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A RADIOTELEMETRIC STUDY OF MOVEMENTS AND SHELTER-SITE SELECTION BY FREE-RANGING BROWNSNAKES (*PSEUDONAJA TEXTILIS*, ELAPIDAE)

Patrick Brian Whitaker and Richard Shine[1]

Biological Sciences A08, University of Sydney, NSW 2006, Australia

Abstract: Radio tracking of 40 free-ranging eastern brownsnakes (*Pseudonaja textilis*) in an agricultural landscape in southeastern Australia clarified the spatial ecology of these highly venomous animals. Most snakes over-wintered in burrows within a small area on the bank of an irrigation canal, dispersing into agricultural land during the warmer months. The snakes sheltered overnight in burrows or soil cracks, reusing the same retreat on successive nights and moving about to forage during the day. Successive shelter-sites averaged 152 m apart, and the snakes moved between them on average every six days. Home ranges of adult snakes were small (average MCP = 5.8 ha), and did not differ significantly between years with varying prey abundance. Movement patterns depended upon the snakes' sex, reproductive condition and body size. Adult males moved earlier in spring than did the (smaller) adult females, moved further and more often, and had larger home ranges. Home range size increased with body size in males, but not in females. Shelter-site selection was influenced by the location of potential prey (House Mice, *Mus domesticus*) and the location of other snakes. When radio-tracked snakes moved, they generally traveled from areas of lower to higher prey abundance (as determined by mammal-trapping). Throughout most of the year, adult male snakes were avoided by females and by other males. Adult males rarely cohabited with other snakes, and their arrival at an occupied burrow generally induced the resident snake to depart. Our study thus provides the first strong evidence that agonistic interactions can influence the spatial ecology of snakes.

Key words: Australia; Habitat; Serpentes; Social behavior; Snake.

While it is relatively straightforward to document movement patterns in free-ranging animals, we frequently have little understanding of what motivates or limits these movements. Interspecific and intraspecific (e.g., sexual, ontogenetic, seasonal) variation in aspects such as home range sizes will be much easier to interpret if we have insight into the stimuli that cause movement, and the underlying functional significance of those movements. For example, animals may move about to forage, to avoid predators or physical extremes, or to find (or to avoid) conspecifics. The relative importance of such factors remains unclear for most kinds of organisms, with a majority of studies on movement patterns simply providing descriptive data on space use rather than tests of specific hypotheses on causal processes. Ideally, we need both kinds of studies (or even better, a combination of both approaches) if we are to understand the mechanisms underlying observed variation in spatial ecology.

There is an extensive scientific literature on the distances animals move, the frequency of such displacements, and the attributes of sites in which they shelter between successive movements (e.g., Dingle, 1980; Reinert and Kodrich, 1982; Gregory et al., 1987; Macartney et al., 1988; Engelstoft et al., 1999). However, there are large taxonomic and geographic biases in such studies, with some kinds of animals largely ignored in these respects. Not surprisingly, little attention has been focused on species that are highly cryptic and secretive, especially if they pose a potential danger to the observer. For these and other reasons, free-ranging snakes are often difficult to study (e.g., Gibbons and Semlitsch, 1987). Fortunately, the development of miniature radio transmitters has allowed us to examine dispersion patterns of free-ranging snakes in detail and clarify not only patterns of movement and shelter-site selection, but also the cues involved in initiating these behaviors. The spatial ecology of snakes has attracted increasing study, albeit much of it focused on a small number of taxa in Europe (e.g., Madsen, 1984; Prestt, 1971; Viitanen, 1967; Nagy and Korsus, 1999) and in North America (e.g., Brown and Parker, 1976; Fitch and Shirer, 1971; Larsen, 1987; Parker and Brown, 1972; Reinert, 1984; Reinert et al., 1984;

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[1] Correspondence: email, rics@bio.usyd.edu.au

Reinert and Kodrich, 1982; Plummer, 1997; Brown and Weatherhead, 1999; Shine et al., 2001). Increasingly, however, other study systems are being exploited (e.g., Voris and Karns, 1996; Tobin et al., 1999; Angelici et al., 2000; Shetty and Shine, 2002; Shine et al., 2002).

There are at least three potential benefits from a study of patterns of space use by highly venomous snakes. First, a better understanding of movements and habitat selection by these animals may help to reduce the incidence of serious snakebite to humans, by identifying the circumstances (times, places) to be avoided. Second, some authors have speculated that venomous snakes may play an important role in the control of agricultural pests, especially rodents (e.g., Curran and Kauffield, 1937; Webber, 1951). Information on the spatial ecology of predators and their prey may aid in assessing the role of snakes in this regard, and in formulating management plans to maximize their effectiveness as agents of pest control. Third, the information is of interest in its own right, apart from the management benefits. For example, there is disagreement about the role (if any) of social interactions in the ecology of snakes (e.g., Carpenter, 1986; Carpenter and Ferguson, 1977). Snakes are generally viewed as being highly asocial, but some authors have suggested that social factors may affect patterns of movement and dispersion in these animals (e.g., Gillingham, 1987; Gregory et al., 1987; Webb and Shine, 1997). We set out to describe patterns of space use in a highly venomous Australian elapid snake, and to gather data to test specific hypotheses about the ways in which the spatial dispersion of prey organisms and conspecifics might influence snake movements.

MATERIALS AND METHODS

Study Species and Area

The eastern brownsnake (*Pseudonaja textilis*, Elapidae) is a large (to 1.7 m snout–vent length [SVL]) slender-bodied venomous snake that is widely distributed in southern Australia (Longmore, 1989). In our study population, adult males averaged 1.25 m SVL (692 g) whereas females averaged 1.17 m (512 g). These fast-moving and agile snakes are highly cryptic in color (brown dorsally), and possess one of the most potent venoms yet investigated (Broad et al., 1979). Based on their numbers in museum collections, *P. textilis* may be the most common snake species in Australia (Longmore, 1989). This abundance reflects the brownsnake's ability to exploit highly disturbed agricultural lands and to feed on the introduced House Mouse (*Mus domesticus*: Shine, 1989). Possibly because of its wide distribution, use of disturbed habitats, potent venom, agility and preparedness to defend itself vigorously when cornered, *P. textilis* causes more human fatalities than does any other snake species in Australia (Sutherland, 1983).

