Life history consequences of nest-site variation in tropical pythons

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We document and interpret microgeographic variation in life history traits of water pythons (Liasis fuscus) on the Adelaide River floodplain in tropical Australia. Subpopulations of pythons separated by [less than] 2 km differ in reproductive timing, in survival rates at three different life history stages (adults, embryos, and hatchlings), in costs of reproduction, and in reproductive frequencies. Remarkably, these differences all seem to result from a minor divergence in nest-site characteristics. Female water pythons use two main types of nest sites: those with relatively low, variable temperatures (especially hollows within paperbark root systems on the edge of the floodplain) and those with higher, constant temperatures (burrows dug by large varanid lizards in the higher, drier ridges [approximately] 2 km away). "Cool" nests delayed reproduction and reduced survival rates of hatchlings in at least one year. Females ovipositing in "cool" nests remained with the clutch throughout the 2-too incubation period, whereas they deserted the clutch within a few days of laying in warmer nests. Most egg-attending females did not feed. Hence, "cool"-nesting females were emaciated by the end of incubation, and many died from starvation or predation; surviving females required two years to replenish their energy reserves before producing another clutch. In contrast, "hot"-nesting females had higher rates of survival, and most could reproduce again the following year. Most females showed strong nest-site fidelity in successive clutches, but some moved between "hot" and "cool" nest sites. We have previously shown that the incubation thermal regime also affects developmental rates and hatchling phenotypes (shape and behavior). Thus, nest-site selection is a phenotypically plastic character, which although superficially trivial, engenders significant microgeographic variation in a wide range of life history traits.

Key words: costs of reproduction; demography; Liasis fuscus; life history; nest-site selection; phenotypic plasticity; python; reproductive frequency; reptile; snake.

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INTRODUCTION

Temporal and spatial aspects of oviposition are crucial life history components for many kinds of animals. Data from several taxa demonstrate that females utilize a wide range of cues to select oviposition sites (Bernardo 1996). However, although oviposition site selection has been well documented in insects (e.g., Rausher 1983), far less is known concerning the ability of female vertebrates to discriminate among potential oviposition sites (Bull et al. 1988, Bernardo 1996). The lack of interest in this topic is surprising, because environmental conditions within the nest can exert a dramatic impact on the developing embryo. For example, abiotic conditions within the nest can affect the offspring's survivorship (e.g., Burger 1993, Resetaris 1996), locomotor performance (e.g., Van Damme et al. 1992, Shine et al. 1997), size (e.g., Packard and Packard 1988), subsequent growth rate (e.g., Brooks et al 1991), and sex (e.g., Bull et al. 1988, Roosenburg 1996).

Nest-site selection by females can influence not only the phenotype and survival probability of the offspring, but also the "costs of reproduction" experienced by the female. For example, alternative nest sites may differ in the degree to which they impose additional energy costs, such as by requiring a long migration, or survival costs, as for example when nest sites expose the nesting female to a high predation risk (Parker and Brown 1972, Madsen 1987). Hence, spatial variation in the availability of nest sites with particular characteristics may induce microgeographic variation in the life history. This paper documents such a case, where available nest sites for water pythons (Liasis fuscus) differ among adjacent areas in ways that cause a cascade of secondary effects that profoundly modify demographic features of the reproducing female pythons.

MATERIALS AND METHODS

Study species and area

Water pythons are large ([less than or equal to] 3 m total length, 5 kg), nonvenomous snakes widely distributed across northern Australia (Cogger 1992). They achieve high population densities in floodplain habitats of the Northern Territory, and since 1986 have been the subject of our detailed ecological research in the Fogg Dam area, 60 km southeast of Darwin. This site is situated in the wet-dry tropics, a region characterized by high temperatures year-round (monthly mean maxima 31 [degrees] 34 [degrees] C, minima 15 [degrees] - 24 [degrees] C), but with highly seasonal rainfall ([greater than]75% of the annual rain falls within the 3-mo "wet

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season" from December to March). The snakes move extensively across the floodplain with the onset of wet-season flooding, but return to the same dry-season areas each year (Madsen and Shine 1996a). Mating occurs in the mid-dry season (July-August), and the eggs are laid about a month later (Madsen and Shine 1996b).

