WHY DO MOST TROPICAL ANIMALS REPRODUCE SEASONALLY? TESTING HYPOTHESES ON AN AUSTRALIAN SNAKE

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Abstract. Most species reproduce seasonally, even in the tropics where activity occurs year-round. Squamate reptiles provide ideal model organisms to clarify the ultimate (adaptive) reasons for the restriction of reproduction to specific times of year. Females of almost all temperate-zone reptile species produce their eggs or offspring in the warmest time of the year, thereby synchronizing embryogenesis with high ambient temperatures. However, although tropical reptiles are freed from this thermal constraint, most do not reproduce year-round. Seasonal reproduction in tropical reptiles might be driven by biotic factors (e.g., peak periods of predation on eggs or hatchlings, or food for hatchlings) or abiotic factors (e.g., seasonal availability of suitably moist incubation conditions). Keelback snakes (*Tropidonophis mairii*, Colubridae) in tropical Australia reproduce from April to November, but with a major peak in May–June. Our field studies falsify hypotheses that invoke biotic factors as explanations for this pattern: the timing of nesting does not minimize predation on eggs, nor maximize food availability or survival rates for hatchlings. Instead, our data implicate abiotic factors: female keelbacks nest most intensely soon after the cessation of monsoonal rains when soils are moist enough to sustain optimal embryogenesis (wetter nests produce larger hatchlings, that are more likely to survive) but are unlikely to become waterlogged (which is lethal to eggs). Thus, abiotic factors may favor seasonal reproduction in tropical as well as temperate-zone animals.

Key words: Australia; climate; developmental plasticity; hydric; oviposition; predation; reptile; Tropidonophis mairii.

INTRODUCTION

Most plants and animals do not reproduce year-round, but instead display distinct seasonal peaks in reproductive activity. In some cases this reproductive seasonality is extraordinarily precise, with all gametes produced within a few days or even hours (e.g., coral spawning; Babcock et al. 1994). In other cases the reproductive activity is spread out over weeks or months, but nonetheless is clearly seasonal rather than continuous (e.g., most temperate-zone species; Fitch 1970, Abts 1988, Aichinger 1992, Bauer 1992*b,* Alkins-Koo 2000). Even *Homo sapiens*, the archetypal example of a continuously breeding species, exhibits significant seasonality in births (Bronson 1995). Because the time of year at which reproduction occurs is a major axis of life-history variation, extensive research has sought to clarify both the proximate and ultimate reasons for the observed diversity in patterns of reproductive timing. Proximate factors generally have proved more amenable to study, with robust evidence that seasonal reproduction can be initiated by stimuli such as variations in day length (Murton and Westwood 1977, Burns 1985, Kumar and Kumar 1991, Wikelski et al. 2000, Chandola-Saklani et al. 2004), temperature (Obbard and Brooks 1987, Hart 2004), rainfall (Patterson

1991, Lampo and Medialdea 1996, Madsen and Shine 1999*b,* Christian et al. 2003), and food supply (Tinney et al. 2001, Clouet 2003, Rubenstein and Wikelski 2003), or interactions between these factors (Janzen 1967, Johannes 1978, Kramer 1978, Garrido et al. 2000, Hau et al. 2000, Hau 2001, Pankhurst and Porter 2003).

It has proven more difficult to identify ultimate causations for reproductive seasonality, that is, the selective advantages and disadvantages associated with reproducing at different times of year. Many hypotheses have been proposed in this respect, but robust empirical tests are rare. For example, many authors invoke thermal requirements for developing offspring to explain the highly seasonal reproductive cycles of cool-climate ectothermic animals (which typically restrict embryogenesis to midsummer; Fitch 1970, Tauber et al. 1986, Vitt 1991, Olsson and Shine 1998). However, the near ubiquity of this constraint makes it difficult to test the hypothesis except in special cases (e.g., Mouton and Herselman 1994, Olsson and Shine 1998). Species with extended breeding seasons, but with clear peaks in the intensity of breeding within that longer period, offer better opportunities for study in this respect (Sexton et al. 1971, Smith and Iverson 1993, Winemiller 1993, Colli et al. 1997, Lemos-Espinal et al. 1999). In these cases we know that breeding is possible over the entire period, and can quantify the conditions at various times as well as their consequences for reproductive females

and their progeny. Such data can then be used to test predictions from alternative hypotheses about the seasonally varying factors (e.g., weather, nest conditions, predation risk, food supply) that might restrict reproductive activity to some subset of time within the broader temporal window when reproduction is physically possible.

