

Spatial ecology of slatey-grey snakes (*Stegonotus cucullatus*, Colubridae) on a tropical Australian floodplain

Gregory P. Brown*, Richard Shine*¹ and Thomas Madsen*†

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

† Biological Sciences, University of Wollongong, NSW 2522 Australia
(Accepted 28 February 2005)

Abstract: The extent, sequence, synchrony and correlates of diel displacements by animals can provide powerful insights into the ecological and social factors that shape an organism's day-to-day activities, but detailed data on spatial ecology are available for very few tropical taxa. Radiotelemetric monitoring of 25 slatey-grey snakes (*Stegonotus cucullatus*) on a floodplain in the Australian wet-dry tropics for periods of 40 to 355 d (mean = 195 d, 136 locations per snake) provided extensive information on habitat use, movement patterns and home range size of these large slender-bodied colubrids. All radio-tracked animals were nocturnal, sheltering by day in soil cracks and beneath tree roots and debris. Snakes did not appear to move between 61% of successive locations and timing of movements was not synchronized among snakes. Most displacements were small (< 50 m), with males moving further and more often than did females. However, nesting females made occasional long-distance movements, travelling 100–400 m to forested areas to oviposit but then returning to their usual home ranges. Snakes of both sexes moved further and more often during the wet-season than the dry-season. Snakes typically moved on a few successive nights then remained sedentary for the next few days, apparently reflecting cessation of activity as soon as a meal was obtained. Home ranges were small (2.9–7.4 ha) and most snakes remained in the same area throughout the year, providing a strong contrast in this respect to the large and seasonally dynamic home ranges of sympatric acrochordid and pythonid snakes.

Key Words: activity, home range, movements, radiotelemetry, reptile

INTRODUCTION

All vertebrate animals must move about to find the resources they need (e.g. food, water, shelter), to locate potential mates and to avoid predators. However, the spatial scale of such movements, and the degree to which they are modified by factors such as sex, season and body size, vary in complex ways (Clutton-Brock & Harvey 1979, Kessing 1998, Mace & Harvey 1983). Empirical evidence on these abiotic and biotic correlates of movement patterns can therefore be used to clarify critical ecological issues such as the role of weather conditions, prey resources, predation pressure, mate availability and intrasexual competition on the day-to-day lives of organisms (Daltry *et al.* 1998, Gibbons & Semlitsch 1987). Knowing when, where, how often and how far an animal is likely to move is also critical to identifying the appropriate spatial scale and attributes

of any area set aside to protect or manage such an organism (Caughley 1994, Caughley & Sinclair 1994). In consequence, ecologists have devoted considerable attention to quantifying spatial ecology of a diverse array of taxa (Gregory *et al.* 1987, Milton & May 1976, Rivera *et al.* 2003, Rolando 2002).

Inevitably, some kinds of animals and some kinds of habitats have attracted disproportionate attention in this respect. Logistical issues are a primary determinant of such biases, although these have changed considerably through time. For example, the development of miniature radiotransmitters has allowed researchers to relocate individual animals even in taxa that were previously too difficult to study (Reinert 1992). Nonetheless, major biases remain. The scientific literature on spatial ecology of snakes provides a good example of this situation. Although radiotelemetric studies on spatial ecology of snakes have proliferated over the last few decades, the vast majority of these studies have been conducted in cool-climate (temperate-zone) habitats in Europe and North America (Gibbons & Semlitsch 1987, Gregory *et al.* 1987).

¹ Corresponding author. Email: rics@bio.usyd.edu.au

Despite the fact that snakes are far more diverse in the tropics than in cooler climates, only a trivial proportion of even the most abundant tropical snake taxa have yet been investigated in any detail (Daltry *et al.* 1998).

Unsurprisingly, the dramatic seasonal shifts in temperate-zone habitats massively affect movement patterns in snakes, with many taxa sedentary during winter and then dispersing long distances to and from communal hibernacula in autumn and spring (Brown & Parker 1976, Gregory & Stewart 1975, Parker & Brown 1980). Do tropical snakes display equivalent seasonal shifts in the amount or location of activity? The scarcity of field-based studies on snake spatial ecology in the tropics precludes any general answer to this question, but several studies have suggested that seasonal shifts in precipitation rather than thermal regimes may drive major patterns in spatial ecology. Many tropical environments are hot year-round but exhibit extreme seasonal variation in precipitation regimes and thus, important components of the habitat. For example, the onset of monsoonal rains can inundate vast areas, massively altering both abiotic conditions (thermal, hydric) and biotic factors (e.g. abundance and distribution of prey) that in turn might favour modifications of movement patterns by predators (Daltry *et al.* 1998, Madsen & Shine 1996, Shine & Lambeck 1985, Webb & Manolis 2002).