Methods

Location and capture of study species. - Most of the water pythons were collected at night by spotlighting, either from a slow-moving car or by walking. In total, we captured and marked [greater than] 5000 pythons for a total of [greater than] 8000 captures. All pythons were individually marked by scale-clipping and (except for the animals implanted with radiotransmitters) were released the following day at their original site of capture.

Because gravid female water pythons do not dig their own nesting burrows, they must rely on existing holes for oviposition. During the oviposition season (August-October), we found gravid snakes primarily in two areas, neither of which contained significant numbers of pythons at any other time of the year (Madsen and Shine 1998a). The first area consisted of open eucalypt woodland containing numerous burrow complexes dug by large varanid lizards (Varanus panoptes). These burrows were situated in a relatively high, dry area of sandy soils [approximately] 1 km from the floodplain fringe. Some of the burrow systems used by the nesting pythons were also in active use by varanid lizards. The second area, [approximately] 2 km from the first, was a forest of paperbarks (Melaleuca cajuputi) growing in cracking black soils along the fringe of the floodplain, in a location that is inundated by wet-season rainfall each year. The roots of the paperbark 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 (see Shine et al. 1997 for a photograph). Occasionally, gravid females and nests were also seen in other parts of our study area. One nest was laid in extensive Eleocharis reed beds within Fogg Dam in a year when the dam was entirely dry, and another was located in a mound of dirt (3 m long x 1 m high) resulting from human activities (bulldozing by the edge of a road).

Nest temperatures. - We monitored ambient temperatures within each type of nest site during the oviposition season (September 1994) using thermal data-loggers (Hobo-temp with external thermistor; Onset Computer Company, Massachusetts, USA) inserted 1 m down the holes, and set to record air temperatures within the burrow every 10 min for 5 d. Four nests of each type were monitored simultaneously in this way.

Radiotelemetry of female pythons. - We gathered additional data by radio-tracking 13 reproductive female pythons to monitor their movement patterns and body temperatures before and after oviposition. Of these 13 snakes, 8 oviposited in varanid burrows and 5 in paperbark root boles. These snakes were chosen to represent the overall range of body sizes and locations of water pythons in our study area. The pythons were captured at least 3 wk prior to oviposition, and miniature radiotransmitters (Holohil model SI-2T, Holohil Systems Ltd., Carp, Ontario, Canada; Televilt model TXT-2sm-TT, Televilt International, Lindesberg, Sweden; ranging from 45 x 15 mm and 35 g to 80 x 18 mm and 55 g) were surgically implanted in the body cavity under ketamine anesthesia. Transmitters weighed [less than] 3% of the body mass of the snake, and had no apparent effect on the snake's survival, feeding, movements, reproduction, or growth (Shine and Madsen 1996). The transmitter circuits incorporated thermistors, so that pulse intervals were proportional to temperature. Each transmitter was calibrated against a certified thermometer at 2 [degrees] C intervals between 10 [degrees] and 40 [degrees] C prior to surgery (NATA calibration certified by Dobbie Instruments, Sandringham, Victoria, Australia). We located our radio-tracked female pythons at least once a day, and recorded pulse intervals of radiotransmitters (by means of a digital processor) so that we could document the snakes' body temperatures and behavior before and after egg-laying.

Characteristics of pythons using each type of nest.Our data set from the mark-recapture program enabled us to compare several attributes of the snakes using the two main types of nest sites. We could unambiguously assign all captured snakes to one or the other type of nest site, for the following reasons. The two nesting areas are separated by 2 km, with low python densities in the intervening area year-round. We never captured gravid females in this intervening area, despite frequent searching. None of our radiotelemetered female pythons moved between these two areas during the time that they were carrying eggs, nor did we record any marked snakes moving between these sites within a single reproductive season. Hence, gravid snakes captured in one or the other of these sites were almost certainly destined to deposit their eggs in the area in which they were captured.

