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A FIELD STUDY OF SPATIAL ECOLOGY AND MOVEMENTS OF A THREATENED SNAKE SPECIES, *Hoplocephalus bungaroides*

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Abstract

Information on movement patterns, home range sizes and site fidelity of endangered fauna may provide a basis for conservation planning (size and location of reserves; vulnerability to habitat fragmentation; feasibility of natural recolonisation of 'restored' habitats, etc.). To obtain such information, we surgically implanted miniature radio transmitters in 25 individual broad-headed snakes Hoplocephalus bungaroides, *a small (mean snout–vent length = 57 cm, mean mass = 51 g) viviparous elapid snake reliant upon sandstone outcrops in southeastern Australia. We also carried out a mark–recapture study of this threatened species. Our telemetered snakes spent long periods of time sequestered inside retreat-sites (rocks, crevices, tree hollows) and thus were active on only 21% of days. Gravid females had small home ranges (mean size = 0·05 ha, convex polygon method) and remained near cliffs during summer, whereas most males and non-gravid females moved long distances (up to 780 m) away from cliff tops during summer and had larger home ranges (mean size = 3·3 ha). Movements by the snakes were more frequent and extensive when they were in the woodland (mean interval between successive moves = 2·9 days; mean displacement per move = 159 m) than when they were in the rock outcrops (means = 6·3 days, 37 m). Home ranges were larger in summer than in spring, and were larger in 1994–95 than in other years. Home ranges of males showed little spatial or temporal overlap in spring, but females were found within the areas used by males. During summer there was little temporal or spatial overlap of home ranges of adults, which suggests that snakes may actively avoid conspecifics of either sex while foraging in the forest. Many adult snakes showed strong site fidelity, frequently returning to the same rocks where they were initially captured. Dispersal of juvenile snakes from their birth sites was relatively limited (maximum recorded distance = 375 m after 6 months).*

Our results have significant implications for conservation of this threatened taxon. The fixed home ranges and high site fidelity of adults coupled with the low dispersal rates of juvenile broad-headed snakes mitigate against successful natural recolonisation of rehabilitated habitats. Thus, habitat restoration may need to be combined with release of captive-bred progeny, or field-caught neonates. The exclusive home ranges of adult snakes suggest that social interactions (avoidance of conspecifics) may limit population densities, and hence that (i) removal of some neonates may not reduce future densities of adults, and (ii) habitat destruction is likely to be a more serious long-term threat than removal or killing of individual snakes. The large home ranges, and frequent and extensive movements, of snakes in woodland indicate that conservation reserves must incorporate large forest areas adjacent to sandstone outcrops. © *1997 Elsevier Science Ltd*

INTRODUCTION

Human-induced disturbances have caused many terrestrial habitats to become increasingly fragmented (e.g. Diamond *et al.*, 1987; Saunders *et al.*, 1991; Hobbs *et al.*, 1992; Askins, 1993). In Australia, extensive clearing of native vegetation over the last two centuries has coincided with the disappearance of at least eight species of mammals (Morton & Baynes, 1985; Caughley & Gunn, 1995) and a decline in the diversity and abundance of birds in some areas (Hobbs *et al.*, 1992). Not surprisingly, habitat fragmentation is seen as one of the greatest threats to biological diversity (e.g. Wilcove *et al.*, 1986). However, the degree to which individual species will be affected by habitat fragmentation will depend on the scale of fragmentation and the biology of the species in question (Wiens, 1989, 1994; Doak *et al.*,

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1992). Clearly, how individuals move between patches and how they respond to different habitats will ultimately determine how populations are affected by fragmentation (Fahrig & Paloheimo, 1988; Opdam, 1990; Hanski, 1991; Wiens *et al.*, 1993; Wiens, 1994). Hence, few generalisations can be made about the effects of habitat fragmentation on individual species, although we might expect species with relatively high mobility and generalised habitat requirements to be less vulnerable to habitat disturbance than sedentary species with specialised habitat requirements (e.g. Warren, 1987; Bierregaard *et al.*, 1992; Thomas *et al.*, 1992; Thomas, 1994; Wiens, 1994).

Despite its importance, detailed information on dispersal and movement patterns is lacking for many threatened species (e.g. Opdam, 1990; Harrison, 1991). This situation is especially true for snakes, which are notoriously difficult to observe (Gibbons & Semlitsch, 1987). Also, studies of snakes have used a wide range of different methods and techniques, so that in most cases few generalisations can be made about their movement patterns (Gregory *et al.*, 1987; Macartney *et al.*, 1988). Hence, although many snake species are currently threatened by man-made habitat changes (Mittermeier *et al.*, 1992; Dodd, 1993), it is virtually impossible to predict which species will persist in habitats altered by man.

In Australia, the broad-headed snake *Hoplocephalus bungaroides* has shown a drastic decline in numbers since European settlement (Krefft, 1869; Hersey, 1980; Shine & Fitzgerald, 1989). This small, brightly coloured, nocturnal viviparous snake was once found in inner suburbs of Sydney, but has not been recorded in the Sydney metropolitan area for over 30 years. The broad-headed snake's reliance on sandstone rocks for shelter sites during the cooler months has made it particularly vulnerable to habitat disturbance, especially the collection of bush-rock for Sydney gardens (Krefft, 1869; Hersey, 1980; Shine & Fitzgerald, 1989; Webb & Shine, 1997). Today the species is confined to a few state forests and national parks within a 200 km radius of Sydney, where populations are very patchy even in apparently suitable habitats (Shine *et al.*, 1995).

The persistence of these remaining populations will depend on many factors, including the ability of individuals to disperse between patches of suitable habitat. Recently we documented seasonal shifts in habitat use by telemetered broad-headed snakes, whereby males and non-gravid females moved away from sandstone cliffs and used hollows of large trees as retreat-sites during summer (Webb & Shine, 1997). Thus, the distance of suitable summer habitat (old-growth forest) from rocky outcrops, and the ability of broad-headed snakes to move to this summer habitat, may well influence overall patterns of persistence shown by this species. The degree of site fidelity of the snakes may also influence their susceptibility to human-induced disturbances such as bush-rock removal. For example, birds that display strong site fidelity may be more vulnerable

to habitat destruction, because they delay migration to new habitat patches until long after conditions in the 'old' patch become unfavourable (e.g. Wiens *et al.*, 1986; Verboom *et al.*, 1991; Belettsky & Orians, 1994; Wiens, 1994). Another factor that might influence the snakes' tolerance to various kinds of human-induced disturbance is the role of social factors in space use. If individuals occupy exclusive 'territories' rather than broadly overlapping home ranges, population densities may be limited by social interactions rather than the availability of resources such as shelter-sites or prey.

We used a combination of techniques (radiotelemetry, harmonic radar, mark–release–recapture) to study the movements and dispersal of free-ranging broad-headed snakes in a study area in south eastern New South Wales. Our work was designed to identify aspects of space use by the snakes that might influence effective conservation planning. Hence, we were interested in issues that might affect the realistic size of reserves, and the effectiveness of alternative management techniques. For example, how often and how far do the snakes move? Do these parameters vary in time and between alternative habitat types? Do the snakes have discrete home ranges? If so, how large are they? Are specific shelter-sites used repeatedly by the same snakes? Do social interactions influence patterns of space use? How far and how quickly do neonates disperse after they are born? Information on these basic questions is unavailable for broad-headed snakes, as for most reptiles, and may provide a rational basis for conservation planning.