The present paper describes a radiotelemetric study of spatial ecology in a poorly known snake taxon living in a tropical habitat exposed to massive seasonal variation in rainfall. We focus on the ways in which factors such as season and sex influence movement patterns and the size and location of the home range, and on quantifying temporal patterns of movements to clarify proximate causes for variation in activity.

MATERIALS AND METHODS

Study species

Slatey-grey snakes (*Stegonotus cucullatus* Duméril, Bibron and Duméril 1854) are slender-bodied terrestrial colubrids distributed widely through near-coastal regions of tropical Australia and New Guinea (Cogger 2000). The genus *Stegonotus* contains 11 species in New Guinea, Borneo and the Philippines (Greer 1997, O'Shea 1996), suggesting that the sole taxon in mainland Australia (*S. cucullatus*) is a relatively recent immigrant from the north (Cogger & Heatwole 1981, Greer 1997, Shine 1991). Despite their largely terrestrial habits, these snakes can climb effectively and rapidly (Mirtschin & Davis 1992, *pers. obs.*). Although harmless, they have large bladelike teeth midway along the maxilla (perhaps adaptive to slitting eggshells: Scanlon & Shine 1988) and defend themselves pugnaciously if harassed (*pers. obs.*). At our

study site, slatey-grey snakes have a diverse diet that primarily comprises frogs, reptile eggs (especially those of keelback snakes, *Tropidonophis mairii* Gray 1841) and native rodents (especially dusky rats, *Rattus colletti* Thomas 1904: Brown *et al.* unpubl. data), but also includes fishes. The diet is diverse even over short time periods: for example, one snake disgorged a freshly ingested eel plus a rat, and six others disgorged both rats and snake eggs. Until recently, all published ecological data on *S. cucullatus* were derived from dissection of museum specimens (Shine 1991). However, we are now conducting a mark–recapture study on this species on the Adelaide River floodplain near Darwin (Brown *et al.* 2001). The present paper describes our radiotelemetric studies at the same site.

Study area

Fogg Dam is an artificial impoundment on the Adelaide River floodplain 60 km east of Darwin in Australia's wet-dry tropics. The dam is surrounded by eucalypt-dominated woodland on three sides and with an extensive floodplain below the dam wall (see Madsen & Shine 1996 for a detailed description of this site). The climate is hot year-round (mean monthly air temperatures > 23 °C in every month) but with pronounced seasonal variation in rainfall. Based on a 30-y average, more than 78% of the high (1402 mm) annual precipitation falls as monsoonal downpours in a 4-mo 'wet-season' (December–March). To compare movement patterns of snakes among seasons, we divided the year into four periods (see Brown *et al.* 2001 for more detail): wet-season (December–March; monsoonal rains), early dry-season (April–May; little rain but continued extensive flooding), middle dry-season (June–September; relatively cool and dry), and late dry-season (October–November; high temperatures and humidity, but little rain). Thus, we recognized two 4-mo periods (the classical 'wet' and 'dry' seasons) separated by 2-mo transitional periods.

Methods

Snakes were captured by hand during nightly surveys, and processed as part of a mark–recapture study before release at their site of capture the following day. All animals were measured (snout–vent length [SVL], head length and tail length), weighed, individually marked (scale-clipped) and palpated for the presence of prey items or eggs. Sex was determined by hemipenal eversion. Gravid females were retained until oviposition, and an additional 25 snakes (7 males (SVL 100–138.25 cm), 18 females (SVL 80.25–127.25 cm)) were used for radiotelemetric monitoring. We used three sizes of transmitter (Holohil Systems Ltd models SB2T, SI2T, PD2T) ranging in size from 3.4–9.7 g. Transmitters were surgically

implanted in the peritoneal cavity of these animals under halothane anaesthesia and using sterile procedures. Whip antennae 20–25 cm long were implanted subcutaneously, using a method similar to that developed by Reinert (1992). Snakes were retained in captivity for an average of 20 d, during which they were used in a variety of thermal preference studies, then released at their original capture site. There was no evidence of reduced or enhanced rate or frequency of movement immediately subsequent to release. For example, rates and distances of movement did not differ among the 1st, 3rd, 5th, 8th or 16th week of liberty (ANOVA with week as the factor, all $P > 0.20$).

