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# SEASONAL MIGRATION OF PREDATORS AND PREY—A STUDY OF PYTHONS AND RATS IN TROPICAL AUSTRALIA[1]

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*Abstract.* Although seasonal migrations of large predatory mammals that follow migrating prey are well documented, no equivalent phenomenon has been described previously in terrestrial reptiles. We surveyed and radio-tracked water pythons (*Liasis fuscus*) in Fogg Dam and its adjacent floodplain in the wet–dry tropics of northern Australia to document patterns of movement, with particular emphasis on the ways in which the snakes exploit their major prey species, the dusky rat (*Rattus colletti*). The distribution and abundance of these rodents vary seasonally. During the dry season the rats live in soil crevices in the floodplain, but wet-season flooding forces them to higher ground, primarily to natural levee banks. Python and rat abundances on the floodplain adjacent to Fogg Dam were significantly correlated through time: both reached a maximum during the dry season, and fell dramatically during the wet season. Activity of pythons was centered around Fogg Dam during the dry season, but all of the radio-tracked snakes moved away from this area during the wet season. Most pythons migrated to the vicinity of levee banks on the floodplain up to 12 km away from their dry-season range. By migrating seasonally, water pythons can efficiently utilize a migratory prey species that would otherwise be unavailable for much of the year.

*Key words: Australia; foraging; home range; predator–prey; rodent; seasonality; snake; weather.*

## INTRODUCTION

Many species of animals show consistent seasonal migratory movements, but the actual stimulus for migration varies considerably. One pattern reported for large mammalian predators involves seasonal migrations to track prey populations that are themselves moving seasonally to follow changing food availability. For example, migrating herds of African ungulates are accompanied by lions, cheetah, and hyenas (Schaller 1972), and North American caribou by wolves (Sinclair 1983). We know of no published reports of equivalent cases in terrestrial ectotherms. Instead, long-range migrations in amphibians and reptiles typically involve return to breeding sites and/or to thermal refugia (e.g., Gregory and Stewart 1975, Larson 1987, Dingle 1980, Bock et al. 1985, Duvall et al. 1990).

Ectothermic vertebrates possess a series of interrelated features that tend to militate against long-distance seasonal migration in response to seasonal changes in prey distribution. Most terrestrial ectotherms are relatively small (and thus, vulnerable to predation), possess a limited capacity for sustained exercise, and often are inactive for much of the year because of thermal constraints (e.g., Pough 1980). Thus, many ectotherms exploit ephemeral resources, waiting out periods of low resource availability, rather than actively tracking highly mobile prey. Additionally, the social system of reptiles often involves strong site attachment and vigorous territorial defense, which may render long-distance migration difficult or impossible. The terrestrial reptiles most likely to show seasonal migrations in pursuit of migrating prey are large tropical snakes. The tropical environment permits year-round activity, the large size of the animals confers relative invulnerability to many predators, and the lack of active territorial defense in snakes (Duvall et al. 1992) facilitates long-distance movements. Our studies in tropical northern Australia have focussed on large ectothermic predators (water pythons, *Liasis fuscus*) that fulfil all of these conditions. We have found that these snakes move considerable distances each year to follow the changing distribution patterns of their major prey (the dusky rat, *Rattus colletti*).

## MATERIALS AND METHODS

### *Study area*

Our study area is centered on Fogg Dam, a permanent waterbody 60 km southeast of Darwin in Australia's Northern Territory. The area is warm year-round (mean daily maximum air temperatures range from 31° to 36°C, and minima from 15° to 24°C) but precipitation is highly seasonal (Fig. 1). More than 75% of the total annual rainfall (1300 mm) falls in the brief wet season from December to March (Fig. 1). Fogg Dam is 1.3 km wide and 2.0 km long. The vegetation in the dam consists mainly of extensive reed beds (*Eleocharis* spp.), water lilies (*Nymphaea spp.*), and red lilies (*Nelumbo nucifera*). The dam wall is a man-made structure across a natural blacksoil floodplain that is inundated during the wet season. Minor differences in elevation