MATERIALS AND METHODS

Study sites

Our study sites were located in Morton National Park, approximately 160 km south of Sydney. Mean daily maximum air temperatures range from 25·9°C in January (mid summer) to 15·8°C in July (mid winter); mean daily minima for these months are 15·9 and 6·0°C, respectively (Bureau of Meteorology, 1988). Four study sites were used for a mark-and-recapture study, but we only radio-tracked snakes at three sites (each approximately 3 km apart) on the western side of a sandstone plateau of 400 m elevation. The plateau is covered by open woodland forest except for the exposed western cliff edge (10–30 m wide) where small rocks have weathered from the underlying sandstone. During winter and spring, broad-headed snakes are found under these rocks or in crevices along the sandstone cliffs. These cliffs are 20–30 m high and are deeply dissected by numerous horizontal crevices. The vegetation of the general area has been described elsewhere (Black, 1988); at our sites, the open woodland was dominated by turpentines *Syncarpia glomulifera*, red bloodwoods *Eucalyptus gummifera*, and blue-leaf stringy barks *E. agglomerata*.

Table 1. Frequency of movement between shelter-sites by free-ranging broad-headed snakes

	Moves per tracking day			Moves per day		
	1992–93	1993–94	1994–95	1992–93	1993–94	1994–95
Mean	0·31	0·33	0·48	0·18	0·17	0·27
SD	0·10	0·09	0·25	0·12	0·08	0·13
Range	0·15–0·53	0·06–0·35	0·12–1·00	0·07–0·53	0·19–0·5	0·07–0·50
N	11	10	10	11	10	10

N = number of individual snakes radio-tracked each year. 'Moves per tracking day' = number of days on which the snake moved between retreat sites, divided by the number of days for which it was tracked radiotelemetrically. 'Moves per day' = number of days on which the snake moved divided by the total number of days for which we could recognise movement (= days radio-tracked + additional days that snake was inactive between field trips). See text for details.

Transmitters and surgical techniques

Transmitters and surgical techniques are described elsewhere (see Webb & Shine, 1997). Thirty-three broad-headed snakes were tracked over 3 years from September 1992 to February 1995. We tracked 11 snakes each year, usually from spring until late summer when the transmitters stopped. The timing of commencement of radio-tracking varied slightly each year, depending on when snakes were captured. Full details of dates of initial capture and release are presented elsewhere (see Table 1: Webb & Shine, 1997). During the final year, four transmitters failed much earlier than usual, so we have a smaller data set for this field season. Of 33 snakes radio-tracked, one snake was tracked in 3 successive years, and six snakes were tracked in 2 years (Table 1: Webb & Shine, 1997). Hence, we have data for 25 individual broad-headed snakes (eight females, mean SVL = 58·7 cm; 17 males, mean SVL = 56·1 cm).

We released the radio-tagged snakes at the point of capture, and commenced radio-tracking them immediately after release. Snakes were located daily during each field trip and usually there were two field trips (each 5–10 days duration) per month. Initial monitoring showed that telemetered snakes rarely moved from their diurnal retreat-sites during daylight hours (movements between retreat-sites occurred around dusk) so there was little point in carrying out multiple locations within a single day. Once this was established, we located each snake's retreat-site daily and flagged it with fluorescent tape.

Harmonic radar

A relatively new tracking device, the harmonic radar, was used to track juvenile snakes. A description of the detection system, range and manufacturer is given elsewhere (Mascanzoni & Wallin, 1986). We used small diodes (Toshiba 1SS-242, size 10×2×2 mm, mass 0·02 g) with wire antennae (0·125 mm enamelled copper winding wire) soldered to each end. Preliminary tests showed that maximum range was attained with one antenna twice the length of the other. We used 6 cm long antennae (i.e. 2+4 cm) for very small snakes (< 35 cm snout–vent length) and 12 cm long antennae for larger snakes. In the field, maximum detection range

of these units was 4 and 10 m, respectively. Diodes with antennae attached were placed inside flexible medical grade silicon tubes (Dow Corning Cat. No. 602-175) and the ends were sealed with 100% silicon. Final weights of sealed units were 0·25 and 0·41 g; hence small units were < 5% of the mass of the smallest juvenile snakes. Surgical procedures used for implanting diodes were the same as that described for transmitter implantation (see Webb & Shine, 1997), except that incisions were much smaller, usually only 4 mm long.

Mark–recapture study

Additional information on dispersal of juvenile snakes was obtained by turning all the rocks at our study sites at least once per month. For each snake we recorded sex, reproductive status, snout–vent length (henceforth SVL) and mass. Small (12×2 mm) passive integrated transponder (PIT) tags were injected under the skin of all individuals to allow subsequent identification. These PIT tags do not appear to affect growth rates or locomotor performance of neonatal snakes (Keck, 1994). One advantage of using PIT tags (as opposed to other marking techniques) was that known 'snake' rocks could be scanned with a hand-held microchip reader to see whether marked snakes were using the rocks. This minimised disturbance to the snakes; we found that snakes usually moved to new rocks after rocks were lifted. All rocks were given a unique number to assess whether they were used by more than one snake, and to see whether snakes showed site fidelity.

Mapping locations

Detailed large-scale maps of all study sites were drawn from aerial photographs. Smaller-scale maps of two sites were made by hand (using a compass and tape measure) and all landmarks and 'snake rocks' were recorded. In spring, we were usually able to plot locations of snakes directly onto these maps. At other times of year, the distance and bearing of snake retreat-sites from known landmarks (such as roads, creeks, swamps, and isolated rock outcrops) were recorded. For displacements of < 150 m, we measured the distance and bearing between successive retreat-sites with a 30 m tape and compass. When snakes moved very long distances,

to physically inaccessible areas, we estimated their positions by triangulation from two landmarks no less than 200 m apart. Locations of all snakes were then plotted directly onto maps. Sizes of home ranges of snakes were estimated using the convex polygon method (Jennrich & Turner, 1969).

Movements

Displacements of snakes were recorded as the straight-line distance between successive retreat-sites. These straight-line distances undoubtedly underestimate the actual distance moved by snakes (e.g. Secor, 1994; Beck, 1995), and we estimated the magnitude of this underestimation by following the exact movements of three different snakes as they moved at night. Snakes were followed as closely as possible (using dim red light) and small pieces of fluorescent marking tape (with time recorded on them) were placed onto vegetation every few minutes. Next morning we accurately mapped the movement of the snake using a tape measure and compass. For each snake we calculated the 'meander ratio' (Secor, 1994) by dividing the total distance moved by the straight-line distance between locations. Total distances moved within a year, and mean distances moved between successive retreat-sites, were calculated for each snake. We used straight-line distances for these analyses, rather than correcting with a 'meander ratio'.

Activity

Two indices of snake activity were calculated: (1) moves per tracking day: the number of moves (i.e. displacements > 1 m) divided by the number of radio-tracking days; and (2) moves per day: the number of moves divided by the total number of days for which we had information on that animal's location (= number of radio-tracking days + additional days that snakes were known to be inactive). Activity index (2) was determined in cases where we recorded body temperatures continuously with an automated system (see Rummery *et al.*, 1995). Movements of snakes from retreat-sites were usually coupled with a sudden change in signal intensity and/or a significant drop in body temperature. Thus, the onset of movement could usually be determined from continuous plots of body temperature vs ambient temperatures, even if we had not been present at the study site at the time (see Webb, 1996).

We used one- and two-factor analyses of variance (ANOVAs) to test the effects of sex, year, and habitat type on our measures of movement frequency and mean and total distances moved. Prior to statistical analyses, we checked all data sets for normality using Kolmogorov–Smirnov tests, and for heterogeneity of variances using Cochran's test (Day & Quinn, 1989). Although our data sets were normally distributed, we log-transformed movement data and arcsine-transformed movement frequencies to achieve homogeneity of variances (Underwood, 1981).