Body sizes of the radio-tracked snakes ranged from 80.3–138.3 cm SVL (140–633 g). Thus, the transmitters weighed 1.1–3.5% of the mass of the snakes into which they were implanted. These 25 snakes were tracked for an average of 196 d (range 40–355 d) between 1998 and 2002. The duration of monitoring varied among individuals because of differences in transmitter life span, and mortality of radio-tracked animals (eight telemetered snakes were killed; normal annual adult mortality rate in the population is 43%; Brown *et al.* unpubl. data). On average, the snakes were located 126 times each with a mean duration between successive fixes of 1.4 d; 79% of fixes were on consecutive days.

Analysis of movement patterns

Twenty-two snakes were located frequently enough to provide robust data on movements. Restricting analysis to cases in which a snake was located on successive days, we calculated two variables to characterize movement patterns: (1) distance moved between successive days, and (2) the proportion of days that snakes moved at all. Statistical analysis of these patterns was based on single mean values for each variable for each snake in each season, to avoid pseudoreplication. To examine seasonal effects, we divided the year into 'wet' (December–March) and 'dry' (April–November) seasons.

To assess synchrony of movements among individuals we adapted the Synchronization Index (SI) method of Ruckstuhl (1999). Analyses were limited to periods when at least six individuals were located on successive days. We used data from 19 snakes that were located on at least 25 d when 5 or more other snakes were also located. Each snake in the data set was designated in turn as a focal individual. The focal individual was assigned an SI value of 1 if $> 50\%$ of the other animals in the group exhibited the same activity (movement vs. no movement) as it did during a 24-h period. If $< 50\%$ of the other animals in the group exhibited the same activity as the focal animal, the focal animal was assigned an SI value of 0. If exactly 50% of the other snakes exhibited activity, the focal animal was assigned an SI value of either 0 or 1 by a random

'coin-flipping' procedure. Thus, the mean SI calculated for each individual measures the extent to which its pattern of movements corresponds to the pattern of movement of the rest of the group of snakes radio-tracked over the same period.

To test the significance of the mean SI value for each snake, we used a randomization procedure whereby the movement patterns of each focal animal were randomly shuffled, and an SI value calculated as above (i.e. relative to activity of the rest of the group: Engel & Lamprecht 1997). This process was repeated 1000 times, and the significance level of the observed mean SI was then determined by its ranking among the 1000 randomly generated mean values (Marsden & Evans 2004).

Analysis of home ranges

Snakes that we monitored for relatively long periods provide information on the degree to which the size and location of the home range is influenced by factors such as sex and season. We used the program HomeRange (Version 1.1; Huber & Bradbury 1995, UC San Diego) to calculate 100% minimum convex polygon (MCP) home ranges (White & Garrott 1990). Home range centres were calculated as the arithmetic mean value of x and y coordinates.

RESULTS

Habitat use

Slaty-grey snakes are entirely nocturnal in our study area. When we located telemetered snakes by day, they were invariably hidden within deep cracks in the soil, or beneath thick grass or tree roots. Although juvenile slaty-grey snakes often are arboreal during their nocturnal activity, most diurnal retreat-sites of our radio-tracked adults were terrestrial, and generally underground. Snakes located in water were always in thick mats of floating vegetation. Anthropogenically modified habitats, especially raised embankments on the floodplain, were often used. Habitat types showed minimal change between seasons. Of three snakes that shifted their home ranges between wet- and dry-seasons (i.e. no spatial overlap between home-ranges in the two seasons: see below), two became more closely associated with the edges of waterbodies during the wet-season. The other snake simply shifted its home range a few metres along the same embankment.