Survival rates of eggs. - During three nesting seasons (1986, 1987, and 1992), we excavated burrows that had been used by gravid female pythons so that we could search for eggshells in an attempt to determine hatching success and rates of egg predation. In a number of these cases, we had seen females enter these burrows when gravid and emerge after laying, so were confident that the eggs had actually been deposited within the burrow. Pilot

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studies (using eggs from captive females) showed that shells of both hatched and unhatched eggs persist, and are easily recognizable, for [greater than] 12 mo after hatching, because there are no local predators that consume the shells from hatched eggs. Thus, [TABULAR DATA FOR TABLE 1 OMITTED] an absence of dried shells within the nesting burrow suggests that the eggs were taken by predators prior to hatching.

Survival rates of hatchlings. - In 1991 and 1992, we maintained gravid female pythons in captivity until oviposition, and artificially incubated their eggs (full details of our methods are given by Madsen and Shine 1996b). We did not find the paperbark nesting area until 1992, so our 1991 sample did not include snakes from this area. However, in 1992 we captured females from both nesting areas, and we incubated 21 clutches from females nesting in varanid burrows and 29 clutches from paperbark nesters (Table 1). All of the 1992 hatchlings were released at the same place in our study area. Because all of the clutches were incubated under identical conditions in the laboratory, our experimental procedure eliminated the delay in hatching due to lower temperatures in the paperbark nests (Shine et al. 1997), but it did not eliminate the delay due to later oviposition of these females. Thus, we can use the information on recapture rates of these marked offspring to compare survival rates of the hatchlings from clutches deposited by females captured in the two main nesting areas.

Statistical analyses. - Statistical tests were carried out using the programs Statview 4.5 and SuperANOVA (Abacus Concepts, Incorporated) on a PowerMacintosh 6100/66 computer. In some cases, the groups to be compared differed significantly in variances as well as in means (see Results). In such cases, tests for differences in mean values were performed on log-transformed data; this transformation successfully removed the variance heterogeneity. For comparisons involving linear relationships among variables, we tested for equivalence of the groups in terms of the slopes of the relationships (homogeneity of slopes test) before testing for differences in intercept (elevation) of the regression lines (i.e., analysis of covariance).

RESULTS

Nest temperatures

Eggs inside paperbark root holes and in the reed-bed nest experienced cooler and more variable temperatures than did eggs inside varanid burrows. Automatic monitoring of nest-site temperatures in September (the egg-laying season) showed that varanid burrows remained at a virtually constant 32 [degrees] C (mean of hourly means =

32.03 [degrees] C, SD = 0.28, n = 24), whereas temperatures inside the paperbark nests were lower (mean = 29.81 [degrees] C, SD = 1.72, n = 24) and more variable (from [less than] 27 [degrees] to [greater than] 32 [degrees] C; [ILLUSTRATION FOR FIGURE 1 OMITTED]). Hence, paperbark nests (henceforth, "cool" nests) were consistently cooler (true for 23 of 24 hourly means; Fisher's exact test, against a null of 12 from 24, P [less than] 0.01) and more variable in temperature (true for 24 of 24 hourly means, using standard deviation as the measure of variation; against a null of 12 from 24, P [less than] 0.01) than were varanid-burrow nests (henceforth, "hot" nests). Thermally, the reed-bed nest was even cooler and more variable than the paperbark nests (mean = 27.8 [degrees] C, SD = 2.96, n = 71). The dirt-mound nest was thermally intermediate, but was substantially warmer and more stable in temperature (mean = 31.02 [degrees] C, SD = 0.52, n = 28) than any of the paperbark nests.