RESULTS

Movement patterns

Frequency of movements

Throughout the study, telemetered broad-headed snakes spent long periods of time inactive in retreat-sites (Webb & Shine, 1997) and thus moved infrequently (Table 1). There was no difference in the frequency of movement of broad-headed snakes between years for either moves per tracking day (one factor ANOVA, $F_{2,28} = 2 \cdot 05$, $p = 0 \cdot 15$) or moves per day (one factor ANOVA, $F_{2,28} = 2 \cdot 38, p = 0 \cdot 11$). There was no difference between the sexes for either of these measures of activity (one factor ANOVAs: moves per tracking day $F_{1,29} = 0 \cdot 17$, $p = 0 \cdot 69$; moves per day: $F_{1,29} = 1 \cdot 74$, $p = 0 \cdot 20$). Pooling data from the three field seasons, snakes moved on only 36% of days on which they were located (overall mean move per tracking day $= 0 \cdot 36$, $SD = 0 \cdot 17$, range $0 \cdot 12$–$1 \cdot 00$, $n = 31$), and only on 21% of days overall (overall mean moves per day $= 0 \cdot 21$, $SD = 0 \cdot 12$, range $0 \cdot 06$–$0 \cdot 53$, $n = 31$). However, snakes moved more frequently in forest habitat than in cliff habitat (moves per day: one factor ANOVA, $F_{1,48} = 11 \cdot 12$, $p < 0 \cdot 01$). Snakes moved on 35% of days in forest habitat ($SD = 0 \cdot 27$, $n = 20$) compared with 16% of days while in cliff habitat ($SD = 0 \cdot 10$, $n = 30$).

'Meander ratios'

Observations of three snakes radio-tracked on summer nights during 1994 and 1995 (exact dates: 16 February 1994, 7 December 1994, 16 January 1995) revealed that the snakes did not move in straight lines between successive retreat-sites. All snakes emerged from their tree hollows just after sunset and rapidly descended from the trees. The snakes spent up to 75 min on the ground (exact times 75, 30, 24 min) and moved significantly further between retreat-sites (trees) than the measured straight-line distances (49, 75, 73 vs 22, 29, 27 m). Straight-line distances between successive retreat-sites clearly underestimate the true distances moved by broad-headed snakes by a factor ranging from $2 \cdot 2$ to $2 \cdot 7$, and the mean 'meander ratio' for this small sample was 2.5.

Distances moved in cliff vs forest habitats

Each year, most of our telemetered snakes moved up to 780 m away from the sandstone cliffs (mean distance snakes travelled from cliffs $= 318$ m, $SD = 187$, range 80–780 m, $n = 20$) into the woodland. The timing of this seasonal shift in habitat use varied among years, and coincided with the onset of hot weather (Webb, 1996). For example, in the first field season it was atypically wet and cool during November and December, and the snakes did not move long distances away from cliffs until January (see Fig. 1). In contrast, during the second field season the weather was warmer and
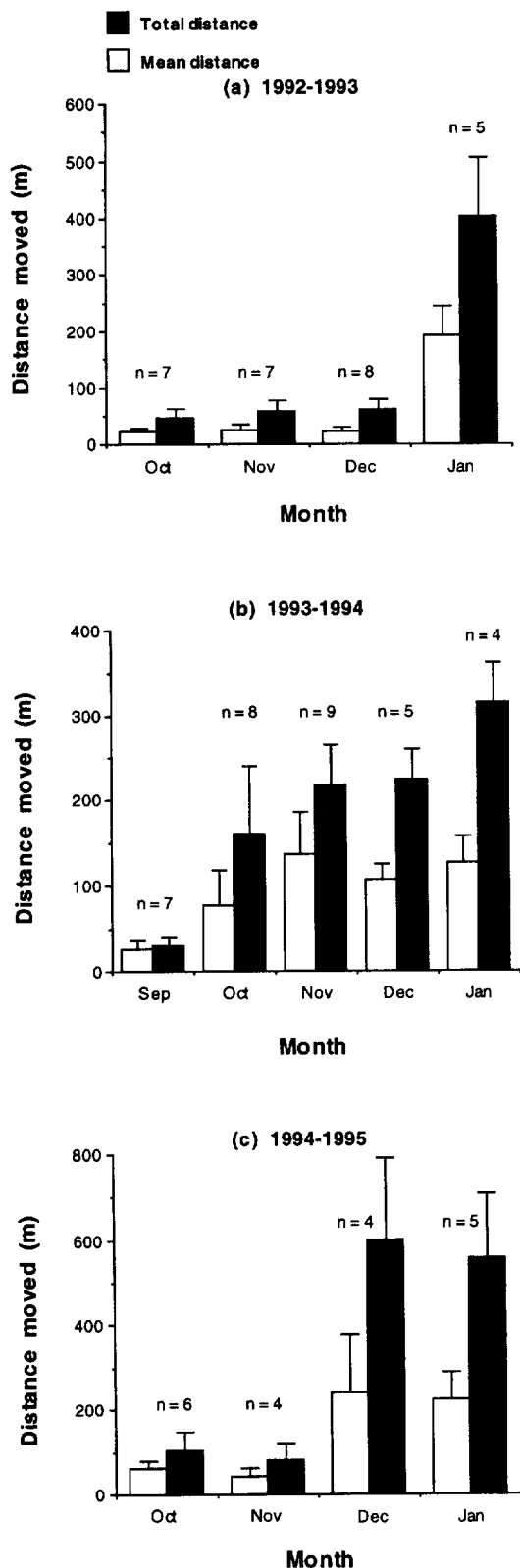
Fig. 1. Distances moved by free-ranging broad-headed snakes, *Hoplocephalus bungaroides*, based on radiotelemetric monitoring over 3 years. The graphs provide data separately for each year, and show both the mean distance moved between retreat-sites (□), and the total distance moved by each snake (■) over the spring–summer period. Sample sizes refer to numbers of snakes. Error bars show one standard error on either side of the mean.

snakes moved away from cliffs in late October and November (Fig. 1).

Two-factor ANOVAs on the mean distances travelled by snakes between successive retreat-sites, and the total distances travelled per month, provided very similar results. For both variables, there were significant differences among months (for distances between successive retreat-sites, $F_{3,59} = 9.06$, $p < 0.0001$; for total distances travelled, $F_{3,59} = 11.87$, $p < 0.0001$) and among years ($F_{2,59} = 6.13$, $p = 0.004$; $F_{2,59} = 4.52$, $p = 0.01$), and the interaction term was not significant. *Post hoc* tests (Fisher's PLSD) revealed that both variables (distances travelled between successive retreat-sites, and total distances travelled) were larger during the final 2 years than in the 1992–93 field season, and were larger during January than in other months.

Mean distances travelled between successive locations by snakes in cliff vs forest habitats were also compared among years, again using two-factor analysis of variance. The analysis revealed that snakes moved further between retreat-sites (locations) in forest habitat than on the rock outcrops ($F_{1,44} = 47.19$, $p < 0.0001$), but there were no significant differences among years ($F_{2,44} = 0.27$, $p = 0.76$), and a non-significant interaction term ($F_{2,44} = 0.06$, $p = 0.94$; see Fig. 2). Overall, snakes travelled an average of 159 m (SD = 84, $n = 20$) between retreat-sites (trees) in the forest, vs only 37 m (SD = 42, $n = 30$) between retreat-sites (crevices and rocks) in the cliff top habitat. We then compared the total distances travelled by snakes in each habitat in different years. This analysis revealed that snakes travelled significantly further in forest than in cliff-top habitat ($F_{1,44} = 42.52$, $p < 0.0001$), but there were no significant differences among years ($F_{2,44} = 0.26$, $p = 0.77$), and a non-significant interaction term ($F_{2,44} = 2.92$, $p = 0.06$). Note, however, that these results are based on log-transformed data, which may obscure biologically meaningful results (e.g. Underwood, 1981; Day & Quinn, 1989). Thus, although snakes travelled similar distances between retreat-sites each year (Fig. 2(a)), total distances travelled by snakes in the forest varied substantially (Fig. 2(b)). This result is not surprising, because the time spent by snakes in the forest (and hence the opportunity to travel farther) varied each year. For example, in the first field season telemetered snakes moved into the forest during January, not long before their radio-transmitters failed. Hence, total distances travelled by these snakes were much smaller than in the final year, when snakes used the forest during December and January.

