Spatial ecology of a threatened python (*Morelia spilota imbricata*) and the effects of anthropogenic habitat change

D. PEARSON,1 R. SHINE2* AND A. WILLIAMS1
1Department of Conservation and Land Management, Wanneroo, Western Australia, Australia and
2School of Biological Sciences A08, University of Sydney, Sydney, New South Wales 2006, Australia
(Email: rics@bio.usyd.edu.au)

Abstract Large predators play important ecological roles, but often are sensitive to habitat changes and thus are early casualties of habitat perturbation. Pythons are among the largest predators in many Australian environments, and hence warrant conservation-orientated research. Carpet pythons (*Morelia spilota imbricata*) have declined across much of south-western Australia presumably because of habitat clearance and degradation. Information on habitat use, home range sizes and movements is needed to plan for the conservation of this important predator. We studied pythons at two study sites (Garden Island and Dryandra Woodland) with markedly different climates, habitat types and disturbance histories. We surgically implanted radio-transmitters in 91 pythons and tracked them for periods of 1 month to 4 years. Dryandra pythons remained inactive inside tree hollows during cooler months (May–September), whereas some (especially small) pythons on Garden Island continued to move and feed. Overall weekly displacements (mean = 100–150 m) were similar at the two study sites and among sex/age classes, except that reproductive females were sedentary during summer while they were incubating eggs. Home ranges averaged 15–20 ha. Adult male pythons had larger home ranges than adult females at Dryandra, but not at Garden Island. Radio-tracked snakes at Dryandra exhibited high site fidelity, returning to previously occupied logs after long absences and reusing tree hollows for winter shelter. Many of the logs used by snakes had been felled during plantation establishment >70 years ago, with little subsequent regeneration of source trees. In contrast, Garden Island snakes usually sheltered under dense shrubs. Habitat usage was similar among different sex/age classes of snakes at each site, except that juvenile pythons were more arboreal than adults. Although carpet pythons demonstrate great flexibility in habitat use, certain habitat elements appear critical for the persistence of viable populations. Fire plays a central role in this process, albeit in complex ways. For example, low-intensity fires reduce the availability of hollow logs on the ground at Dryandra and fail to regenerate shrub thickets required by prey species. Paradoxically, high-intensity fires stimulate shrub thickets and fell trees creating new logs – but might also threaten overwinter trees. Thus, the impact of disturbances (such as wildfires) on the viability of python populations will be mediated in complex ways by alteration to important microhabitats such as vegetation cover or log availability. At Dryandra, landscape management should include occasional fire events to generate new logs as well as shrub thickets used by prey. Strategic burning may also be required at Garden Island to regenerate some vegetation communities.

Key words: carpet python, fire, geographical variation, habitat use, movement, seasonality, telemetry.

INTRODUCTION

In order for wildlife populations to persist, they need access to suitable habitat of sufficient size and contiguity to provide adequate resources (i.e. food, shelter, etc.) and to cope with environmental perturbations. Habitat destruction and fragmentation can reduce the ability of wild populations to persist, or to reinvade after major natural and anthropogenic disturbances. Some types of animals may be particularly vulnerable to such changes and among snakes, large ambush predators may be at most risk (Webb & Shine 1998). Such species depend upon vegetation structure for concealment from potential prey and predators, and even minor modifications to habitat can have serious effects on their population viability (Reed & Shine 2002). Also, habitat changes may alter the composition and abundance of prey assemblages and so reduce hunting success.

The south-western carpet python (*Morelia spilota imbricata*) is a large ambush predator with a wide distribution across southern Australia (Pearson 1993). It is considered a threatened taxon (Cogger et al. 1993) and is a ‘specially protected taxon’ under State legislation on the basis of declines in parts of its range, presumably because of habitat destruction (Smith 1981). The diet consists of vertebrates, particularly mammals, and logs are important for shelter (Barker & Barker 1994). Thus, this taxon is likely to be vul-
nerable to any reduction in ground cover (and therefore ambush opportunities) or in the abundance or diversity of vertebrate prey (Shine 1994). Although carpet pythons from eastern Australia have attracted considerable ecological research (Slip & Shine 1988a,b,c,d,e,f; Shine & Fitzgerald 1995, 1996), the south-western subspecies has been virtually unstudied. Because information on the spatial ecology of this python can guide decisions regarding its conservation and management, we undertook a detailed radio-telemetry study of two populations of this species in south-western Australia.

Despite the proximity of our two study sites (separated by 130 km; 35° of latitude), they differ markedly in climate, landform, vegetation types, prey resources and potential shelter sites. This contrast allowed us to compare activity patterns, seasonal movements, habitat use and home ranges in an effort to identify the ways in which habitat and climatic diversity influence python spatial ecology. To this end, we radio-tracked juvenile pythons, adult males, and reproductive and non-reproductive female pythons over several years. An understanding of how pythons use the varying resources of these two sites should clarify their responses to environmental change and disturbances such as fire, logging and land clearance.

METHODS

Study animal

The south-western carpet python (*M. s. imbricata*) is a large non-venomous snake, measuring up to 2.5 m in total length with a mass of up to 6 kg. It is an ambush predator of vertebrates including birds, reptiles and mammals ranging in size up to small wallabies. The sexes are strongly size dimorphic with adult females averaging more than 10 times the mass of adult males in some populations (Pearson *et al.* 2002a,b). Mating occurs from October to mid-December, eggs are laid in December and the female coils around the eggs and incubates them until hatching in March. Adult males are probably reproductively active every year, but females only breed every second year or less frequently because of the time required for emaciated post-reproductive females to rebuild energy stores (Pearson *et al.* 2002a).

