Spatial subdivision within a population of tropical pythons (*Liasis fuscus*) in a superficially homogeneous habitat

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Abstract Based on 10 years of intensive fieldwork, we describe the spatial and temporal distribution of water pythons (*Liasis fuscus*) on the Adelaide River floodplain, Northern Territory, Australia. Our study provides a cautionary tale, because it was only after several years' work that we realized that our apparently panmictic study 'population' in fact consisted of three subpopulations that were separated during breeding activities although they intermingled for most of the year. The partitioning of the populations is due to the restricted availability and spatial separation of suitable nest-sites (varanid burrows *vs* root complexes of paperbark trees). Groups of snakes using each type of nest-site comprise quite separate breeding populations, because females move to these sites prior to mating. Snakes return to the same breeding sites year after year, with little dispersal between populations (even though snakes from each population often move through other breeding sites during the non-breeding period). The three subpopulations differed in many traits, including body-size distributions, age structures, the proportions of reproductive animals, survival rates, timing of reproduction, and reproductive frequencies. Thus, if our study had involved only one of the subpopulations (as would typically be the case with studies of this kind), we would have obtained a misleading view of the 'real' (i.e. average) ecological characteristics of our study organisms.

Key words: genetic fragmentation, metapopulation, population ecology, snakes, tropics.

INTRODUCTION

Species that are distributed over large geographical areas often consist of a series of more-or-less isolated local populations (Andrewartha & Birch 1954). Subdivision into local populations is likely to be particularly pronounced if the habitat is heterogeneous, and if the species has limited vagility, and/or is a habitat specialist (e.g. Sjögren Gulve 1994). Even when a vagile, habitat-generalist species is widely distributed in homogeneous habitats, however, detailed investigation often reveals that the taxon actually occurs as a series of small separate subpopulations rather than as one huge panmictic assembly (Ehrlich *et al.* 1975). Spatial subdivision of populations may have several significant ecological consequences, including the induction of significant local heterogeneity in the dynamics and genetics of the different subpopulations. The recognition of these implications has stimulated the rapid development of metapopulation theory (e.g. Levins 1969; Hanski *et al.* 1995).

Population subdivision has many significant implications, but one of the most important is a simple logistical one: an investigator can substantially misinterpret the ecological traits of a population if the 'population' actually consists of a series of discrete subpopulations that differ in these traits. For example, if the subdivided populations differ in characteristics such as dynamics,

habitat use, age structure and/or reproductive rates, then studies that are restricted to a single subpopulation may provide an erroneous view of the 'real' (i.e. average) ecological characteristics of the species in that general area (Ehrlich *et al.* 1975).

Thus, we need to know, for different kinds of animals in different kinds of habitats, the degree to which superficially 'large panmictic' populations in relatively homogeneous habitats are in fact separated into more-or-less discrete subpopulations; and if so, whether the separate subpopulations differ significantly in important ecological traits. Very little has been published on the spatial subdivision of populations of reptiles, and nothing at all on large snakes living in tropical habitats. Since 1986 we have carried out an ecological study on a python species that is well suited to such an analysis. Remarkably, despite the superficial homogeneity of the floodplain habitat that these snakes occupy for most of the year, subgroups of snakes within this population migrate back to separate breeding grounds each year. Thus, although the population appears completely intermingled, it actually consists of a series of discrete breeding units.

METHODS

Study area

The lower reaches of the Adelaide River, 60 km southeast of Darwin in the Northern Territory of Australia,

are surrounded by a large floodplain up to 20 km in width. Much of the floodplain is inundated by monsoonal rains each year, and is covered with dense sedges (*Eleocharis*) and grasses (e.g. *Oryza, Mnesithea, Panicum*). Paperbark (*Melaleuca*) forest fringes the floodplain, giving way to open woodland (dominated by *Eucalyptus*) in higher drier regions. The area lies within the 'wet–dry' tropics; temperatures are high year-round (mean daily maximum air temperatures > 30°C) but precipitation is highly seasonal. More than 75% of the 1300 mm mean annual rainfall occurs during the brief (December to March) 'wet-season' (Taylor & Tulloch 1985).

The data in this paper were gathered at three sites.

(1) The wall of Fogg Dam, a 1.3 km long, man-made structure across a narrow section of the blacksoil floodplain (Fig. 1). The dam is inundated year-round (except for occasional dry years), whereas the backswamp (a low-lying area of the floodplain north of the dam wall) is dry for up to 8 months each year.

