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### Abstract

Young snakes are rarely seen in the field and little is known about their habits, mostly because they are too small for radio-telemetry (the primary method for studying snake spatial ecology). However, the offspring of some larger species can be fitted with transmitters and we investigated the spatial ecology and habitat use of ten hatchling water pythons (*Liasis fuscus*: Pythonidae) in the floodplain of the Adelaide River, tropical Australia. Patterns of habitat use in the late wet season and during the dry season were similar to those of adults tracked in the same vicinity in an earlier study. Soon after release the young snakes moved to the floodplain, avoiding pasture areas. Diurnal refuge sites were typically in the base of grass clumps or below the soil surface, especially in sites with thick vegetation and deep, wide soil cracks. Adult snakes are more sedentary but move longer absolute distances (mean  $\pm$  SE = 252  $\pm$  50 m wk<sup>-1</sup>) than hatchlings (66.3  $\pm$  41 m wk<sup>-1</sup>). However, hatchling snakes moved longer distances relative to body size (84.4  $\pm$  1.1 body lengths wk<sup>-1</sup>) than did the previously studied adults (66.0  $\pm$  1.1 body lengths wk<sup>-1</sup>). Mean and minimum body temperatures of the hatchlings were correlated with mean and minimum air temperatures, respectively.

### Keywords

liasis, fuscus, tropical, ecology, australia, hatchling, spatial, water, pythons

### Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

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# Spatial ecology of hatchling water pythons (*Liasis fuscus*) in tropical Australia

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**Abstract:** Young snakes are rarely seen in the field and little is known about their habits, mostly because they are too small for radio-telemetry (the primary method for studying snake spatial ecology). However, the offspring of some larger species can be fitted with transmitters and we investigated the spatial ecology and habitat use of ten hatchling water pythons (*Liasis fuscus*: Pythonidae) in the floodplain of the Adelaide River, tropical Australia. Patterns of habitat use in the late wet season and during the dry season were similar to those of adults tracked in the same vicinity in an earlier study. Soon after release the young snakes moved to the floodplain, avoiding pasture areas. Diurnal refuge sites were typically in the base of grass clumps or below the soil surface, especially in sites with thick vegetation and deep, wide soil cracks. Adult snakes are more sedentary but move longer absolute distances (mean  $\pm$  SE =  $252 \pm 50$  m wk<sup>-1</sup>) than hatchlings ( $66.3 \pm 41$  m wk<sup>-1</sup>). However, hatchling snakes moved longer distances relative to body size ( $84.4 \pm 1.1$  body lengths wk<sup>-1</sup>) than did the previously studied adults ( $66.0 \pm 1.1$  body lengths wk<sup>-1</sup>). Mean and minimum body temperatures of the hatchlings were correlated with mean and minimum air temperatures, respectively.

**Key Words:** habitat, habitat selection, hatchling, movements, snake, thermoregulation

## INTRODUCTION

In many endothermic species (birds and mammals), offspring remain with their parents until they achieve body sizes relatively close to adult size. In such species, the ecology of young individuals after the termination of parental care may be broadly similar to the ecology of their parents. In most ectotherms, however, offspring begin their independent life at a size far below mean adult size: often, an order of magnitude smaller than their parents (Shine 2005). In such cases, we might expect the ecology of juvenile animals to differ substantially from the ecology of adult conspecifics. For example, neonates may be exposed to greater risk from predators, eat different types of prey, be less capable of buffering rates of thermal and hydric exchange with the environment, and be less able to tolerate long periods without feeding (Hjelm *et al.* 2000, Lankford & Targett 2001, Pizzatto & Shine 2008, Seebacher & Alford 2002, Werner & Gilliam 1984). Such size-related shifts may generate ontogenetic

variation in behaviour, growth rates, diel cycles, habitat use, movement patterns and home ranges (Harestad & Bunnell 1979, Hjelm *et al.* 2000, Keren-Rotem *et al.* 2006, Pizzatto & Shine 2008, Schoener & Schoener 1984, Werner & Gilliam 1984, Wilson *et al.* 2006). Understanding how animals occupy and use space is important for conservation purposes (Groom *et al.* 2006). For an ectotherm, that understanding should include information on ontogenetic shifts in spatial ecology. For example, we can only assure conservation of a population by protecting the areas where individuals live at all stages of their lives.

Most snakes have very secretive habits, but the increasing availability of miniature radio-transmitters has yielded substantial progress in understanding patterns of movements and habitat use in many species (Brown *et al.* 2005, Glaudas *et al.* 2007, Macartney *et al.* 1988, Shine 1987, Wilson *et al.* 2006). The extent of the home range varies among and within species depending on factors such as reproductive status, sex, body size, season, prey availability and geographic location (Brown *et al.* 2005, King & Duvall 1990, Macartney *et al.* 1988, Madsen & Shine 1996a, Shine 1987, Whitaker & Shine

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2003). However, small (young) snakes are rarely included in such studies (Macartney *et al.* 1988). One obvious problem is that methods used for large snakes (such as surgical implantation of transmitters) often are inapplicable to small ones (Macartney *et al.* 1988, Shine *et al.* 2002). Another problem is that young snakes are difficult to find in the field: their small size facilitates hiding, their greater vulnerability to predators may favour secretive behaviour, and their higher rates of heating may limit time of exposure during basking (Asplund 1974, Sun *et al.* 2001). Such biases affect most mark-recapture studies of snakes (Pike *et al.* 2008). Thus, although newborn snakes are often seen immediately after birth/hatching when they leave the nest, they then tend to disperse and are often not encountered again until they reach larger size. Aiming to understand what young snakes do in their first months of life we studied the spatial ecology of hatchlings of the water python (*Liasis fuscus* Peters 1873: Pythonidae) in the wet-dry tropics of northern Australia, comparing our results to those available for conspecific adults in a neighbourhood area. We hypothesize that (1) like the conspecific adults, hatchling water pythons use the floodplain as main habitat, take refuge in soil cracks and under the vegetation, (2) differently from the adults and due to their smaller size they do not undertake very long distance dispersion/migration and (3) as typical tropical ectothermics they are exposed to very high temperatures and their movements are limited/related to the weather conditions.