Reproductive cycles of squamate reptiles (lizards and snakes) offer excellent model systems with which to investigate these topics. In cool-climate species, major events within the female reproductive cycle (ovulation, pregnancy, oviposition, and parturition) are almost entirely restricted to the warmest times of year (Fitch 1970, Ota 1994). This rigid seasonality breaks down in warmer climates, with females of many tropical species reproducing over several months each year (Gorman and Licht 1974, Fleming and Hooker 1975, Rocha 1992, Griffiths 1999, Ramirez-Bautista et al. 2000, Luiselli et al. 2002, Aldridge et al. 2003, Mojica et al. 2003), sometimes all year (James and Shine 1985, Shine 1991, Clerke and Alford 1993, Dearing and Schall 1994). Nonetheless, truly aseasonal (continuous) reproduction by female reptiles is rare, even in equatorial climates (Saint Girons and Pfeffer 1971, Colli 1991, Vitt and Blackburn 1991, Shine et al. 1998). Two major kinds of hypotheses have been invoked to explain the seasonality of female reproduction in tropical reptiles: (1) Biotic factors—egg production may be restricted to periods when predation on eggs or nesting females is low, or timed such that newly emerged offspring will encounter optimal conditions of food availability or low vulnerability to predation (Tinkle 1967, Tinkle et al. 1970, Saint Girons and Pfeffer 1971, Fitch 1982); or (2) Abiotic factors—although ambient temperatures are high year-round, precipitation is seasonal in many tropical areas and hence, reproduction may be restricted to periods when optimal nest conditions (e.g., moist but not flooded soils) are available (Fitch and Fitch 1967, Barbault 1975, 1976, Wolda 1989).

The same kinds of explanations have been advanced to explain seasonality of reproduction in other types of animals (e.g., Wikelski et al. 2000, Aung et al. 2001). James and Shine (1985) attempted to test between these hypotheses with a comparative analysis of reproductive seasonality in squamate species from the wet–dry tropics of northern Australia. Precipitation is highly seasonal in this area (McDonald and McAlpine 1991), and James and Shine found that some species bred mostly in the dry season whereas others bred in the wet season. Critically, a species' seasonal timing of reproduction was linked to the geographic distribution of its relatives. Species in the wet–dry tropics that were closely related to arid-zone lineages tended to breed in the dry season, whereas taxa related to those from more mesic habitats were wet-season breeders. James and Shine (1985) interpreted this pattern as support for the ''abiotic'' hypothesis above, with lineages preadapted to

dry-soil incubation retaining that preference when they invaded a seasonally arid habitat, and the reverse occurring for mesic-habitat animals. They argued that because many of these taxa used similar kinds of prey and were vulnerable to similar predators, the ''biotic'' hypothesis would predict similarity not divergence in reproductive timing and hence, was less consistent with their data. Similar comments have been made by other studies that have documented divergent reproductive seasonality within sympatric squamate faunas, especially when the diversity appears to fall along taxonomic lines (Barbault 1976, Vitt 1991; see also Zimmerman and Simberloff 1996).

Our long-term studies on a small colubrid snake species (the keelback, *Tropidonophis mairii*) in tropical Australia provide an opportunity to test among alternative hypotheses on the possible advantages and disadvantages of seasonal breeding. This species breeds over most of the year, but with a strong peak of breeding activity in May–June; the eggs hatch about two months later (Fig. 1). In this paper, we attempt to identify the optimal timing of breeding with respect to a series of seasonally varying biotic and abiotic factors that might plausibly act as selective forces for reproductive seasonality: (1) food availability (and thus, growth rates) of hatchlings produced at different times of year; (2) predation risk (and thus, survival rates) for hatchlings produced at different times of year; (3) predation rates on eggs at different times of year; and (4) availability of optimal nest conditions (cool, moist but not flooded soils).

For each of the variables identified by these hypotheses, we examine our data to see whether there is indeed significant annual variation in the putative selective force, and if so whether the timing of optimal conditions coincides with the observed reproductive seasonality of the keelback population.

METHODS

Study area and species

Fogg Dam is an artificial empoundment on the Adelaide River floodplain 60 km east of Darwin, in the Australian wet–dry tropics. The floodplain is dry for most of the year, but is shallowly inundated for up to five months with the onset of seasonal monsoonal rains (Madsen and Shine 1996b; see Plate 1). In contrast to the highly seasonal precipitation regime, maximum temperatures remain warm year-round (monthly mean maxima 31–34°C) although with lower minima during the dry season (monthly mean minima 15–24°C: Brown et al. 2001).