Our study was conducted in the intensely farmed Murrumbidgee Irrigation Area (MIA) in southeastern Australia (146° 28′ E, 34° 39′ S). This region is typical of habitats occupied by eastern brownsnakes over much of their geographic range. Summers are hot (mean maximum daytime air temperature in January = 31.6 C) and winters are cool (mean in July = 13.5 C: Watson, 1997). Rainfall averages 440 mm per year, and droughts are common. Rainfall over the four years of our field study (1993–1996) was 550, 270, 511 and 468 mm. Thus, one year (1994/95) was strongly drought-affected, particularly so during the snakes' active season. The area consists of flat pasture land separated by irrigation channels. The work was focused on a three-kilometer length of canal running through paddocks used for sheep grazing and cereal crop production. A relatively undisturbed area on one bank of this canal contained many deep burrows that acted as over-wintering sites for the snakes (see below). This central refuge area was not grazed by stock over the 10-year period leading up to and including our study. Further details on the study area are provided elsewhere (see Whitaker and Shine, 1999*a,b*, 2000, 2001).

Monitoring Snake Movements and Locations

We surgically implanted miniature radio transmitters in 40 brownsnakes and monitored their activity and movements over the next 2 to 32 months (mean duration of monitoring = 12 months). Details of transmitter types and sizes, surgical techniques and overall monitoring schedules are given elsewhere (Whitaker and

Shine, 1999*a,b*). Briefly, the snakes were returned to a nearby laboratory immediately after capture, and miniature temperature-sensitive transmitters were placed in the peritoneal cavity under inhalation anesthesia. Some snakes were recaptured and had transmitters replaced partway through the study. Movement was monitored twice each month, in five to seven day periods, over three active seasons between September 1993 and May 1996. Because these snakes are difficult to observe in the field when active, and can move very rapidly, we could not quantify actual distances moved per day. However, the animals are almost exclusively diurnal (Whitaker and Shine, 2001), so that it was straightforward to locate a snake's overnight shelter-site. Our analyses of movement patterns are based on the locations of these shelter-sites (i.e., displacements between sites used by a snake for shelter on successive nights) rather than the total distances that animals moved during their daily activities. Thus, our estimates do not allow for the meandering that undoubtedly occurred (e.g., Secor and Nagy, 1994).

We treated shelter-sites (usually holes in the ground, see below) as different from each other if their entrances were >2 m apart (Weatherhead and Charland, 1985); otherwise, we could have recorded a snake as having moved between shelter-sites simply when it used a different entrance to the same retreat. The distance that a snake moved between shelter-sites was calculated as the straight-line distance between these two sites (to the nearest meter). The location of each shelter-site was plotted onto a map with reference to fence posts spaced at 4.5 m intervals, running parallel to the relatively narrow and approximately linear central refuge area (x coordinates). Latitudinal bearings (y coordinates) were measured by pacing, recorded on metal tags wired to corresponding points on fence-lines, logged, and later confirmed using plot overlays on a 1:6500 aerial photograph. Locations of the telemetered snakes were recorded after sunset and were confirmed where possible before the snakes emerged from their retreats the following day. Direct observations and telemetrically monitored body temperatures confirm that the snakes rarely emerged from their burrows during the night (one record: Whitaker and Shine, 2001).

Measuring Shelter-Site Characteristics

The physical characteristics that we recorded at night time retreats included location (as above), diameter, slope, aspect and percentage vegetation cover. Shelter-site diameter was calculated at the burrow entrance, using calipers positioned one centimeter inside the entrance used by the snake. Slope was measured using an inclinometer over the entrance. Aspect was measured using a hand-held compass and calculated from true north. Cover refers to vegetation $\geq$4 cm height (i.e., high enough to obscure an adult brownsnake), which we estimated in 4×0.5 m^2 quadrats centered over the entrance.

Calculation and Analysis of Home Range and Core Area Size and Overlap

We restricted our location records for estimating home range to nocturnal shelter-sites, and only data for snakes that were regularly monitored over entire active seasons were used to calculate home range and core area sizes. Individual home range and core area sizes were calculated using the program Calhome (Kie et al., 1994). We used the minimum convex polygon method to calculate overall home range sizes. Because of the large numbers of locations per snake, the resulting polygons did not need sample-size correction (Jennrich and Turner, 1969). The adaptive kernel method was used to calculate core areas (50% isopleth: that is, the area of home range that includes the central 50% of shelter-sites). In all adaptive kernel analyses, we used the optimal bandwidths (smoothing parameters) as calculated automatically by Calhome. Spatial overlap among the home ranges of radio-telemetered snakes was quantified as the average percentage of home range containing other snakes during a 12-month period. We estimated shared areas using 10 m grids placed over convex polygons. Percentages of shared area were arcsine-transformed to achieve homogeneity of variances (Sokal and Rohlf, 1969).

Sample sizes for different analyses on snake movements in this paper vary because dates of onset and conclusion of tracking, and thus duration of tracking, varied among individual snakes. In turn, this reflected transmitter failure and mortality of telemetered snakes (Whitaker and Shine, 2000).

Monitoring the Abundance of Mice

Between October 1993 and April 1996, live mice were captured using Elliott live traps (similar to Sherman traps) baited with a mixture of vanilla essence and rolled oats. Regular trapping on a transect allowed us to assess the abundance of mice along the long axis of the central refuge area. This trapline consisted of 52 traps placed at 22.5 m intervals to form a 1.2 km transect along a fenceline between the refuge area and adjoining farmland. We also trapped opportunistically when radio tracked snakes moved between shelter-sites, to quantify mouse abundance at previous locations compared to newly selected ones. In this way, we could directly test the hypothesis that brownsnakes move to areas with higher prey abundance. To do this, we laid two 4.5 m nine-trap grid patterns with the central traps placed 30 cm from the "old" and "new" shelter-site entrances used by the snakes. Both methods involved setting traps over three nights: at two-weekly intervals on the refuge area transect and opportunistically as the snakes moved over surrounding farmland.

RESULTS

Prey Abundance and Snake Diets

The numbers of House Mice (*Mus domesticus*) caught during three years of study varied in time and space, and corresponded to a tri-phasic model of mouse abundance on farmland (i.e., plagues build up slowly over a three-year cycle: Redhead, 1988; Twigg and Kay, 1995). The capture rate (number of mice per trap per month) on the refuge area varied significantly among the active seasons (one-factor ANOVA with active season as the factor, $F_{2,21} = 6.344$, $P < 0.01$). Overall mean capture rate (mice per trap per day) was 0.58 (SD = 0.54) in the first active season, 0.01 (SD = 0.01) in the second, and 0.22 (SD = 0.14) in the third. Mouse density peaked in late autumn (mean number of mice per trap = 1.37, in May) during the first activity season, when the refuge area traps became saturated (i.e., all traps filled with mice almost every night). Moreover, mice in the general farmland area (edge habitat around pasture and cereal crops) were highly abundant during the first activity season, when they approximated "Phase 3" of Redhead's (1988) tri-phasic model, were virtually absent in the second and were locally common in the third. Hence, we examined the tendency for brownsnakes to move to areas of greater mouse abundance in the second and third active seasons, when mice were less common (below). This could not be done during the first season, because mice were dense and approximately uniformly distributed in areas occupied by the snakes during this time.