Home ranges

For the analyses in this paper, we define home range as the area used by broad-headed snakes during spring and summer. Breaking home range down into separate components for spring and summer (as some workers have done: e.g. Slip & Shine, 1988) was not feasible for our study because of the short life (maximum 6 months) of the radio transmitters.
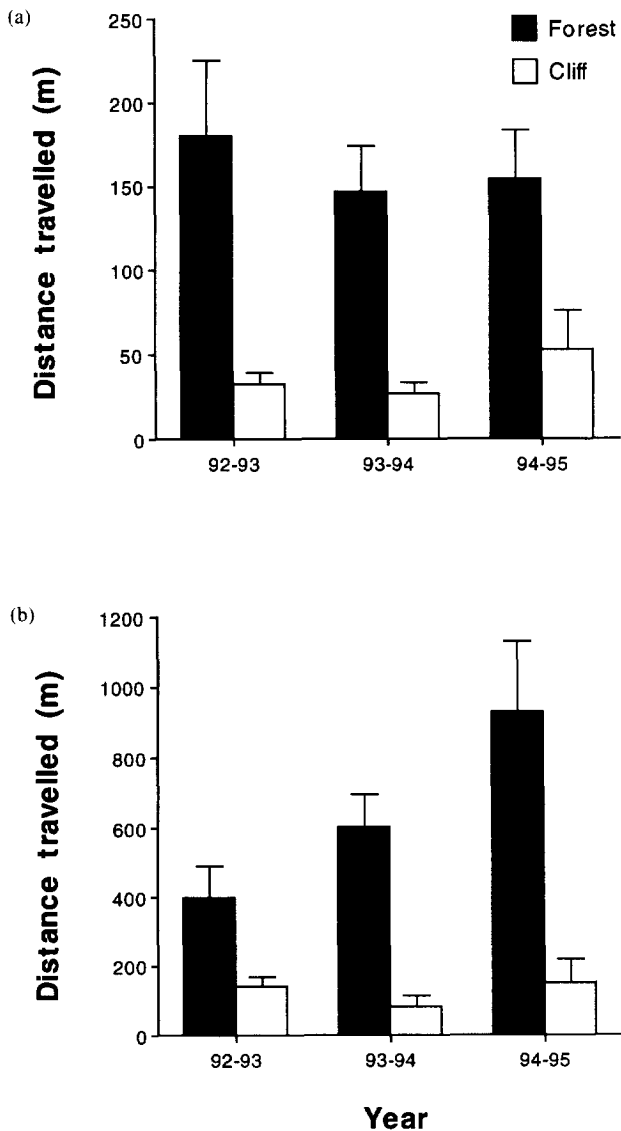
(a)

(b)

Year

Fig. 2. Distances moved by free-ranging broad-headed snakes, *Hoplocephalus bungaroides*, in two distinct types of habitat. In each year of the study, snakes moved much further when they were in forest habitats (■) than when they were on the rock outcrops (□). This was true for the mean distance between successive retreat-sites (a) as well as for the total distances moved over the entire spring–summer period (b). Error bars show one standard error on either side of the mean. See text for further explanation.

Is there a discrete home range?

To determine whether broad-headed snakes restricted their movements to a well-defined home range, or wandered randomly, we examined the spatial arrangement of successive locations (see below) and plotted the distance of snakes from their original release points vs days since release (Slip & Shine, 1988). If snakes wander randomly then later locations should be further away from the initial release sites (Slip & Shine, 1988), although such a pattern could also result from highly directional long-distance migration (see Gregory *et al.*,

1987). In fact, there was no significant relationship between the distance a snake was located from its initial release site and the number of days since release (1,62 d.f., $r^2 = 0.006$, $p > 0.05$), suggesting that broad-headed snakes restrict their movements to discrete home ranges.

Further evidence that broad-headed snakes move within well-defined home ranges can be seen from chronological positions of three snakes radio-tracked during 1993–94 (Fig. 3). The snakes remained relatively close to their original release points, and frequently revisited specific sites (Fig. 3). During the second field season two snakes returned to the same trees after long absences (Webb & Shine, 1997). The snake with the largest recorded home range (11.43 ha, convex polygon) moved a total of 2.6 km (corrected distance using a meander ratio of 2.5) during late December and early January, but by mid January it was found 20 m from a tree it had used in early December. One female radio-tracked at Site 1 during 1994–95 moved back towards the cliff after it had digested a mouse in the forest habitat. This snake moved 176 m in a single night, and was found in the forest some 60 m from its initial release point on the cliff in mid January 1995. A male radio-tracked at the same study site moved back to the cliff in mid January 1995 and was found in a crevice less than 10 m from its original release point.

Site fidelity

Rock outcrops

Additional evidence that snakes restrict their activities to well-defined home ranges comes from our recaptures of telemetered snakes. Even though adult snakes moved long distances (up to 780 m) away from rocky outcrops during summer, they consistently returned to the same cliff tops where they were initially captured. Five telemetered snakes (two males, three females) were recaptured under the same rocks that they had used during previous years. Indeed, we captured one female under the same rock in spring in 4 years (1992, 1993, 1994 and 1996). Hence, some broad-headed snakes showed very strong site fidelity, and consistently used the same rocks year after year.

However, our long-term mark-and-recapture data suggest that site fidelity may be more pronounced in females than in males. Nine females recaptured after long periods of time (mean = 25.6 months, SD = 9.9, range = 10–43 months) were found relatively close to their original capture points (mean distance = 59 m, SD = 36, range 0–120 m). In contrast, males were found further away from their original capture points than females ($n = 12$, mean distance = 129 m, SD = 143, range 0–500 m) after a similar amount of time (mean = 19.0 months, SD = 12.7, range = 5–39 months), but this difference was not statistically significant (one factor ANOVA, $F_{1,18} = 2.02$, $p = 0.17$). Like females, some males continued to use the same rocks each year.
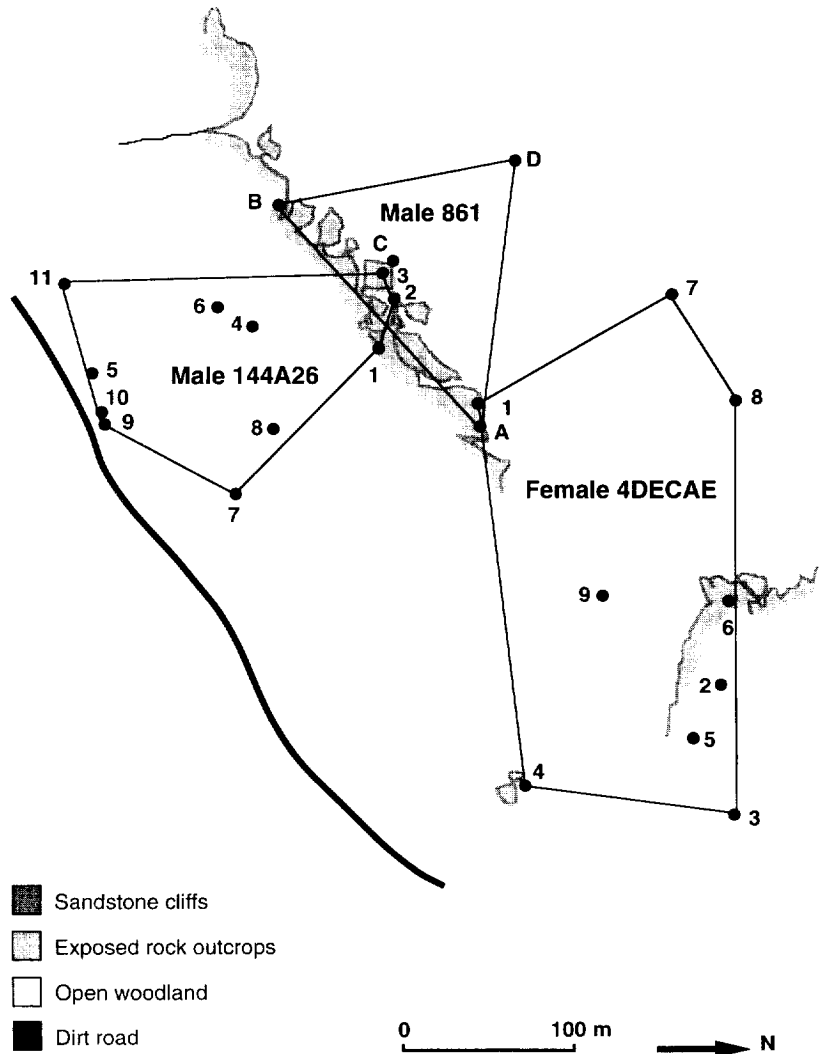
Fig. 3. Home ranges (convex polygons) of three adult broad-headed snakes monitored radiotelemetrically at Site 4 during the 1993–94 field season. Snakes often spent long periods of time at the same location, so relatively few retreat-sites were used by each snake over the long (5-month) monitoring period. The numbers within each home range refer to the sequential locations (retreat-sites) of each snake.