Carpet pythons use a range of habitats including coastal shrublands, heath, forest, woodlands, the margins of agricultural land and outer metropolitan areas (where they sometimes utilize the roof spaces of buildings: Shine & Fitzgerald 1996; Slip & Shine 1988a; Fearn *et al.* 2001). Despite this flexibility, the south-western carpet python has disappeared from large tracts of its historic range. It is now rarely recorded in most of the ‘Wheatbelt Region’, an area of intensive cereal production in inland Western Australia, and the Swan Coastal Plain, now largely covered by metropolitan development around the city of Perth (Smith 1981; Pearson 1993).

Study areas

Garden Island (32°12′S, 115°40′E) lies 15 km southwest of the port of Fremantle and has an area of 1200 ha (Fig. 1). It experiences hot dry summers, tempered by reliable afternoon sea breezes and mild wet winters. Figure 2 summarizes the mean maximum

![Fig. 1. Map showing the location of study areas.](image-url)
other shrubs on dune sands; (iii) mixed low forest of *Olearia axillaris* and *Acacia rostellifera* with a thick understory of shrubs and herbs; (ii) shrublands of *Acanthocarpus preissii* with a thick understory of prickly *Acanthocarpus preissii* and a variety of other shrubs on dune sands; (iii) mixed low forest of *C. preissii*, *Melaleuca lanceolata*, *Melaleuca huegelli* and *A. rostellifera* with *Ac. preissii* understory on undulating sand plain; and (iv) low (0.5–1.5 m) heath dominated by *Alyxia buxifolia*, *Scaevola cassinifolia* and *Olearia axillaris* on shallow soils over limestone or in exposed positions along the west coast. There were also minor areas of littoral shrubland of variable composition around the coastal margin (McArthur & Bartle 1981). Trees on Garden Island only grow to a maximum height of 10 m, with few tree hollows or hollow logs.

The second site, Dryandra Woodland (32°47'S, 116°55'E), lies 140 km SE of Perth and 130 km ESE of Garden Island (Fig. 1). Dryandra also experiences hot, dry summers, but without mediating maritime influences. Winters are cold and wet. Figure 2 summarizes climatic data for the town of Wandering, 28 km NW of Dryandra. It has lower rainfall and more pronounced temperature extremes than Garden Island. Dryandra Woodland consists of 24 fragmented woodland and forest blocks separated by areas cleared for wheat production (Coates 1993). The total area of the State Forests that make up Dryandra Woodland is 28 066 ha, but our study was carried out entirely within the largest contiguous area of the Woodland (in areas known as Dryandra, Frank and Peters forest blocks). This area is vegetated by: (i) undulating open woodlands of *Eucalyptus wandoo* with a variable understory of *Gastrolobium* spp. and heath; (ii) areas of residual lateritic plateau vegetated by tall *Dryandra* spp.-dominated heath (to 3 m) with occasional *Corymbia calophylla*; (iii) mixed woodlands of *Eucalyptus accedens*, with scattered *Eucalyptus astringens* and *Co. calophylla* on the erosional slopes of these plateaux; (iv) low woodland of * Allocasuarina huegelia* and emergent *E. wandoo* with little understory on granitic soils; and (v) areas of mallet plantation (*E. astringens* and *Eucalyptus gardneri*) planted on areas where natural woodlands were cleared from the late 1920s to the 1940s for tannin production (Coates 1993). *Eucalyptus wandoo* and *E. accedens* are susceptible to termites so these woodlands are rich in hollow branches and logs. Wildfires commonly entered the woodland before the 1960s, usually originating from fires used to clear wheatfields. There has been no major fire since that time and the lack of fire appears to be leading to the senescence and collapse of *Gastrolobium* thickets important for a number of mammal species utilized by pythons as prey (Burrows et al. 1987; Friend et al. 1995). Hot fires regenerate *Gastrolobium* thickets which re-establish from soil-stored seed (Burrows et al. 1987).

**Capture of study animals**

Most pythons were captured at night by road-driving, but some were captured by naval police, rangers, other researchers and weed-spraying contractors. Several pythons at Dryandra were captured after they consumed radio-telemetered mammals. Over 650 pythons were captured, marked and released on Garden Island during the study (1995–2000) and 50 of these animals were implanted with transmitters. Adult size was determined for males by the smallest individual (in snout-vent length, SVL) found involved in reproductive activity or based on the presence of turgid testes and convoluted vas deferens of dissected road kill ani-
mals (complete data are available from the authors). Minimum adult female size was calculated on the smallest female (in SVL) found to lay a clutch of eggs. Of 63 pythons captured at Dryandra, 41 were fitted with transmitters.

**Implantation of radio-transmitters**

Four sizes of implantable transmitters (Holohil Systems Ltd, Carp, Canada) were used depending on the size of the python. All transmitters were <5% of the python’s mass. Snakes >100 cm in SVL were fitted with SI-2T transmitters (13 or 21 g with a life of 18–24 months, depending on battery size). Smaller snakes were fitted with either BD-2T or PD-2T transmitters (3 and 5 g, with battery lives of 28 and 35 weeks, respectively). Aerials were encased in 2 mm non-toxic Silastic tubing and the entire unit sealed with 734 flowable sealant (Dow Corning Corporation, Midland, MI, USA).