Dissection of road killed adult snakes, and palpation of prey items from live animals when they were captured for transmitter insertion or replacement, revealed that 34 of 174 brownsnakes examined in the study area (19.5%) contained identifiable prey. The snakes consumed a variety of frogs ($n = 7$), reptiles (2 scincid lizards, 2 snakes) and mammals (15 mice, 2 rats, 2 rabbits). Introduced mammals were not found in juvenile snakes (which consumed small scincid lizards), while small mice were found in subadult snakes (80 to <95 cm SVL). Young rabbits (to approximately half-grown) were consumed only by adult male snakes. Although the overall pattern is thus that House Mice comprised about half of all prey items in adult snakes, diets varied significantly through time. In the drought year, no mice were recorded in snake stomachs; instead, the animals had consumed larger mammals (2 rats, 3 rabbits) as well as ectothermic prey (2 snakes, 3 lizards, 3 frogs). In contrast, prey items during the average rainfall years comprised mostly mice ($n = 15$), plus single records of a rat and a rabbit, and four frogs. These data indicate that the snakes switched to alternative prey during the drought affected (second) active season (comparing the proportion of diet composed of mice during the drought versus near average rainfall active seasons, $\chi^2 = 16.62$, df = 1, $P < 0.0001$).

General Movement Patterns

Eighty-five percent ($n = 34$) of the radio tracked snakes spent their winters in burrows on the central refuge area, whence they dispersed into surrounding farmland in warmer months. Ninety-four percent (32) of these snakes displayed burrow fidelity by returning to previously used sites. We recorded the locations of 34 over-wintering burrows for 17 of these snakes in two successive winters. Of these, 18% (3: 1 female and 2 males) returned to the same winter burrows they had used the previous year, and 82% used different burrows. The mean distance between successive winter burrows was 99.0 m (SD = 99.9, range 0–274.1 m), and there was no significant difference between males ($n = 8$) and females ($n = 9$) in the displacement distance between successive winters (one-factor ANOVA with sex as the factor, $F_{1,15} = 0.03$, $P = 0.86$). While the snakes showed a high level of burrow fidelity, each snake used many burrows over the course of the study.

During the active season, the snakes spent >90% of nights in burrows, and basked, foraged and moved about during the day. The same nocturnal shelter-site was typically used several times in succession, before the animal moved to a new site. However, visual and radio tracking records show that the snakes (especially males) often moved large distances during foraging activities, even when they later returned to the same overnight retreat. We frequently recorded snakes moving >400 m from the overnight retreats they used on successive nights. The maximum distance recorded away from a night time burrow was during drought, when a female traveled 1.16 km from a rocky hill in order to drink; she returned to her shelter-site the following morning. Thus, during most of the active season, a shelter-site (burrow) was used as a central base from which to forage for a period of several days, before the snake moved to another location. Because of this pattern of daily movement, our data on displacement between successive shelter-sites may substantially underestimate the total distances moved. Instead, they serve as a measure of the distances between successive centers of short-term activity ranges. Successive shelter-sites selected by adult males and non-reproductive females in farmland tended to form a "loop" (e.g., Gregory et al., 1987; Madsen, 1984) or "remigration" (Parker and Brown, 1980). Each snake (especially adult males) typically traveled over two or more such loops during the year (as migration typically was interrupted once or twice by returns to the refuge area during the active season).

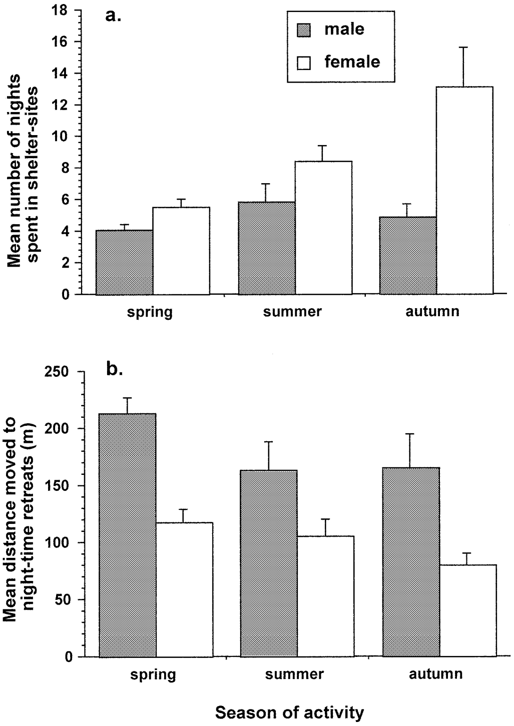

FIG. 1.—(a) Seasonal and sexual variation in the overall mean number of nights that radio-tracked snakes spent in shelter-sites during the active season. (b) Seasonal and sexual variation in the mean distances that radio-tracked snakes moved between successive shelter-sites. Histograms show means ± one standard deviation. Seasons were defined as follows: Dec–Feb = summer; March–May = autumn; June–Aug = winter; Sept–Nov = spring.

Frequency of movement.—On average, the 40 radio tracked snakes moved to new locations every six days ($n = 517$, SD = 8), with the overall frequency of movement differing among seasons (repeated-measures ANOVA for frequency of movements between early-spring and late-autumn, $F_{2,32} = 4.41$, $P = 0.02$; for definition of seasons see caption to Fig. 1). During the active season, the snakes moved most frequently in spring and least in autumn. The frequency of movement differed significantly between the sexes (one-factor ANOVA with sex as the factor and overall mean frequency of movement for each snake in each season of the year as the dependent variable, $F_{1,19} = 7.65$, $P = 0.01$). On average, males moved to a new shelter-site every 5.5 days (SD = 2.0) whereas females moved every 8.6 days (SD = 2.8). Adult males moved more frequently than did females in all seasons (Fig. 1a).