(2) A 2 ha area of paperbark forest at the fringe of the backswamp, about 2 km northeast of the dam wall (Fig. 1). This site is ~ 1 m lower than the surrounding forest. In consequence, during the wet season this area is inundated more deeply, and for longer periods, than is the surrounding forest. As a result, the roots of the paperbark trees in this area form large buttresses, with the complex root systems interwining to form mounds at the base of each tree. These mounds range up to 3 m in diameter and > 1 m in height (see Shine *et al.* 1997 for a photograph), whereas paperbark trees in the adjacent forest lack these root mounds altogether.

(3) An 8 ha area of higher drier ground covered by open eucalypt forest, 2 km east of the paperbark area and about 4 km northeast of the Fogg Dam wall (Fig. 1). The site contains numerous burrow complexes dug by large varanid lizards (*Varanus panoptes*). The areas have been described in detail in earlier papers (Madsen & Shine 1996a,b; Shine & Madsen 1997).

Study species

Water pythons (*Liasis fuscus*) are large (to 3 m), non-venomous, nocturnally active snakes widely distributed across tropical Australia (Cogger 1992). They are very abundant in the vicinity of Fogg Dam, and have been the subject of our detailed ecological research in this region since 1986. Radiotelemetric studies have shown that these snakes engage in regular long-distance (up to 12 km) seasonal migrations, moving from Fogg Dam or the adjacent backswamp down to the lower reaches of the floodplain with the onset of wet-season flooding (Madsen & Shine 1996a). The stimulus for this migration is the flooding-induced concentration of dusky rats (*Rattus colletti*, the primary food for water pythons in this area) on isolated patches of higher and drier ground. As wet-season floods subside, the pythons migrate back to their dry-season habitats (Madsen & Shine 1996a).

Methods

Most of the water pythons were collected at night by spotlighting, either from a slow-moving car (on the
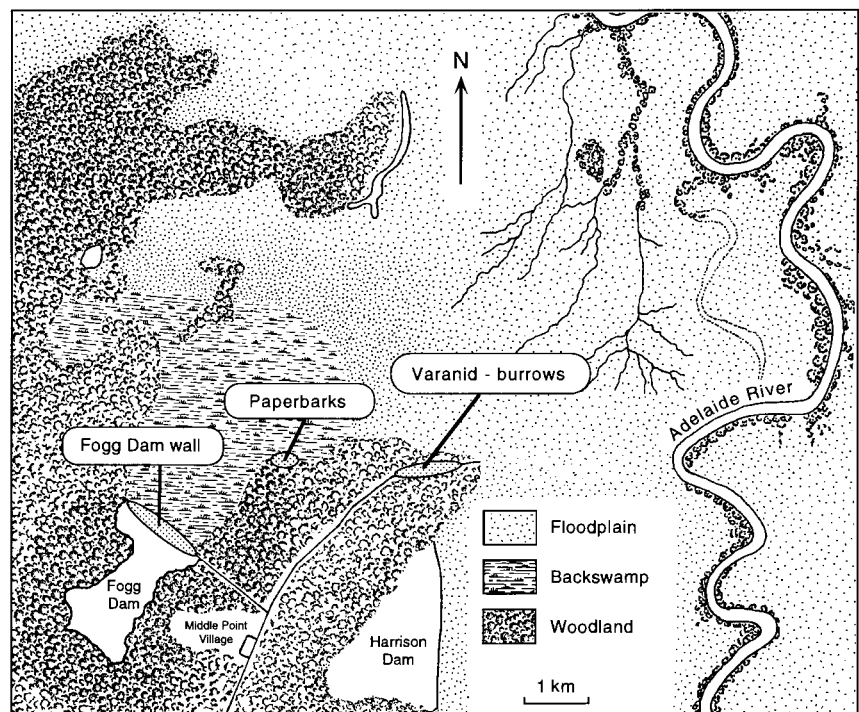

Fig. 1. Map of study area, showing vegetation types and the three study sites (Fogg Dam wall, paperbarks and varanid burrows).

Fogg Dam wall and at the varanid burrows) or by walking (at the paperbarks). The pythons were weighed, measured and individually scale-clipped prior to their release the following day at their site of capture.

From 1986 to 1990 the focus of our work was on the Fogg Dam wall, because capture rates in this area were very much higher than in any of the surrounding habitats. In July–August 1990, however, we encountered large numbers of pythons at the varanid burrows also. Then, two years later (in July 1992), we found another area, the paperbarks, where large numbers of pythons appeared during this time of year. Although recapture rates were very high by 1990 at our primary study site (the dam wall), most of the snakes we captured near the varanid burrows or in the paperbarks were unmarked. Thus, we realized that pythons at the three sites might represent three separate populations.