## MATERIALS AND METHODS

### Study species

The water python *Liasis fuscus* is a large nocturnal snake (up to 3 m in snout-vent length (SVL)) widely distributed in tropical Australia (Cogger 1992). Many aspects of the ecology of adult and sub-adult pythons have been studied in great detail in the Adelaide River floodplain in the Northern Territory, Australia. The dusky rat (*Rattus colletti*) is the major prey of these snakes (Shine 1993) and during the wet season the pythons follow the rats in a migration of up to 12 km (Madsen & Shine 1996a). Python breeding is highly seasonal, with reproductive frequency and output largely dependent on prey availability (and thus, maternal body condition), but also affected by availability of specific thermal conditions within nesting burrows (Madsen & Shine 1996b, 1999, 2000; Shine & Madsen 1997). Most female pythons show fidelity to their breeding sites (Madsen & Shine 1998). The only study to date on hatchling water pythons was conducted in the laboratory, and focused on the influence of incubation temperature on the snakes' phenotypes at hatching (Shine *et al.* 1997). However, the large size of

newborn water pythons (mass 28–33 g and 410–430 mm in SVL, Shine *et al.* 1997) makes them a good candidate for studies on spatial ecology by radio-tracking in the field.

### Study area

Our study site (Beatrice Hill Farm) comprises 2600 ha of predominately alluvial clay soil (blacksoil) in the floodplain of the Adelaide River, approximately 60 km south-east of Darwin in Australia's Northern Territory. Most areas of the floodplain can be accessed by all-terrain vehicles, even during the height of the wet season. The climate is generally hot year-round but with pronounced seasonal variation in rainfall: more than 78% of the 1402 mm annual precipitation falls during monsoonal downpours from December to March. Vegetation in the area is composed mainly of native and introduced plants: *Imperata cylindrica* (L.) Beauv., *Dichanthium eriantha* (R.Br.) A.Camus, *Digitaria eriantha* Steud., *Urochloa mutica* (Forsk.) T. Q. Nguyen, *Urochloa humidicola* (Rendle) Morrone & Zuloaga, *Setaria apiculata* K. Schum., *Hymenachne amplexicaulis* (Rudge) Nees (occurring in thick mats floating on waterways), and the sedges *Eleocharis spiralis* (Rottb.) Roem. & Schult. and *E. dulcis* (Burm.f.) Trin. ex Hensch.

### Radio-tracking

Water python eggs from five different clutches, found under hay bales stored in a building on the study site, were incubated in moist vermiculite at approximately 30 °C. A total of 16 hatchlings were retained and kept at room temperature (about 30 °C) in individual plastic boxes (32 × 20 × 10 cm) lined with paper towel and with a dish containing water *ad libitum*. After the first slough each young snake was offered a mouse every week. The first ten snakes to attain sufficient size (50 g body mass) were chosen for radio implantation. These 10 individuals were all females and comprised two offspring from each of the five litters. Each temperature-sensitive radio-transmitter (model LTM, Titley Electronics, Australia) weighed 2.5 g and was calibrated in a water bath ranging from 10 °C to 40 °C. We used the program Curve Expert 1.3 to find the best fitted curve describing the relationship between temperature and pulse rate of the transmitter. The transmitters were surgically implanted in the peritoneal cavity of the animals under halothane anaesthesia and using sterile procedures. After a recovery period of 7 d we offered each animal a mouse. After they fed successfully, the snakes were released on the tenth day post-surgery. All snakes were released during the night at the hay shed where they had been collected as eggs. The first snake was released on 16 February and the tenth snake released on

7 June, in 2007. This delay was due to the differences in hatching times (from 20 December 2006 to 14 January 2007), body masses (mass at birth varied from 16 g to 34.5 g) and growth rates of the snakes ( $0.13\text{--}0.38\text{ g d}^{-1}$ , mean number of days to reach 50 g was  $104.2 \pm 28.1$  SD, range = 58–145 d).

Snakes were located daily at different times of the day and night. At each location we recorded the time of the day, the pulse rate of the transmitter and the coordinates using a hand-held GPS receiver. If the snake was visible, we also recorded its activity and behaviour. We scored the vegetation type, height of the vegetation and depth of the leaf litter. If the snake was in a soil crack, we recorded the minimum width of the opening and minimum depth. To compare these microhabitat attributes to those available in the general vicinity, we measured these same variables in a location 3 m from the snake, in a random direction (determined by spinning a pen on a clip board).

We calculated the bearing of each movement for each snake using Hawth's Tools 3.26 for ArcView (ArcMap 9.1) and used Rayleigh's test to assess the directionality of this parameter in Oriana 2.02. Principal components analysis (PCA) was carried out on microhabitat measures. We compared the first two PCs between the used and non-used locations with a Mann–Whitney test (Zar 1999) using the software Statistica 6.0. We compared the proportion of location-points of snakes that were in the floodplain with the proportion of random points in this habitat using a Z ratio test. Using the Hawth's Tools, we obtained the random points by selecting 1000 points inside a circular area of radius equal the maximum distance that the snakes dispersed from the point of release.