Woodland

To see whether broad-headed snakes restrict their foraging activities to the same general areas of forest each year, we compared locations of home ranges of individual snakes radio-tracked during successive years. Although we radio-tracked seven snakes in more than 1 year (see Table 1, Webb & Shine, 1997), early transmitter failure meant that we could only compare the locations of 'woodland' home ranges of two males during successive years (see Table 2). One male (No. 14597E) moved within the same area of forest during both years, such that 93% of its 1993–94 home range (0·96 ha) fell within the home range of the previous year (3·66 ha). In contrast, a second male (144935), showed less overlap in home ranges from consecutive years, with only 34% of the 1992–93 home range (0·88 ha) falling within its 1993–94 home range (1·40 ha). These data, together with observations of snakes revisiting particular trees (Webb & Shine, 1997), tentatively suggest that some

broad-headed snakes may reuse the same areas of forest each year.

Sizes of home ranges

Sizes of home ranges of telemetered broad-headed snakes determined using the convex polygon method (Jennrich & Turner, 1969) are shown in Table 2. Mean sizes of home ranges of males and females for the 3 years of the study are shown in Table 3. During the 1993–94 field season (when sample sizes were largest), there was no difference in home range size between males and non-gravid females (unpaired t-test, $T_{1,7} = -0.06$, $p > 0.05$). Overall, sizes of home ranges of males and non-gravid females were similar in the 1992–93 and 1993–94 field seasons (see below). Hence, sizes of home ranges of gravid females were compared with those of non-gravid females (one from the first field season, and two randomly chosen females from the second field season). Gravid females had significantly

Table 2. Home ranges of radio-tracked broad-headed snakes, *Hoplocephalus bungaroides*

Year	Snake no.	Sex	SVL (cm)	Mass (g)	N	Duration (days)	Home range (Ha)
1992–93	1273	M	50·5	38	27	105	1·56
1992–93	1151	M	51·5	41	21	105	2·24
1992–93	469	M	56·0	49	25	127	0·05
1992–93	14597E	M	56·0	47	16	82	3·66
1992–93	144935	M	61·0	43	19	118	0·88
1992–93	1DB5AFE	F	54·0	40	20	87	1·58
1992–93	D32A8	F(g)	54·5	51	18	127	0·04
1992–93	13268F2	F(g)	58·0	53	20	121	0·05
1992–93	1181	F(g)	58·5	53	18	76	0·03
1993–94	D428D	F	55·0	44	25	124	2·78
1993–94	D32A8	F	55·0	41	27	175	1·07
1993–94	D56DB	F	59·0	47	17	182	1·18
1993–94	4DECAE	F	63·5	59	29	129	3·53
1993–94	144A26	M	52·0	39	32	132	1·44
1993–94	D89C2	M	53·7	50	21	168	2·59
1993–94	D3C5F	M	54·5	53	14	124	4·57
1993–94	14597E	M	56·5	46	26	86	0·96
1993–94	861	M	59·0	62	26	92	1·99
1993–94	144935	M	61·0	46	21	98	1·40
1994–95	1339F7B	F	67·0	70	33	122	6·59
1994–95	1BBF261	M	52·0	40	27	122	11·43
1194–95	1E9B1A	M	55·5	42	8	36	5·36
1994–95	1341AE1	M	61·5	57	19	78	8·13
1994–95	1DA64AD	M	62·5	60	4	36	2·60

SVL = snout-vent length; M = male; F = female; F(g) = gravid female; N = number of locations made on different days. Home range was calculated by the convex polygon technique, without correction for differing sample sizes.

smaller home ranges than did non-gravid females (unpaired *t*-test, $T_{1,4} = 3·8$, $p < 0·05$). In the one case where we radio-tracked a female in two successive years (female D32A8, Table 2), the snake had a smaller home range during pregnancy (0·04 ha, 1992) compared with the following year when she was non-gravid (1·07 ha, 1993).

Unlike males and non-gravid females, radio-tagged gravid females did not move away from the sandstone cliffs during summer. Instead, these snakes remained quite sedentary, sheltering in crevices and hollow logs. Our field observations tend to support the idea that gravid broad-headed snakes remain in the sandstone cliffs during late spring and summer. On 18 November 1994 we found a small gravid female (SVL = 54·5 cm) basking next to a large slab of rock underneath a rock overhang 5 m below the top of a 30 m high cliff. A larger gravid female (SVL = 76·0 cm) was observed basking next to a crevice on a cliff-top on 10 January 1995. Both females were captured, and subsequently gave birth in the laboratory during early March 1995.

Temporal variation in home range size

Home ranges of individual snakes radio-tracked during successive years varied significantly (see Table 2). We pooled data on home range sizes of males and non-gravid females to examine year-to-year variation. This analysis revealed significant differences in mean home range size between years (one factor ANOVA, $F_{2,18} = 12·8$, $p < 0·001$). Home ranges were similar in size in 1992–93 and 1993–94, but much larger during 1994–95 (Table 3). Overall, the mean size of home ranges of snakes utilising forest habitat was 3·3 ha $n = 19$, SD = 2·8, range 0·9–11·4 ha).