In consequence, we modified our collecting schedule in 1993. From July to November each year, our nightly collecting trips consisted of a routine patrol of all three areas, with approximately equal time being spent in each. During September the number of pythons captured at the paperbarks and the varanid burrows decreased rapidly; very few were observed in October and November (see below). Therefore, in order to compare data from the three sites, results presented in the current paper are based on snakes captured during July to September from 1992 to 1996. During this period 576 pythons were marked at the Fogg Dam wall, 671 in the paperbarks and 195 at the varanid burrows.

The snout–vent length (SVL) of the smallest reproductive female (i.e. gravid or containing large vitellogenic ovarian follicles) was 140 cm, identical to the SVL of the smallest reproductive male (i.e. recorded courting and/or mating). We therefore consider snakes with a body length of less than 140 cm as juveniles.

We have previously reported on movements of 25 radiotracked Fogg Dam pythons monitored from 1990 to 1993 (Madsen & Shine 1996a). In the current paper we also present telemetric data on movements of an additional six adult females from the varanid burrows and five adult females from the paperbarks. All of these snakes were monitored over the period from 1991 to 1993. For more detailed information on our radiotelemetric methods, see Madsen and Shine (1996a).

RESULTS

Seasonal abundance of pythons at the three sites

Over the period July to November, capture rates of pythons increased on the Fogg Dam wall but decreased in the paperbarks and at the varanid-burrows area (Fig. 2). Snakes had virtually disappeared from the two latter areas by November (Fig. 2). Hence, there was a significant difference in the monthly distribution of capture rates at Fogg Dam *vs* the paperbarks and the varanid burrows. Using a two-factor ANOVA with month (August through November) and location as the factors, the number of pythons collected was influenced by location ($F_{2,15}$ = 669.0, P = 0.0001) and month ($F_{4,15}$ = 4.28, P = 0.02). More importantly, the three areas differed in the ways in which capture rates changed among months (interaction $F_{8,15}$ = 73.91, P = 0.0001).

The time of the year at which we encountered pythons in the paperbarks and around the varanid burrows (July to September), corresponded with the time of the year at which the snakes reproduced. Despite the high temperatures year-round, these tropical pythons are highly seasonal in their reproductive activity (Madsen & Shine 1996b). Of a grand total of 289 records of female water pythons captured in reproductive condition during our study (i.e. gravid, or with enlarged ovarian follicles detectable by palpation), 286 (99%) were captured during these three months. The location (as well as the timing) of reproductive activities supported the inference that the usage of paperbarks and varanid burrows was somehow related to reproduction. This was true at two levels. First, the spatial distribution of pythons was non-random; the snakes were highly associated with particular habitat features. Pythons encountered in the paperbarks were close to (or partly inside) holes of the huge paperbark root mounds, whereas pythons in the varanid-burrow area were consistently found close to (often, entering or emerging from) the burrows. These root mounds and burrows are the primary nesting sites for *L. fuscus* in our study area (Shine *et al.* 1997). Second, of the 32 instances in which we observed reproductive behaviours (courtship sequences and matings), most were in
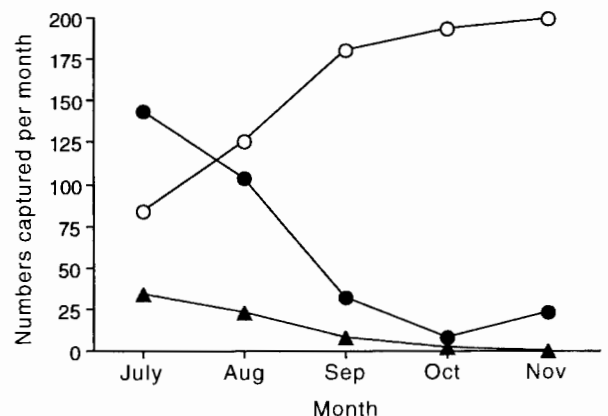

Fig. 2. Number of water pythons captured per month at the three study areas, showing that capture rates decline seasonally in the paperbarks and varanid burrows, but not on the dam wall. All data from 1993. (—○—) Fogg Dam, (—●—) paperbarks, and (—▲—) varanid burrows.

the paperbarks ($n = 18$) or near the varanid burrows ($n = 11$) rather than on the dam wall ($n = 3$). These observations, and the concentration of pythons in the paperbarks and the varanid burrows during the reproductive season, suggest that these two sites are used specifically for reproductive purposes. If this inference is correct, we might expect that the body-size distributions of pythons captured in the different areas might also differ, with the paperbark and varanid-burrow sites containing mostly reproductive adult snakes. We test this idea below.