Telemetrically determined body temperatures of ovipositing female pythons provided additional information on nest temperatures [ILLUSTRATION FOR FIGURE 2 OMITTED]. Mean temperatures of snakes were higher during the oviposition period (i.e., the period of 1-16 d between the last sighting of a female when she was gravid and her first sighting as nongravid) than either before or after this time, but the two nest types did not differ in this respect ([ILLUSTRATION FOR FIGURE 2 OMITTED]; two-factor repeated-measures ANOVA with nest type as the "between" factor and stage of reproductive cycle as the "within" factor, and mean body temperature per snake as the dependent variable; effect of nest type, $F_{1,26}$ = 0.27, P = 0.62; effect of reproductive stage, $F_{2,26}$ = 11.09, P [less than] 0.003; interaction, $F_{2,26}$ = 0.25, P = 0.78). However, variances of body temperatures tended to be lower in "hot"-nesting females than in "cool"-nesting females, at the time of oviposition [ILLUSTRATION FOR FIGURE 2 OMITTED]. A two-factor repeated-measures ANOVA (as above, but with standard deviation of body temperature per snake as the dependent variable) showed that snakes using the two types of nest site did not differ in thermal variances overall ($F_{1,26}$ = 0.08, P = 0.79) but that these thermal variances changed with the stage of the reproductive cycle ($F_{2,26}$ = 3.76, P [less than] 0.04; interaction, $F_{2,26}$ = 1.51, P = 0.24). The snakes maintained very stable body temperatures while they were ovipositing in varanid burrows [ILLUSTRATION FOR FIGURE 2 OMITTED] because of the stable environmental temperatures in this microhabitat [ILLUSTRATION FOR FIGURE 1 OMITTED].

Indeed, monitoring body temperatures of female pythons at around the time of oviposition suggested that their choice of nest sites was driven mainly by thermal variance. We have detailed data on the temperatures of eight gravid

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females that oviposited in varanid burrows after moving from burrow to burrow during the 2 wk preceding oviposition. Typically, they stayed for 1-2 d in a burrow before moving on to another. Often, females moved among three to seven burrows before finally ovipositing in one of them. We could thus compare the thermal characteristics (as measured by the females' body temperatures) of the burrows that were sampled and rejected with those that were finally selected as oviposition sites.

We analyzed the body-temperature data of these eight gravid females using one-factor repeated-measures ANOVA, with burrow category (used or not used as an oviposition site) as the factor and maternal body temperature as the dependent variable. Analysis detected no significant differences between the mean temperatures of the burrows used for nesting vs. those that were sampled but rejected ($[F_{1,7}] = 0.55$, $P = 0.48$), but the females consistently chose to lay their eggs in burrows with a lower thermal variance than the burrows that they had occupied but not used for oviposition (using the standard deviation of maternal body temperature while in the burrow as the dependent variable; $[F_{1,7}] = 7.48$, P [less than] 0.04). These analyses suggest that burrow-nesting females move among potential nest sites and eventually oviposit when they find a burrow with lower thermal variance (but with a similar mean temperature) than the sites they have previously sampled but rejected. This sequential "sampling" behavior was not evident in the paperbark-nesting females, as all of the five radio-tracked females were recorded moving directly into very large paperbark boles.

Characteristics of female pythons using each nest site

Table 1 compares the snakes using the two main types of nest site. Females from the varanid burrows were larger than those from the paperbark. However, there were no significant differences in reproductive output (relative clutch mass, clutch size, mean egg size, offspring size) between snakes from the two areas, nor in body condition either before or after oviposition (single-factor ANCOVA with nest type as the factor, snout-vent length as the covariate, and body mass as the dependent variable; for pre-oviposition, homogeneity of slopes $[F_{1,46}] = 0.77$, $P = 0.38$, intercepts $[F_{1,47}] = 2.09$, $P = 0.15$; for post-oviposition, homogeneity of slopes $[F_{1,46}] = 0.28$, $P = 0.60$, intercepts $[F_{1,47}] = 3.53$, $P = 0.07$).

Timing of reproduction

The date of oviposition of the first brood laid by our captive females was set to zero, and subsequent broods were assigned a relative date accordingly. The females captured in the varanid-burrow site laid their eggs significantly earlier than did conspecifics from the paperbarks (mean dates = 14.7 vs. 24.4 d after the first clutch was laid; unpaired two-tailed t test, $[t_{48}] = 4.19$, P [less than] 0.0005). Consequently, the clutches from our captive varanid-burrow females also hatched earlier than the clutches from paperbark females (mean dates = 17.7 and 29.2 d, respectively, $[t_{48}] = 4.30$, P [less than] 0.0005). The difference of [approximately]10 d in mean date of oviposition may reflect the warmer temperatures in burrows [ILLUSTRATION FOR FIGURE 1 OMITTED], with consequent acceleration of embryogenesis prior to oviposition. In the field, this difference in timing is increased by the longer incubation periods of eggs from the (cool) paperbark nests (means = 59.4 vs. 68.0 d; Shine et al. 1997).