Spatial and temporal overlap of home ranges

The degree of overlap between home ranges of different individuals can give insights into the mechanisms determining use of space. If the presence of one snake in an area makes the site less attractive to another snake, we might expect to see low overlap between individuals in space and/or time. Our analysis reveals effects of this kind:

Table 3. Mean home ranges (convex polygons) of male and female broad-headed snakes, *Hoplocephalus bungaroides*, over the three years of study

Year	Males				Females			
	N	Mean	SD	Range	N	Mean	SD	Range
1992–93	5	1·68	1·37	0·05–3·66	4	0·43	0·77	0·03–1·58
1993–94	6	2·16	1·71	0·96–4·57	4	2·11	1·25	1·07–3·53
1994–95	4	6·88	3·78	2·60–11·43	1	6·59	—	—

Rock outcrops

The areas occupied by seven adult snakes (5 males, 2 gravid females) radio-tracked at Site 2 during spring and early summer of 1992–93 are shown in Fig. 4. We are confident that we had captured most or all of the adult snakes at this site. The home ranges of males showed virtually no overlap with other males, yet the locations of females were clearly within the home ranges of male snakes (Fig. 4). Although males were sometimes found as close together as 5 m, only one male trespassed into the area used by another male (Fig. 4). In order to see whether the spatial arrangement of the home ranges of males shown in Fig. 4 would be expected by chance, we calculated the nearest neighbour distances

Fig. 4. Home ranges (convex polygons) of five adult male broad-headed snakes and locations of two gravid females monitored radiotelemetrically at Site 2 from early September to late December 1992. The snakes' movements were restricted to the exposed sandstone cliff during this period. Notice that the home ranges of males show little or no overlap, whereas the locations of females are largely within the home ranges of males.

from the centres of the home ranges (Clark & Evans, 1954). The mean nearest neighbour distance between male home ranges was 49 m, which was significantly greater than would be expected by chance (expected distance $= 24 \pm 11$ m, $p < 0.05$). For this population the ratio R (observed/expected distance) was 2·04, which indicates that males were spaced fairly evenly in the population (Clark & Evans, 1954).

Additional evidence that males avoid each other comes from our observations of groups of snakes found under the same rocks. These groups consisted of a male–female pair of newborn snakes (SVLs = 25 cm, 21 August 1995), two adult male–female pairs (28 July 1994, 15 August 1995), an adult male and subadult female (14 November 1995), and a trio consisting of one adult male and two adult females (18 August 1993). Thus, although males occasionally shared rocks with females, pairs of males were never observed under the same rock. Interestingly, the adult females found with males during 1993 and 1994 were non-gravid animals that subsequently moved long distances in the forest. Hence, mating may not always be the reason why adult males and females occasionally share the same rocks.

Woodland

At first sight, the high spatial overlap between some snakes in the woodland suggests a lack of any social effects (e.g. Fig. 5; but see Fig. 3). However, closer analysis indicates that the snakes may be actively avoiding each other through time, but not space. That is, two or more snakes may use the same area of woodland, but tend not to use it at the same time. To test this we calculated the nearest neighbour distances from the centres of the home ranges (convex polygons) of five snakes (three males, two females) radio-tracked at Site 2 between 25 November and 13 December 1993. Note that these home ranges were sometimes smaller than the 'total home ranges' because two snakes were sedentary during this period. The mean nearest neighbour distance between the home ranges of these snakes was 243 m, which was significantly greater than would be expected by chance (expected distance $= 132 + 61$ m, $p < 0.05$, Clark & Evans, 1954). For this sample $R = 1·85$, which indicates that the areas used by the animals were fairly evenly spaced in the forest (Clark & Evans, 1954). Thus, snakes appear to avoid each other, regardless of sex, while in the woodland.

Further evidence that broad-headed snakes avoid conspecifics is provided by examination of the *smallest* nearest neighbour distances of snakes using woodland during the 3 years of the study. These were measured only in instances where we were confident most adults had been captured. Thus, we measured nearest neighbour distances of snakes radio-tracked at Site 2 during 1992–93 (total of seven snakes radio-tracked) and 1993–94 (six snakes radio-tracked) and at Site 1 during 1994–95 (six snakes radio-tracked). We then selected the smallest nearest neighbour distances of snakes using
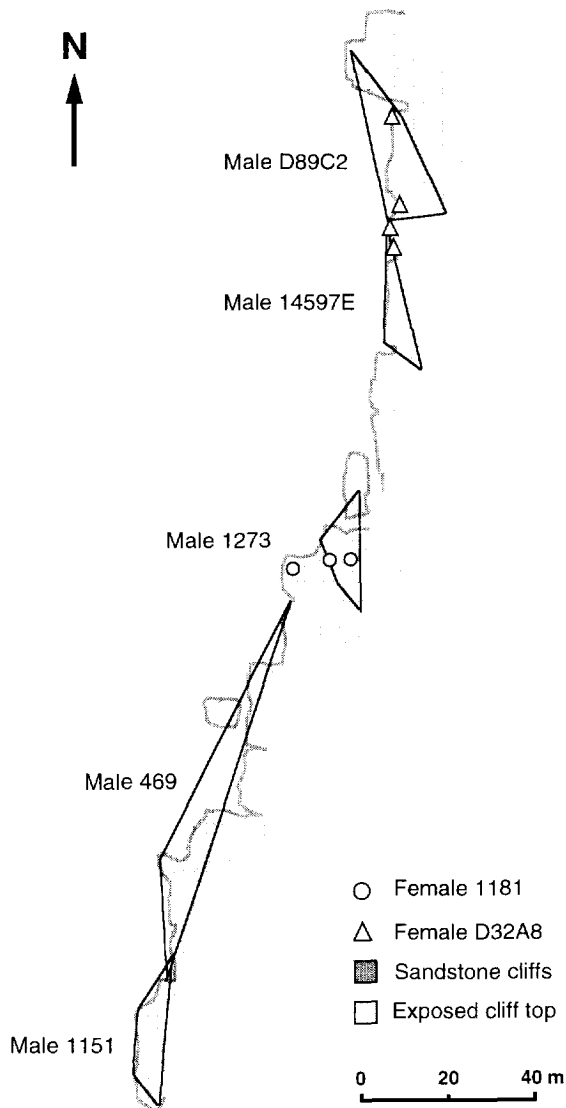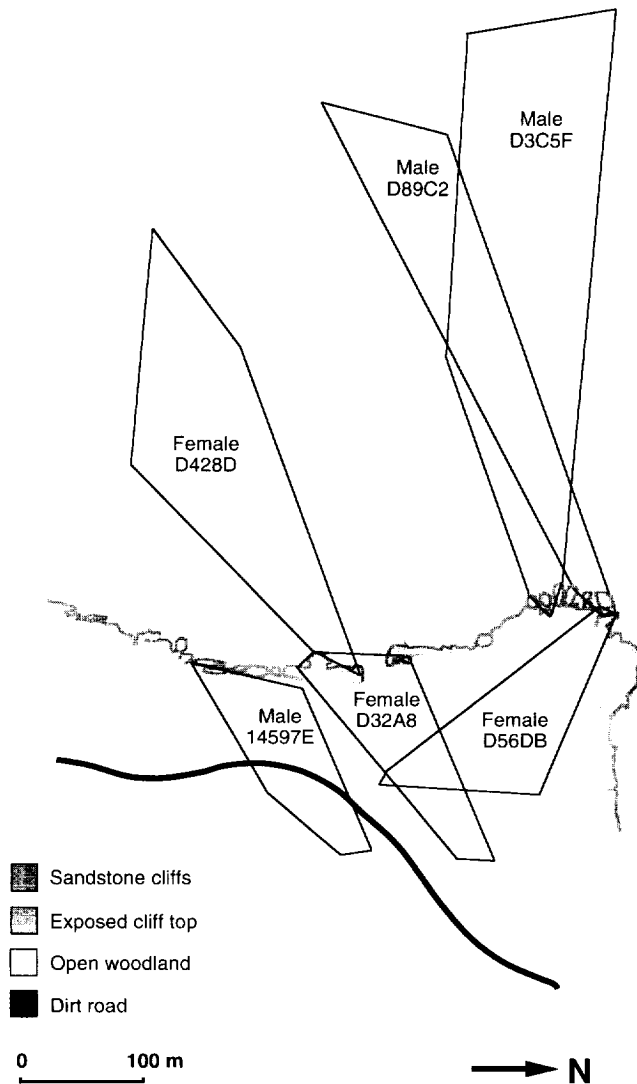
Fig. 5. Home ranges of six adult broad-headed snakes monitored radiotelemetrically at Site 2 during the 1993–94 field season. Note that female D32A8 did not move into the forest habitat until late January, whereas the other snakes moved into the forest during November.

woodland, and only included one measurement for each pair of snakes. Overall the mean smallest nearest neighbour distance of snakes in the forest was 203 m ($n = 8$, SD = 45), and snakes were never found closer than 115 m together. There was no difference between male–male or male–female nearest neighbour distances (one factor ANOVA, $F_{1,6} = 2.0$, $p = 0.20$). Collectively, these data suggest that snakes actively avoided conspecifics (of either sex) while they were in the woodland.