For surgery, pythons were maintained under isoflurane (‘Forthane’, Abbott Pty. Ltd, Sydney, Australia) anaesthesia while the transmitter and aerial were being inserted into the peritoneum through a mid-lateral incision 10% of the snake’s SVL anterior to the vent (Pearson & Shine 2002). Absorbable sutures were used to close the incision and the python was released 1–3 days later. A few of these pythons later excreted their transmitters through the alimentary tract (Pearson & Shine 2002). When possible, snakes were recaptured close to the end of battery life and the transmitter was removed or replaced. To quantify reproductive frequency, several large females were tracked for >4 years each. In contrast, the smaller transmitters implanted in males limited the duration of tracking, although some were reimplanted and monitored for up to 2 years.

**Radio-telemetry**

During the first 2 years of the study (1995 and 1996), we located most pythons on a weekly basis. In later years, Dryandra pythons were located fortnightly for most of the year but less often during their sedentary overwintering period. Pythons were tracked on foot using a 3-element yagi aerial (Sirtrack Ltd, Havelock North, New Zealand) and receiver (RX3, Biotelemetry Services, Norwood, Australia). Most pythons did not flee from observers, allowing direct observation of microhabitat use. The exact position of pythons in trees was determined by scaling the tree, or by using a directional antennae attached to an extendable pole. Distances and directions between locations were determined by compass and pacing at the start of the study and later with a differential Global Positioning System (GPS) system (Omnistar, Perth, Australia) to determine accurate positions (+–1–3 m) for most locations. Remaining locations were calculated from distances and directions to known points using the program ‘Numtrack’ (M. Choo, Conservation and Land Management, pers. comm. 2003).

**Movement patterns**

To compare how far pythons moved at various times (seasons) of the year, we calculated distances between locations at approximately weekly intervals (defined as 5–8 days since the previous location). These distances represent the minimum distance travelled over that period, because some pythons may have wandered extensively between the two points. We divided the year into four general time periods based on biological criteria, as follows:

1. **Winter** (June, July and August) – Pythons at Dryandra usually retired to tree hollows for winter while those at Garden Island stayed on the ground and sheltered below shrubs. The end of the winter period was defined for Dryandra pythons as the last time they were located in their overwinter tree and for Garden Island pythons, it was arbitrarily defined as the end of August.

2. **Spring** (breeding season) – For Dryandra pythons, the start of the spring period was defined as the first time they were located on the ground away from their overwinter tree and for Garden Island, arbitrarily as September 1. For pythons at both sites, spring was deemed to finish on December 15 each year, around the latest date reproductive activity was ever observed (mating or close male–female proximity was noted from October 13 to December 20 with only one observation after December 15). We distinguished between reproductive and non-reproductive females, but all males were considered reproductive (Pearson et al. 2002a).

3. **Summer** – This season was defined as December 16 to the end of March at both sites. Reproductive females during this period were developing eggs, with oviposition in mid-December to early January and incubation of eggs into March. Males and non-reproductive adult and juvenile females fed extensively during this period.

4. **Autumn** (April, May) – This was a time of cooler days and nights, when reproductive females had left their nests following the hatching of eggs, and when both sexes, but particularly post-incubation females, fed.

Because of the differences in transmitter battery life and the duration of tracking, data were available for only one season for some snakes (n = 5), but up to 16 seasons for other individuals. Table 1 provides a summary of the size of pythons and the duration of tracking. Extensive simulations show that treating successive seasons of data from the same snake as
independent should not invalidate statistical analyses so long as the differences in movement patterns across seasons within a single animal are similar in magnitude to (or larger than) the variation among individual animals within a single season (Leger & Didrichson 1994). Our data fulfil this assumption (see below), and so we treated the mean movement distances for each python in each season of each year that it was radio-tracked as independent for the purposes of our analyses. In this and other analyses, we tested data for normality and variance homogeneity before analysis, and any deviations from these requirements were corrected by appropriate transformation (ln or arcsine).

Home range analysis

We followed Burt's (1943) definition of 'home range' as 'that area traversed by the individual in its normal activities of food gathering, mating and caring for young', but noted the need to include a temporal component when reporting home ranges (White & Garrott 1990). A wide range of home range estimators are available, with the accuracy of calculated home ranges depending on the characteristics of the sampling techniques used, particularly the number of fixes (Jennrich & Turner 1969; Seaman et al. 1999), the interval between fixes (Swihart & Slade 1985a), how the locations were determined (e.g. trapping, triangulation of telemetry fixes; Otis & White 1999) and the home range estimator used (White & Garrott 1990; Garton et al. 2001). In this study, we were interested in determining the seasonal movements of pythons, yearly home ranges, habitat use in terms of broad vegetation/habitat types and microhabitat preferences. Where sample sizes permitted, we compared these factors between sexes, between juvenile and adult pythons and between the two study sites. We calculated yearly home ranges from July 1 to June 30.

We employed three home range estimators (as recommended by Harris et al. 1990; Kernohan et al. 2001) available within Ranges V (Kenward & Hodder 1995). The Minimum convex polygon (MCP; Mohr 1947) has been widely reported in the literature and so was calculated to enable general comparison with other studies on snake home ranges. However, MCP only uses a proportion of location data, is sensitive to outliers and sample size and incorporates large areas that may never be used (White & Garrott 1990; Seaman et al. 1999; Powell 2000). We also employed the harmonic mean estimator (Dixon & Chapman 1980) because it has been commonly used in previous studies on snake home ranges (e.g. McCartney et al. 1988; Secor 1994). The third estimator used was the kernel method (Worton 1987, 1989), recommended by recent reviews (Powell 2000; Kernohan et al. 2001). A fixed band width and least squares cross validation (Worton 1995) were applied to select the smoothing parameter, a method that provides more accurate estimates than the adaptive kernel (Seaman & Powell 1996; Seaman et al. 1999).