We compared movements of hatchlings to those of the six non-pregnant adult females and four adult males studied by Madsen & Shine (1996b, and unpublished data) from 1991 to 1993. As the adults were studied at a much larger spatial scale (tracking was done from a helicopter much of the time, Madsen & Shine 1996b) it was not possible to precisely measure movements shorter than 10 m. Thus we considered any relocation smaller than 10 m as 'no movement' for both adults and hatchlings. Considering only the data from consecutive days, we compared movement parameters between adults and hatchlings using climatic characteristics as covariates. The climatic variable was represented by the first axis (explaining 52.5% of variation) of a PCA analysis that included mean, maximum and minimum values for air temperature, air pressure, relative air humidity and rainfall. Weather data for this PCA analysis were obtained from the Bureau of Meteorology from daily measurements taken every 3 hours (00h00–21h00) in Darwin Airport for the studied years (1991, 1992, 1993 and 2007), from which we calculated weekly means. The movement parameters used as dependent variables

were: (1) Mean weekly distances moved including no movements; (2) Mean weekly distances moved excluding no movements; (3) Mean of the total weekly distance moved (include no movement); and (4) Proportion of days moved per week. Because distances moved may depend on the body size of the snake, we also calculated size-corrected movement parameters. Because there was no overlap in body sizes between hatchling and adult snakes, it was not appropriate to include body size as a covariate in the analyses. Instead we divided each movement by the ln-transformed body length of the snake that made it. This calculation transformed movements from distances measured in m to distances measured in body lengths. Snake ID was used as a random factor nested within age-class (adult vs. hatchling) in all analyses to limit pseudo-replication.

### Body temperatures

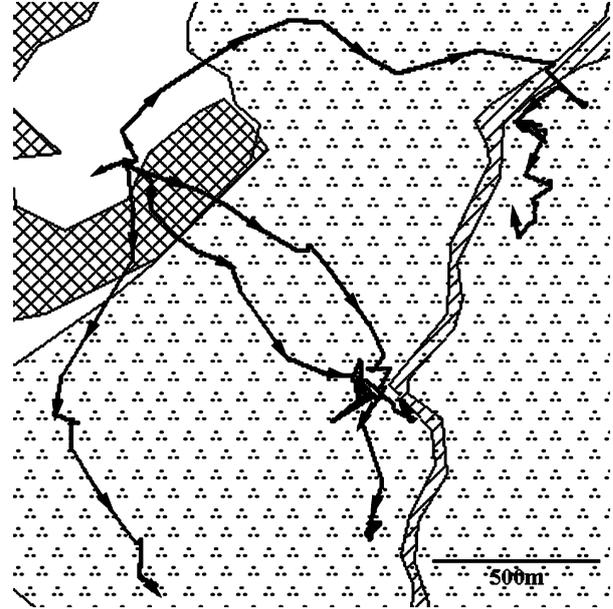
We recorded body temperature (obtained by the transmitter pulse) for the tracked hatchling snakes mostly in the early morning (07h00–10h00) but some snakes had temperature recorded during other times of the day, mainly in the late dry season when air temperature was more variable. We related mean monthly values of body temperature and concurrent air temperature (obtained from the Bureau of Meteorology, for Middle Point Village, in the vicinity of the Beatrice Hill farm) using linear regressions. For the comparisons we divided the data into wet (November–March) and dry (April–October) seasons. Published temperature data for adults (Shine & Madsen 1996) were used for comparative purposes in the discussion. As the frequency distribution of body temperature with respect to time of day was very similar in both groups, the mean overall temperatures of hatchlings and adults were compared by t-test, based on the mean values of each individual snake.

## RESULTS

In 2007, the tracking period of newborn snakes varied from 24 to 110 d (mean =  $53.9 \pm 23.4$  SD,  $N = 10$  snakes) between 16 February (late wet season) and 24 September (dry season). One snake was lost during the wet season, 24 d after release, when it entered an inaccessible area of the floodplain. Three snakes died during the tracking: one was predated by a water rat, *Hydromys chrysogaster* E. Geoffroy, 1804 (all the soft organs were eaten and there were many marks of rodent incisors along the body) after 51 d; another was consumed after 62 d by an adult water python (found with the transmitter in its stomach); and the other died from bacterial infection. The other snakes were tracked until their transmitters failed.



**Figure 1.** Movement patterns of radio-tracked hatchling water pythons *Liasis fuscus* in the Adelaide River floodplain. Each symbol represents one individual and each point is a day-location. Dotted area = floodplain; white area = savanna; hatched area = lagoon; cross-hatched area = pasture; ellipse = release point.



**Figure 2.** Direction of movement in four selected hatchling water pythons *Liasis fuscus* in the Adelaide River floodplain. Each line represents one individual and the arrow-heads indicate the direction of the movement. Dotted area = floodplain; white area = savanna; hatched area = lagoon; cross-hatched area = pasture.

One snake was observed to contain recently ingested prey (inferred from bodily distension) on two occasions.

**Habitat and microhabitat of newborn snakes**

All hatchling pythons moved from the relatively high ground and pasture area of the release point eastwards onto the floodplain. None moved westwards into the savanna habitat and main pasture (Figure 1). Snakes used the floodplain more than expected by chance ( $Z = -6.61, P < 0.0002, N = 427$  locations) and despite the apparently directional movement (Figures 1 and 2), Rayleigh’s tests indicated that only one snake moved in a non-random direction (snake 11,  $Z = 3.14, P = 0.043, N = 89$  locations; for all others  $Z < 2.0, P > 0.1$ ; sample sizes varying from 21 to 72 locations). Some snakes were observed swimming or partially immersed in the water. The snakes were found moving mainly at night, and less often in the early morning. During the day snakes were rarely visible, typically hidden amongst vegetation, down soil cracks or inside farm machinery. Occasionally (during mornings in the mid-dry season), snakes were seen partially exposed, apparently basking. The first two axes in the PCA analysis explained 70.2% of the observed variation for microhabitat use. Crack width and depth were the main components in the first axis, and water and vegetation depth were the main components in the second. Snakes chose larger cracks (wider:  $U = 2108, P < 0.0001$ ; and deeper:  $U = 1601, P < 0.0001$ ) and sites where vegetation was higher ( $U = 14588, P = 0.009$ ) than those available in non-used sites (Table 1). Mean

**Table 1.** Characteristics of shelter-sites used by hatchling water pythons, compared with randomly chosen nearby sites that were not used by the snakes. Sample sizes (N) refer to the number of measurements for each microhabitat trait.