Body-size distributions at the three sites

The body-size distributions of the pythons that we captured in each of the three sites differed substantially (using a nonparametric Kruskal–Wallis test because of unequal variances, $H = 936.4$ with 2 d.f., $P = 0.0001$). The vast majority of pythons captured in the paperbarks and near the varanid burrows consisted of adult
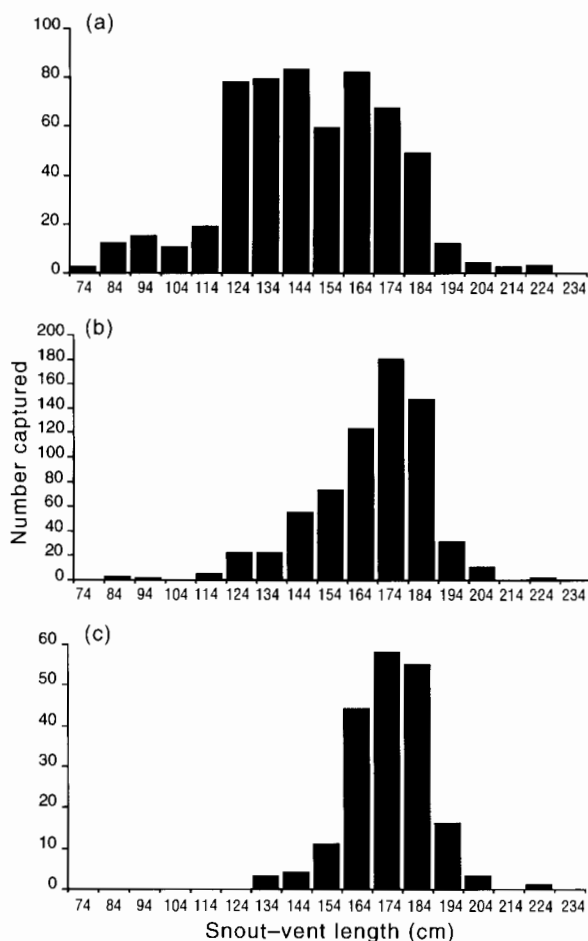

Fig. 3. Snout–vent length distributions of water pythons captured at (a) Fogg Dam (mean = 148.5 cm, SD = 26.0, $n = 576$), (b) in the paperbarks (mean = 167.7 cm, SD = 18.1, $n = 671$) and (c) at the varanid burrows (mean = 174.7 cm, SD = 12.7, $n = 195$).

snakes (Fig. 3). In contrast, we found snakes of a much wider range of body sizes on the Fogg Dam wall (Fig. 3).

Thus, the paperbark and the varanid-burrow areas contained mostly adult snakes, and the only time that we encountered large numbers of pythons in these areas was during the breeding season. Inspection of data on the proportion of adult-size females that were reproductive when collected, further supports the inference that the paperbarks and the varanid burrows are breeding areas. Because the proportion of reproductive animals varies with female body size (Madsen & Shine 1996b), the exact proportion of reproductive females depends on the size range examined. However, considering females with a snout-vent length of more than 140 cm as adults (see above), a significantly larger proportion of the females captured in the varanid burrows and the paperbarks were reproductive than were those from the Fogg Dam wall [varanid burrows: 93% (82/88); paperbarks: 60% (108/180) and Fogg Dam: 23% (39/167); paperbark vs Fogg Dam: $\chi^2 = 46.2$, $P = 0.0001$, d.f. = 1; varanid burrows vs Fogg Dam: $\chi^2 = 109.9$, $P = 0.0001$, d.f. = 1]. We therefore conclude that the snakes collected in the paperbark and varanid-burrow areas had migrated to these sites for the purpose of breeding. In contrast, the Fogg Dam sample comprised juvenile as well as adult snakes, most of the adult females were non-reproductive, and the animals were found on the wall over a much longer period of time than at the other two sites (Fig. 2).

