snake species.

Thus, the continued existence of viable populations of these large pythons in eastern Australia probably results from several factors. Chief among these is the inconspicuousness of the animal (due to its crypsis, habitat selection, and sedentary nature) and its willingness to utilise non-natural prey types and habitats so long as these have the appropriate general characteristics. Available data suggest the same situation in the southeastern subspecies (*M. s. spilota*), although the cooler climate, less abundant commensal prey and sparser vegetation may render it more difficult for these animals to remain hidden from humans (Slip & Shine, 1988*a,b,c*; Shine, 1994). *Morelia spilota* thus appears to have tolerated man-made habitat modifications — in some cases, very extreme modifications — throughout its range along the eastern coast of Australia.

Why, then, have populations of the same species from inland regions, and from large areas of Western Australia, been unable to cope with disturbances wrought by agricultural activities (Smith, 1981; Pearson, 1993; Shine, 1994)? The fundamental difference between the two cases may lie in the nature of the habitat remaining after land-clearing. Although carpet pythons are flexible in terms of habitat use, they require access to dense cover where they can hide — to lie in wait for prey, to avoid predators, and to brood their eggs. In areas where precipitation is low, so that the natural vegetation cover is already sparse (such as the mallee country of inland southeastern Australia, and the Western Australian wheatbelt), the end result of land-clearing for agriculture is virtually to eliminate any heavy cover suitable for a large cryptic ambush predator. This trend is exacerbated by the nature of the land-use patterns. Because the inland areas are level, and production is on a broadacre scale, proportionally more native vegetation is removed. The steeper topography and higher rainfall of the northeast coast mean that creeklines cannot be profitably cultivated without considerable erosion, and such sites are therefore usually left to grow belts of trees and woody thickets that can furnish habitat for pythons. Although commensal rodents may be abundant in the open grasslands of western regions, the foraging strategy of pythons is unsuited to open areas. Instead, the only snakes to persist in large numbers in these areas are fast-moving active searchers like *Pseudonaja textilis* (Shine, 1989). The maintenance of python populations in these areas is an important conservation issue, because *M. spilota* of the semi-arid zone are morphologically distinctive and are accorded subspecific status by many authorities (see Shine, 1994). The results of our study suggest that maintenance or replacement of thickly vegetated habitats — even if only in small patches — is the crucial first step towards halting the decline of this species over the western part of its range.

## ACKNOWLEDGMENTS

We thank E. Kosack and M. Fitzgerald for surgical implantation of radiotransmitters, and W. Hatton and M. Mathison for allowing us to work on their farm. M. Whicker donated several pythons for the study, and P. Whitaker analysed faecal samples. The Australian Research Council provided financial support for this study.

## REFERENCES

Andren, C. (1985). Risk of predation in male and female adders, *Vipera berus* (Linné). *Amphib.-Reptil.*, **6**, 203–6.

Brunner, H. & Coman, B. J. (1974). *The identification of mammalian hair*. Inkata Press, Melbourne.

Cann, J. (1986). *Snakes alive*. Kangaroo Press, Sydney.

Cogger, H. G. (1992). *Reptiles and amphibians of Australia, 4th edn*. Reed Books, Sydney.

Covacevich, J. (1970). *The snakes of Brisbane*. Queensland Museum, Brisbane, Qld.

Dickman, C. R. (1994). Native mammals of western New South Wales: past neglect, future rehabilitation. In *Future of the fauna of Western New South Wales*, ed. D. Lunney, S. Hand, P. Reed & D. Butcher. Royal Zoological Society of NSW, Sydney, pp. 81–91.

Dodd, C. K. J. (1993). Strategies for snake conservation. In *Snakes: ecology and behavior*, ed. R. A. Seigel & J. T. Collins. McGraw-Hill, New York, pp. 363–94.

Gow, G.F. (1976). *Snakes of Australia*. Angus and Robertson, Sydney, NSW.

Gregory, P. T., Macartney, J. M. & Larsen, K. W. (1987). Spatial patterns and movements. In *Snakes: ecology and evolutionary biology*, ed. R .A. Seigel, J. T. Collins & S. S. Novak. Macmillan, New York, pp. 366–95.