The number of fixes required to estimate the home range accurately depends on the type of estimator used, the degree of autocorrelation between fixes and the time period under investigation. Seaman et al. (1999) suggested that robust kernel estimates required 30–50 observations per animal. However, the wide temporal spacing of data collection during our study (predominantly 7–14 days between fixes; see below) meant that fewer fixes were needed than if the time between successive locations was shorter (Swihart & Slade 1985b; Hansteen et al. 1997; Kernohan et al. 2001). We arbitrarily set 20 fixes (equivalent to around 20 weeks telemetry) as the minimum required for the calculation of home range, with the additional proviso that most locations were obtained during the active season. The pythons do not undertake any regular seasonal migrations, so that the seasonal timing of data

| Table 1. Summary of the sexes, body sizes and duration of radio-tracking for south-western carpet pythons used in this study |
|---------------------|----------------|----------------|----------------|----------------|----------------|----------------|
|                     | Number | Mean snout-vent length (cm) | Range of snout-vent lengths (cm) | Mean body mass (g) | Range of snake body mass (g) | Mean days telemetered | Range of days radio-telemetered |
| Dryandra             |        |                            |                                |                  |                            |                      |                                  |
| Adult male           | 21     | 132.7 (30.7)               | 109.6–176.5                    | 639.2 (271.0)    | 248–1244                   | 300.5 (180.0)        | 43–721                          |
| Juvenile male        | 1      | –                           | 94.4                           | –                | 141                        | –                     | 77                              |
| Adult female         | 12     | 191.1 (7.8)                | 178.5–205.7                    | 2255.6 (527.0)   | 1433–3253                  | 610 (190.1)          | 256–867                         |
| Juvenile female      | 7      | 124.7 (35.5)               | 72.2–172.0                     | 565.9 (489.2)    | 94–1401                    | 438.2 (349.0)        | 34–988                          |
| Garden Island        |        |                            |                                |                  |                            |                      |                                  |
| Adult male           | 18     | 112.1 (16.5)               | 94.7–157                       | 380.1 (235.6)    | 189–1011                   | 188.8 (158.6)        | 38–442                          |
| Juvenile male        | 1      | –                           | 86.6                           | –                | 218                        | –                     | 112                             |
| Adult female         | 21     | 213.6 (9.4)                | 195.5–231.8                    | 4173.7 (775.7)   | 2639–5200                  | 673.4 (220.6)        | 74–876                          |
| Juvenile female      | 10     | 132.7 (41.7)               | 80.6–195.0                     | 948.3 (941.9)    | 124–2429                   | 401.4 (241.5)        | 83–756                          |

Standard deviations given in brackets after mean values.
acquisition within the active season is relatively unimportant for calculating home ranges. The use of 20 fixes as a criterion allowed us to retain data on juvenile and small male pythons that could only be fitted with short-term transmitters.

For the calculation of data on distances moved, we used fixes taken 5–8 days apart (see above). For home range calculations, we relaxed this requirement to a minimum time between fixes of 3 days, because pythons are capable of traversing their entire home ranges within a 3-day period.

Habitat and microhabitat type scoring

Whenever we located telemetered pythons, we recorded a range of physical and biotic features of the surrounding habitat as well as data on snake behaviour. Observed habitat selection by pythons was compared with availability of the various vegetation associations. For the Dryandra Woodland study site, the relative proportions of vegetation units (determined from the maps of Coates 1993) were compared with telemetry observations. Areas occupied by the various vegetation types in the Garden Island study area were determined by interrogation of available Department of Defence digital vegetation mapping, based on the units of McArthur and Bartle (1981).

The type of microhabitat occupied was reduced to four categories for data analysis: (i) in tree hollows; (ii) in or under shrubs, leaf litter, or fallen branches; (iii) in logs; or (iv) underground.

RESULTS

General activity patterns

Telemetered pythons at the two sites displayed similar general activity patterns, with some variation between sites apparently because of climatic differences (Fig. 3). Adult males at both sites were active and moving in search of females in spring (October to mid-December) and continued to move around and feed during summer. In winter, Dryandra adult male and female pythons typically retreated up trees to shelter in hollow limbs, apparently ceased to feed and were occasionally observed basking near their overwinter refuge (see Discussion below). Dryandra experiences minimum temperatures close to freezing throughout winter and pythons were able to escape severe conditions at ground level by utilizing elevated refuges where they could bask when conditions were suitable.

In contrast, Garden Island adult males continued to move about on the ground and feed during winter. Adult female pythons at both sites moved extensively in spring and summer, although reproductive individuals (<30% of the group) were more sedentary, and eventually stationary, during the incubation of their eggs. Although adult females at Garden Island did not retreat to overwinter refuges like their Dryandra counterparts, they reduced their movements and most lay coiled under shrubs or under fallen timber, occasionally emerging to bask on sunny days. They were not observed to feed at this time.
Movement patterns

We calculated mean weekly movements for each snake in each season, and analysed the resulting data using a three-factor ANOVA. The factors were: (i) sex/age class (juveniles, adult females, adult males); (ii) season (spring, summer, autumn, winter); and (iii) site (Dryandra, Garden Island). The analysis did not identify any significant three-way interaction between these factors \(F_{6,201} = 0.42, P = 0.86\), but did generate a significant two-way interaction between sex/age class and season \(F_{6,201} = 2.28, P = 0.037\), as well as highly significant main effects of season \(F_{6,201} = 11.63, P = 0.0001\) and sex/age class \(F_{2,201} = 5.33, P = 0.006\). There was no significant difference between the two study sites in terms of mean distances moved per week \(F_{1,201} = 0.19, P = 0.66\). Because of the significant interaction term, we then tested seasons separately to look at whether weekly movements by the sex/age classes differed in any season. There was a marginally significant difference between sex/age classes in winter \(F_{2,30} = 3.32, P = 0.05\), with males moving further than adult or juvenile females, and a strong difference in summer \(F_{2,66} = 5.67, P = 0.005\) with juvenile females moving less than did the other groups.