Life-history characteristics of snakes at the three sites

In earlier papers, we have documented significant small-scale heterogeneity in life-history traits of water pythons, due to subtle differences in the thermal regimes available in different types of nests (Madsen & Shine 1996b; Shine et al. 1997). For example, the eggs of pythons reproducing in the varanid burrows are laid earlier in the year, and incubate more rapidly (because of high nest temperatures) than do eggs in the other sites (Madsen & Shine 1996b). Hence, varanid-burrow eggs hatch much earlier, with a consequent enhancement of hatchling survivorship in some years (Shine et al. 1997). The difference in incubation temperatures between varanid-burrow nests and paperbark-root nests also directly affects the phenotypes of the hatchling pythons, as well as modifying the duration of maternal nest-attendance (Shine et al. 1997). The longer maternal attendance at paperbark-root nests translates into lower maternal survival rates, and a reduced reproductive frequency in the adult females nesting in this area (Madesn & Shine in press a). Lastly, rates of egg survival also differ between clutches laid in the two main types of nest-sites (Madsen & Shine in press a). Thus, life history traits differ substantially

between python subpopulations nesting in adjacent areas.

How discrete are these populations?

The data presented above show that the three adjacent subpopulations of water pythons differ in terms of body-size, seasonality, reproductive status, and other life-history traits, but do not tell us whether the subpopulations are discrete. In particular, adult snakes might move from one of these sites to the other, either within or between reproductive seasons. For example, adult pythons might remain near the Fogg Dam wall until they are ready to reproduce, and then migrate to one of the other sites. Alternatively, each of the three subpopulations may be separate, with little or no exchange. Table 1 shows that water pythons are highly philopatric, with very few snakes moving from one site to another, despite the small distance separating these areas (Fig. 1). Furthermore, we did not detect any dif-

ferences in the degree of site-fidelity between juveniles vs adult snakes ($\chi^2 = 2.62$, $P = 0.10$, d.f. = 1), nor between juvenile males vs juvenile females ($\chi^2 = 0.35$, $P = 0.56$, d.f. = 1), or adult males vs adult females ($\chi^2 = 0.30$, $P = 0.58$, d.f. = 1; all calculations were based on comparisons of number of recaptures at the original site vs number of recaptures at other sites, Table 1).

The spatial subdivision between the three subpopulations is further supported by our telemetric monitoring of the movements of six adult females from the varanid burrows and five adult females from the paperbark area, from 1991 to 1993. None of these females were ever recorded on the floodplain close to Fogg Dam (Figs 4, 5). However, our telemetric data clearly show that pythons from all of the three areas move towards the Adelaide River during the late dry-season and the early wet-season. Thus, during the wet-season, pythons from the three different sites mingled into one large 'population' on the Adelaide River floodplain (Fig. 5).

Table 1. Number of male and female water pythons marked and recaptured at three sites (the Fogg Dam wall, the paperbarks and the varanid burrows) during July to September from 1992 to 1996

		Number marked		Number recaptured at Fogg Dam		Number recaptured at paperbarks		Number recaptured at varanid burrows	
		snout–vent length (cm)		snout–vent length (cm)		snout–vent length (cm)		snout–vent length (cm)	
		<140	>140	<140	>140	<140	>140	<140	>140
Fogg Dam	Males	128	193	55	46	1	7	0	1
	Females	83	167	51	23	1	0	0	0
Paperbarks	Males	37	438	0	4	7	141	0	2
	Females	13	180	0	1	0	16	0	1
Varanid burrows	Males	2	104	0	0	0	2	0	16
	Females	1	88	0	0	0	1	0	13

Only recapture records that were taken at least 12 months after the previous capture and release are included. The sexes of five Fogg Dam snakes and three pythons from the paperbarks were not determined.

Table 2. Subcaudal scale counts of water pythons from the three subpopulations

	Area of capture					
Subcaudal scale count	Fogg Dam ($n = 347$)		Paperbarks ($n = 375$)		Varanid burrows ($n = 114$)	
	Number	%	Number	%	Number	%
∞D	147	42.4	167	44.5	46	40.4
1D1E∞D	38	11.0	37	9.9	13	11.4
2E∞D	34	9.8	38	10.1	14	12.2
3E∞D	37	10.7	34	9.1	13	11.4
1D2E∞D	27	7.8	22	5.9	10	8.8
4E∞D	21	6.1	19	5.1	9	7.9
5E∞D	17	4.9	23	6.1	5	4.4
1D3E∞D	14	4.0	20	5.3	3	2.6
1D4E∞D	12	3.5	15	4.0	1	0.9

The count refers to the numbers of undivided (E, entire) and divided (D) subcaudal scales, starting from the vent and proceeding posteriorly. Thus, '1D1E∞D' describes a snake with one divided subcaudal immediately behind the vent, then one entire subcaudal, then all the rest divided. Data presented are based on all scale counts observed that occur relatively frequently (i.e. have been recorded in more than 20 snakes).