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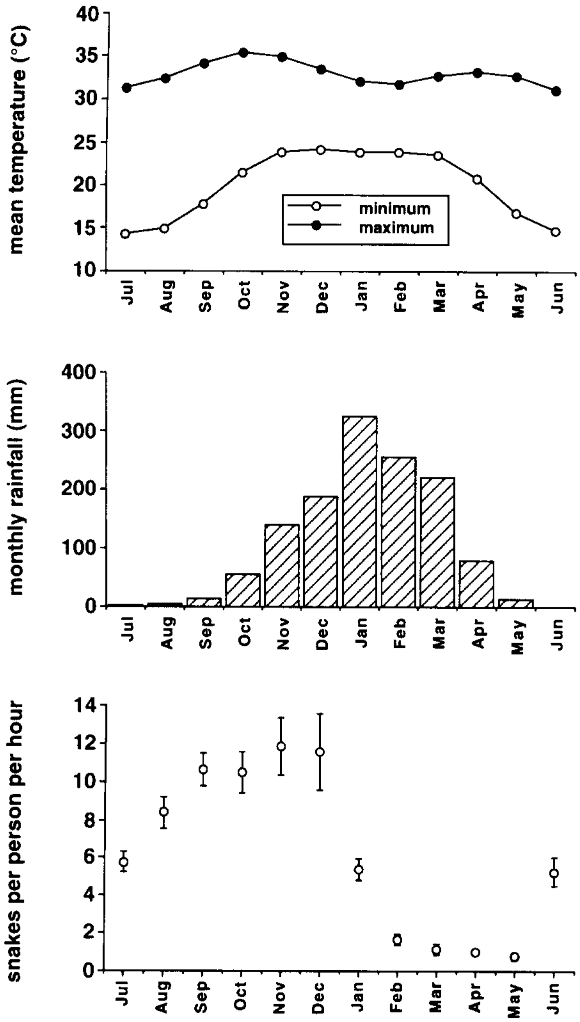


FIG. 1. Climatic data for the Fogg Dam study area based on average values over 15 yr (1978–1992), and mean monthly capture rates of water pythons on the Fogg Dam wall. Climatic data come from records taken at the Coastal Plains Research Station in Middle Point Village, 2 km from Fogg Dam. Data (with means ± 1 SE) on capture rates of snakes taken from nocturnal surveys.

have profound effects on soil moisture and vegetation on the plains. The floodplain adjacent to Fogg Dam, and up to 4 km northeast of the dam, is ≈1 m lower than the floodplain closer to the Adelaide River, where levee banks are formed by silt deposition from the river (Fig. 2). These low-lying areas of the floodplain adjacent to Fogg Dam are termed the "backswamp." In most years torrential monsoons fill Fogg Dam to overflowing and inundate the backswamp to a depth of >1 m, whereas inundation on the rest of the floodplain is <0.4 m. Consequently, the backswamp is underwater for longer periods after the end of the wet season than is the rest of the floodplain. The vegetation on the backswamp consists of plants that can survive heavy inundation for long periods of time, mainly wild rice (*Oryza* spp.), sedges of the genus *Eleocharis* and *Cyperus*, the legume *Sesbania cannabina*, and the herb *Polygonatum attenuatum*. The drier parts of the floodplain are covered by sedges (*Eleocharis* spp.), grasses (*Echinocloa, Paspalium, Coelorachis,* and *Sorghum*) and herbs such as *Passiflora foetida* (Fig. 2).

The floodplain below Fogg Dam is bordered by higher ground to the northwest and northeast, and these areas are covered by woodland dominated by trees of the genera *Eucalyptus, Acacia, Terminalia, Syzygium,* and *Lophostemon* (Fig. 2). Even during and after the wet season, the nutrient-poor sandy soils of the woodland support only scattered stands of grasses and herbs. The fringes of the floodplain are dominated by paperbark trees (*Melaleuca* spp.) and screw palms (*Pandanus spiralis*). The woodland northeast of Fogg Dam also contains a small area (≈ 600 × 200m) of monsoon rain forest.

### *Monitoring and radio-tracking snakes*

Water pythons are large (to 3m total length) nonvenomous constricting snakes, that, in our study area, feed primarily on dusky rats throughout the year (>95% of prey items [Shine 1993]). We have been studying water pythons in this area since 1984. The data used in the present paper were gathered from 1989 to 1993, and are based on surveys (capturing snakes on a regular basis at night on the dam wall) as well as radiotelemetric monitoring of selected individuals. No data were gathered during the months April to June in most years, due to our absence on other fieldwork. Because water pythons are primarily nocturnal, we estimated snake abundance by walking or driving along the dam wall for a specified time period (1–2 h), commencing < 60 min after sunset. We attempted to capture all pythons seen, and succeeded in catching >98% of animals sighted.