Effects of sex and season on movement patterns

Two-way ANOVAs with sex and season (wet and dry only, 'between' seasons excluded) as factors showed that the mean distances moved per day were greater for male

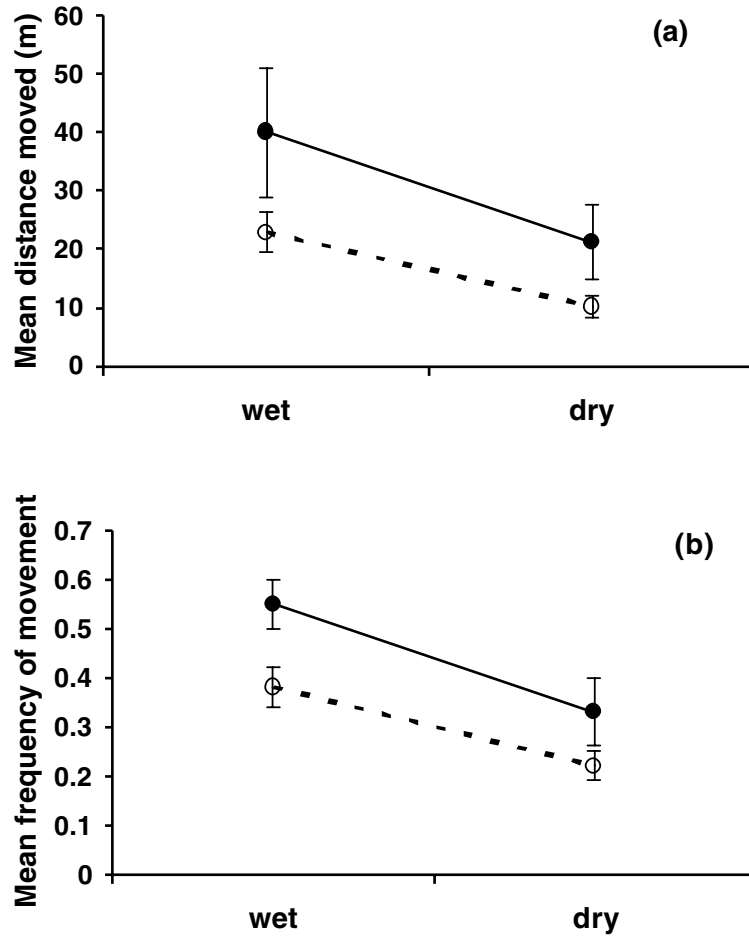


Figure 1. Mean distances moved between locations (a) and frequency of movements (proportion of radio fixes) (b) for male (solid symbols and lines) and female (open symbols broken lines) slatey-grey snakes during the wet-season (December–March) and dry-season (June–September). Note that males move further and more often than females, and that movements are more frequent and more extensive in the wet-season than in the dry-season. Error bars represent standard errors.

snakes than for females ($F_{1,36} = 7.5$, $P < 0.01$) and greater during the wet-season than the dry-season ($F_{1,36} = 9.5$, $P < 0.004$), with no significant interaction between these factors ($F_{1,36} = 0.4$, $P = 0.56$; see Figure 1a). The same patterns were evident for the frequency of movements (sex effect, $F_{1,36} = 9.6$, $P < 0.004$; season effect, $F_{1,36} = 17.1$, $P < 0.002$; interaction, $F_{1,36} = 0.6$, $P = 0.45$; see Figure 1b). Any such sex differences in a dimorphic species such as *S. cucullatus* might be due to body size rather than to sex per se. To test this possibility, we repeated the above analyses after including snout–vent length [SVL] as a covariate (that is, did sex and season affect movement patterns after body-size differences between the sexes had been factored out of the analysis?). None of our major conclusions (above) was affected; SVL did not explain significant variance in any of the models, and its inclusion did not influence the significance of the previously entered main effects except for the male–female difference in frequency of movements (which may thus be due to body size rather than sex per se).

Proximate cues for movement

On average, our radio-tracked snakes moved on 26% of days during the dry-season and on 43% of days during the wet-season. However, movements often occurred on successive days followed by longer sedentary periods. To test this pattern against a null hypothesis of random intervals between days with movement, we used contingency table analysis to examine the relationship between movement probabilities on successive days. Pooling data from all individuals, this test confirmed that a move tended to be followed by another move whereas a sedentary day was likely to be followed by another sedentary day ($N = 2282$, $\chi^2 = 266$, $P < 0.0001$). Examining data for the 25 snakes separately, the association was statistically significant for 16 cases, marginal ($0.05 < P < 0.10$) for five and clearly non-significant ($P > 0.10$) for only four snakes.