Later in the year, as the flooding recedes, the pythons return to their dry-season home ranges; many snakes were recaught at their original capture locations in successive dry-seasons, despite their extensive migration during the intervening wet-seasons (Madsen and Shine 1996a).

Finally, morphological differences between the pythons captured at these three sites might provide some insight into the degree to which the populations constitute genetically separate entities. The most useful data in this respect come from subcaudal scale counts, which we recorded routinely from all captured snakes (as an aid to individual identification, if scale-clips prove to be ambiguous). The scales under the tail

Fig. 4. Locations of radio-tracked water pythons during the breeding season (July to September), based on locations of 36 pythons (25 from Fogg Dam, 6 from the varanid burrows and 5 from the paperbarks), monitored from 1990 to 1993. (●) Fogg Dam pythons, (■) snakes from the paperbark area, and (▲) pythons from the varanid burrows.
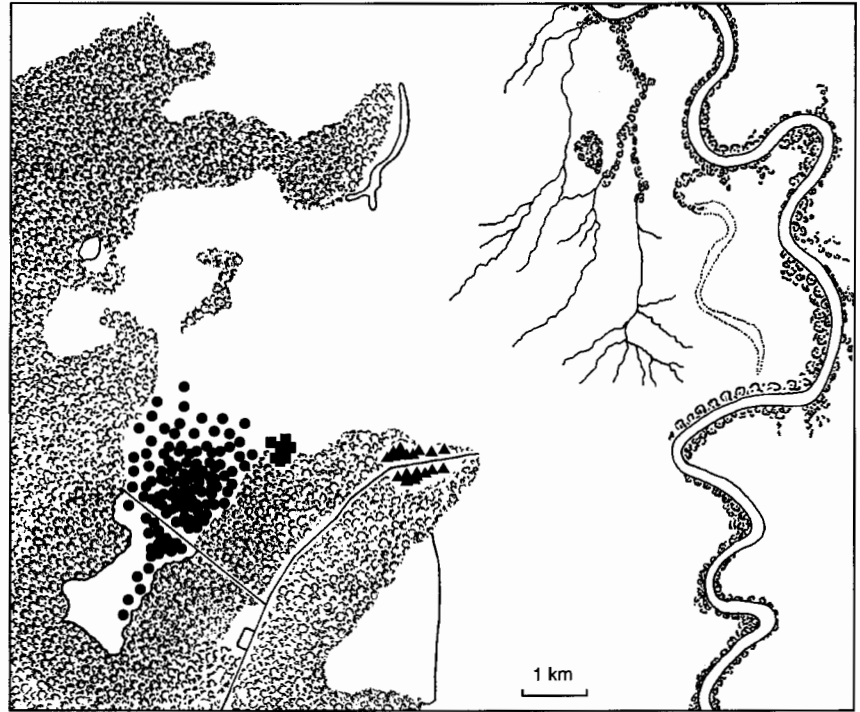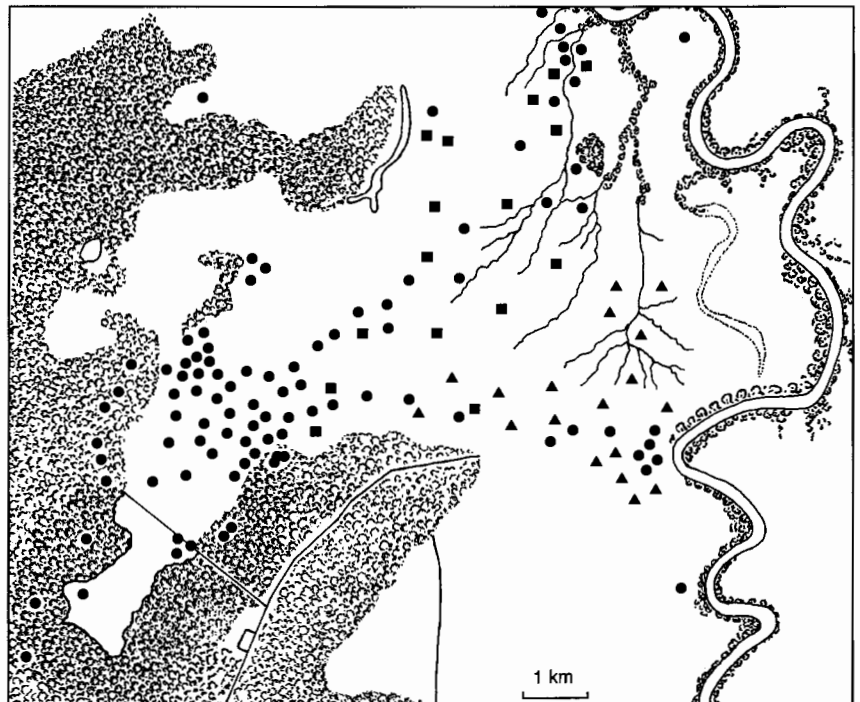