Behavior of pythons after oviposition

Radio-tracked female pythons that oviposited in "cool" nests usually remained with their eggs until they hatched, a period of [approximately]2 mo (n = 7 females; mean = 58.43 d, SD = 14.36, range = 32-73 d). This was true of the females that nested in the earth mound (73 days) and the reed bed (67 d), as well as the paperbarks (mean = 53.8 d). In contrast, females that oviposited in "hot" nests usually deserted the clutch after a few days (n = 8 females, including 2 that nested in "cool" nests in other years; mean = 6.50 d, SD = 5.21, range = 1-16 d). The difference between the two nest types in duration of maternal attendance after laying was highly significant (unpaired two-tailed t test, $[t_{13}] = 9.57$, P [less than] 0.001). The facultative nature of nest attendance is well illustrated by two females recorded to change their nest types during the study. A female that remained with her clutch in the reed beds throughout incubation (67 d) in 1992 deserted her subsequent clutch (laid in a varanid burrow) [less than]2 days after oviposition. Similarly, a female that deserted her varanid-burrow eggs [less than]5 days after oviposition in 1992 attended her subsequent clutch (laid in the cooler earth mound) throughout incubation (73 d) in 1993.

Nest-site fidelity

Water pythons lay only a single clutch per year (Madsen and Shine 1996b), and recapture records show that most females return to the same nesting areas each year. Of 13 females that were initially captured in the paperbark nesting area and then recaptured when gravid in a later year, 12 (92%) were recaptured in the same area. The single exception (number 3497) was captured when gravid in the paperbarks in 1993 and recaptured beside a varanid burrow 3 km away in 1995. Similarly, 28 (97%) of 29 reproductive females from the varanid burrows returned to the burrows to deposit subsequent clutches. The sole

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exception (number 2083) oviposited in the varanid burrows in 1991, 1992, and 1993. She was not captured during the reproductive season in 1994, but laid her 1995 clutch 2 km away in the paperbarks. The female that nested among Eleocharis reeds in Fogg Dam in 1992 laid in a varanid burrow one year later. Another record of nest-site change may have been due to disturbance: a radio-tracked female oviposited in a varanid burrow that we later excavated in our search for eggshells, and the following year she laid her eggs in the large earth mound.

Energy "costs" of reproduction

Body condition. - Female water pythons were never recorded to feed (i.e., contain freshly ingested prey) during the period from ovulation to oviposition. The only female that was recorded to feed during clutch attendance was the animal that oviposited in the dry reed beds in 1992. Rats were abundant in the reed beds, whereas they were rare in the paperbarks (Madsen and Shine, personal observation) Perhaps for this reason, the females that remained with their clutches in the paperbarks did not feed during this period. These egg-attending females often emerged from the paperbark burrows to bask, but were never recorded to move [greater than] 1 m from the nest hole. They became increasingly emaciated over this period. Females captured in the paperbark forest during November-December, soon after their eggs hatched, were in significantly poorer condition than were females after laying. This effect is most easily seen by comparing mass/length relationships of paperbark-nesting females vs. burrow-nesting females. The two groups were similar in body shape after ovipositing, but within 2 mo (i.e., at about the time the eggs hatched) the paperbark nesters were substantially thinner, whereas the burrow nesters had actually gained in mass.

This pattern is shown in Fig. 3, using residual scores from the general linear regression of In(mass) vs. snout-vent length (SVL) as an index of maternal body condition (from a two-factor ANOVA on these data, with each individual represented only once in the data set; effect of population, $F_{1,76}$ = 24.10, P [less than] 0.0001; effect of stage of the reproductive cycle, $F_{1,76}$ = 1.20, P = 0.28; interaction, $F_{1,76}$ = 13.63, P [less than] 0.0005). For a large (200 cm SVL) female python brooding in a paperbark nest, the decrease in body mass during incubation was [approximately]300 g (an average of 15% of post-laying body mass).