Neither sex continued to move about during winter. The snakes spent an average of 140 consecutive days (n = 26, SD = 21.0, range 103–182) in overwintering burrows, and there was no significant difference between the sexes in the number of days spent sequestered over winter. Males spent an average of 137 days (SD = 21.9) residing in winter burrows compared to 143 days (SD = 19.7) by females (one-factor ANOVA, $F_{1,24}$ = 0.42, P = 0.52). However, the timing of winter inactivity differed between the sexes, with most males entering their winter burrows earlier than females in autumn, and emerging earlier in spring. Overall, most males (75%) occupied winter burrows before May (although they sometimes emerged to bask and move about on warm days) whereas most females did not enter over-wintering burrows until mid-May. This delay in entering winter burrows was pronounced in females which had reproduced the preceding active season. All of the telemetered snakes occupied over-wintering burrows by the end of May. Females often remained inside over-wintering burrows until the onset of mating activity at the end of September (test for the number of females versus males which remained in their over-wintering burrows until the onset of mating, n = 26, χ^2 = 6.0, df = 1, P = 0.01). Thus, adult males tended to leave their winter burrows earlier than did adult females (by an average of 13 days) in spring. Most males left their winter burrows during the first week of September, whereas most females did not depart until nearer the end of that month.

Extent of movement.—The average distance moved between successive locations was 152.0 m (n = 583, SD = 163.0, maximum = 860 m), with a nonsignificant tendency for shorter movements as the active season progressed (repeated-measures ANOVA for the mean distance moved by individual snakes between early spring and late autumn, $F_{2,34}$ = 3.08, P = 0.06; Fig. 1b). The major contributor to this trend was the more extensive movements by adult males during spring.

The overall mean distance covered during successive moves by the snakes differed significantly between the sexes (one-factor ANOVA with sex as the factor and overall mean distance moved by each snake in each season as the dependent variable, $F_{1,18}$ = 7.02, P = 0.02). Males moved an average of 173.0 m (SD = 39.7) and females an average of 108.6 m (SD = 60.4) to new shelter-sites. Adult males consistently moved over greater distances between successive shelter-sites than did adult females, in all seasons (Fig. 1b).

Home Range and Core Area

Overall mean home range and core area size.—The average size of the home range for adult snakes over a 12-month period was 5.83 ha (n = 26, SD = 9.58; range 0.14 to 43.8 ha), with an average core area of 2.29 ha (SD = 2.68). These estimates changed little when we included all snakes monitored over 12 months in all years (i.e., repeated-measures). Calculated in this way, the home range averaged 6.01 ha (n = 35, SD = 9.39), and the core area averaged 2.28 ha (SD = 2.53).

Difference in home range and core area sizes among years.—To analyse these data, we treated each year's data on a snake as a separate observation. Hence, some snakes were represented by data from two years not one (Table 1). Annual adult home range size did not differ significantly among years (one-factor ANOVA with year as the factor, $F_{2,23}$ = 0.43, P = 0.65). Thus, the size of home ranges did not differ significantly between years with contrasting amounts of rainfall (drought versus near average) and associated prey abundance (mouse plague versus virtual absence) (one-factor ANOVA with drought as the factor, $F_{1,21}$ = 0.06, P = 0.81). Similarly, core area size did not differ among years (one-factor ANOVA, $F_{2,23}$ = 0.83, P = 0.45), nor with drought as the factor (one-factor ANOVA, $F_{1,21}$ = 0.03, P = 0.87). Consequently, we pooled our data on home range and core area sizes for all years in order to test for differences between the sexes with respect to body size and reproduction (below). We also found no significant difference between years in the home range size of nine snakes (4 males and 5 females) which we continuously monitored over two years (repeated-measures ANOVA, $F_{1,8}$ = 2.09, P = 0.19). Nonetheless, the overall mean size of male home ranges tended to increase when mice became scarce, from a mean of 3.83 ha (n = 12, SD = 5.37) in the first (near-average rainfall) year to 5.86 ha ($n = 10$, SD = 6.79) in the second (drought) year (see Table 1).

Differences in home range and core area size between the sexes.—Adult home range size differed significantly between the sexes (one-factor ANOVA with gender as the factor, $F_{1,24} = 10.04$, $P < 0.005$). Home ranges of males (mean = 11.79 ha, $n = 11$, SD = 12.95) were much larger than those of females (mean = 1.46 ha, $n = 15$, SD = 1.48). Core areas also were larger in males (mean = 3.79 ha, $n = 11$, SD = 3.17) than in females (mean = 1.19 ha, $n = 15$, SD = 1.61; $F_{1,24} = 7.55$, $P = 0.01$). These analyses include reproductive as well as nonreproductive females; the influence of reproductive status on female movements is examined below.

Influence of body size on home range and core area.—The eightfold difference in mean home range and threefold difference in mean core area sizes between the sexes were at least partly due to allometry of these gender-related traits, combined with sexual size dimorphism (adult males are larger than adult females, above). These differences indicate more extensive movements by the larger snakes (below). However, because adult males therefore were more likely to occur on surrounding farmland, these differences may also indicate that male snakes moved because they were more frequently disturbed. One male occupied a large and frequently disturbed farmland area during extensive construction work, and this animal showed by far the largest home range (43.8 ha, see Table 1). The distances traveled by this snake between successive shelter-sites were atypical of the population (below). Consequently, this snake was excluded from analyses of the relationship between home range and body size.

Among the remaining animals, there was a significant relationship between body length and the size of the home range ($r^2 = 0.43$, $P < 0.01$) and core areas ($r^2 = 0.35$, $P < 0.05$). Overall, larger animals had larger home ranges and core area sizes than did smaller animals (Fig. 2a). However, the sexes differed in these respects. Home range size was dependent on body size within males ($r^2 = 0.69$, $P < 0.01$) but not within females ($r^2 = 0.10$, $P > 0.1$) (Fig. 2b). Similarly, core area size was dependent on the body size of males ($r^2 = 0.58$, $P < 0.05$), but not on the size of females ($r^2 = 0.09$, $P > 0.1$).

TABLE 1.—Twelve-month home range sizes (minimum convex polygons in hectares) of 26 adult brownsnakes (*Pseudonaja textilis*). These data include the proportion of home ranges shared with snakes of either sex during the active season (September to May). Where snakes were monitored for two or more years, only the first year's data were used in the analyses (see text). * = yes.