Why did movements of radio-tracked snakes occur in pulses followed by periods of (apparent) inactivity? If the

proximate stimuli for such a pattern occur simultaneously across the study area (e.g. meteorological, astronomical, biological conditions) we would expect the activity pulses to be synchronized among snakes. We tested this prediction by calculating synchronization indices for each snake. The prediction was not supported. None of the mean SI values calculated for the 19 snakes was outside the 2.5–97.5 percentiles of the distributions of randomly generated values. Overall, the mean values of SI for the 19 snakes did not differ significantly from mean SI values calculated from 1000 random permutations (mean SI 0.519 vs. 0.522, $t = 0.138$, $P = 0.89$). Thus, there is no evidence of synchronized activity (at least on the basis of changing location) among slatey-grey snakes.

Nesting migrations

Most nightly displacements by slatey-grey snakes were relatively small (> 60% were < 50 m). However, unusually long movements were recorded from four radio-tracked females monitored during the peak nesting period (September–December). All four of these animals made sudden, rapid movements of 100–400 m, taking them well outside their usual home ranges. Two females captured as soon as they made these movements were gravid, and both oviposited in captivity within 2 d. The other two females were not captured; they stayed in their unusual locations for 2–7 d and then moved directly back to their original areas. In all cases these apparent nesting migrations took snakes from relatively open treeless areas to forested microhabitats comprising paperbark trees (*Melaleuca*, two cases), mangroves (*Aegiceras*, one case) and monsoonal forest (one case).

Home ranges

Figure 2 maps seasonal home ranges for four snakes that were monitored in all four seasons. These snakes remained within the same general area throughout the year: the centres of wet- and dry-season home ranges (circles in Figure 2) were separated by < 100 m for each of the five snakes for which we had data in all four seasons. Home ranges were surprisingly small for such large (to 1.5 m) snakes, ranging from 2.9–7.4 ha for these five examples. An additional nine snakes were tracked during both the wet- and dry-seasons. For all 14 animals, the distance between the centres of wet- and dry-season home ranges averaged 119.4 m (SE = 37.1, range = 5.9–478.8 m). For seven of these 14 snakes, centres of wet- and dry-season home ranges were < 55 m apart. On average, wet- and dry-season home ranges overlapped by 34.6% (SD = 33.3, range = 0–100%). Mean home range areas did differ significantly between wet- and dry-seasons (13.7 ha vs. 15.8 ha, $t = 0.47$, $P = 0.65$).

DISCUSSION

The most remarkable aspect of the spatial ecology of slatey-grey snakes is the lack of any obvious seasonal shift. The Adelaide River floodplain changes dramatically with the onset of monsoonal rains at the beginning of the wet-season; extensive low-lying areas covered by bare deeply cracked blacksoil throughout the dry season abruptly become shallow lakes for the next few months, and vegetation grows prolifically. This sudden shift in habitat characteristics initiates major changes to the activity patterns and home ranges of many species of native fauna. For example, the closure of the soil cracks that had provided dry-season shelter drives native rodents (*Rattus colletti*) to areas of higher ground several kilometres away, in turn stimulating an equivalent migration by water pythons (*Liasis fuscus*) that feed upon these rats (Madsen & Shine 1996). Similarly, the rapid development of extensive shallow-water habitat induces a major increase in movements and home range sizes of aquatic taxa such as acrochordid filesnakes (*Acrochordus arafurae*: Shine & Lambeck 1985), homalopsine water snakes (*Enhydryis polylepis*: Shine *et al.* 2004, unpubl. data), saltwater crocodiles (*Crocodylus porosus*: Webb & Manolis 2002), and longneck turtles (*Chelodina expansa*: Kennett 1999, Kennett *et al.* 1998). Although slatey-grey snakes also rely upon soil cracks for dry-season shelter, they do not shift either the sizes or locations of their home ranges in response to the disappearance of this habitat type underwater. Instead, they simply shift to slightly higher ground within their usual home range, and increase the rate and distance of their nightly movements.

Why do slatey-grey snakes show so little modification of their spatial ecology in the face of this dramatic seasonal inundation? Part of the answer lies in their generalist and flexible dietary habits; examination of faeces from freshly captured snakes shows a seasonal shift in the relative proportions of reptile eggs and rodents in the diet (Brown *et al.*, unpubl. data). Studies on other reptile taxa in the same area have revealed other cases where the size and/or location of the home range shows little variation between seasons (e.g. frillneck lizard *Chlamydosaurus kingii*: Griffiths 1999; death adder *Acanthophsis praelongus*: J. Webb, *pers. comm.*), suggesting that there may be a considerable diversity of responses in this respect.