Our observations of individual snakes also support this interpretation. During the 1994–95 field season, a male and non-gravid female radio-tracked at Site 1 were relatively close together during spring and had home ranges that overlapped considerably during summer. The home range of the male overlapped the home range of the female by 49%, while the home range of the female overlapped that of the male by 61%. However,

these snakes showed no temporal overlap in home ranges while in the forest. The closest distance these two snakes were from each other while in the forest was 229 m (mean distance = 344 m, range = 229–405 m), yet prior to moving into this habitat they were less than 20 m apart in the cliff top.

Snake characteristics vs home range size

For both sexes, there were significant positive correlations between SVL and mass (males: $r^2 = 0.77$, 1, 38 d.f., $p < 0.0001$; females: $r^2 = 0.76$, 1, 13 d.f., $p < 0.0001$), and we used residuals from these regressions as indicators of snake body condition. For males, there was no correlation between home range size and either SVL, mass, or residual mass (regression analyses, 1,14 d.f., $p > 0.05$ in all cases). However, home range sizes of the non-gravid females were positively correlated with each of the three morphological traits (SVL: $r^2 = 0.70$, 1, 4 d.f., $p = 0.04$; mass: $r^2 = 0.85$, 1, 4 d.f., $p < 0.01$; residual mass: $r^2 = 0.82$, 1, 4 d.f., $p = 0.01$). These results show that larger, heavier-bodied females had larger home ranges.

Juveniles

Activity and movements

Owing to the low detection range (< 10 m) of the harmonic radar, only limited information was obtained on the movements and activity of juveniles. Four juveniles (SVLs < 35 cm) tracked during spring spent long periods inactive in retreat-sites (mean = 10 days, SD = 13, range 2–30 days) and moved relatively short distances along the sandstone cliffs (mean = 39 m, SD = 48, range 1–110 m). Two juveniles located in February 1993 had moved long distances (225 and 250 m) away from the exposed cliffs and were found on a small sandstone rock outcrop in open woodland. One of these snakes was subsequently recaptured 15 m from its original capture point on the exposed cliff edge in November 1993.

Dispersal

A total of 44 juvenile snakes (SVL < 35 cm) were marked with PIT tags (15 with PIT tags only, 29 with PIT tags and diodes) during 3 years of field work. Of these, 12 (four males, six females, two not sexed) were recaptured after periods of 6 months or more (mean time between recaptures = 18.6 months, SD = 11.1, range 6–34 months). Overall, these snakes had travelled an average of 161 m from their original capture points (SD = 120, range 10–375 m). There was no difference in the mean distances moved by males vs females (one factor ANOVA, $F_{1,8} = 0 \cdot 46$, $p = 0.95$). We then compared the distances moved by juveniles and adults of the same sex. Among females, juveniles had moved significantly further between captures compared with adults (mean distance 187 vs 59 m: one factor ANOVA, $F_{1,13} = 14 \cdot 78$, $p = 0.002$). In contrast, juvenile males had travelled similar distances compared with adults (mean distance 136 vs 129 m: one factor ANOVA,

$F_{1,13} = 0.36$, $p = 0.56$). Collectively, these results suggest that juveniles do not disperse over long distances. The low dispersal of juveniles is unlikely to be due to locomotory problems caused by implantation of miniature harmonic radar diodes, because distances dispersed by snakes with and without implanted diodes were not significantly different (one factor ANOVA, $F_{1,10} = 0.64$, $p = 0.44$).

DISCUSSION

Our data paint a complex picture of the determinants of movement patterns and home range size in broad-headed snakes. The distances moved by the snakes, and the overall area they use, are affected by factors such as the time of year, the nature of the habitat, the snake's size and condition, and its reproductive activities. The significant year-to-year variation in home range sizes during our study suggests that resource (especially, prey) availability may also play a role in this respect. It is not surprising to discover that these kinds of factors influence a snake's frequency of movement, and how far it travels when it does move, because one would expect that these traits would be very flexible and responsive to local conditions. However, the particular details of influences on snake movements would have been very difficult to predict *a priori*. The striking seasonal shift in activity patterns offers a good example of this unsuspected diversity. Undoubtedly, however, the most surprising result from our analysis is the suggestion that . social interactions constrain home range parameters in *H. bungaroides*. In the following discussion, we focus on two main questions: (i) why do the snakes use the available habitat in way that they do?; and (ii) what are the implications of these results for conservation planning?

First, we examine the question of why the snakes display these patterns of movement. Most of the main features of movements by *H. bungaroides* are consistent with other information on this species, and on other snakes:

(a) *the low frequency of movement* of the radio-tracked snakes (regardless of whether they were sheltering in tree hollows or under rocks) is probably related to the snakes' 'sit-and-wait' feeding strategy (Webb, 1996), and is consistent with activity levels of other 'sit-and-wait' predators (e.g. Slip & Shine, 1988; Secor, 1994; Beck, 1995; Shine & Fitzgerald, 1996). Clearly, frequent movement would be incompatible with ambush predation.

(b) *the variable distances moved* by our snakes are likely to reflect the spatial distribution of essential resources such as food and shelter (Gregory *et al.*, 1987). Our radio-tracked snakes moved further between retreat-sites and travelled further in

woodland than in cliff top habitat, presumably because essential resources (food and shelter) were more dispersed in the forest. Alternatively (or additionally), the risk of predation may be lower for moving snakes in the thick woodland than on the open outcrops. Foraging rattlesnakes continue to move until they encounter patches of prey (e.g. Duvall *et al.*, 1985; King & Duvall, 1990). A similar system may operate here, as broad-headed snakes fed mainly on small mammals while they were in the forest (Webb, 1996).

(c) *the well-defined home ranges* of our snakes, and their revisitation of specific shelter-sites in tree hollows and under rocks, reflects a pattern that has been seen among many other snake species (e.g. Slip & Shine, 1988; Weatherhead & Hoysak, 1988; Durner & Gates, 1993; Ciofi & Chelazzi, 1994), including at least one other elapid (the blacksnake *Pseudechis porphyriacus*: Shine, 1987). Strong site fidelity may be very widespread among snakes.

(d) *the dependence of home range size on the snake's size, body condition and reproductive state* accords with intuition, and again mirrors results from other studies. The overall home ranges of males and non-gravid females were similar in magnitude, as might be expected from the similarity in adult body sizes and diets between the sexes (Webb, 1996). Unlike their non-gravid counterparts, gravid females did not move long distances into the forest; instead they remained within small home ranges (mean size = 0.05 ha) in the cliff tops. Several studies on viviparous snakes have found that gravid females are more sedentary or use different habitats than their non-gravid counterparts (e.g. Andren, 1982; Reinert & Zappalorti, 1988; Charland & Gregory, 1995), and such differences may be related to physiological or ecological changes associated with pregnancy (e.g. Reinert, 1993). Gravid females of many snake species feed rarely, and bask often (e.g. Shine, 1980). The open outcrops offer better thermoregulatory options than the relatively shaded woodland, and the scarcity of food in the outcrops in summer is not a problem if the snakes are anorexic at this time. Larger home ranges of larger and better-conditioned snakes (at least in females) may be due to individual variation in a snake's ability and willingness to move about in search of prey.