Keelbacks are medium-sized (to 0.8 m snout–vent length [SVL], 280 g) nonvenomous natricine colubrid snakes. Widely distributed in near-coastal habitats throughout much of tropical and subtropical Australia (Cogger 1992), these snakes feed primarily on frogs (Shine 1991). Female keelbacks produce multiple

PLATE 1. Seasonal shifts in habitat characteristics over the course of the extended nesting season for keelback snakes. The upper photograph shows the Adelaide River floodplain below Fogg Dam during the wet season (early March) when the area is inundated and vegetation-covered, whereas the lower photo shows the same location late in the dry season (October) after a wildfire has removed most vegetation and left bare, deeply cracked soil. Photo credit: G. P. Brown.

clutches within a single breeding season, with oviposition from April through November each year (Brown and Shine 2002a, b; see Fig. 1). Two natural nests at Fogg Dam were 10–20 cm beneath the soil surface (Webb et al. 2001). Thermal and hydric conditions during incubation strongly influence the phenotypic traits of hatchling keelbacks, including body size, shape, and muscular strength (Webb et al. 2001, Brown and Shine 2004). Incubation under cool moist conditions generates larger hatchlings, which in turn have a higher probability of survival through the first year of life (Brown and Shine 2002b, 2004).

Field methods

Data in the present paper were gathered over the period May 1998 to December 2003. We surveyed the 1.3 km long dam wall for snakes on 1851 nights during this period, on an average of 27.2 nights per month (range 4–31). We attempted to catch all keelbacks that we encountered on the dam wall; these individuals were then measured and individually marked prior to release at their capture site the following day. Snakes were palpated prior to release to obtain fecal samples, in order to quantify feeding frequencies, and if possible to identify the nature of the prey that had been consumed. Gravid females were retained until oviposition 1–28 days later (mean = 6.5 days, SD = 3.4) before release; their eggs were incubated in the laboratory and

all hatchlings weighed, measured, and individually marked prior to release at their mother's site of capture. In total, we collected 2317 individual keelbacks over the study period (2839 captures), and released 3523 marked hatchlings. Beginning in March 1999 we also conducted nightly surveys of frog abundance at Fogg Dam. Ten survey grids were established 100 m apart, each encompassing 2×3 m sections of the road surface along the dam wall. Each evening, we recorded the numbers and species of frogs in each grid (Brown and Shine 2002b).

Shaded air temperature and relative humidity were measured hourly over the study period using dataloggers located ~1 km from Fogg Dam. Daily rainfall values were recorded using a rain gauge located 2 km from Fogg Dam. Beginning in July 2001 we collected monthly soil samples in potential nesting sites along the dam wall. These were weighed, then dried and re-
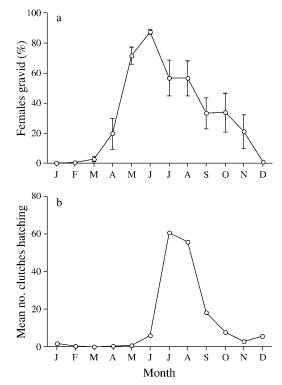

FIG. 1. Seasonality of reproduction in female keelbacks, *Tropidonophis mairii*, at Fogg Dam in tropical Australia. The upper graph shows the mean percentage of adult female keelbacks containing shelled oviductal eggs (total $N = 809$ snakes) during each month over 5.5 years. Error bars represent standard errors. The lower graph represents the distribution of expected hatch dates of the mean number of clutches produced each month, based on a two-month incubation period. Note that the two graphs do not coincide completely, because of monthly variation in the numbers of females captured. For example, very few clutches hatch in January despite a reasonably high percentage of gravid females two months earlier (in November), because very few females overall were captured in November compared to the numbers captured earlier in the year.

weighed to determine their water content (Shine and Brown 2002). Thus, we have two to five years of monthly data for the above variables; our statistical analyses and figures are based on means of monthly values calculated over those periods. As an additional index of soil moisture, we interpolated monthly values of ''soil moisture storage'' from the 60-year averages presented in Fig. 15 of McDonald and McAlpine (1991). Soil moisture storage was calculated from weekly rainfall and evaporation rates, and estimates the amount of moisture available to plants (McDonald and McAlpine 1991).