Mean distances moved were remarkably similar at the two study sites, despite their considerable divergence in climate and vegetation cover (Fig. 3). Unsurprisingly, snakes moved less in winter than in the warmer seasons. Mean weekly movements of adult male snakes and reproductive females were similar in spring (the mating season), but reproductive females were highly sedentary in summer (by this time, they were incubating their eggs; see Fig. 3). The apparent similarity in mean movements for adult males during winter in the two sites (Fig. 3a) is deceptive. Males at Garden Island continued to move, albeit over short distances, throughout winter. In contrast, males at Dryandra were inactive for many weeks, but then began making large moves soon after they emerged from winter inactivity. Inclusion of a few such moves in the ‘winter’ category thus suggests a (misleading) similarity in movement patterns between males in the two sites.

Site fidelity

Telemetered pythons were sometimes observed to return to sites where they had been located previously. At Garden Island, such observations were relatively rare (33 observed from a total sample of 2672 locations; or 1.2%), and appeared to have no seasonal pattern. Only two pythons (one male, one juvenile female) were observed to return to the same site on more than two occasions. In comparison, when we excluded overwinter trees from the analysis (because Garden Island pythons did not utilize them, but see below), Dryandra pythons still revisited previously occupied sites more often (154 of 1743 records; or 8.8%), but not significantly so \((z = 1.14, P = 0.25)\). Most revisited sites were logs (51%) and hollows in trees (37%), with all other microhabitats (including burrows, under rocks and below shrubs) comprising the remaining 12%. There was considerable individual variation, with one subadult female reusing a few hollows on 15 occasions within her small home range of only 3.73 ha.

The timing of revisitation of previously occupied sites may reveal seasonal movements. Dryandra telemetry data were scanned to identify and extract non-overwinter refuges that were occupied on more than two occasions. There were seven instances (one adult male, two juvenile females and four adult females) of repeated visitation to logs or tree hollows during the active months. Some pythons did revisit certain refuges over several years and often these visits occurred at similar times each year, particularly in spring and early summer.

Overwinter refuge fidelity

At both sites, adult males and juvenile and adult females reduced their movements during winter. The retreat to overwinter refuges by Dryandra pythons was the most striking difference in habitat use and seasonal activity patterns between the two studied populations. Most of the overwinter refuges used by Dryandra pythons were hollows in trees, with many pythons returning to the same hollow in consecutive years (see Table 2). Sample sizes were too small to detect any differences in site fidelity among the three sex/age groupings of pythons, but all used overwinter refuges. The duration of time spent in the overwinter refuge differed between sex/age groups at Dryandra. Minimum overwinter refuge durations averaged briefer for adult males than for adult or juvenile females (Table 2; one-factor ANOVA, \(F_{2,37} = 3.81, P = 0.03\), but Tukey-Kramer post hoc pairwise comparisons found no significant difference between any pair of means).

At Garden Island, adult females reduced their movements markedly during winter. Several sheltered under the same shrubs for up to 67 days, although most continued to move small distances to new clumps of shrubs throughout winter. No radio-tracked adult female python on Garden Island returned to the same area in consecutive winters. Males continued to move (albeit smaller distances) in winter and did not show any site fidelity.

Home ranges

Mean home ranges as estimated by three methods were broadly similar, and showed similar patterns with
respect to the effects of location and sex/age class on home range size (Fig. 4). Minimum convex polygon (100%) estimates averaged 17.6 ha, harmonic mean (95%) estimates averaged 19.3 ha, and kernel (95%) methods averaged 19.9 ha. All three were highly correlated with each other \( (r > 0.68, P < 0.0001) \). Two-factor ANOVA with location and sex/age class as factors revealed a significant interaction term \( (F_{2,87} = 5.81, P < 0.005) \); for harmonic mean, \( F_{2,87} = 5.45, P < 0.006) \); that is, the effect of sex/age class on home range size differed between the two study areas. This interaction term reflects the fact that adult male pythons had larger home ranges than did females at Dryandra, but smaller home ranges than females on Garden Island (Fig. 4). To further investigate these patterns, we conducted one-factor ANOVAs (with sex/age class as the factor) separately for data from each location. In each case, home ranges did not differ significantly among adult males, adult females and juveniles at Garden Island, but did so at Dryandra.

Table 2. Overwinter refuge fidelity of carpet pythons at Dryandra Woodland, including minimum and possible maximum duration of use, type of refuge and reuse of refuges between years

<table>
<thead>
<tr>
<th></th>
<th>Number of snakes</th>
<th>Number of seasons</th>
<th>Minimum overwinter duration (days)</th>
<th>Maximum overwinter duration (days)</th>
<th>Number of winters in tree hollows (no. of snakes)</th>
<th>Number of winters in logs (no. of snakes)</th>
<th>Proportion of records with site fidelity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult male</td>
<td>8</td>
<td>13</td>
<td>86.3 (33.0)</td>
<td>100.4 (32.1)</td>
<td>11 (7)</td>
<td>1 (1)</td>
<td>2 of 5</td>
</tr>
<tr>
<td>Adult female</td>
<td>10</td>
<td>18</td>
<td>121.6 (36.8)</td>
<td>130.63 (37.3)</td>
<td>13 (8)</td>
<td>5 (4)</td>
<td>4 of 4</td>
</tr>
<tr>
<td>Juvenile female</td>
<td>4</td>
<td>9</td>
<td>130.5 (29.6)</td>
<td>140.2 (29.6)</td>
<td>8 (4)</td>
<td>0 (0)</td>
<td>no data</td>
</tr>
</tbody>
</table>

Mean values for overwinter duration based on means per snake (i.e. each snake provided only a single mean value); standard deviation is given in parentheses. For location of overwinter sites, data are given on total number of seasonal records, then (in parentheses) the number of individual snakes on which those records were based.