Twelve adult pythons (7 females and 5 males) were selected for radiotelemetric monitoring during 1990–1991, 10 adult pythons (7 females and 3 males) during 1991–1992 and 3 adult pythons during 1992–1993 (1 female and 2 males, one of them a male previously monitored 1990–1991 and the other male monitored 1991–1992: Table 1). The snakes were anesthetized by interperitonal injection of ketamine hydrochloride (1.5 mg/kg), and radiotransmitters were surgically implanted in the peritoneal cavity. The snakes were kept in captivity for 10–20 d after surgery to ensure complete healing of the wound. The transmitters used (Holohil model number SI-2T; Televilt model number TXT-2sm-TT) measured 45 × 15 mm (35 g) and 80 × 18 mm (55 g), with a 30-cm whip antenna encased in silicone rubber. The transmitters constituted < 3% of the body mass of the snakes into which they were implanted, and battery life ranged from 9 to >14 mo. Reception range of the telemetry signal ranged from 0.2 to 2.0 km (mean = 600 m) depending on the location of the snake. All of our radio-tracked pythons fed actively,

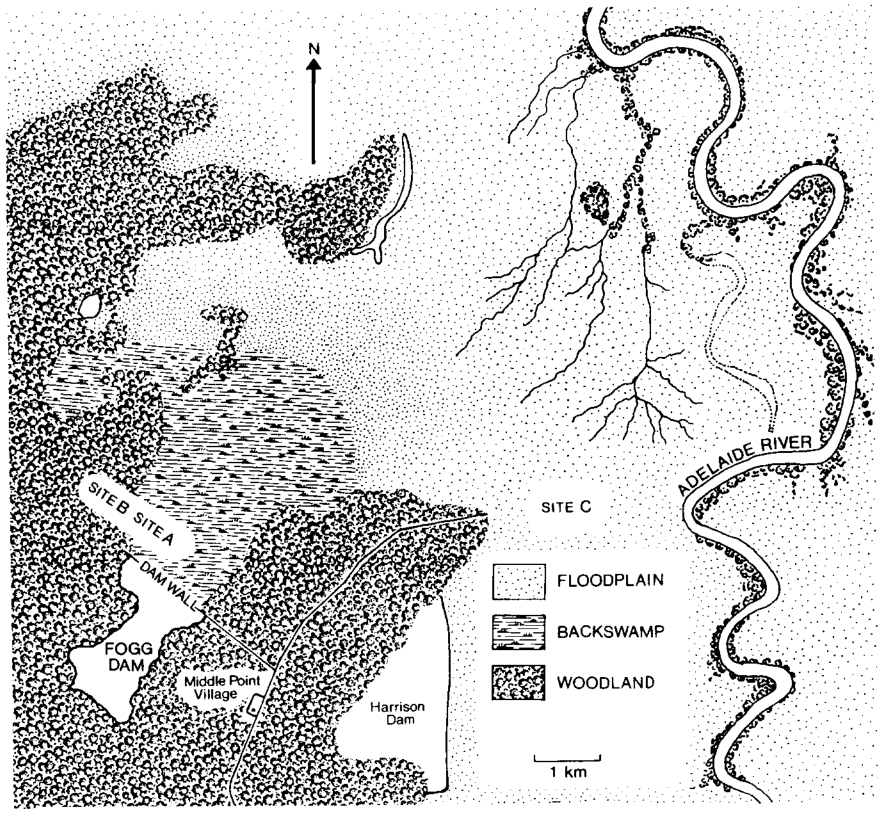


FIG. 2. Map of study area, showing vegetation types and rat-trapping sites (Site A, B, and C).

and most grew substantially during the monitoring period. Of six pythons recaptured after long periods (12–24 mo after transmitter insertion), five had increased in both length and mass whereas the remaining animal (a large male) had not changed significantly in either dimension. Growth rates of snakes carrying transmitters were indistinguishable from growth rates of similar-sized animals without transmitters, but individually marked by scale-clipping. Thus, the transmitters seemed to have had little negative effect on the snakes.