Soil temperatures at Fogg Dam were recorded over a 12-month period using thermal dataloggers buried 0, 10, and 30 cm under the soil surface at two locations. To assess the ability of keelback eggs to withstand immersion in water (as might occur if a nest was flooded by heavy rain), we placed eggs of different developmental stages (newly laid, mid-incubation, and near the end of incubation) in water for lengths of time varying from 1 to 30 h. The eggs were then returned to moist vermiculite for incubation, and we recorded whether or not they survived the exposure. In total, these data allow us to address assumptions and predictions from alternative hypotheses.

Some of our time-series data exhibit positive autocorrelation, inflating the risk of Type I error in correlation analyses. One means of compensating for this risk is to reduce the ''effective'' sample size of correlations, hence making them more conservative (Bence 1995, Pyper and Peterman 1998). We used an even more conservative approach to adjust the sample sizes of such correlations, by calculating overall monthly means and thereby limiting the sample size of correlations to a maximum of $N = 12$.

RESULTS

Hypothesis 1. Oviposition is timed such that hatchlings emerge when food availability (and thus, hatchling growth) is maximized

Many authors have invoked this hypothesis to explain reproductive seasonality in tropical reptiles (e.g., Saint Girons and Pfeffer 1971, Fitch 1982). To test the idea, we need to establish which times of year offer the best feeding opportunities for hatchling keelbacks at our study area. First, do frog abundances vary seasonally, and second, are the feeding rates and body condition of hatchling snakes influenced by frog abundance?

Although mean frog abundance increased twofold following the onset of the wet season (Fig. 2a), overall variation in frog numbers among months was not statistically significant (Table 1). Because no small keelbacks (<35 cm SVL) were captured during June or July and few were captured between August and October, we pooled data on feeding rates and body condition over the August–October period. Body condition
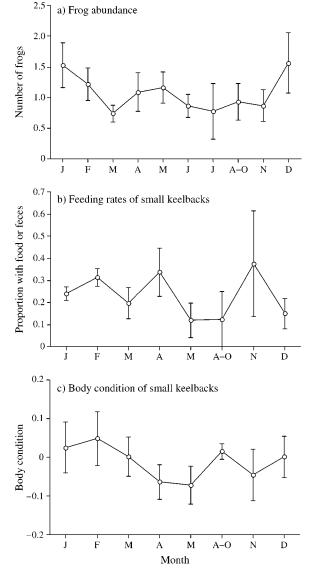

FIG. 2. (a) Number of frogs seen per month in 10 survey grids monitored over 1465 nights over five years; (b) monthly feeding rates of 458 small (<35 cm SVL) keelback snakes over five years; (c) body condition (residuals from general linear regression of ln(body mass) vs. ln(snout–vent length) of 458 small (<35 cm SVL) keelback snakes over five years. Values in all three panels are shown as mean ± SE.

(mass relative to length, using residual scores from the general linear regression of ln mass vs. ln SVL) of small (<35 cm SVL) keelbacks also did not vary among months, but tended to be lowest during the early dry season (April–May; Fig. 2c). Feeding rates tended to be lower during the dry season May–October (Fig. 2b), but like frog abundance and body condition, feeding rate did not vary significantly among months (Table 1). Correlation analyses using mean monthly values show that the numbers of frogs seen on our nightly surveys were not correlated with body condition of young keelbacks ($N = 10$, Spearman $r = -0.01$, $P =$

Table 1. Results of statistical analysis (ANOVA) to examine variation among months in nesting activity of keelback snakes, and in abiotic and biotic factors that might affect the fitness consequences of nesting seasonality in this species.

Variable	F	df	P
Proportion of females gravid	11.2	11, 51	<0.0001
Daily maximum air temperature	5.6	11, 42	<0.0001
Daily minimum air temperature	9.7	11, 42	<0.0001
Daily mean air temperature	17.7	11, 42	<0.0001
Rainfall	19.2	11, 56	<0.0001
Maximum soil moisture	1.3	11, 19	0.31
Minimum soil moisture	5.0	11, 19	0.001
Mean soil moisture	2.8	11, 19	0.02
Abundance of frogs	1.1	11, 46	0.42
Abundance of slatey-grey snakes	1.4	11, 56	0.18
Proportion of slatey-grey snakes eating keelback-sized eggs	0.4	11, 46	0.96
Body condition of hatchling keelbacks	0.7	7, 29	0.69
Proportion of hatchling keelbacks with food	1.0	7, 29	0.49
Proportion of hatchling keelbacks recaptured	1.1	3, 14	0.38

Note: Data on these variables were gathered over periods of 2–5 years (degrees of freedom are based on number of months for which data were obtained).