Fig. 5. Locations of radio-tracked water pythons during the non-breeding part of the year (late dry-season plus wet-season, October to March), based on locations of 36 pythons (25 from Fogg Dam, 6 from the varanid burrows and 5 from the paperbarks), monitored from 1990 to 1993. (●) Fogg Dam pythons, (■) snakes from the paperbark area, and (▲) pythons from the varanid burrows.

of *L. fuscus* show considerable individual variation in terms of the numbers and positions of paired *vs* single scales, and these arrangements are highly heritable (Shine *et al.* 1988; Madsen & Shine unpublished data). If the pythons from the three populations rarely interbreed, we would expect to see significant difference in the distributions of subcaudal scale counts among the three populations. However, analysis indicates that the populations are extremely similar in this respect (Table 2). A contingency table test of these data fails to reveal any significant differences among the three populations, despite the very high power of the test ($\chi^2 = 14.3$, $P = 0.57$, d.f. = 16). Given the high heritability of this trait, this result strongly suggests that the three populations are not genetically isolated from each other.

DISCUSSION

Our major result is highly counter-intuitive. We studied a population of large, highly vagile organisms in a floodplain habitat that appears (at least superficially) to be very homogeneous. Our telemetric monitoring showed that individuals captured in one part of this area regularly travelled across the entire study area, and that animals located side-by-side in the wet-season habitat (the lower reaches of the floodplain) included representatives from drier ground areas on all sides of the floodplain. Given these results, it seems remarkable that the water pythons of the Adelaide River floodplain are actually subdivided into at least three separate breeding populations, which differ significantly in important life history traits. However, our data show that this is exactly what occurs. Even though the breeding areas are separated by distances that are trivial in comparison to the seasonal migrations undertaken by the snakes (Madsen & Shine 1996a), the areas are sufficiently discrete and the snakes so highly philopatric that individual snakes can be reliably assigned to consistent membership of one *vs* another of these discrete breeding groups (Table 1).

This result introduces an apparent paradox: adult snakes move very large distances, and many of the pythons caught at Fogg Dam moved down the floodplain and through the paperbark area (Madsen & Shine 1996a; see Fig. 5). Why, then, were more Fogg dam snakes not captured in the paperbarks during the breeding season? The answer lies in the seasonal distribution of movements. During most of the dry-season (including the period when breeding occurs), the adult Fogg Dam snakes are found in the vicinity of the dam (Fig. 4). Nine female pythons have been recorded laying eggs in varanid burrows on the wall or in burrows on high ground close to the dam wall, and one of these females was also recorded to oviposit in a reed bed in Fogg Dam when the dam dried out in 1992 (Shine 1991; Madsen & Shine 1996a). Not until the late dry-

season or early wet-season (November–December) do the Fogg Dam pythons migrate to their 'wet-season habitat' (Madsen & Shine 1996a). Thus, very few Fogg Dam pythons are likely to be found in the paperbarks or the varanid burrows during the breeding season in July to September.

The mechanism responsible for the partitioning of the population is straightforward. Because female water pythons do not dig their own nesting burrows, they must rely on existing holes for oviposition. The areas surrounding the floodplain contain few suitable nesting areas, and these fall into two discrete categories: holes inside paperbark root mounds, and the burrows dug by varanid lizards on the higher, drier soils. Female water pythons travel to these nesting grounds prior to mating, so that most breeding occurs very close to the final oviposition site. Hence, the relatively subtle heterogeneity in nest-site availability results in geographical subdivision of mating activities as well as egg-laying.

Why were so few juvenile pythons encountered on the breeding grounds compared to the Fogg Dam wall (Fig. 3)? The probable answer is that prey availability is considerably lower in the paperbarks and the varanid-burrows area than on the backswamp close to Fogg Dam (Madsen & Shine 1996a; Shine & Madsen 1997). Because of gape-limitation, hatchling water pythons are unable to ingest adult rats, and thus depend upon juvenile rats for their first few meals (Shine *et al.* 1997). These small rats are most abundant in the backswamp, especially late in the dry-season (close to the time of hatching of the snakes) when rat reproduction has ceased over most of the rest of the floodplain (Madsen & Shine in press b). Hence, in order to find ingestable prey, all juvenile pythons (regardless of where they hatch) must migrate to the backswamp close to the Fogg Dam wall.