	Median (cm)	Interquartile range	Range
Crack width			
Used (N = 85)	2.3	1.0–4.6	0–10
Non-used (N = 85)	1.1	0–4.0	0–22
Crack depth			
Used (N = 85)	11.4	5.3–30.0	0–30
Non-used (N = 85)	3.0	0.0–18.6	0–38
Water depth			
Used (N = 36)	7.5	0.9–67.9	0–70
Non-used (N = 36)	8.2	0.0–67.9	0–70
Vegetation depth			
Used (N = 186)	3.6	0.0–10.0	0–100
Non-used (N = 186)	3.0	0.0–7.0	0–34

water depth did not differ significantly between used and non-used sites ( $U = 612, P = 0.689, Table 1$ ).

**Movements and area of use**

The PCA on climatic conditions produced a primary axis which explained 52.5% of the variation. This axis was comprised (eigenvectors  $> 0.2$ ) mainly by mean and minimum air temperature, mean and minimum relative humidity, mean, maximum and minimum air pressure and mean maximum and minimum rainfall. With the

**Table 2.** Results of a statistical comparison (ANCOVA) of movement traits between free-ranging adult and hatchling water pythons (*Liasis fuscus*). The ANCOVA included weather conditions and number of days tracking as covariates, and snake behaviours (movement parameters) as dependent variables. NA = non-applicable. Sample sizes:  $N_{\text{adults}} = 93$ ,  $N_{\text{hatchlings}} = 85$  records, when zero-movements are excluded  $N_{\text{adults}} = 43$ ,  $N_{\text{hatchlings}} = 75$  records. PC1 is the first principal component of the principal component analysis (PCA) for the weather variables.

Response variable	Age class			PC1 (weather conditions)			Number of days of tracking		
	F	df	P	F	df	P	F	df	P
Mean weekly distances moved (m wk <sup>-1</sup> )	6.48	1, 17	0.021	7.83	1, 98	0.006			NA
Proportional distances moved (body lengths wk <sup>-1</sup> )	4.62	1, 18	0.045	8.97	1, 99	0.003			NA
Mean weekly distances moved, including zeros (m wk <sup>-1</sup> )	1.63	1, 18	0.218	8.56	1, 155	0.004			NA
Total distances moved, including zeros (m wk <sup>-1</sup> )	2.32	1, 18	0.145	8.98	1, 154	0.003	8.11	1, 154	0.005
Total distances moved, including zeros (body lengths wk <sup>-1</sup> )	3.40	1, 18	0.082	5.39	1, 154	0.021	9.83	1, 154	0.002
Proportion of days moved	12.8	1, 173	< 0.0001	6.88	1, 173	0.009			NA

exception of eigenvectors for air pressure, all the others had positive values.

The ANCOVA analysis showed that mean weekly distances moved differed between adults and hatchlings (Table 2): adults travelled longer absolute distances ( $252 \pm 50.3$  m wk<sup>-1</sup>) than hatchlings ( $66.3 \pm 41.2$  m wk<sup>-1</sup>; Figure 3a) and these dependent variables were also influenced by climatic conditions (Table 2). Although larger (adult) snakes moved longer distances than smaller (hatchling) snakes, the smaller animals actually moved further in terms of body lengths per unit time. When movement distances were converted to body-length units, neonates moved 1.34 times further ( $84.8 \pm 1.12$  body lengths wk<sup>-1</sup>) than did adults ( $66.0 \pm 1.15$  body lengths wk<sup>-1</sup>, Table 2; Figure 3b). These body-size-corrected movements were also influenced by climatic conditions (Table 2). Inclusion of zero-distance movements in the analyses revealed no significant difference between hatchlings and adults, in terms of absolute means (Table 2; hatchlings:  $33.3 \pm 24.8$  m wk<sup>-1</sup>, adults:  $89.6 \pm 25.1$  m wk<sup>-1</sup>) or total absolute distances travelled (i.e. sum of all distances: Table 2; hatchlings:  $204 \pm 46.6$  m wk<sup>-1</sup>, adults:  $195.1 \pm 46.1$  m wk<sup>-1</sup>; Figure 3a). In both cases, weather conditions influenced the distances travelled (Table 2) and the number of days the snakes were tracked also influenced the total distances travelled (Table 2). In terms of distance relative to body size, the total distance travelled was marginally significantly higher in hatchlings (Table 2), with most of the difference in distances travelled (hatchlings:  $329 \pm 32.4$  body lengths wk<sup>-1</sup>, adults:  $89.8 \pm 32.1$  body lengths wk<sup>-1</sup>; Figure 3b) due to the number of days the snakes were tracked (Table 2) and weather conditions (Table 2).

Adult snakes were more sedentary, staying for longer in the same place, than were the neonates (proportion of days moved =  $0.48 \pm 0.06$  days wk<sup>-1</sup> for hatchlings, and  $0.31 \pm 0.06$  days wk<sup>-1</sup> for adults; Table 2) and the proportion of days on which snakes moved were related to weather conditions (Table 2).