Part of the mass loss of female pythons during clutch attendance may be due to the additional energy costs of shivering thermogenesis (Harlow and Grigg 1984, Slip and Shine 1988). Female pythons of many species wrap around their eggs during cool conditions and warm the

clutch by regular muscular contractions (e.g., Shine 1988). This behavior has been recorded in captive water pythons from Fogg Dam (G. Bedford, personal communication), but may not occur frequently in the wild because nest temperatures remain relatively high even without additional metabolic thermogenesis [ILLUSTRATION FOR FIGURE 1 OMITTED]. Our telemetry data show that means and variances of body temperatures differ in only trivial ways among individual snakes and between reproductive and nonreproductive seasons (Shine and Madsen 1996; see also [ILLUSTRATION FOR FIGURE 2 OMITTED]). Hence, the primary energy cost for brooding females may be the decreased food intake, rather than metabolic expenditures in shivering thermogenesis.

Interval between successive clutches. - Recaptures of marked female snakes also reveal a difference in reproductive frequency between females using "cool" vs. "hot" nests. Five varanid-burrow nesting females were recorded as gravid near the burrows in each of three successive years. Another female was caught in this area in four of five years, and was gravid on each occasion; she was not captured in the intervening year. An additional 10 females from the varanid burrows were recorded as gravid in each of two successive years. Fewer paperbark-nesting females were recaptured, and most of these (7 of 10) did not reproduce in successive years. Counting all records of snakes in successive years, 24 of 27 cycles (89%) from varanid-burrow nesters were annual (i.e., the snake reproduced in both years), whereas this was true for only 3 of 10 paperbark nesters (30%). The difference in reproductive frequency was highly significant ($[Chi]^2$ = 10.0, df = 1, P [less than] 0.002). Overall, the pattern is clear: "hot" nesting females typically reproduced again the following year, whereas "cool"-nesting females usually did not reproduce again until two years later.

Survival "costs" of reproduction

In order to assess the probability of survival of female pythons nesting in varanid burrows vs. paperbark boles, we can compare the recapture rates of these two groups of snakes. However, the difference in reproductive frequency complicates this analysis. Because we spent much of our time in the nesting areas, we were more likely to capture a snake in a year when she was nesting than in a year when she did not reproduce. As most of the paperbark-nesting females did not reproduce annually, their probability of recapture would be less than that of the varanid-burrow nesting females, even if the two groups of females had the same survival rates. We can avoid this bias by restricting analysis to recapture records obtained at intervals of two years after the snake's initial capture (i.e., in the years when the paperbark females would also be expected to reproduce). When calculated in this way,

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the recapture rate of the varanid-burrow nesting females captured in 1992 was significantly higher (9 of 34 = 26%) than that of the paperbark-nesting females captured the same year (3 of 44 = 7.3%, $[Chi].sup.2$ = 4.3, df = 1, P [less than] 0.04). The comparison is a conservative one, because any survival costs of reproduction would have been experienced twice as often by the (annually reproducing) varanid-burrow nesting females as by the (biennial) paperbark-nesting females in this comparison. The difference in recapture rates between these two groups of snakes apparently relates to reproduction by the females, because recapture rates of males were actually higher for the paperbark males (67 of 145 = 46%) than for the varanid-burrow males (10 of 44 = 23%, $[Chi].sup.2$ = 6.8, df = 1, P [less than] 0.01).

Because of their high nest-site fidelity, the low recapture rate of paperbark-nesting females is likely to reflect higher mortality rates rather than movement to other nesting areas. In support of this hypothesis, we recorded deaths of five of the paperbark-nesting females during our study. One of these snakes was a radio-tracked female. Three of the snakes (including the radio-tracked female) died of starvation after the cessation of brooding, and the other two were killed by varanid lizards when basking outside their nesting holes in the later stages of brooding. Both of these snakes were in extremely poor condition when killed. Over the same period, none of the varanid-burrow nesting females were found dead.