Snake	Wintered on refuge	Year	Sex	Total home range area (ha)	% area where solitary	% area shared with males	% area shared with females
T1	*	1	m	3.246	16.45	72.92	50.74
T2	*	1	m	12.600	58.45	41.55	2.0
T3	*	1	f	2.241	73.14	1.65	26.86
T5	*	1	f^1	0.796	54.25	22.86	45.75
T6	*	1	f^1	0.142	3.52	95.07	97.18
T7	*	1	f^1	0.240	0	100.0	89.99
T8	*	1	f	2.479	12.59	74.95	53.25
T9	*	1	m	17.010	80.53	19.47	1.31
T10	*	1	f^1	0.198	0	100.0	100.0
T11	*	1	f^1	0.350	0	100.0	100.0
T12	*	1	m	3.312	5.04	94.38	47.91
T13	*	1	m	3.385	93.91	6.09	0.74
T14		1	m	43.800	n.k.	n.k.	n.k.
E1	*	2	m	5.940	98.1	0	1.9
F2		2	f	1.629	n.k.	n.k.	n.k.
H1		2	f	1.372	n.k.	n.k.	n.k.
S17		2	f	4.953	n.k.	n.k.	n.k.
S51	*	2	f	0.574	0	100.0	73.34
T1	*	2	m	19.260	73.36	22.98	6.87
T3	*	2	f	2.137	3.28	96.72	57.23
T5	*	2	f^2	0.818	8.81	73.71	84.84
T7	*	2	f	2.290	37.25	61.92	11.75
T8	*	2	f	1.106	0	99.15	96.84
T9	*	2	m	25.700	72.83	27.03	1.61
T10	*	2	f	0.611	0	100.0	100.0
T12	*	2	m	0.683	0	100.0	97.8
T13	*	2	m	5.871	17.12	63.77	19.66
T19	*	2	f	3.221	11.74	88.26	46.2
T21	*	2	m	0.992	16.33	68.85	56.86
T24	*	2	f	3.282	24.83	71.05	33.27
T25	*	2	m	18.430	38.96	54.15	26.02
T26	*	2	m	18.220	38.65	53.47	20.56
T33	*	3	f^1	0.270	0	n.k.	100.0
T34	*	3	m	2.732	n.k.	n.k.	n.k.
T36	*	3	f^1	0.208	0	n.k.	100.0

f^1 = reproductive female; f^2 = female mated but we found no evidence of eggs via endoscope in burrows; n.k. = not known.

Influence of female reproduction on home range and core area.—Reproductive females oviposited in burrows close to their overwintering sites, and moved about relatively little before laying. Moreover, they generally remained within the nesting burrow for one to five weeks after oviposition (possibly guarding the eggs). Overall, reproductive females moved about most frequently from mid-October to late November (post-mating), and again after nesting. Reproductive females

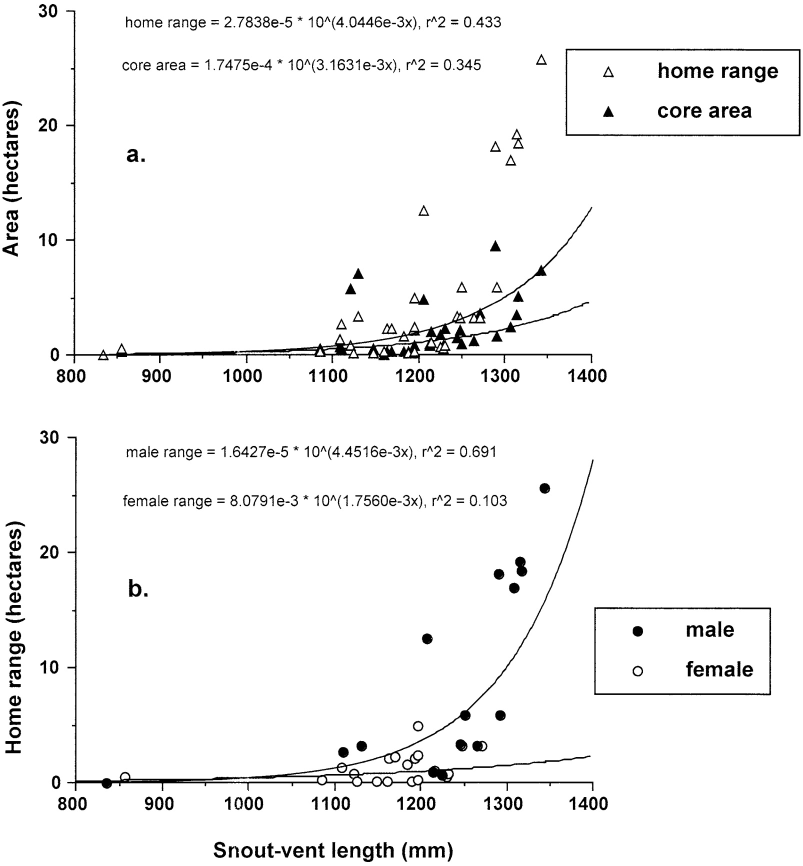

FIG. 2.—Home ranges and core area sizes of individual brownsnakes as a function of the snake's body size and gender. (a) Overall, larger animals occupied larger home range and core areas than did small animals. (b) The size of the home range depended on the body size in males but not females. Data for one outlier, a male which occupied a highly disturbed area, are not included (see text).

thus had smaller home ranges than did non-reproductive females (one-factor ANOVA with female reproduction as the factor and the annual home range as the dependent variable, $F_{1,18} = 15.42$, $P = 0.001$). The eight reproductive females we monitored during the study had an average home range of 0.38 ha (SD = 0.27) compared to 2.16 ha ($n = 12$, SD = 1.25) for non-reproductive females and 11.79 ha for males (above). Two gravid females made relatively long movements just prior to oviposition. The maximum such distance was 315 m, when a gravid female moved to a nesting burrow in late December. Other reproductive females ($n = 6$) remained in the vicinity of nesting burrows from spring emergence until the time of oviposition in early summer. Thus, reproduction did not influence the size of female core areas (one-factor ANOVA with female reproduction as the factor, $F_{1,18} = 0.015$, $P = 0.91$). Reproductive females generally restricted their movements between successive shelter-sites to within relatively small and frequently used areas until after oviposition. Conversely, the non-reproductive females occupied larger areas, including farmland.

Spatial and Temporal Overlap

Home range overlap between years.—Adult snakes residing on the central refuge area for at least part of two full years ($n = 9$ males and 10 females) provided useful data with which to examine social interactions, based on the proportion of their 12 month home range shared with other snakes. We restricted our analyses to these snakes because we knew the numbers of resident adults on the refuge area at those times (N = 41 to 45 through the duration of the study: Whitaker and Shine, 1999*b*).