0.99), or their feeding rates ($N = 10$, Spearman $r = 0.20$, $P = 0.59$).

These analyses suggest that prey availability may not be a limiting factor for young keelbacks. Although frogs tended to be more abundant during the wetter months, they were common year-round. Thus, frogs may remain sufficiently abundant that young keelbacks will encounter prey frequently throughout the year. Additionally, if keelback hatching was timed to coincide with frog abundance (December–January) we would expect to see a majority of nests laid in October–November. In fact, few clutches are laid at this time of year (Fig. 1). This mismatch between prediction and data falsifies the hypothesis that the seasonal timing of oviposition has evolved to maximize food availability for hatchlings.

Hypothesis 2. Oviposition is timed such that hatchlings emerge when predation risk (and thus, hatchling mortality) is minimized

Neonate keelbacks are small (9.5–17.0 cm SVL, 0.8–3.8 g) and nonvenomous and thus, presumably are eaten by a wide variety of predators including waterbirds, snakes, and varanid lizards. Hence, the most important determinant of the optimal timing of oviposition might be to produce hatchlings at times of year when the young snakes are most likely to survive. Our mark–recapture data provide estimates of survival rates of snakes hatching at different times within the prolonged (7-mo) emergence period. To maintain acceptable sample sizes we have combined data for hatchlings released between October and January, when numbers were low (Fig. 3). This leaves four time periods for comparison. Recapture rates were low (5.2%) and did not differ significantly among these periods (Table 1). Neonates released during September had slightly but nonsignificantly higher rates of recapture. If females timed their reproduction to produce hatchlings during this period, their nesting activity should peak in July (allowing a

2-mo incubation). This is not the case, and therefore we can reject the hypothesis as inconsistent with our data. In keeping with this conclusion, the most important potential predators of hatchling keelbacks (wading birds, snakes, and varanid lizards) are abundant year-round at our study site, and thus seasonal fluctuations in predator pressure are unlikely.

Hypothesis 3. Oviposition is timed such that eggs are laid when rates of egg predation are low

High rates of egg predation might drive reproductive seasonality, with females favored to oviposit at times of year when their eggs are at less risk from predators. Keelback nests are vulnerable to a range of mammals and reptiles (e.g., bandicoots, varanid lizards; G. P. Brown and R. Shine, *unpublished data*), but the most important predator may be an oophagous colubrid snake, the slatey-grey snake *Stegonotus cucullatus*. Abundant at Fogg Dam, this species belongs to a phylogenetic lineage in which oophagy is frequent, and *S. cucullatus* possesses egg-eating adaptations such as enlarged bladelike teeth at the rear of the maxilla that
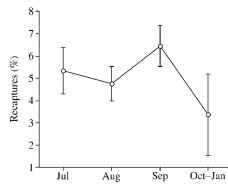

Fig. 3. Recapture rates (mean ± SE) of marked baby keelbacks by hatching period, calculated from 183 recaptures of 3523 hatchlings released over five years.
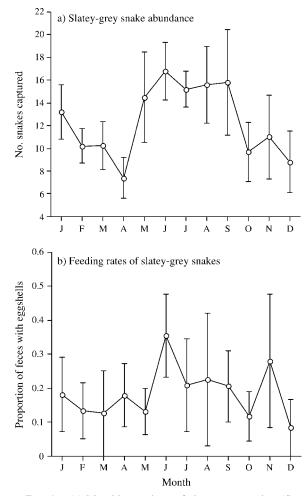
FIG. 4. (a) Monthly numbers of slatey-grey snakes (*Stegonotus cucullatus*) caught (*N* = 756 over five years); (b) monthly proportion of slatey-grey snake fecal samples (from a total *N* = 246) containing keelback-sized eggshells. All values are shown as mean ± SE.

function to penetrate leathery eggshells (Shine 1991). Reptile eggs comprise >20% of all prey items identified in our studies of *S. cucullatus* at Fogg Dam (G. P. Brown and R. Shine, *unpublished data*). Although some of these eggs are small and likely belong to lizards, the vast majority of eggshells found in *Stegonotus* feces unambiguously belong to keelback snakes.