### Thermal data

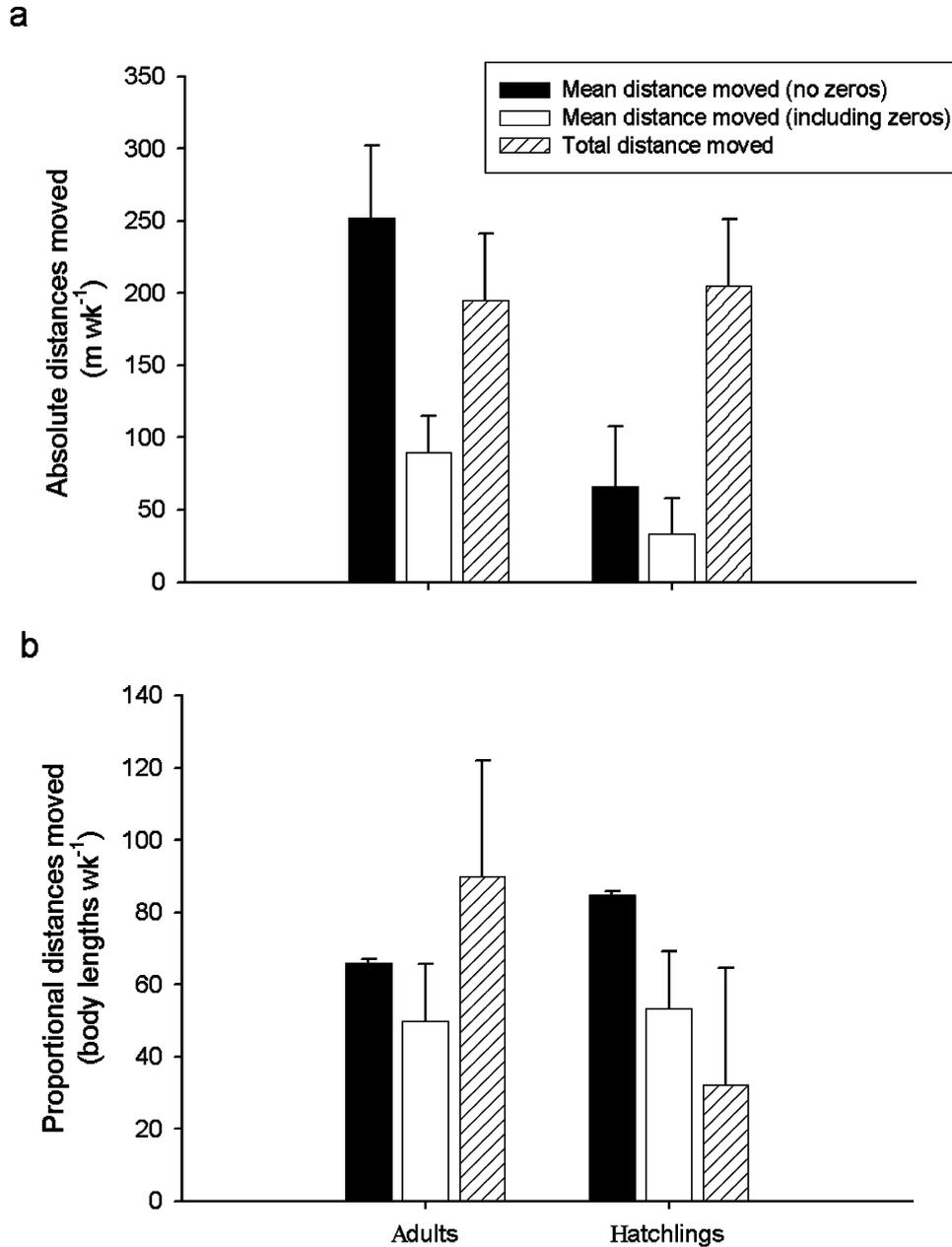
Air temperature varied more over the course of the day during the dry season than during the wet season (Figure 4a, b). Most of the newborn snakes were tracked during the dry season, when they often experienced a considerable (but short-term) decrease in environmental temperature, especially in the early mornings (Figure 4d).

Mean body temperatures were positively correlated with mean air temperatures (Figure 5a,  $r^2 = 0.85$ ,  $P = 0.003$ ,  $N = 7$ , mean values per month) per month, and minimum body temperatures with minimum air temperatures per month (Figure 5b,  $r^2 = 0.73$ ,  $P = 0.01$ ,  $N = 7$ , mean values per month). However, the relationship between maximum body and maximum air temperatures was not statistically significant (Figure 5b,  $r^2 = 0.45$ ,  $P = 0.097$ ,  $N = 7$ , mean values per month). In general, snake body temperatures were slightly higher than the recorded air temperatures, with most records between  $27.5^\circ\text{C}$  and  $29^\circ\text{C}$  for snake body temperatures and between  $23^\circ\text{C}$  and  $24.5^\circ\text{C}$  for air temperature (Figure 6). The overall mean temperature of hatchlings was  $29.3^\circ\text{C} \pm 0.65^\circ\text{C}$  ( $N_{\text{total}} = 545$ ), not significantly higher than  $27.8^\circ\text{C} \pm 2.72^\circ\text{C}$  ( $N_{\text{total}} = 773$ ), the overall mean temperature of the adults ( $t = 1.70$ ,  $df = 18$ ,  $P = 0.106$ ).