The breeding ground philopatry exhibited by water pythons on the Adelaide river floodplain (Table 1) is similar to that reported for several other vertebrate taxa, including fishes (e.g. Dittman & Quinn 1996), amphibians (e.g. Gill 1978; Berven & Grudzien 1990; Reading *et al.* 1991), reptiles (e.g. Werner 1983; Burger & Zappalorti 1992), birds (e.g. Southern 1977; Osorio-Beristain & Drummond 1993) and mammals (e.g. Buechener & Roth 1974). Thus, there is the potential for population subdivision in all of these groups, but the actual degree of subpopulation separation will depend crucially not only on philopatry of adults, but also on whether or not hatchlings tend to return to the site of their own hatching when they grow old enough to breed. In some groups, this condition is certainly fulfilled: for example, neonatal salmonid fish become imprinted on their natal breeding grounds (e.g. Dittman & Quinn 1996) and in some amphibians, 70–80% of the metamorphs return to breed in their natal pond (Breden 1987; Berven & Grudzien 1990).

We did not mark any hatchling pythons in the paperbarks or at the varanid burrows, and thus do not know whether or not the young snakes exhibit any form of natal imprinting. However, our recapture data suggest that the young pythons are highly philopatric: 98% (115 out of 117) of the snakes that we marked as juveniles, and later recaptured as adults, were recaptured at their original location (Table 1). If these juveniles hatched close to the site where they were first captured, a large proportion of hatchling pythons may return to breed at their natal sites. In other snake species, it has been suggested that the young find their way back to den sites by following scent trails left by adults (Brown & MacLean 1983; Reinert & Zappalorti 1988). Alternatively, Lawson (1994) suggested that neonatal garter snakes might imprint on solar cues at the birth site. We simply do not know whether or not some kind of natal imprinting occurs among hatchling water pythons.

Clearly, the effective division of the water-python population into discrete breeding groups has the potential to induce genetic divisions also. However, we have no evidence that this has occurred. Subcaudal scale counts show considerable individual variation and are highly heritable, yet do not differ between water pythons from the different subpopulations (Table 2). Similarly, our measures of genetic traits (Mhc polymorphism) reveal no consistent differences between these groups of snakes (Madsen & Shine unpubl. data). These data suggest that the rates of dispersal, although low (Table 1), have probably been sufficient to prevent any genetic differentiation of the subpopulations.

The major implication of our results is a methodological one, and very similar to that stressed by Ehrlich *et al.* (1975). If our study had been restricted to sampling animals at a single locality, at a single time of year (even if the sampling was repeated in the same season in subsequent years), we could have been led to some of the following serious errors in interpretation.

(1) The size (age) structure is 'biased' in all populations that we sampled, because of age-specific habitat shifts (i.e. migration of hatchlings to the 'backswamp' close to Fogg Dam). Juvenile pythons are overrepresented in the Fogg Dam population, and under-represented in the other two groups (Fig. 3). Thus, studies of any single 'population' would provide misleading estimates of age structure (and thus, recruitment and mortality rates, etc.) for the python population as a whole.

(2) Similarly, estimates of the proportion of reproductive animals from such a study could substantially underestimate or overestimate the 'real' (i.e. population-wide) mean value.

(3) Population estimates based on studies of a single subpopulation would considerably underestimate the total numbers and biomass of the water-python population using the floodplain.

(4) If the subpopulations differ in life-history characteristics, then studies based on a single subpopulation would fail to reveal this diversity. For example, minor thermal differences between the paperbark-root and varanid burrow nests induce a cascade of other life-history modifications, including effects on female 'tactics' (abandon *vs* attend the eggs), female survival rates, female reproductive frequencies, the seasonal timing of reproductive events, survival rates of embryos and hatchlings, and hatchling phenotypes (Shine *et al.* 1997; Madsen & Shine in press a).

Hence, as pointed out by Ehrlich *et al.* (1975), investigators should be aware of the possibility that superficially homogeneous 'panmictic' populations are in fact composed of relatively discrete subunits, and that such subgroups may display distinctive ecological traits. Our own study acts as a cautionary tale, because we had been engaged in detailed studies of the water pythons of the Adelaide River floodplain for six years before we stumbled across the paperbark mating grounds, and realised that 'the study population' at Fogg Dam actually comprised a highly non-random group of individuals (i.e. biased towards small size classes) and that we had been restricting our study to a discrete subset of the water python population in this area. We are fortunate that our study continued for long enough to enable us to recognize the important role of spatial subdivision in interpreting ecological processes in this system.

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