The most plausible reason for seasonal variation in predation rates on keelback eggs would be if slatey-grey snakes show seasonal shifts in habitat use or diet such that they contain fewer keelback eggs at some times of year than at others. Contrary to this prediction, (1) numbers of slatey-grey snakes encountered on the dam wall did not vary significantly among months (Table 1), but (2) numbers tended to be highest during May–September, corresponding to the keelback nesting period (Fig. 4a). The proportion of the slatey-grey snake diet composed of keelback eggs (as based on shells in the feces of recently captured specimens) also

did not vary significantly among months but peaked in June (Fig. 4b), suggesting that slatey-grey snakes key in on keelback eggs at the time when most keelback eggs are incubating (Fig. 1). Thus, the observed timing of keelback nesting does not reduce rates of egg predation. Qualitative observations on abundance of the only other potential predators also fail to support the "seasonal egg predation" hypothesis. Varanid lizards are active on the dam wall year-round, but especially in the dry season (the peak period of keelback nesting). Bandicoots are rarely seen in the area, with no clear seasonality in occurrence (G. P. Brown and R. Shine, *unpublished data*).

Hypothesis 4. Oviposition is timed such that eggs are laid when incubation conditions are optimal

As is the case for many other reptile species, the thermal and hydric conditions experienced by a keelback egg can affect not only its probability of successful hatching, but also many aspects of the phenotype of the young snake (including its overall body size, shape, and muscular strength; Webb et al. 2001, Brown and Shine 2004). Experimental studies have shown that relatively cool, moist conditions are optimal for keelback incubation, generating larger (and thus, fitter; Brown and Shine 2004) hatchlings. Hence, the peak period of keelback reproduction might be restricted by nest availability.

Either temperature or moisture (or both) could be significant in this respect. Monthly mean values reveal that air temperatures are lowest mid-year (Fig. 5a), whereas rainfall is highly concentrated in the midsummer wet season (Fig. 5b). Reflecting these climatic patterns, soil temperatures (Fig. 5c) and soil water content (Fig. 5d) in potential nest sites also vary through the course of the year (Table 1). Correlation analyses reveal that the relative intensity of nesting activity (Fig. 1) was not related to either monthly maximum air temperature (N = 12, Spearman r = −0.20, P = 0.53) or to monthly mean air temperature (N = 12, Spearman r = −0.46, P = 0.14). However, relative intensity of nesting activity was significantly (and inversely) related to monthly minimum air temperature (N = 12, Spearman r = −0.83, P = 0.001) and to monthly rainfall (N = 12, Spearman r = −0.94, P < 0.0001). Similar correlation analyses for soil parameters showed a strong link between nesting activity and minimum monthly soil temperature (N = 12, Spearman r = −0.76, P = 0.004) but no relationship between nesting activity and soil water content (N = 12, Spearman r = −0.22, P = 0.50).

Thus, peak nesting by keelbacks occurs when rainfall is scarce and temperatures are relatively low. The correlation is less than perfect, however: temperatures are lowest in July but nesting is rare at that time (compare Figs. 1 vs. 5a), and rainfall is low from May through September but nesting is concentrated in the earliest part of the dry season (May–June; compare Figs. 1 vs.
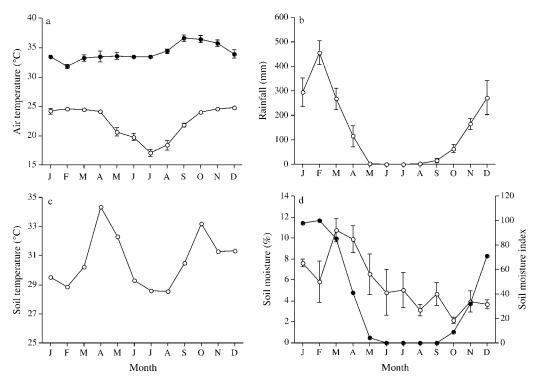
FIG. 5. Monthly variation in thermal and hydric conditions at Fogg Dam: (a) daily minimum and maximum air temperatures; (b) rainfall; (c) soil temperatures; and (d) soil water content. Data for soil temperature were available for only one year, but for all other variables, values are shown as mean ± SE. In (d) the soil moisture percentage (open circles) was measured from monthly soil samples from Fogg Dam; the soil moisture index (solid circles) was taken from McDonald and McAlpine (1991: Fig. 15).

5b). Soil water content is higher during the wet season than during the peak breeding period (Fig. 5d). The latter pattern suggests an additional abiotic consideration: flooding. Eggs laid prior to May are likely to experience heavy rain and wet substrate (Fig. 5b,d), raising the possibility that they might drown in waterlogged nests.