Grigg, G. & Harlow, P. S. (1984). Shivering thermogenesis in a brooding diamond python, *Python spilotes spilotes*. *Copeia*, 1984, 959–65.

Houston, D. L. & Shine, R. (1993). Sexual dimorphism and niche divergence: feeding habits of the arafura filesnake. *J. Anim. Ecol.*, **62**, 737–49.

Houston, D. L. & Shine, R. (1994). Population demography of arafura file snakes (Serpentes: Acrochordidae) in tropical Australia. *J. Herpetol.*, **28**, 273–80.

Jennrich, R. I. & Turner, F. B. (1969). Measurement of non-circular home range. *J. theoret. Biol.*, **22**, 227–37.

Madsen, T. & Shine, R. (1993). Costs of reproduction in a population of European adders. *Oecologia, Berl.*, **94**, 488–95.

Morton, S. R. & Baynes, A. (1985). Small mammal assemblages in arid Australia: a reappraisal. *Aust. Mammal.*, **8**, 159–69.

Parker, W. S. & Plummer, M. V. (1987). Population ecology. In *Snakes:ecology and evolutionary biology*, ed. R.A. Seigel, J. T. Collins & S. S. Novak. Macmillan, New York, pp. 253–301.

Pearson, D. J. (1993). Distribution, status and conservation of pythons in Western Australia. In *Herpetology in Australia*, ed. D. Lunney & D.Y. Ayers. Royal Zoological Society of NSW, Sydney, pp. 383–96.

Shine, R. (1989). Constraints, allometry and adaptation: food habits and reproductive biology of Australian brownsnakes (*Pseudonaja*, Elapidae). *Herpetologica*, **45**, 195–207.

Shine, R. (1990). The broad-headed snake. *Aust. Nat. Hist.*, **23**, 442.

Shine, R. (1991). Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *Amer. Nat.*, **138**, 103–22.

Shine, R. (1993). Ecological studies on Australian pythons. In *Proc. Int. Herpetol. Symp.*, 15th, ed. M. Uricheck. International Herpetological Symposium, Inc., Seattle, WA, pp. 29–40.

Shine, R. (1994). The biology and management of diamond pythons *Morelia s. spilota* and carpet pythons *M. s. variegata*. NSW National Parks and Wildlife Service, Sydney.

Shine, R. & Fitzgerald, M. (1995). Variation in mating systems and sexual size dimorphism between populations of the Australian python *Morelia spilota* (Serpentes: Pythonidae). *Oecologia, Berl.*, **103**, 490–8.

Slip, D. J. & Shine, R. (1988*a*). Habitat use, movements and activity patterns of free-ranging diamond pythons, *Morelia s. spilota* (Serpentes: Boidae): a radiotelemetric study. *Aust. Wildl. Res.*, **15**, 515–31.

Slip, D. J. & Shine, R. (1988*b*). Reptilian endothermy: a field study of thermoregulation by brooding diamond pythons. *J. Zool. (Lond.)*, **216**, 367–78.

Slip, D. J. & Shine, R. (1988*c*). The reproductive biology and mating system of diamond pythons, *Morelia spilota* (Serpentes, Boidae). *Herpetologica*, **44**, 396–404.

Slip, D. J. & Shine, R. (1988*d*). Thermoregulation of free-ranging diamond pythons, *Morelia spilota* (Serpentes, Boidae). *Copeia*, 1988, 984–95.

Slip, D. J. & Shine, R. (1988*e*). Feeding habits of the diamond python, *Morelia s. spilota*: ambush predation by a boid snake. *J. Herpetol.*, **22**, 323–30.

Smith, L. A. (1981). A revision of the python genera *Aspidites* and *Python* (Serpentes: Boidae) in Western Australia. *Rec. West. Aust. Mus.*, **9**, 211–26.

Wilson, S. K. & Knowles, D. G. (1988). *Australia's reptiles.* Collins, Sydney.

Zinner, H. (1985). On behavioral and sexual dimorphism of *Telescopus dhara* Forscal 1776 (Reptilia: Serpentes, Colubridae). *J. Herpetol. Assoc. Afr.*, **31**, 5–6.