Slatey-grey snakes found above the ground surface at night are almost always active, moving slowly at ground level and tongue-flicking intensively at any crevices they encounter. This behaviour suggests that they use the vomeronasal system to locate reptile nests and rodent burrows by scent. The high proportion of reptile eggs in their diet (> 58% of identifiable remains in faeces: Brown *et al.*, unpubl. data) provides strong evidence of reliance on active foraging rather than sit-and-wait (ambush) predation. Why, then, did our radio-tracked snakes show

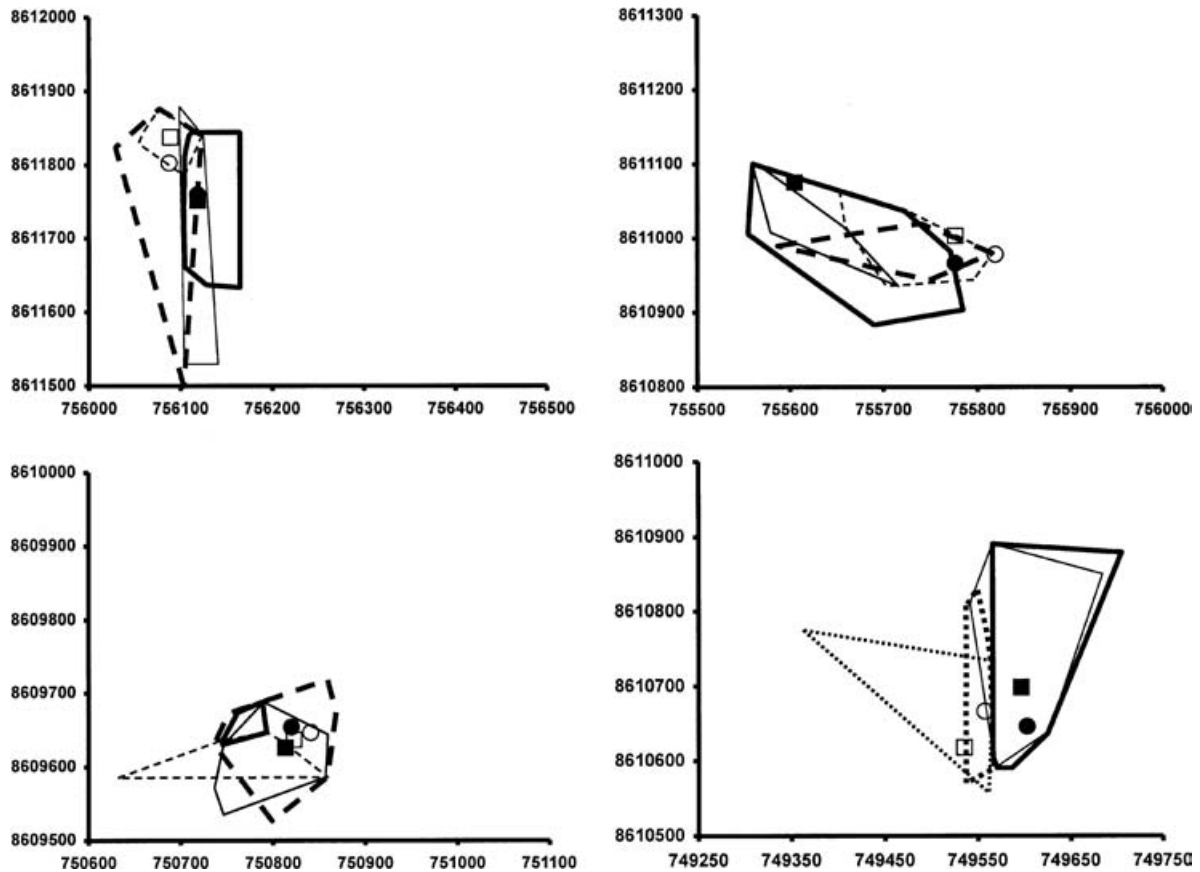


Figure 2. Home ranges of four representative slatey-grey snakes radio-tracked through four seasons. The four polygons in each figure indicate the Minimum Convex Polygon home ranges for each season and the four symbols represent the home range centres (based on arithmetic means of x and y coordinates). The area shown in each figure is the same (500 m \times 500 m), allowing home range areas and distances to be compared among figures. Wet-season (December–March) = thick dashed line, open circle; early dry-season (April–May) = thin solid line, filled square; mid dry-season (June–September) = thick solid lines, filled circle; late dry-season (October–November) = thin dashed line, open square. Note that home ranges are small, and do not shift markedly among seasons.