To assess the ability of keelback eggs to withstand inundation for varying periods, we submerged eggs of different stages of development in water for 1–30 h. At each time period we used six eggs (two newly laid, two mid-incubation, two near the end of incubation). All eggs survived 1 and 4 h immersion, but mortality rates were 50% after 8.5 h; 67% after 12, 17.5, and 21 h; and 100% after 25 and 30 h. The egg's stage of development did not affect its probability of survival; a multiple logistic regression with survival as the dependent variable showed that the duration of immersion significantly affected the probability of egg mortality ($\chi^2 = 8.57$, 1 df, $P = 0.003$) but that an egg's stage of development did not ($\chi^2 = 3.87$, 2 df, $P = 0.15$; interaction $\chi^2 = 0.83$, 2 df, $P = 0.66$). Thus, eggs are likely to die if submerged for more than about eight hours, possibly explaining why keelbacks do not begin nesting until the cessation of monsoonal rains (Figs. 1 and 5b,d).

DISCUSSION

In several respects, keelback snakes offer an ideal study system with which to test alternative hypotheses about the advantages and disadvantages associated with different seasonal schedules of reproduction. In particular, the broad range of nesting dates but with a clear peak (Fig. 1) allows us to compare the fate of hatchlings from clutches produced at different times of year. Our unusually large data set (809 clutches totaling 3523 hatchlings, produced over five years) further enhances our ability to detect any benefits or costs associated with reproduction at different times of year. Results from these analyses challenge conventional paradigms that invoke biotic factors as selective forces for reproductive seasonality in tropical reptiles. Factors such as egg predation rates, prey availability, and survival probabilities for hatchlings either did not vary through the year, or peaked at times inconsistent with predictions from hypotheses invoking these factors as causal influences on reproductive cyclicity. Instead, our data broadly support predictions from the hypothesis that abiotic factors constrain nesting in keelbacks. Experimental studies identify cool, moist (but not flooded) nest sites as ideal incubation environments for this species, and our field data show that the peak timing of keelback nesting coincides with the availability of such

conditions. That is, keelbacks nest during the period when the soil is moist but heavy rain is unlikely, and when soil temperatures are relatively low.

Inevitably, we have failed to consider some other hypotheses about the factors that modify reproductive seasonality. For example, many authors have suggested that reproductive output within a population may be concentrated both in time and space because of benefits related to predator satiation (Janzen 1967, Barbault 1975). That is, hatchlings are most likely to survive if they hatch in a large group, so that many inevitably escape even if there is predator pressure soon after hatching. Unlike the hypotheses reviewed above, the ''predator satiation'' hypothesis does not predict seasonal timing of reproduction, only that selection will favor both temporal and spatial concentration of nesting activity. Contrary to this prediction, keelback nests at our study site are not spatially concentrated, instead occurring along the entire dam wall (G. P. Brown and R. Shine, *unpublished data*). On a temporal scale, we might expect predator satiation to generate hatching synchrony at a scale of hours or days rather than the weeks and months seen in keelbacks at Fogg Dam (Fig. 1).

How general are our results? Although most tropical reptile species reproduce seasonally, there is considerable interspecific diversity in reproductive seasonality even within a single area (Barbault 1976). At first sight, this phenomenon looks to be inconsistent with any single hypothesis (either biotic or abiotic) for the determinants of reproductive seasonality. However, this paradox is easily resolved at least in theory, in a way that is amenable to further empirical testing. There are at least three reasons why sympatric taxa might reproduce at different times, even if in all cases it is abiotic (incubation) conditions that restrict their reproductive timing:

1) Eggshell structure and embryonic physiology differ among species, and can generate significant divergence in incubation requirements (e.g., Badham 1971). In an area with strong seasonal variation in soil moisture content (like Fogg Dam), taxa with differing hydric requirements would be forced to breed at different times of year. The most dramatic divergence in this respect involves the evolution of a water-resistant calcareous shell in some lineages of gekkonid lizards (Bauer 1992a, Thompson and Russell 1999). Presumably, the independence from substratum hydric conditions might allow a wider range of egg-laying seasons in such taxa, especially if the eggs are laid in elevated locations secure from flooding (G. P. Brown and R. Shine, *unpublished data*).

2) Nest-site selection can modify the physical conditions that eggs experience in the nest. For example, slatey-grey snakes (*Stegonotus cucullatus*) and golden tree snakes (*Dendrelaphis punctulatus*) at Fogg Dam nest in the wet season rather than the dry season (Shine 1991; G. P. Brown and R. Shine, *unpublished data*).

Radiotelemetric monitoring of *S. cucullatus* suggests that most females nest in the hollows of standing trees, thus eliminating any risk of flooding (Brown et al. 2005). The highly arboreal habits of *D. punctulatus* suggest that the same will be true for them also.