## DISCUSSION

### Habitat- and microhabitat-use by newborn snakes

The hatchling water pythons that we studied moved to and inhabited floodplain areas, which are typically used by adults as well (Madsen & Shine 1996a). The young snakes also temporarily used areas highly modified by human activities. Especially during the wet season, the young pythons frequently inhabited aquatic areas for several days at a time. Differences in microhabitat availability according to the seasons may change the habitat use by the snakes. Our sample sizes, especially

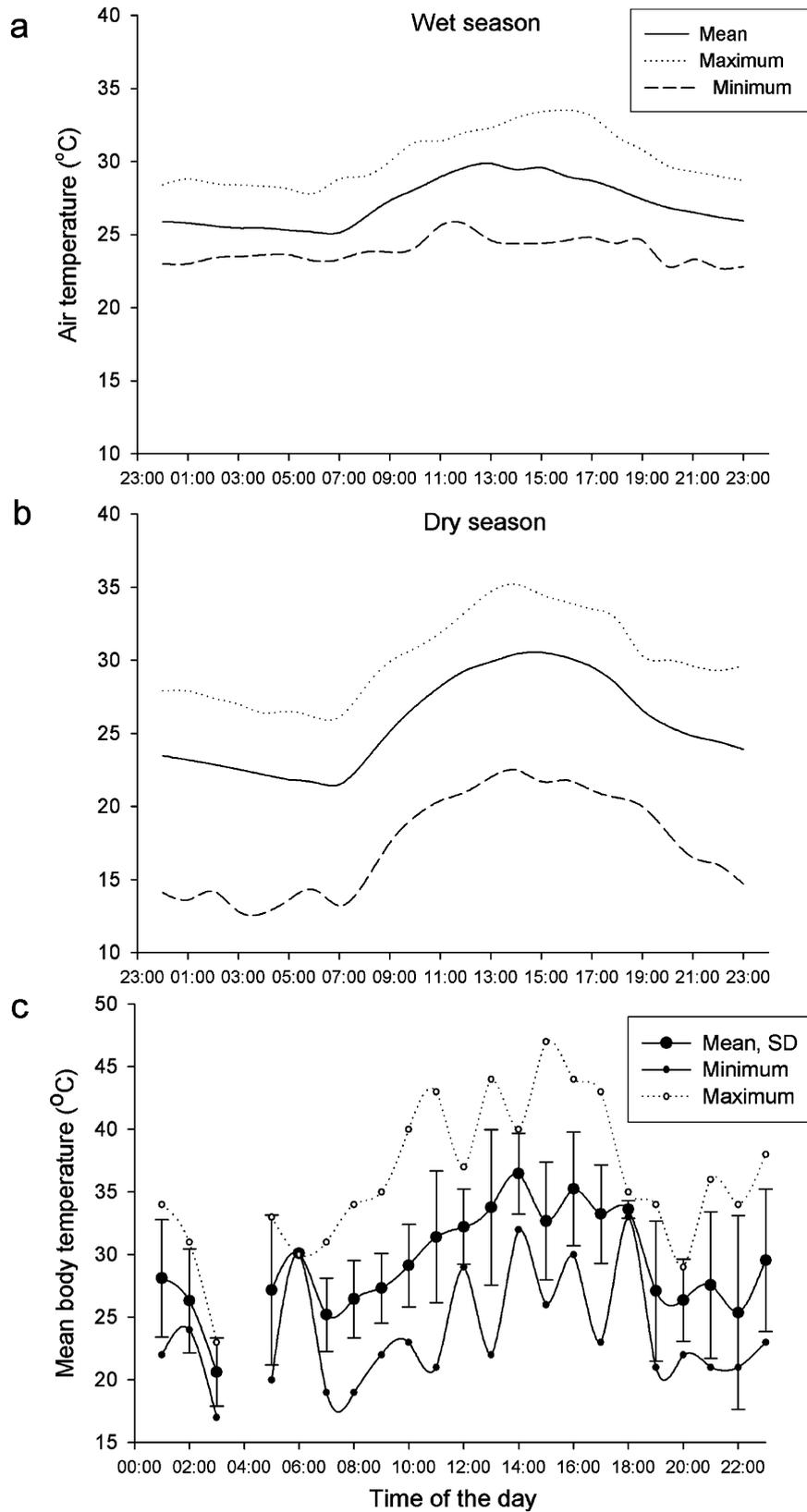


**Figure 3.** Characteristics of weekly movements of adults and hatchlings water pythons in the Adelaide River floodplain. Absolute distances travelled (a). Distances travelled in body lengths (i.e. corrected for body size) (b). Error bars represent SE. Data for hatchlings from the present study, and for adults from the previous radio-tracking study by Madsen & Shine (1996a).