frequent periods without displacement? Radio-tracking studies on snakes generally have recorded such periods of immobility during ambush predation (Greene & Santana 1983, Reinert *et al.* 1984, Secor 1994). In contrast, the episodic brief periods of immobility in *S. cucullatus* almost certainly represent cessation of activity immediately following ingestion of a meal. Reliance on foraging inside narrow crevices may constrain foraging effectiveness when the body is distended by a prey item; and the high temperatures of this tropical site mean that digestion of prey does not require overt basking. In keeping with these speculations, we have recorded freshly ingested prey (i.e. in the stomach rather than the hindgut) in only 20 of 1756 slatey-grey snakes (1.1%) captured during our mark-recapture study. Thus, feeding must entail an almost immediate retreat to a shelter-site (although the occasional presence of multiple prey items in the stomach at capture, as summarized above, indicates that on occasions the foraging bout must be prolonged). The lack of synchrony in activity pulses among simultaneously

monitored snakes falsifies the most plausible alternative explanation for this episodic activity: the idea that slatey-grey snakes move about only on nights with specific weather conditions.

Most other aspects of our results are readily interpretable in light of our extensive dataset from mark-recapture studies on this population. The trend for more frequent and extensive movements by males than by conspecific females is seen throughout the year, whereas reproduction is highly seasonal (> 90% of clutches are produced from September through to December: Brown *et al.* 2001, unpubl. data). This contrast suggests that the sex difference in movements may reflect the larger body sizes attained by males (mean adult SVLs of 117.1 vs. 98.6 cm in our study population: Brown *et al.*, unpubl. data) rather than mate-searching or other reproduction-associated activities. However, our analyses that included SVL as a covariate cast doubt on this interpretation, except for frequency of movement. More frequent and extensive movements during the wet-season than the dry-season

were accompanied by an increase in the feeding rate (as indicated by the proportion of snakes containing faeces at capture in the wet-season 24.5% vs. the dry-season 19.3%, $N = 1221$, $\chi^2 = 4.13$, $P = 0.04$). When the wet-season inundates (and thus closes) soil cracks that provide abundant shelter for both the snakes and their prey during the dry-season, slatey-grey snakes may have easier access to prey; and also, the reduced availability of soil cracks may force them to travel further to find alternative diurnal shelter-sites.

Although female slatey-grey snakes generally moved over shorter distances than did the (larger) males, the most extensive movements were by four heavily gravid females. In each case, the displacement took the snakes from their relatively treeless home ranges to forested areas, suggesting that they may use arboreal sites for oviposition. Similar long-distance movements away from the usual home range have been reported in many other squamate species, and may entail substantial risks for the heavily burdened females (Blair 1960, Bonnet *et al.* 1999, Parker & Brown 1972). However, our mark–recapture studies suggest that survival rates do not differ between female slatey-grey snakes and conspecific males (Brown *et al.*, unpubl. data).

The small home ranges of slatey-grey snakes, despite the large body sizes of these animals, presumably reflect the abundant prey resources in this tropical ecosystem – especially for a generalist predator that is able to switch among alternative prey types on a seasonal basis. Additionally, the raised embankments preferred by slatey-grey snakes as their year-round residences are important as refuges for rats with the onset of wet-season flooding (Madsen & Shine 1996) and are frequently used as oviposition sites by keelback snakes, that may travel long distances to these sites (Brown & Shine 2004). Hence, prey tend to come to the slatey-grey snakes rather than vice versa. Under these circumstances, there may be little benefit (but significant risk) to long-distance movements by this species.

In summary, our data reveal that slatey-grey snakes on the Adelaide River floodplain occupy small home ranges, move episodically over short distances, and do not change their activity patterns in dramatic ways between the wet-season and the dry-season. The striking contrast between these results and those from previously published studies on other snakes in the same region (the acrochordid *Acrochordus arafurae*, the python *Liasis fuscus*, the aquatic colubrid *Enhydryis polylepis*) suggest that we will need many more field studies, of a wide array of phylogenetic lineages, if we are to understand the factors generating interspecific diversity in spatial ecology within tropical snakes. However, the same diversity suggests that tropical snakes may provide excellent model systems in which to tease apart the correlates and causes of divergent patterns in spatial ecology.

ACKNOWLEDGEMENTS

We thank the staff of Beatrice Hill Farm for logistical support, and the Australian Research Council for funding.

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