During the dry season telemetered snakes were usually located at least once per day. It was rarely possible to see the snakes when their position was determined, because they were hidden down in deep cracks in the soil, or inside dense clumps of vegetation. Nonetheless, we could generally determine the animal's location to within $<1$ m throughout the dry season. During the wet season, large areas of the floodplain became inaccessible to vehicular access, and the presence of large saltwater crocodiles (*Crocodylus porosus*) posed a significant danger to humans on foot. At these times, we were forced to rely on telemetric monitoring by helicopter, with a consequent decrease in frequency of monitoring and in precision of location. However, we could regularly triangulate the position of some of the snakes from dry ground.

### *Monitoring rats*

We monitored dusky rat populations at three different sites (see Fig. 2). The first is the backswamp 400 m northwest of Fogg Dam (site A, trapped since October 1990), the second is the adjacent woodland (site B, trapped since January 1991), and the third area is the floodplain 6 km northeast of Fogg Dam (site C, trapped since January 1991, Fig. 2). Site C is situated in an area formerly used for rice growing and thus contains man-made levee banks, enabling us to trap throughout the wet season. At each site 50 Elliot traps were placed at 10-m intervals along a 500-m transect. Each site was trapped for 5 d every 4–6 wk unless it was under water. The rats were marked by toe-clipping and ear-tagging. In the present paper we use an index of rat abundance, the number of different rats captured per trap per night.

## RESULTS

### *Surveys of python abundance*

Capture rate of pythons on the dam wall showed significant monthly variation (one-factor ANOVA with month as the factor $F_{8,206} = 7.85$, $P < 0.001$; note that we were absent during the period April-June in most years) (Fig. 1). Overall, capture rates were lowest during the wet season and then gradually increased

TABLE 1. Gender, size and tracking period of 25 water pythons monitored with radiotransmitters.

| Identi-fication number | Sex | SVL (cm)* | Tracking period: Dates | Tracking period: Duration (d) |
|---|---|---|---|---|
| 287 | F | 201 | 27 Sep–4 Dec 1990 | 68 |
| 213 | F | 210 | 27 Sep 1990–16 Feb 1991 | 142 |
| 808 | F | 204 | 27 Sep–8 Nov 1990 | 42 |
| 344 | F | 202 | 27 Sep–18 Dec 1990 | 82 |
| 862 | M | 175 | 20 Oct 1990–16 Feb 1991 | 119 |
| 1727 | F | 202 | 20 Oct 1990–16 Feb 1991 | 119 |
| 709 | M | 186 | 25 Oct 1990–16 Feb 1991 | 114 |
| 51 | M | 168 | 25 Oct 1990–16 Feb 1991 | 114 |
| 555 | F | 180 | 25 Oct 1990–16 Feb 1991 | 114 |
| 448 | M | 185 | 25 Oct 1990–16 Feb 1991 | 114 |
| 192 | M | 178 | 25 Oct 1990–5 Jan 1991 | 72 |
| 1101 | F | 184 | 26 Oct–28 Nov 1990 | 33 |
| 1897 | M | 185 | 22 Jul 1991–2 Mar 1992 | 224 |
| 1715 | F | 225 | 1 Aug 1991–20 Jan 1992 | 172 |
| 1286 | F | 205 | 9 Sep 1991–2 Mar 1992 | 175 |
| 1185 | F | 170 | 4 Nov 1991–25 Jul 1992 | 264 |
| 2471 | F | 190 | 4 Nov 1991–2 Mar 1992 | 119 |
| 2464 | M | 198 | 4 Nov 1991–19 Jul 1992 | 258 |
| 2430 | F | 250 | 4 Nov 1991–21 Jul 1992 | 260 |
| 1575 | M | 177 | 9 Nov 1991–11 Feb 1992 | 94 |
| 1484 | F | 180 | 4 Dec 1991–7 Mar 1992 | 94 |
| 2489 | F | 181 | 4 Dec 1991–3 Aug 1992 | 243 |
| 2293 | F | 180 | 14 Sep 1992–30 Nov 1993 | 442 |
| 709 | M | 197 | 26 Nov 1992–30 Nov 1993 | 369 |
| 1575 | M | 180 | 9 Dec 1992–20 Nov 1993 | 346 |

* SVL = snout–vent length.

throughout the dry season, reaching a peak immediately before the onset of the monsoons. The number of snakes then fell abruptly (Fig. 1).