Among these resident adult snakes, females had smaller home ranges than males (above). The females remained within 240 m of the refuge area during the entire active season (irrespective of reproductive condition) whereas males frequently moved further away (to approx. 1 km from the refuge area). Thus, female home ranges were concentrated along a 25 m-wide strip of land (the refuge area) with consequently high overlap among individuals (up to 100% of their total home range). Four of the adult males also used this area (other than over winter and in the mating season) when mice were plentiful, although they generally remained well away from each other (approximately 150–350 m apart) at this time (below).

The overall mean percentage of home range overlap was 67.03% (SD = 33.73) when estimated using the first 12 months of data for each snake. Including snakes in all years (repeated measures) made little difference to this estimate (70.03%, SD = 32.46). Despite the tendency for the snakes to range over wider areas when mice were scarce (above), the mean percentage of spatial overlap changed very little among years (one-factor ANOVA with year as the factor, $F_{1,17} = 0.001$, $P = 0.98$). Home range overlap averaged 66.84% (SD = 36.04) in the first year, and 67.34% (SD = 30.49) in the second (drought) year. There was also no significant difference in the percentage of overlap between these years for the nine snakes we continuously monitored over two years (repeated-measures ANOVA, $F_{1,8} = 0.96$, $P = 0.36$). Hence, while the overall mean size of brownsnake home ranges tended to decrease when prey became more abundant (above), mean home range overlaps (and core areas) remained unchanged.

Dependence of home range overlap on the snakes' sex.—Adult males shared significantly less of their home range than did adult females (one-factor ANOVA with sex as the factor, $F_{1,17} = 5.104$, $P < 0.05$). Mean overlap was 50.34% (SD = 34.96) in males, and 81.99% (SD = 25.77) in females. This difference remained essentially unchanged among years (two-factor ANOVA with year and sex as the factors, $F_{1,15} = 0.031$, $P = 0.86$) and reflects the relatively wide dispersal of males during the active season, compared to the close proximity of females on the refuge area.

Characteristics of Shelter-Sites

More than 98% of shelter-sites selected by the snakes were holes (cavities, burrows or cracks) in the ground. The rest (all selected by males) included retreats in or under hay or straw, under metal debris (e.g., sheeting, girders and tracks), and inside hollow logs. Most of the holes selected on farmland were House Mouse burrows and, less frequently, crayfish burrows and rabbit warrens. Holes used by the snakes as shelter on the refuge area included relatively deep and complex burrow systems. These holes were originally formed (and/or enlarged) by lizards (*Ctenotus robustus* and *Tiliqua scincoides*) and rodents (*Mus domesticus* and *Rattus rattus*), and by long-term erosion due to repeated animal use and rainwater. We did not observe the snakes forming their own burrows, but we did see them enlarging pre-existing holes (including spider burrows) by pushing in moist soil.

Shelter-sites were not selected during winter, because the snakes were largely inactive during that time. Consequently, tests for seasonal differences in the physical attributes of shelter-sites (below) did not include winter. The tests below treat data on attributes of successive burrows used by the same snake as independent data points, and thus are technically pseudoreplicates at this level. There is no straightforward way to avoid this problem, but any *P* values from these analyses should be treated as indicative only.

Aspect.—The overall aspect of shelter-sites used by the snakes was significantly nonrandom. Comparing the number of locations in each quadrant of the compass to a null hypothesis of equal numbers in each quadrant, the snakes selected significantly more sites on north-facing slopes than expected by chance ($\chi^2 = 450.80$, df = 3, $P < 0.0001$). The sexes differed in this respect. Females were more likely than males to choose north-facing slopes ($\chi^2 = 59.92$, df = 3, $P < 0.0001$); 81.6% of female retreats were on north-facing slopes, compared to 62.4% of male retreats. This in part reflected the greater tendency of males to

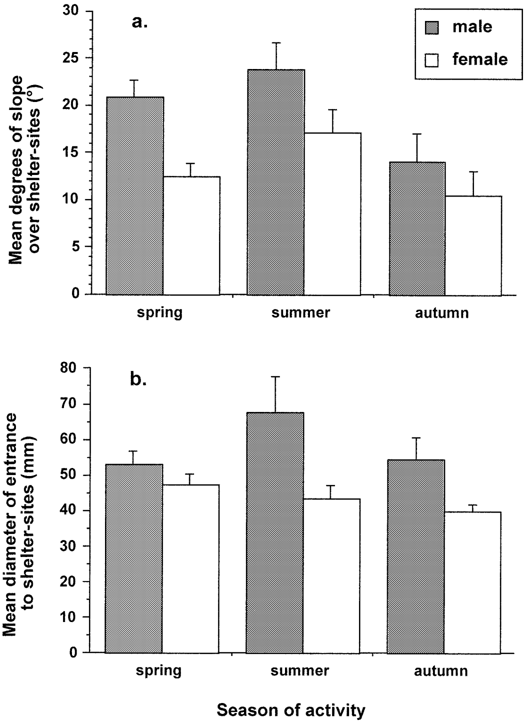

FIG. 3.—The steepness of slope over shelter-sites, and the diameter of burrows selected, as a function of the radio-tracked snakes' sex and the season in which it was monitored. Histograms show means ± one standard error.

select shelter sites on farmland rather than on the canal bank, especially in summer when many females occupied nesting burrows on north-facing aspects. Consequently, the choice of aspect differed among seasons ($\chi^2 = 66.74$, df = 6, $P < 0.0001$). Overall, most of the snakes selected north-facing (relatively warm) aspects in spring (75.3%) and autumn (79.6%), but were less likely to do so in summer (62.3%).

Slope.—Males selected shelter-sites on steeper slopes than did adult females in all seasons (one-factor ANOVA with sex as the factor, $F_{1,634} = 15.20$, $P < 0.0001$). The mean slope of entrances to male shelter-sites was 20.6° ($n = 320$, SD = 24.5), compared to 13.6° ($n = 316$, SD = 20.3) selected by females. This was also partly due to the greater male occupancy of farmland (including steep embankments and burrows in stored fodder). However, we found no interaction between sex and season in the degree of slope selected (two-factor ANOVA, $F_{2,630} = 0.52$, $P = 0.59$). Both sexes selected steeper slopes (e.g., channel banks) in summer than they did in other seasons (one-factor ANOVA with season as the factor, $F_{2,633} = 4.61$, $P = 0.01$; Fig. 3a).