The final column shows the proportions of repeat records (snakes monitored in more than 1 year) for which we could reliably judge whether or not the animal used the same overwinter site.

Patterns in macrohabitat use

Because habitat availability at the two study sites differed profoundly, so did habitat usage by the pythons. Dryandra snakes were located primarily in open *E. wandoo* woodland (65.6% of 1504 records) and *E. accedens* woodland (15.2%); with the remainder in heath, *Al. huveliana/E. wandoo* communities or in disturbed habitats such as mallet plantation and in huts. In contrast, pythons on Garden Island were found mainly in vegetation associations dominated by *A. rostellifera* (shrublands and low forest: 68% of 2451 locations) or *C. preissii/Me. lanceolata* forest (23%).

Assuming that pythons had similar access to all vegetation types (a reasonable assumption given the fine-scale interdigitating vegetation pattern of the study area), pythons showed a high level of habitat selection (analysis of contingency table listing the five major habitat types: *E. wandoo*, *E. accedens*, *Al. huveliana*/*E. wandoo* woodlands, heath and mallet plantations; \( \chi^2 = 359.21, P < 0.001 \)). *Eucalyptus wandoo* woodland was a preferred habitat type (66% of python locations vs. availability of 35%), whereas other major habitats were used in approximate proportion to their availability (*E. accedens* woodland 15% vs. 19%; and *Al. huveliana/E. wandoo* woodland 10% vs. 6%). However, mallet plantations were avoided (8% usage vs. 32% availability; test of proportions, \( z = 15.11, P < 0.001 \)). None of the snakes we tracked had home ranges completely within the mallet plantations; all made extensive use of neighbouring native woodlands.

On Garden Island, python usage of the four major habitats (*A. rostellifera*-dominated shrubland or woodland, *C. preissii/Me. lanceolata* forest, heath and littoral communities) was significantly different to availability \( (\chi^2 = 926.92, P < 0.001) \). Pythons showed a preference for communities dominated by *A. rostellifera* (68% usage vs. 41% availability) and heath (8.3% vs. 4%), but *C. preissii/Me. lanceolata* forest (22.7% usage vs. 41% availability) and littoral communities (0.1% vs. 13.5%) were used less than expected from their availability.

Within each of the study sites, our analyses did not detect any differences between sex/age groups in macrohabitat use. At Garden Island, one-factor ANOVA with sex/age class as the factor revealed no significant
Patterns in microhabitat use

To facilitate comparisons between snakes at our two study sites, we classified microhabitats into four broad categories: (i) in logs; (ii) in or under shrubs or fallen branches; (iii) in tree hollows; or (iv) underground. We analysed these data (mean proportions in each category for each snake) using two-factor ANOVA, with factors being location and sex/age class (see Fig. 5 for graphical presentation). The proportion of observations of snakes located in logs was higher at Dryandra than Garden Island (means of 46% vs. 4%; $F_{1,66} = 73.67, P < 0.0001$), but there was no difference among sex/age classes in this respect ($F_{2,66} = 0.66, P = 0.52$), nor any significant interaction between the two factors ($F_{2,66} = 2.17, P = 0.12$). Exactly the reverse pattern was evident for the proportion of observations of snakes located in or under shrubs, with means of 12% at Dryandra versus 91% at Garden Island ($F_{1,66} = 841.0, P < 0.0001$) and again, no sex/age class difference ($F_{2,66} = 1.28, P = 0.28$) or significant interaction ($F_{2,66} = 0.32, P = 0.73$). Usage of tree hollows showed a more complex pattern, differing not only between sites ($F_{1,66} = 59.28, P < 0.0001$), but also between sex/age classes ($F_{2,66} = 3.30, P < 0.045$; see Fig. 5c). The interaction between the two factors was also close to statistical significance ($F_{2,66} = 3.07, P = 0.05$). Post hoc Tukey-Kramer tests showed that juvenile snakes used tree hollows more than did adult females ($P < 0.05$).

The final microhabitat category involved snakes that were underground when located. The proportion of observations of snakes in holes or burrows did not differ between the two study sites (4% in both; $F_{1,66} = 0.01, P = 0.92$), but was higher in adult females than in other sex/age classes (Fig. 5d; $F_{2,66} = 3.76, P < 0.03$; but Tukey-Kramer post hoc tests non-significant). Additional data on microhabitat variables at Dryandra allowed us to examine effects of snake size and sex on log use. The three sex/age classes did not differ in the sizes of logs that they used (log diameter, $F_{2,23} = 2.58, P = 0.10$; log length, $F_{2,23} = 0.34, P = 0.72$).
DISCUSSION

Our study provides the first detailed data on movements and habitat use for carpet pythons in south-western Australia, and is the largest data set of its kind for a radio-telemetric study on any Australian snake species. The unusually large number of snakes radio-tracked, and the use of two study areas that differed markedly in climate and habitat types, provided an opportunity to tease apart the influences of environmental factors versus attributes of the snake (sex/age class) on variables such as movement patterns and home range sizes. Although our study revealed many such effects, perhaps the most striking aspect was the broad similarity in overall patterns. Snakes at the two sites perforce used very different habitats, but they did so in relatively similar ways. Thus, a snake’s sex and body size influenced its behaviour only within relatively narrow limits (e.g. Fig. 3).