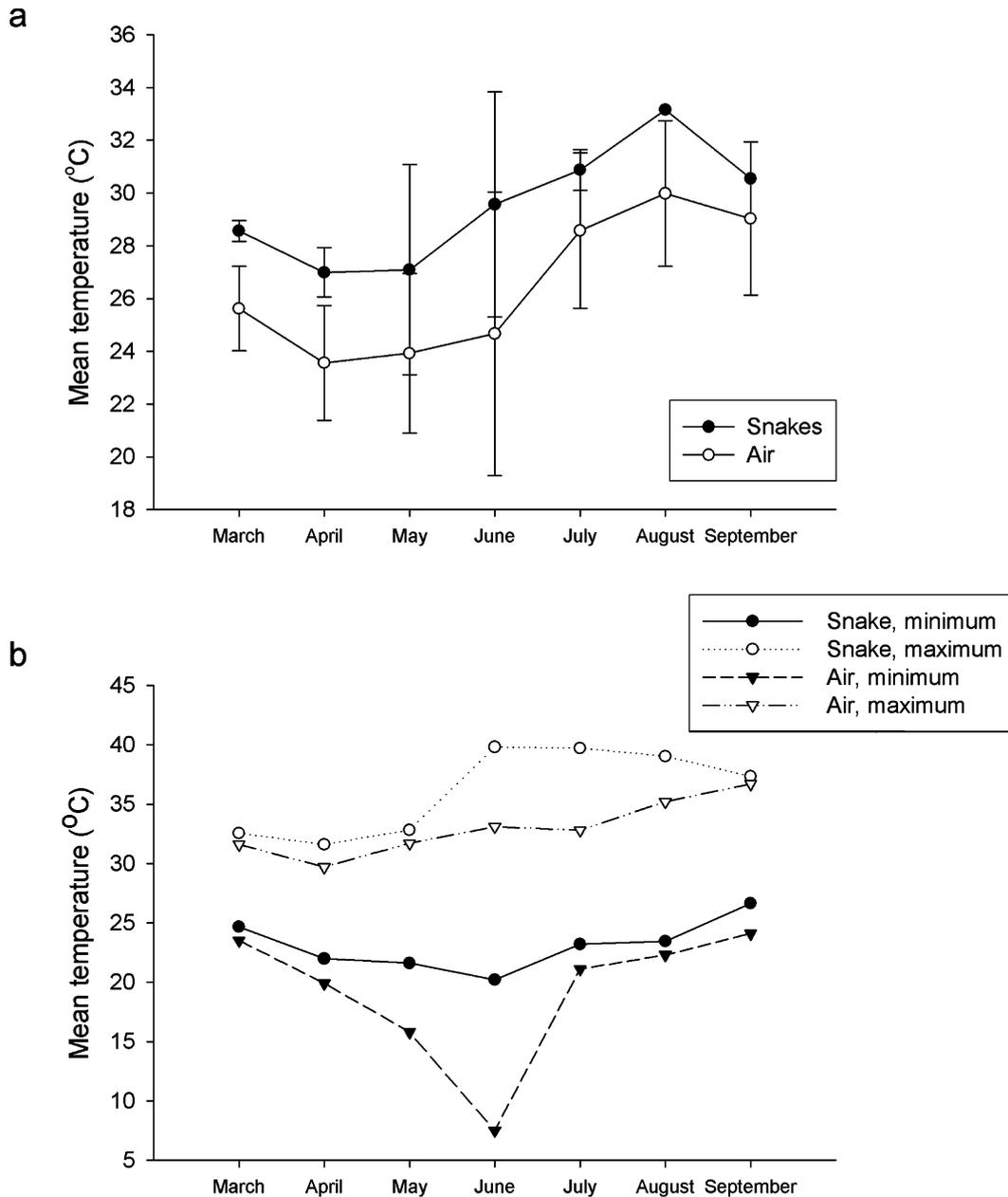
during the wet season, are too small to properly address this question, but in general snakes sheltered under the vegetation and spent time in water bodies (either permanent or temporary) in both seasons. However, we can expect that snakes will spend more time in the water during the wet season (as most of the habitat is flooded) and will take refuge inside the soil cracks only in the dry.

Little is known of dispersal patterns in neonatal reptiles. All the hatchling water pythons in our study moved onto the floodplain soon after release. This was

clearly non-random, although there was no statistical evidence of non-random directionality in movement for most individuals. The lack of significant directionality using the Rayleigh's test is due to the pattern of movements of these snakes: they tended to move around a small area for about 20 d and then travelled for about 4 d to another area and the Rayleigh's test analyses trends in the angles the animals travel. Previous studies have reported that hatchling lizards tend to move in a directional fashion (Imansyah *et al.*



**Figure 4.** Hourly variation in temperature. Mean air temperature in the wet (November to March) (a) and dry (April to October) seasons (b) in Middle Point Village, on the Adelaide River floodplain, in 2007. Mean body temperatures of hatchling water pythons in the wet season (mean values for all individuals pooled together) (c), in the Adelaide River floodplain. Due to the small sample size data on body temperature during the wet season are not illustrated.

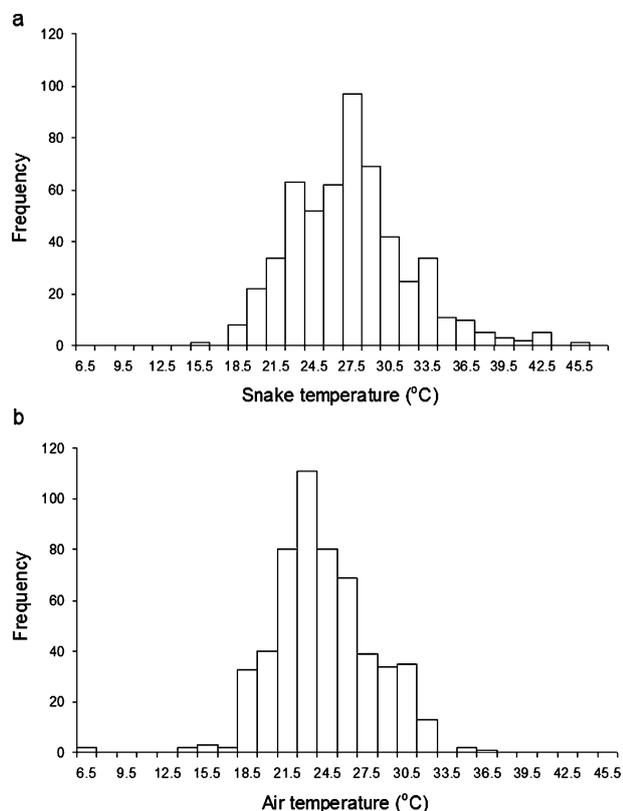


**Figure 5.** Relationships between monthly snake body temperatures and air temperatures at the time the snakes were tracked in the Adelaide River floodplain. Mean temperatures (a). Maximum and minimum temperatures (b). Data points for body temperatures represent means of means, maximum and minimum body temperature of each individual in each month. Error bars represent SD. Air temperatures were recorded by the Bureau of Meteorology in Middle Point Village at the time of snake location.