### *Radiotelemetric monitoring*

The pythons used for radiotelemetric monitoring were captured on the dam wall during the mid-to-late dry season (July to December, Table 1). During the dry season the habitat most frequently used by the radio-tracked pythons was Fogg Dam and/or the backswamp up to ≈3 km northeast of the dam (Fig. 3). Snakes on the dry backswamp were most frequently located within soil cracks or under dense vegetation (*Eleocharis* spp. and *Oryza* spp.). As the soil crevices closed at the beginning of the wet season, the radio-tracked snakes typically moved onto higher ground, usually to the floodplain northeast of the backswamp (Figs. 3 and 4). Some snakes commenced moving weeks prior to the first heavy rains, whereas a few remained in the backswamp until the rains were already in progress. However, no snakes stayed in the backswamp throughout the wet season. Of the 25 telemetered snakes, only five moved to the woodland. At least nine snakes moved to the floodplain, and the same was probably true for the other nine (all of which were moving towards the floodplain when we lost "radiocontact" with them). During the wet season all snakes located on the floodplain were in deep pools (>0.5 m deep) formed by inundation of small "feeder" creeks running into the floodplain, or in man-made (abandoned) rice field channels. All of these locations were within 20 m of higher, dry ground. Six of these radio-tracked pythons were recaptured on the dam wall during subsequent dry seasons (after their transmitter batteries had expired).

Another six snakes were tracked over two successive dry seasons. One of these pythons, an exceptionally large female (number 2430, Table 1), remained in the vicinity of Fogg Dam throughout the tracking period, moving between Fogg Dam and the monsoon rain forest. However, the female was never recorded feeding in the backswamp and her diet consisted of large mam-

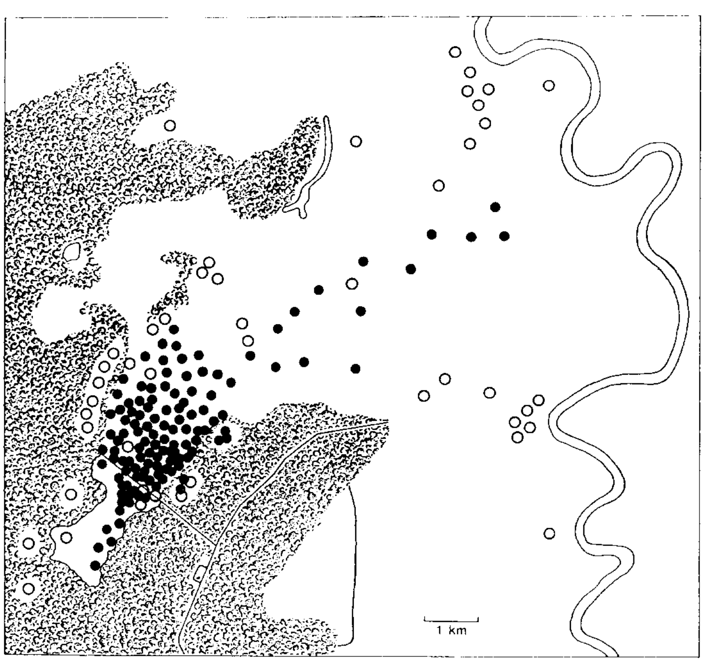


FIG. 3. Locations of 25 radio-tracked water pythons, monitored from 1990 to 1993. ● denote dry season (July–November) locations and ○ wet season (December–March) locations. Data based on 411 locations.