(e) *the among-year variation in home range size* may reflect underlying year-to-year variation in prey availability. At least one of the mammalian species used by *H. bungaroides* a shows yearly fluctuations in population size (*Mus domesticus*; Singleton & Redhead, 1990).

(f) *social influences on space use* comprise the most surprising result from our study. Previous studies

on the spatial ecology of snakes have concluded that these animals lack territoriality, and individuals within the same population generally display widely overlapping home ranges (see review by Gregory *et al.*, 1987; Weatherhead & Hoysak, 1988; Ciofi & Chelazzi, 1994; Secor, 1994). Our study has found a different pattern. Home ranges of male broad-headed snakes overlapped very little in space and time during spring, but females were found within the home ranges of males at this time (see Fig. 4). However, during summer both sexes appeared to avoid each other when they were foraging in the forest (Figs 3 and 5). Our statistical analyses showed that these patterns are unlikely to occur by chance, and so may reflect some active process of avoidance of conspecifics by the snakes. The mechanism for such avoidance is likely to involve olfaction (chemical communication is well developed in snakes: e.g. Ford, 1986), but it is unclear as to why broad-headed snakes should actively avoid the scent trails of conspecifics. We have no records of cannibalism or any agonistic interaction among individuals, but are unable to be sure that such interactions do not occur. Another possibility is that avoidance of conspecifics increases the probability of encountering prey, because a snake entering an area recently used by a conspecific might experience lower foraging success (Charnov *et al.*, 1976).

(g) *the limited dispersal by neonatal snakes* is difficult to interpret, because there is little information on dispersal by juveniles in other species of snakes, so we do not know whether *H. bungaroides* is atypical in this respect. However, our data also offer a contrast between the degree of philopatry in adults (high) and juveniles (low). Juveniles comprise the main dispersive phase for most vertebrates (e.g. Greenwood, 1980), including lizards (e.g. Andrews & Rand, 1983; Doughty *et al.*, 1994) but we know of no previous comparison that shows such an ontogenetic shift within any snake species.

Implications for conservation

What kind of reserve would be adequate?

Clearly, effective conservation of broad-headed snakes requires reserves that include exposed rock outcrops as well as a relatively large area of adjacent woodland with suitable (i.e. hollow-bearing) trees. Logging, and burning after logging, may significantly impact on the availability of habitat for broad-headed snakes. We have discussed the importance of forest habitats to this species elsewhere (Webb & Shine, 1997), but the important message from our data on home ranges and movements is that the woodland areas involved must be relatively large — far larger than the rock outcrops. It is surprising that

such a small snake will travel up to 780 m from the outcrops, and existing conservation measures do not incorporate forested 'buffer zones' of this extent (e.g. Forestry Commission of NSW, 1982). Clearly, the distances of mature forests from rock outcrops will vary from place to place, and may affect the overall size and shape of reserves. Additionally, the frequent and extensive travels of radio-tracked snakes through the forests in summer suggest that vehicular traffic on bush roads in these areas (which often run relatively close to outcrops) may pose a substantial risk to foraging snakes.

What are the major threats to the persistence of broad-headed snakes?

The main present-day threats to *H. bungaroides* are likely to be the collection of bush-rock for suburban gardens, the clearing of private lands and the felling of trees during forestry operations. Our data on movement patterns emphasise yet again the importance of rocks (which provide thermally distinctive diurnal shelter-sites: Webb, 1996) as well as hollow-bearing trees (Webb & Shine, 1997), and also clarify the spatial scale needed for these resources. The virtual lack of home-range overlap between adult broad-headed snakes, however, introduces a new dimension into this discussion. This spatial pattern implies that social factors may limit the maximum population density of broad-headed snakes in a given area, as is known to be the case for several species of lizards (review by Stamps, 1983). If social interactions set the upper limit to densities, then broad-headed snakes may be unable to attain very high numbers even in 'ideal' habitats with abundant shelter sites and prey resources. We emphasise that we have no records of agonistic encounters between snakes, and we do not know whether the snakes change the size and exclusivity of their 'territories' in response to changes in prey abundance, as numerous species of lizards and birds do (e.g. Simon, 1975; Franzblau & Collins, 1980; Smith & Shugart, 1987). Despite this, the possibility that social interactions may influence population densities of *H. bungaroides* has several implications for conservation, including:

1. Efforts to 'restore' degraded habitats (e.g. by replacement of rocks) should aim to provide evenly separated shelter-sites, rather than clumping suitable shelters. The latter spacing has been advocated as the optimal form of post-logging habitat retention for arboreal marsupials by some authors (e.g. Smith & Lindenmayer, 1988) but is unlikely to be useful for highly territorial mammals (Lindenmayer *et al.*, 1990) or broad-headed snakes.

2. If recruitment to the adult population is limited by social factors rather than resource levels, removal of significant numbers of neonatal or juvenile snakes may have little impact on long-term viability

of populations. These 'excess' juveniles could then be relocated to restored habitat.

3. The removal of individual snakes (e.g. via illegal collecting by amateur snake-fanciers) may be a less severe conservation problem than it first appears. Under density-dependent population regulation, removal of animals may simply enhance the survival of younger snakes. Although we support the continued legislative prohibition on collection of *H. bungaroides* from the field, the conservation problems associated with illegal collecting are likely to be trivial, compared with the problems arising from legal or illegal removal of rocks from natural habitats of this species.

How feasible are proposals to 'restore' anthropogenically degraded habitats?

Elsewhere, we have suggested that it might be possible to 'restore' degraded habitats using concrete paving blocks as replacement shelter-sites (Shine *et al.*, 1995). It should be technically feasible to construct 'rocks' that mimic natural shelter-sites, at least thermally (by virtue of their size and exposure: Webb, 1996). However, our data on movements cast strong doubt on the snakes' ability to recolonise such 'restored' habitats without additional human intervention. Given the relatively low dispersal distances of juvenile broad-headed snakes, and the discrete home ranges and site fidelity of adults, these snakes are unlikely to move into 'vacant' habitat unless it is very close to areas that are already occupied.

This phenomenon may help to explain an otherwise puzzling result from field surveys on the distribution and abundance of *H. bungaroides* (Shine *et al.*, 1995). These surveys revealed that large areas of apparently suitable habitat did not contain broad-headed snakes. Although these results suggest that some other (unmeasured) factor may also limit *H. bungaroides* distributions (Shine *et al.*, 1995), our data on movements and dispersal of free-ranging snakes suggest an alternative interpretation. The low vagility and high site fidelity of broad-headed snakes may result in low rates of colonisation, so that suitable habitat is simply not 'discovered' by snakes for very long periods of time. Thus, stochastic extinction of local populations, combined with low recruitment (infrequent production of small litters — Webb, 1996) and low dispersal (present study) may be important contributors to the current 'patchy' distribution of this taxon. Habitat fragmentation through human disturbance has undoubtedly exacerbated this problem. If this scenario is valid, then 'restocking' restored habitats with juvenile *H. bungaroides* may be a viable option. The juveniles could come either from captive breeding (Shine & Fitzgerald, 1989) or from field captures of juveniles or gravid females. If population densities are limited by social factors (as we tentatively suggest above), then removal of neonates from the field may not impact too heavily on local source populations.

In conclusion, our study highlights the value of detailed research on the movements of individuals within a population. Although detailed autecological studies of every threatened species are simply not feasible or necessary, studies on selected species like ours may serve as models for other taxa that share similar ecological, life-history or distributional features (Wiens, 1994).

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