2008, Pérez-Buitrago & Sabat 2007) and in the field, some hatchlings of massasauga snakes (*Sistrurus catenatus*: Viperidae) seem to follow the mother's trail (Jellen & Kowalski 2007). Laboratory experiments show conspecific scent-trailing and discrimination in newborn pine snakes, *Pituophis melanoleucus* (Burger 1989), plains garter snakes *Thamnophis radix* (Graves & Halpern 1988) and timber rattlesnakes *Crotalus horridus* (Brown & MacLean 1983), but the nature of the cues that

hatchling water pythons use to find the floodplain remains unknown.

The main activities (e.g. dispersion and foraging) of water pythons occur at night, both for adults (Madsen & Shine 1996a) and hatchlings (current study); the animals are hidden during the day. In the dry season, soil cracks are the main refuge not only for these young snakes but also for the adults (Madsen & Shine 1996a), as well as for other species of snake and for other animals (such as



**Figure 6.** Frequency of observed body temperatures of hatchling water pythons (a) and air temperatures during the radio-tracking period (b).

anurans and rats) (Brown *et al.* 2005, pers. obs.). The snakes apparently select the cracks by size, preferring those wider and deeper than average, probably because it is easier to move and hide inside. As well as providing physical protection, the cracks also provide a thermal refuge and food, as rodents live and reproduce inside such cracks (Madsen & Shine 1996a). When not in a crack, the neonatal snakes were hidden in the base of vegetation, or under the soil surface where the roots or dry cover are tangled, making a protected, soft and camouflaged spot. Thus, the animals tend to select sites where vegetation cover is higher than average. Ontogenetic changes in microhabitat use are common in many animals, including reptiles (Asplund 1974, Heatwole 1977, Imansyah *et al.* 2008, Irschick *et al.* 2000, Pérez-Buitrago & Sabat 2007). Although there have been no studies on microhabitat selection by adult water pythons, our observations suggest that adults and hatchlings use the same kind of environment.

### Movements and area of use

The area used by newborn water pythons was large and increased with the duration of tracking. This pattern

suggests that the snakes were still dispersing over the course of our study; or alternatively, that they are nomadic at this stage of the life history. In the Adelaide River floodplain, adult *Liasis fuscus* engage in long-distance migration every year (Madsen & Shine 1996a). As observed in other reptiles (e.g. Komodo dragon *Varanus komodoensis*, Imansyah *et al.* 2008; massassauga snake, Jellen & Kowalski 2007), newborn water pythons travelled shorter distances than did older conspecifics. However, in contrast to hatchling Komodo dragons (which are about twice the body mass of our snakes, Imansyah *et al.* 2008) the newborn pythons moved more often than did conspecific adults. In many species small snakes may have more difficulty finding prey of suitable size (Sazima & Martins 1990). This may be the case for small water pythons which depend almost exclusively on young dusky rats. Hence, newborn pythons may need to move around to look for food more often than do the adults or a more generalized predator such as a newborn Komodo dragon. Small snakes also may fit into a greater variety of refuges than would a larger snake. In the dry season, soil cracks are available all over the floodplain and a newborn python can easily hide in most of them. Thus, the cost of leaving a refuge may be lower for newborn snakes, and the risk of starving (especially in years of low rodent abundance, like 2007, T. Madsen unpubl. data, L.P. and G.B. pers. obs.) probably outweighs the benefits of staying for longer in the same spot. When travel distances are measured in terms of body lengths rather than absolute distances, newborn water pythons moved further than adults, similarly to hatchlings of Mona Island iguana, *Cyclura cornuta stejnegeri* (calculated from García *et al.* 2007 and Pérez-Buitrago & Sabat 2007). However, older Komodo dragons and massassauga snakes have been reported to travel relatively longer distances than do newborn conspecifics (calculated from Imansyah *et al.* 2008 and Jellen & Kowalski 2007).

### Temperature

Water pythons typically display high body temperatures (Shine & Madsen 1996, and this study) and for most of the year, the main challenge for the animals may be to keep cool rather than to warm up (Shine & Madsen 1996). However, in the dry season, the snakes experienced low temperatures at night and in the early morning, inducing the hatchlings to thermoregulate by sun-basking during the day. Snake body temperatures were usually a few degrees higher than air temperature, probably due to thermal heterogeneity among microhabitats (Shine & Madsen 1996) as well as occasional basking. As observed for adult water pythons in the same area, minimum (but not maximum) body temperature was positively

related to minimum air temperature (Shine & Madsen 1996).

Overall, keeping in mind that hatchlings and adult water pythons were tracked in different years, in adjacent areas of the floodplain and the transmitters were relatively heavier to the neonates (and these facts could affect the comparison between the two groups), the most striking result from our study was the broad similarity in spatial ecology and habitat use between hatchling water pythons and conspecific adults, despite the enormous disparity in body sizes between the two groups (mean body masses of 50 g vs 2 kg). That similarity in turn may be due to a broad similarity in the ecological requirements of hatchling and adult water pythons – for example, both depend on the same major prey species (dusky rats) and appear to have similar thermal preferences. The floodplain landscape provides relatively few types of refuge from the (otherwise lethally high) operative temperatures in this area, and thus both juvenile and adult pythons utilize soil cracks for shelter. The similarity in prey resources may also generate similarity in the spatial scale of movements, which presumably relate to the spatial dispersion of feeding opportunities. In summary, then, our study is encouraging: the age class most neglected in previous studies of snake ecology appears to be broadly similar in many respects to the age classes that have been more intensively studied, at least in a species that does not exhibit major ontogenetic changes in diet. By analogy, a recent analysis suggested that annual survival of juvenile snakes likely is more similar to those of adult conspecifics than has generally been assumed (Pike *et al.* 2008). Many more species need to be studied before we can frame generalities about such ontogenetic conservatism, but accumulating evidence suggests that at least in some species, the ecology of juvenile snakes may not be too dissimilar from that of their parents.

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