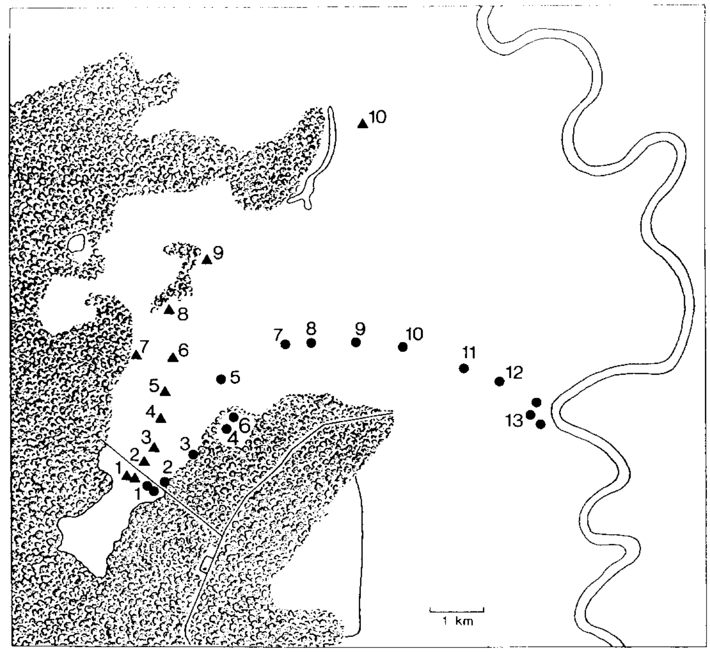


FIG. 4. Movement of two radio-tracked water pythons monitored during 1990–1991 (female number 555, ▲) and 1991–1992 (male number 1897, ●). Numbers denote successive locations.

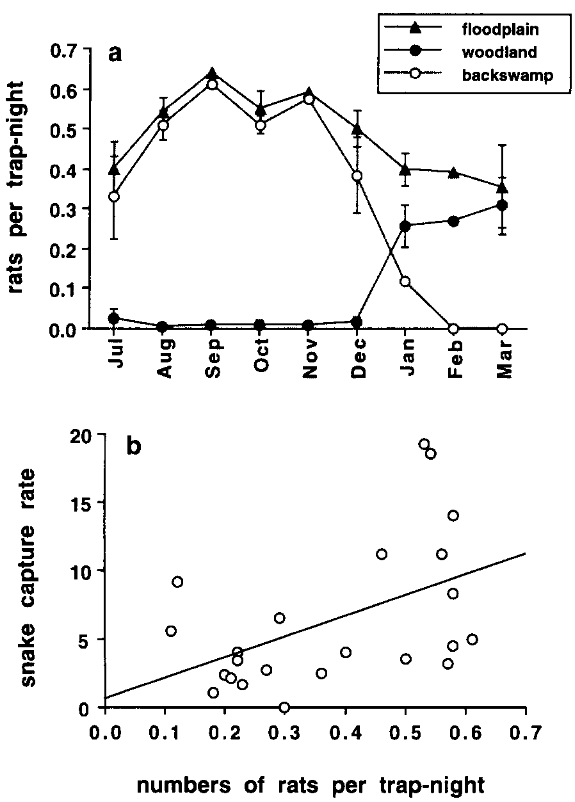


FIG. 5. (a) Mean monthly number of dusky rats (rats/trap-night) captured on the backswamp (○), in the woodland (●) and on the floodplain (▲). Graph shows means ± 1 SE. (b) Temporal correlation between capture rates of rats in the backswamp, and water pythons on the adjacent dam wall. Each data point is based on mean values for 1 mo, and line of best fit is based on least squares regression.

mals such as bandicoots (*Isoodon macrurus*) and feral cats (*Felis catus*). Thus the atypical movement pattern, compared to smaller snakes, most likely reflected her unusual dietary composition. The remaining five snakes left Fogg Dam during the wet season and moved to the vicinity of the Adelaide River. Four of these snakes returned to Fogg Dam during the subsequent dry season, whereas the fifth python remained on the floodplain during the subsequent dry season.

### *Rat abundances and body sizes*

Rat numbers on the floodplain, the backswamp, and the adjacent woodland showed significant monthly variation (two-factor ANOVA with month and location as the factors: month $F_{7,41} = 2.53$, $P < 0.03$; location $F_{2,41} = 39.12$, $P < 0.001$; interaction $F_{5,41} = 6.07$, $P < 0.001$). Rat numbers in both the floodplain and the backswamp increased during the early dry season (July to September), remained high during the dry, and decreased during the wet season (Fig. 5). Very few rats were recorded in the woodland during the dry season, but their numbers increased with the onset of wet-season flooding in adjacent low-lying areas. Most rats in the backswamp apparently moved further down the floodplain with the advent of flooding, rather than dispersing into woodland (which, for most of the floodplain, was >1 km away). Of eight rats marked in the backswamp and recaptured in the woodland after flooding commenced, all had been originally marked very close to (within 100 m of) the woodland fringe. In combination with Redhead's (1979) data, these results suggest that most rats moved down to the lower floodplain rather than dispersing into the woodland. Thus, the spatial distribution of rats changed considerably over the year: rats were abundant in the floodplain all year, but moved from the backswamp to the lower floodplain and adjacent woodland during the wet season (Fig. 5).