Survival rates of eggs

In November 1986 and August 1987, excavation of three varanid-burrow nests (where we had recorded radio-tracked females that had abandoned their clutches after [less than]14 d) revealed unaccompanied egg clutches in each case. Approximately half of the eggs in each clutch remained viable, despite maternal desertion for up to 2 wk. However, six of the eggs on the upperside of one egg mass were severely dehydrated, and the embryos had died. An additional four varanid burrows were excavated to a depth of 1 m in January 1993. All were burrows in which three to eight gravid female pythons had been seen but not captured, suggesting that several clutches had been deposited in each of these holes. One of our radio-tracked females (number 2971) had definitely oviposited in one of the burrows. Nonetheless, we found a total of only three eggshells, all from a single burrow and all having hatched successfully (judged by slits in the eggshells). We do not know the identity of the predators that removed these eggs, but suspicion falls heavily on varanid lizards. When we placed recently laid eggs beside burrow entrances, varanids soon emerged and consumed the eggs. The single paperbark root system that we excavated in January 1993 contained [greater than]50

eggs, all of them hatched. Judging by their appearance, some had probably come from previous years rather than the current breeding season. The clutch laid in the Eleocharis reed beds in Fogg Dam was also examined after hatching: 12 of 13 eggs had hatched successfully.

Survival rates of hatchlings

We observed a significantly higher recapture rate of hatchlings from the varanid-burrow females compared to hatchlings from the paperbark females. Hatchlings from the varanid-burrow females were about six times more likely to be recaptured than were those from the paperbark-nest clutches (11 out of 266 hatchlings = 4.1% vs. 2 out of 293 hatchlings = 0.68%; $[Chi].sup.2$ = 5.9, df = 1, P [less than] 0.02). We cannot be sure of the reason for this difference, but delayed hatching of the paperbark-nest eggs seems a likely candidate (Madsen and Shine 1998a). In keeping with this prediction, the recaptured offspring originated from broods that hatched significantly earlier than broods from which no hatchlings were recaptured (mean relative hatching dates = 17.0 and 25.7 d, respectively; unpaired two-tailed t test, $[t.sub.48]$ = 2.16, P [less than] 0.04).

DISCUSSION

The habitat of the Fogg Dam water pythons is characterized by significant small-scale spatial heterogeneity in nest-site availability. Because the snakes do not construct their own nesting burrows, most females oviposit in existing holes. In some years, the drying of Fogg Dam offers an additional choice, with extensive dried reed beds also providing sites suitable for egg incubation. However, the dam is dry only rarely, probably less than 1 year in 20 (E. Cox, personal communication). Thus, the basic choice for a nesting female python is between paperbark roots and varanid burrows. These two nest types differ considerably in thermal characteristics, as well as in the risk of varanid predation on eggs.

The two main types of nest sites are separated geographically by [less than]2 km, a trivial distance relative to the snake's seasonal migration of up to 12 km across the floodplain (Madsen and Shine 1996a). Nonetheless, most females consistently choose the same type of nest site year after year, and this choice has a considerable impact on major life history traits. The cooler and more variable thermal environment of the paperbark nests delays hatching, through a delay in oviposition as well as a more prolonged incubation (mean incubation periods = 59.4 vs. 68.0 d, respectively; Shine et al. 1997). Hence, eggs from "hot" nests hatch about 3 wk earlier than eggs from "cool" nests.

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Plausibly, this delay in hatching might affect subsequent hatchling survival. In our study area, the pythons feed almost exclusively on dusky rats, Rattus colletti (Shine and Madsen 1997). However, due to gape limitation and the scarcity of alternative prey, hatchling pythons have to rely on juvenile rats for their first few meals. During most years, rats are still breeding when the hatchlings emerge during November-December, and thus small-sized prey are readily available (Madsen and Shine 1998b). However, the 1992 dry season was preceded by an extremely dry "wet" season, and rat reproduction stopped several months before the pythons began to hatch (Madsen and Shine 1998b). Because the rats rapidly grow too large to be swallowed by a hatchling python (Shine et al. 1997), very few ingestible-sized rats were available for the hatchling pythons in 1992. In our experiment, clutches from the paperbark and varanid-burrow females were incubated at the same temperature. Although this procedure halved the difference in time of hatching (from approximately 20 to 10 d), we still recorded a significant difference in recapture rates of hatchlings from the two areas. This difference in survival probably reflects the advantage of early hatching, mediated by the higher availability of ingestible-sized prey for early-hatching pythons.