3) Parental behavior can modify nest-site conditions, and ameliorate climate-imposed constraints. For example, water pythons *Liasis fuscus* at Fogg Dam nest late in the dry season (September–October), and females generally remain with their clutch throughout incubation (Madsen and Shine 1996a, 1999a). Attending female pythons can hold the eggs off a flooded substratum (Barker and Barker 1996) and/or coil tightly to reduce desiccation of the clutch in dry conditions (Aubret et al. 2003). Embryonic development in water pythons proceeds more effectively in relatively hot conditions, as are typical of the late dry season (Shine et al. 1996: Fig. 5a), so that parental protection from desiccation allows water pythons to exploit optimally high temperatures for incubation of their eggs.

4) Reproductive mode (viviparity vs. oviparity) profoundly modifies the abiotic conditions experienced by developing embryos. Inside the maternal uterus, an egg is exposed to relatively constant and high water potential independent of seasonal variations in soil water content (Packard et al. 1977, Tinkle and Gibbons 1977). Maternal thermoregulation also can buffer the thermal regimes experienced by developing embryos to a substantial degree (Peterson 1987, Peterson et al. 1993), albeit not entirely (Lourdais et al. 2004).

5) The mode of body-temperature regulation (endothermy vs. ectothermy) can further buffer embryos against environmental variation. Thus, endothermic parents (pythons, birds, mammals) can regulate (and hence optimize) developmental temperatures of their offspring (Farmer 2000, 2003).

In summary, adaptations of reproductive biology can significantly buffer the vulnerability of a developing embryo to seasonally variable incubation conditions. Hence, seasonal rather than aseasonal reproduction in tropical viviparous taxa (Shine 1986), especially endotherms (Bolton et al. 1982), likely reflects biotic rather than abiotic factors. Adaptations such as parental care also can influence the offspring's vulnerability to biotic risks such as predation and starvation (via parental protection and feeding) but overall, biotic factors likely will be less buffered than will the thermal and hydric conditions of incubation. Hence, we might expect that the causal factors generating reproductive seasonality in tropical organisms will differ according to the kinds of reproductive features outlined above. Many (probably most) tropical organisms are oviparous ectotherms with water-permeable eggs and no parental care, and for such taxa we expect that seasonal variations in hydric conditions (and perhaps thermal regimes) may be the most important constraints on the seasonal timing of egg production. However, traits such as calcareous eggshells, parental care, viviparity, and

endothermy will render organisms increasingly less vulnerable to such environmental variations in ambient temperatures and water potentials. This shift to a greater importance of biotic rather than abiotic factors may be reinforced by other features. For example, endothermy compromises an animal's capacity for long-term storage of energy (because extensive fat stores impede physiological thermoregulation; Bonnet et al. 1998). Hence, endotherms cannot dissociate the seasonal timing of feeding (energy intake) from the seasonal timing of reproduction (energy expenditure) as readily as can ectotherms (Bonnet et al. 1998). In this situation, endotherms may be forced to act as ''income breeders'', such that their seasonal timing of offspring production is constrained by seasonal availability of food resources for either the reproducing female or her offspring (e.g., Bolton et al. 1982, Duquette and Millar 1995).

Given the immense diversity of tropical reptiles, presumably there are species for which reproductive seasonality is the result of biotic rather than abiotic factors (e.g., see Rubenstein and Wikelski 2003). Similarly, phylogenetic constraints may limit variation in reproductive timing in some lineages. Nonetheless, the relatively simple abiotic hypothesis, that reptiles breed at the times of year when suitable physical conditions for incubation are available, appears likely to hold true for a broad range of tropical as well as temperate-zone taxa. Thus, the processes driving reproductive seasonality in these two types of habitats, and in these two groups of taxa, may be more similar than would be expected a priori. Thermal conditions are a more important constraint than moisture in most cool-climate systems, and the high frequency of viviparity in such areas (Shine 2002) presumably removes any significant regulatory role for ambient hydric conditions. Nonetheless, even in relatively cool and highly seasonal habitats, especially in the arid zone, seasonality of rainfall may be a major influence on seasonal patterns of reptile reproduction (Andrews 1988, 1991). Thus, there may be strong parallels between the forces driving reproductive seasonality in tropical, arid-zone, and temperate-zone reptile species. In turn, the central influence of embryonic requirements on reproductive seasonality emphasizes the intimate dependence of reptilian embryogenesis on the physical conditions available for incubation (Deeming 2004).

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