Although rat numbers during the dry season were similar in the floodplain and backswamp (based on capture rates: Fig. 5), the average body size of rats was much higher in the backswamp. Female rats were similar in size in the two areas (backswamp mean [±1 SD] mass = 69.5 ± 28.3 g, $n$ = 140; floodplain mean mass = 71.2 ± 32.2 g, $n$ = 155; unpaired $t$ = 0.47, 293 df, $P$ = 0.64), but males were much larger in the backswamp (mean mass = 102.3 ± 42.1 g, $n$ = 87) than in the floodplain (mean mass = 70.1 g, SD = 36.6, $n$ = 113; unpaired $t$ = 5.82, 198 df, $P < 0.0001$). This size difference is highly relevant to prey availability for water pythons, because the snakes feed primarily on very large, male rats (65 of 74 rats regurgitated by pythons captured on the dam wall weighed >100 g; 51 of these 65 large rats were males).

The end result of these annual shifts in habitat use is to produce a significant correlation between the distributions of rats and snakes in space and time. Both groups exploit low-lying areas during the dry season, and move considerable distances to higher ground with the advent of the monsoons. Analysis of rat and python abundance data on Fogg Dam wall (adjacent to the backswamp) reveals a strong and consistent correlation between the numbers of prey and predators (Fig. 5): capture rates of pythons and rats are significantly correlated (using mean capture rates of rats and pythons per month: $n$ = 23 months, $r$ = 0.49, $P < 0.02$).

## Discussion

Before considering biological aspects of this system, we deal with some methodological issues that could affect interpretation of our results. First, do our counts of python numbers on the dam wall (Fig. 1) provide an accurate index of the number of snakes in that area? Simple counts are open to many inaccuracies due to differential observability of snakes in different habitats (e.g., Weatherhead and Charland 1985), but this kind of bias is unlikely to be a problem in our study. The number of pythons seen does offer a good index of actual densities, because seasonal changes in vegetation cover (and hence, ability of snakes to evade detection) are negligible on the open dam wall.

Secondly, why does python abundance change so dramatically through time, especially the rapid decline at the onset of the wet-season monsoons (Fig. 1)? These temporal changes cannot be attributed to mortality or recruitment, because water pythons are long-lived animals (many of our recaptured snakes are known to be > 7 yr old) and recruitment of hatchlings occurs only in October–December (Madsen and Shine 1995). Thus, the increase in snake numbers during the dry season was not due to recruitment, because most of these animals were large adults, not hatchlings. Likewise, the rapid decrease in numbers of snakes on the dam wall at the beginning of the wet season reflects a movement of pythons to other areas rather than a precipitous increase in mortality, because many of the marked animals were recaptured on the dam wall during the dry season year after year (T. Madsen and R. Shine, *unpublished data*). In combination, these results indicate seasonal movements of animals, rather than methodological artifacts or abrupt changes in mortality and recruitment rates.

This interpretation is further supported by our radiotelemetric studies. All of our radio-tracked pythons consistently moved from Fogg Dam and/or the backswamp prior to or during the wet season, and several of these snakes were recorded on the dam wall or in Fogg Dam during subsequent dry seasons. This shift was not due to any lack of suitable cover, or thermal stress; the inundated backswamp offers ample thermal refuges and suitable shelter sites (Shine and Madsen 1995). Instead, our data suggest that the pythons' seasonal migration from Fogg Dam and the adjacent backswamp to the floodplain and/or the woodland during the wet season occurred in response to the disappearance of dusky rats from the backswamp. This inference is supported by the high temporal correlation between rat abundances and python abundances.