Burrow diameter.—The burrows occupied by male brownsnakes were wider than those occupied by females (one-factor ANOVA with sex as the factor, $F_{1,571} = 11.78$, $P < 0.001$). There was no significant interaction between sex and season in the diameter of burrows selected (two-factor ANOVA, $F_{2,567} = 2.28$, $P = 0.1$). The overall mean size of burrows (entrance diameter = 51 mm, SD = 44) varied only slightly among seasons (one-factor ANOVA with season as the factor, $F_{2,570} = 0.99$, $P = 0.37$). During summer, however, adult males were more likely to occupy larger burrows in surrounding farmland, including those of the introduced European rabbit (*Oryctolagus cuniculus*) (Fig. 3b). Mean burrow diameter selected by males in summer was 67.7 mm ($n = 67$, SD = 82.4), compared to 43.6 mm ($n = 92$, SD = 32.4) selected by females. In autumn, mean burrow diameter was 54.5 mm for males ($n = 57$, SD = 45.9), and 40.1 mm for females ($n = 73$, SD = 13.4).

Vegetation cover.—We found no significant difference in the percentage of vegetation cover over shelter-sites selected by males versus females (one-factor ANOVA with sex as the factor, $F_{1,649} = 3.09$, $P = 0.08$), nor in the percentage of vegetation cover selected in different seasons (one-factor ANOVA with season as the factor, $F_{2,648} = 1.80$, $P = 0.17$). Similarly, we found no significant interaction between sex and season in the percentage of cover selected (two-factor ANOVA, $F_{2,645} = 2.76$, $P = 0.06$). The snakes selected shelter-sites with a similar percentage of cover in all seasons they were active. On average, male shelter-sites were 55.9% ($n = 338$, SD = 34.4) covered by vegetation, and female shelter-sites 51.1% ($n = 313$, SD = 34.1) covered. Hence, over-wintering burrows (which were mostly located on northerly aspects and generally became more exposed as vegetation died in summer) tended to be less frequently occupied by the snakes in the mid-active season.

Effects of Mouse Abundance on Snake Movements and Shelter-Site Use

Brownsnakes frequently shifted from one nocturnal retreat to another (above). If the presence of prey (mice) stimulated these movements, we would expect mouse numbers to be consistently higher at the "new" sites than at the "old". Data for the number of mice trapped on both types of site following 27 such movements (all in months when mice were detected in the general area) revealed a significant tendency for the snakes to move to sites where mice were more abundant (test for an equal probability of movement to areas with more or fewer mice, $\chi^2 = 6.26$, df = 1, $P = 0.01$); 74.0% of these movements ($n = 20$) were to sites with more mice. Both male and female snakes tended to move to areas where mice were more common.

The spatial association between snakes and mice varied among seasons (comparing the overall number of snakes which moved to areas of higher versus lower mouse abundance in each season, $n = 58$, $\chi^2 = 5.90$, df = 2, $P = 0.05$), presumably because movement was also affected by other stimuli (e.g., mate searching in spring). The snakes were most likely to move to higher numbers of mice during late spring and summer. Forty-five percent of the total movements to areas with more abundant mice occurred in summer, and 100% of all summer movements in near-average rainfall years were to sites where mice were more common. The snakes also were more likely to select sites in mouse rich areas in late autumn. Comparing mouse numbers in late May near 14 occupied over-wintering burrows on the refuge area versus 14 unoccupied randomly selected burrows in the same area (in comparable situations and used by the snakes the preceding active season), a one-factor ANOVA with burrow occupancy as the factor shows a significant difference ($F_{1,26} = 7.34$, $P = 0.01$).

Effects of Other Snakes on the Use of Shelter-Sites and Movement

Adult females and subadults of both sexes were more likely to be found together (i.e., in the same burrow) than were adult males (comparing all occasions, including the breeding season, when 29 adult females and one adult male [with a subadult] were found residing in the company of other snakes; against an equal probability of cohabitation between the sexes, $\chi^2 = 16.71$, df = 1, $P < 0.0001$). Adult males were solitary at all times other than during the mating season and, hence, were far less likely than females to be in the company of other snakes (comparing the frequency of cohabitation among adult males versus adult females, other than during the breeding season, $n = 25$, $\chi^2 = 4.84$, df = 1, $P < 0.05$). This difference partly resulted from communal nesting and over-wintering by females.

Social interactions also affected the movement patterns of our radio tracked snakes. When an adult male moved to a burrow already occupied by another brownsnake (whether it was another adult male or female), the "resident" usually moved away within a few hours to another location. Adult females tolerated adult males in close proximity only during the mating season, when males sometimes courted reproductive females for up to three days before mating. When adult males moved to burrows occupied by adult females at other times (e.g., on return to the central refuge area in autumn), the females promptly moved elsewhere. This movement away always occurred within 14 hours (mean = 9.2 hours, SD = 5.6, $n = 13$), even if the timing of male entry into the burrow forced the female to cohabit overnight. We compared the number of hours to displacement after males moved into burrows occupied by females versus the mean number of hours these females were expected to reside in the absence of males (outside of the breeding season) based on general patterns of residence times (above). The tendency for a male's arrival to stimulate the female's departure was highly significant (unpaired *t*-test, $t_{1,11} = 9.95$, $P < 0.0001$). Hence, the movements and locations of brownsnakes were strongly influenced by the location of adult males.

DISCUSSION

Our data provide the first detailed information on the spatial ecology of brownsnakes (*Pseudonaja*), and are among the first data on this topic for any large species of elapid snake (see Dredge, 1981; Schwaner, 1991; Shine, 1987; Shine and Lambeck, 1990). Our study identifies several factors that influence the frequency and extent of movement, and the size and type of areas occupied by brownsnakes. Attributes of the snake are at least as important as are attributes of the environment. Indeed, we found stronger relationships between spatial ecology and the snakes' sex, size and reproductive status, than between spatial patterns and environmental factors such as drought, cover and prey availability. Nonetheless, both types of factors undoubtedly play a role.

Many of these results fit well with intuition, and with what is known of other snake taxa in different parts of the world. For example, male snakes tend to emerge from winter refugia before females, at least in species which mate in spring (e.g., Gregory, 1974; Parker and Brown, 1980). This early emergence may allow males to produce spermatozoa, and ready themselves for reproductive activities (Volsoe, 1944). Also, male snakes frequently show increased activity and movement during the mating season, presumably to enhance reproductive success (Aldridge and Brown, 1995; Bonnet et al., 1999; Gibbons and Semlitsch, 1987; Gregory et al., 1987). The home ranges of snakes may often differ in size among seasons (e.g., Durner and Gates, 1993), and be larger in males than in conspecific females (reviewed by Gregory et al., 1987; Macartney et al., 1988). Male *P. textilis* grow larger than conspecific females, and males in our study population moved more often and over greater distance than did females. Foraging snakes probably often move to areas where prey are more common, although this pattern has rarely been demonstrated empirically (e.g., Duvall et al., 1985; Madsen and Shine, 1996; and see Schwaner, 1991).