Why do some female pythons lay their eggs in varanid burrows and then leave them, whereas others oviposit among paperbark roots and remain with the clutch throughout incubation? The link between maternal attendance and nest temperatures is straightforward, but the maintenance of these two different maternal "strategies" within a single population is surprising. One might expect that one strategy would confer higher maternal fitness than the other, and thus replace its alternative over evolutionary time (Gillespie 1973). Possible explanations for the persistence of this polymorphism include the following:

1) Paperbark roots may be the optimal nest site for some females (e.g., those in better condition, which can better afford the costs of brooding their eggs) and varanid burrows more appropriate nest sites for others. However, the overall similarity between paperbark and varanid-burrow snakes (Table 1) suggests that the persistence of these alternative tactics does not reflect a matching of maternal traits to oviposition-site characteristics.

2) The two types of females may be genetically divergent, so that genes coding for the two maternal strategies do not actually coexist in the same gene pool. Our data do not support this possibility; the snakes are very similar in sizes and reproductive output, as well as in a scalation characteristic (subcaudal scale division) that shows strong heritability (Shine et al. 1988, Madsen and Shine 1998a).

Also, we have [greater than] 10 records of snakes (including two nesting females) moving between the two nesting areas from one breeding season to the next.

3) Nest type may be determined early in ontogeny (perhaps as a result of the female's own incubation environment), in the same way that salmonid fishes return to their own hatching stream to breed as adults (e.g., Eiler et al. 1993). The records of females moving between alternative nest types for successive clutches do not fit this interpretation, although most females did return to the same nest type as they had used for their previous clutch. Hence we cannot rule out imprinting as an explanation of this between-clutch consistency, although the dichotomy in nest-site selection and duration of maternal attendance seems more likely to be a phenotypically plastic character rather than being "hard-wired" through genetics or experience early in a female's life.

4) Each nest type confers costs as well as benefits, such that the overall reproductive success of females using the two types of nests is relatively similar. Our data do, in fact, suggest such trade-offs. A female that nests in the varanid burrows (a) faces lower costs because she lays her eggs earlier and does not attend them (and therefore she is more likely to survive and to breed again in the following year) and (b) produces offspring that hatch earlier (which in some years may increase hatchling survival) but are exposed to a higher risk of egg predation. In contrast, a female nesting in the paperbarks experiences (a) higher costs of reproduction per clutch (a longer delay between successive clutches and a lower probability of survival) and (b) in some years, reduced hatchling survival (because of late hatching). These disadvantages are balanced by the advantage of the eggs having a higher probability of survival to hatching.

The fitness consequences of nest-site choice thus represent a balance among these different variables. However, even if the mean fitness payoff to the two strategies is not identical, temporal variation in their relative success may enable both types to persist within the population over evolutionary time (e.g., Hedrick 1986). For example, the costs to oviposition in the paperbarks vary with maternal condition (females are less emaciated after oviposition if they are in better condition before laying; Shine and Madsen 1997). The condition of the snakes, in turn, varies enormously from year to year, due to rainfall-induced annual variation in prey availability (Redhead 1979, Shine and Madsen 1997, Madsen and Shine 1998b). The survival benefits to early hatching might also vary among years. Similarly, fluctuations in the abundance of varanid lizards might substantially alter relative hatching success in the two nest types.

Life history consequences of nest-site variation in tropical pythons

Overall, our study suggests that a small-scale spatial dichotomy in the thermal characteristics of available nest sites can engender major shifts in fundamental aspects of the life history, such as maternal behavioral strategies; reproductive frequencies; survival rates of females, eggs, and hatchlings; and phenotypic traits of the offspring. It is surprising to see that such traits can be so easily modified. One of these traits (maternal nest attendance) has previously been regarded as invariant within all python species (e.g., Shine 1988), and variation in the other traits (e.g., reproductive frequencies, survival schedules) has generally been reported from among-population, rather than within-population comparisons. Often, such variation has been attributed to life history adaptation rather than phenotypic plasticity (e.g., Fitch 1970, 1982, Tinkle and Ballinger 1972). Instead, our data suggest that minor variation in nest-site characteristics can induce major modifications to the life history. This example reinforces other recent work on reptilian nest-site selection (Shine and Harlow 1996, Qualls and Shine 1996) in suggesting that spatial and temporal variation in the physical conditions available for embryogenesis may generate substantial variation in life-history traits.

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