As is the case with the pythons, the rats' disappearance from the backswamp was most likely due to migration (inundation forcing the rats to move to higher ground) rather than to mortality. The abrupt increase in rat numbers in the woodland during the wet season (in contrast to the situation in the backswamp and the floodplain: see Fig. 5) supports this interpretation. We also have direct evidence from our mark–recapture studies: eight marked rats were recorded migrating from the backswamp to the woodland. A previous study of dusky rats on the same floodplain (Redhead 1979) recorded similar seasonal fluctuations in rat numbers and migration patterns as we observed during our study.

The deep soil crevices, the habitat used by the rats in both the backswamp and the floodplain during the dry season, were no longer available after the onset of the wet season. However, only in the backswamp were the rats forced to undertake long-distance migrations to reach higher ground. This difference in migratory response results from the different degrees of inundation of the backswamp (up to 1 m) vs. the floodplain (<0.4 m). Thus the backswamp contains no dry ground whereas the more shallowly inundated floodplain, especially in the vicinity of the Adelaide River, contains both natural and man-made levee banks.

Why do most of the rats travel so far (to the levee banks on the lower floodplain), rather than simply move to the dry woodland surrounding the backswamp? The movement of rats onto the floodplain rather than the woodland during the wet season probably reflects the higher availability of food in the dense vegetation on the floodplain than in the sparsely vegetated woodland. Inundation of the vegetation does not inhibit foraging by the rats; we have often observed them swimming in open water and biting off grass flowers from the emergent stems, returning to dry ground to consume their food. Thus, the rats' spatial distribution on the floodplain is highly clumped during the wet season, with most rats being restricted to areas close to dry ground. Similarly, all of the water pythons monitored by helicopter were located in deep pools close to dry ground. These pools enable the snakes to avoid temperature extremes, as the shallow water on the floodplain may exceed 40°C. However, the consistent occupancy of pools close to higher dry ground, rather than the many deep pools far from dry ground on the inundated floodplain, suggests that rodent availability is a more important determinant of python distribution than are thermal constraints.

Why do most pythons migrate between the backswamp and the floodplain, rather than simply remaining on the floodplain where rat densities remain high year-round (Fig. 5)? The answer may lie in the different body sizes of rats in the two areas. Large male rats, the sex and size class most frequently consumed by the pythons, are much more common in the backswamp area, presumably because of its higher levels of moisture and nutrients. Thus, the costs of long-distance migration by the pythons may be offset by higher foraging success during the dry season.

The major results to emerge from this study are (1) that the pythons show consistent seasonal movements and (2) that these movement patterns are readily explicable in terms of a shift in the distribution of the snakes' prey. By migrating seasonally, water pythons can efficiently use a migratory prey species that would otherwise be unavailable for much of the year. We know of no other examples of prey-mediated seasonal migration in squamate reptiles. Perhaps the closest analogues to the system we have described in water pythons come from studies of other large reptiles in the Australian wet–dry tropics. Two aquatic species, the freshwater crocodile (*Crocodylus johnstoni*) and the filesnake (*Acrochordus arafurae*) spend the dry season in isolated billabongs (small waterbodies) but move into shallowly inundated areas with the advent of wet season flooding (Webb et al. 1982, Shine and Lambeck 1985). Both of these aquatic species feed on fishes, which show the same seasonal habitat shift (Bishop et al. 1980). However, in freshwater crocodiles and filesnakes it is the temporal variation in habitat, not prey, that is the main stimulus for the observed migrations; aquatic reptiles living in seasonally arid areas have no option but to move into small residual waterbodies during the dry season.

Perhaps the closest analogy to the annual migration of water pythons and rats in the Fogg Dam area is the migration of mammalian predators and prey on the African savannahs (Schaller 1972). Notably, the Australian example involves a large ectothermic predator rather than endotherms as in Africa. The low and variable productivity of many Australian habitats seems to suit ectotherms rather than endotherms, because the low maintenance energy requirements of ectotherms allow them to survive through long periods of low resource availability (Pough 1980, Braithwaite 1990). Nonetheless, there are strong parallels between these two geographically and taxonomically distinct systems. The factor causing the migration of predators in both of these ecosystems appears to be the same: the migratory response of herbivorous mammals to seasonal, rainfall-induced shifts in food availability in different habitat types.

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