Reproduction affects movement patterns of females as well as males. Home ranges of non-reproductive female snakes frequently are larger than those of reproductive females (e.g., Andren, 1982; Brown et al., 1982; Reinert and Kodrich, 1982; Webb and Shine, 1997; Viitanen, 1967). In our study, reproductive females moved less and occupied smaller areas than did non-reproductive females. Reproductive and non-reproductive females also differed in the way in which movement patterns shifted over the course of the year. Reproductive females oviposited in burrows close to their over-wintering sites, and generally remained within the nesting burrow for one to five weeks after oviposition. Overall, reproductive females moved about most frequently from mid-October to late November (post-mating), and again after nesting. At these times they often moved to sites with higher numbers of mice—but the distances traveled by the snakes generally were small. Thus, most hunting by reproductive females occurred in rodent burrows in the refuge area or only a short distance away from it. In contrast, males and non-reproductive females hunted over much larger areas of the surrounding farmland (although these females remained within 240 m of the refuge area).

Because reproductive activities generate differences in habitat use, the sexes differed in many other habitat attributes that we scored (such as the slope and aspect of shelter-sites). These differences probably were by-products of the males' occupancy of a more varied landscape: males spent much of the year in a habitat (farmland) only rarely used by females. Such sex divergence in foraging habitats may be common in snakes (e.g., Durner and Gates, 1993) and result in significant sex divergence in attributes such as dietary composition (e.g., Houston and Shine, 1993). The larger diameters of male (versus female) burrows simply may reflect the larger mean body size of males in our study, combined with the fact that (perhaps because of this larger size) males sometimes take larger prey than those taken by females (Shine, 1989). The burrows of these larger prey (such as rabbits) are larger than the burrows of smaller prey types (mice), and are more common in farmland than on the canal bank frequented by female brownsnakes.

Although many of our results thus accord with intuition, some of our data generate surprising conclusions. In particular:

(1) These agile animals have remarkably small home ranges (mean = 5.8 ha) relative to their large body size. We recorded individuals to travel >2.3 km in a 24-hour period, but nonetheless the snakes generally restrict their movements to small areas. This was true both under conditions of high and low prey availability, suggesting that it is a consistent feature of the animals in the study population. In contrast, radio-telemetric studies on other taxa have generally revealed much larger home range sizes, even in smaller and less mobile species than *P. textilis* (Macartney et al., 1988). This result provides a strong cautionary tale: it

is difficult to predict spatial ecology from body size and agility of the study species. We confidently expected these large, fast-moving snakes to travel over very large distances, and we were comprehensively wrong.

(2) Although the snakes moved about in the course of activities such as foraging and mate searching, they typically returned to the same shelter-site for several nights before moving on. Moreover, our study animals consistently returned to the same parts of the refuge area (frequently to the same burrows) and their core areas remained approximately fixed over time (confirmed by records from snakes monitored over three years, data not shown). The trend for adult males and non-reproductive females to move in "loops" (e.g., Gregory et al., 1987; Madsen, 1984) or "remigrations" (Parker and Brown, 1980) has not been documented for other Australian elapids (but see Webb and Shine, 1997), perhaps reflecting the paucity of long-term studies on this group. Remigration was lacking in the six subadults we studied (81 to 94 cm SVL), all of which behaved similarly to reproductive females by remaining on the refuge area during the two to seven months we monitored them. Unfortunately, we have no comparable data concerning the movement of smaller snakes.

(3) A relatively small area (the canal bank "refuge area") is disproportionately important to the brownsnake population. Virtually all of the snakes in the surrounding region returned to this small area to over-winter, all of the eggs were laid there, and many animals (especially reproductive females and subadults) spent the majority of their time within this area. This concentration of snakes has obvious implications for conservation and management, but it is difficult to identify why this particular area is so attractive to the snakes. The most important factor may be its lack of disturbance: farmers rarely walk through it, there is no livestock grazing there, and the soil contains numerous deep tunnels frequently used by the snakes. The surrounding farmland has much more frequent human presence, considerable grazing pressure and agricultural activity. This activity includes frequent ploughing, which destroys the burrow systems and sometimes kills snakes in the process (PBW, personal observation). Because the refuge area is bordered on one side by a canal, and on the other by several hundred meters of open farmland, it also appears to have fewer predators (e.g., foxes, cats, varanid lizards) and in consequence, may be safer for the snakes (Whitaker and Shine, 2000). It also supports higher densities of prey, such as frogs, lizards and mice (PBW, personal observation).

(4) Social interactions among individuals play a significant role in determining patterns of movement and space use. The prevailing paradigm in this respect is that snakes are highly non-social (e.g., Brattstrom, 1974; but see review by Gillingham, 1987). This view, however, has been challenged by popular writings (e.g., Isemonger, 1968), and by laboratory research (e.g., Almeido-Santos et al., 1999; Carpenter, 1984; Firmage and Shine, 1996; Halpern and Kubie, 1984; Kelleway, 1982). Although observations in the field suggest that social bonds may be involved (e.g., the delayed dispersal of neonatal pitvipers, and scent-trailing of mothers: Duvall et al., 1985; Greene, 1997), field studies have provided little evidence of social behavior, apart from that intimately involved with reproduction (e.g., ritualized combat bouts in males: reviewed by Gillingham, 1987; Shine, 1994).

Our study suggests a much stronger role for social interactions than has been generally accepted for snakes. Female brownsnakes aggregate not only for communal nesting (above), but also at other times of the year. In contrast, male brownsnakes appear to actively avoid each other, and to be avoided in turn by conspecifics of both sexes. Previously, the only quantitative evidence for avoidance of conspecifics in free-ranging snakes came from a telemetric study on a small Australian elapid species, *Hoplocephalus bungaroides* (Webb and Shine, 1997). Non-overlap of home range suggests these snakes may actively avoid each other, but the inference was indirect. In the present study, the evidence for active avoidance of conspecifics is much stronger: (i) adult males cohabited less often than did other members of the population; (ii) home ranges of males overlapped much less than did those of females; and (iii) the entry of an adult male into an occupied burrow at times other than during the mating season was rapidly followed by egress of the prior resident. We thus conclude that the spatial dispersion of eastern brownsnakes is affected by interactions among individuals. Snakes may be much more "social" than has generally been believed.

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