Telemetered *M. s. imbricata* typically moved approximately 100 m per week during the active season, similar to distances reported for adults in the eastern subspecies *Morelia spilota medowelli* in a densely forested area (Shine & Fitzgerald 1996). Our study animals also remained relatively sedentary during winter, as has been reported for eastern subspecies of carpet pythons (Slip & Shine 1988a; Shine & Fitzgerald 1996). The cooler night and day time temperatures at Dryandra Woodland presumably resulted in all python sex/age classes retreating to overwinter shelters for on average over 3 months, as well as the apparent cessation of feeding. Garden Island male and juvenile pythons continued to move and feed during winter and consequently might be expected to be able to maintain more rapid growth rates than their inland conspecifics. The most pronounced feature of movement patterns was the differences between non-reproductive and reproductive adult females, the latter remaining sedentary throughout the period when they were incubating eggs (Fig. 3). The same phenomenon occurs in all egg-brooding pythons (Shine 1988). Thus, overall patterns of movement for females were influenced more strongly by differences in reproductive state within a single population, than by major differences in habitat type across our two study areas, or even thousands of kilometres from south-western to eastern Australia (Slip & Shine 1988b).

One apparent paradox when comparing the data for Garden Island versus Dryandra Woodland animals was that home ranges of adult male pythons were much larger than those of females at Dryandra but not Garden Island (Fig. 4), despite the fact that mean

Fig. 5. Microhabitat use (a) in logs, (b) in shrubs, (c) in tree hollows and (d) underground by radio-tracked carpet pythons at two study locations (○) Dryandra and (●) Garden Island in south-western Australia. See text for further explanation and statistical analysis.
weekly distances moved were similar in both sexes in both areas (Fig. 3). This difference reflects the tendency for adult male pythons at Dryandra to undertake long distance movements to locate a female, but then to remain with her for a long period (up to a few weeks). In contrast, adult male pythons at Garden Island typically moved shorter distances, but did not stay with each female for long, and instead, visited several females during the mating season (Pearson et al. 2002a). The end result was a broad similarity in mean weekly displacements for adult males at the two sites (128.62 m at Dryandra vs. 107.79 m at Garden Island), but this similarity masked a substantial difference in the distances and frequency of mate-searching activities. The likely reason for this difference is the much higher density of snakes (including reproductive females) at Garden Island than at Dryandra (note that we captured more than 10 times as many snakes at the former site as the latter). Thus, a mate-searching male at Garden Island would be likely to locate a female without having to undertake a major search. Given this high density, males may also be more likely to leave a female after mating because they are very likely soon to encounter another one. The same hypothesis has been used to explain divergence in male mate-searching tactics between populations of eastern Australian carpet pythons (Shine & Fitzgerald 1995).

Home ranges of our radio-tracked snakes were broadly similar between the two study areas (means = 17.3 and 17.7 ha), and similar to previous MCP estimates from studies on eastern Australian carpet pythons (mean home range of 17 ha for female *M. s. spilota* (Slip & Shine 1988a) and 22 ha for *M. s. mcdowelli* (Shine & Fitzgerald 1996)). However, male *M. s. spilota* travelled over larger areas than females (mean = 43 ha; Slip & Shine 1988a). In our study, exclusive territories were not apparent, with the home ranges of male, female and juvenile pythons showing extensive overlap (as was reported for *M. s. spilota*, Slip & Shine 1988a). Given the strong geographical variation both in sexual size dimorphism and in mating systems within this species (Pearson et al. 2002a), such differences in spatial ecology are not surprising.

Our estimates of home range size in south-western carpet pythons fit within the general range of those reported for other ambush predators in the recent literature (where radio-telemetry has been used; for a review of reported home ranges up to 1987, see McCartney et al. 1988). Many vipers tend to have very small home ranges (MCP 0.19–8.0 ha), but others such as *Crotalus horridus* have home ranges as large as 207.4 ha, although this figure includes migratory movements to hibernacula (McCartney et al. 1988; Beck 1995). Our data for carpet pythons show some similarity to patterns described by Secor (1994) for sidewinders, *Crotalus cerastes*. Although males moved greater distances than females in breeding periods, mean home ranges of both sexes and subadults were similar (means 22.9, 19.0 and 22.3 ha, respectively).

It is interesting to note that reported mean home range sizes of snakes are all comparatively small (typically <1–25 ha, although there is considerable individual variation), and that of ambush predators such as vipers and carpet pythons are within the same range as active foragers amongst the colubrids (Madsen 1984; McCartney et al. 1988; Weatherhead & Hoysak 1989) and elapids (Shine 1987).

Macrohabitat use by the pythons was highly flexible, responding to the great disparity in available habitat types in our two study areas. Pythons at Garden Island were almost always terrestrial, generally sheltering beneath prickle lily shrubs that cover most of the island. In contrast, pythons at Dryandra were usually found in hollows, either in standing trees or in logs on the ground. The proportion of arboreal records at the two sites thus spans the diversity reported in previous studies from widely separated localities (16% for *M. s. spilota*, 45% in *M. s. mcdowelli*), and reveals a high degree of flexibility in habitat use by these large snakes. The common factor is concealment. Pythons were rarely found in exposed situations, and instead sheltered within whatever type of retreat was available. This result fits well with previous reports of carpet pythons utilizing a broad range of habitat types, including the highly modified habitats of suburbia (e.g. Fearn et al. 2001).

Despite this apparent flexibility, carpet pythons at Dryandra avoided mallet plantations. The small diameter of mallet trees, their lack of hollows, logging practices that remove them at small diameters (the timber is used primarily for tool handles), and the suppression of undergrowth in dense plantations restricts the number of shelter and potential ambush sites available to pythons. When we did locate pythons in mallet plantations, they were almost invariably in logs (76 of 103 locations) or lying under bushes in close proximity to logs. Of particular importance is the origin of these logs. We never found pythons in mallet logs (they are rarely of sufficient diameter) and all the logs occupied by pythons were from *E. wandoo* or *E. accedens* trees cut down during the establishment of the plantation or in subsequent thinning. Most of these logs are now extremely old (some >70 years) and many are in advanced states of decay. This observation suggests that mallet plantations will become increasingly unsuitable for pythons with the loss of logs and no possibility of replacement. The loss of logs in mallet plantations is also likely to impact heavily on various mammals (and hence, python prey) in Dryandra Woodland including such species as the threatened numbat (*Myrmecobius fasciatus*). While the management of these plantations is primarily for timber production, their value to pythons would be increased by...
retaining the small patches of native vegetation that have regrown in some areas, avoiding the use of fire (which will destroy existing logs) and retaining the fallen canopies (branches and leaves) of cut mallet trees as these provide some shelter for pythons.

Much of the behavioural diversity that we observed is readily interpretable in light of the characteristics of the snakes and the study areas. For example, the reasons why juvenile snakes were more arboreal than adults at Dryandra (Fig. 5) probably involves the availability of suitably sized prey (juveniles take birds and small arboreal mammals whereas adults concentrate on larger terrestrial mammals: Pearson et al. 2002b) and refuges (adult female pythons are too large to fit into many tree hollows). The potential role of predators (primarily the introduced fox, Vulpes vulpes and feral cats) in determining habitat use by pythons remains unresolved and may warrant further study.

The general picture that emerges from our study is of a species that displays extreme ecological flexibility. It uses whatever habitats are available, at both macro and micro scales. Although the massive disparity in body sizes (lengths) between hatching (25 cm) and adult (>200 cm) snakes inevitably requires shifts in traits such as retreat site selection, ambush location and prey types (Mushinsky 1987), the same general patterns of spatial ecology are seen in individuals over a substantial range of body sizes and habitat types. The same is true for comparisons across our two very dissimilar study areas, as well as for wider comparisons that encompass previously studied populations of M. spilota in eastern Australia (Slip & Shine 1988a; Shine & Fitzgerald 1996).

The ability of carpet pythons to utilize such a wide range of habitat types and prey taxa suggests that these snakes would fare well in anthropogenically disturbed habitats, and indeed this is the case in coastal areas of eastern Australia (Shine 1994). Paradoxically, however, this flexible generalist has disappeared from much of its range in south-western Australia (Smith 1981; Pearson 1993) as well as in semiarid to arid parts of its range in eastern Australia (Shine 1994). Our study suggests that one of the critical resources needed for populations of this large predator is the availability of suitable hiding places in which the snakes can shelter, from which they can ambush prey, and in which they can brood their eggs. Well-watered coastal habitats with uneven topography typically provide such places (often in densely forested gullies within disturbed landscapes), whereas agricultural development often removes extensive areas of habitat in semiarid areas with little topographic relief, as in the Western Australian Wheatbelt, where only 7% of the native vegetation remains (Saunders 1979). Although land-clearing for agriculture has undoubtedly played a major role in the destruction of python habitat, wildfires also may be significant. There is a substantial complexity to the effects of fire, however. Because of the great spatial diversity in the types of retreat sites and ambush sites used by carpet pythons, fires would substantially reduce the availability of critical ground cover in some areas but not in others. Gastrolobium thickets are important shelter and foraging sites for small marsupials such as Woylies (Bettonia penicillata), an important prey item for adult female pythons at Dryandra. If unburnt, these thickets senesce and collapse. Fire stimulates the germination of soil-stored seed and the reinvigoration of thickets (Friend 1994; P. Christensen, pers. comm. 2003). The timescale over which the cover items regenerate would differ considerably depending on the habitat involved (e.g. logs vs. shrubs), the area and its climate. The seasonal timing (and thus, intensity) of fire may also be significant. Relatively ‘cool’ fires used for prescribed fuel reduction at Dryandra Woodland may destroy logs (and thus, remove the pythons’ primary places of concealment). On the other hand, ‘hot’ fires while burning many logs, also kill and fell standing trees thus resulting in a new generation of logs. ‘Hot’ fires may also remove many of the hollow limbs used as overwintering sites (often, year after year) by snakes. Friend (1994) reported that in an October experimental burn at Dryandra, 25% of logs were destroyed, with only 3% of these replaced by fallen trees. In contrast, a hot March fire led to 50% of logs being destroyed, with half of these replaced by trees falling during the fire. After 2 years, further logs had fallen so log abundance was similar to pre-fire conditions (Friend 1994). These complexities suggest that we need a much clearer understanding of the processes that determine the abundance of potential shelter sites (especially, logs) in semiarid areas. The keys to maintaining populations of carpet pythons may be twofold: sufficient mammals of the appropriate size to be prey for adult snakes (Pearson et al. 2002b), and sufficient protected refuges (logs and shrub thickets) at ground level for effective shelter and ambush predation. 

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