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Responses of three sympatric snake species to tropical seasonality in northern Australia

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ABSTRACT. In the Australian wet–dry tropics, temperatures are high year-round but rainfall is concentrated in a 4-mo wet season. Regular nightly surveys in the Fogg Dam Nature Reserve provided data on temporal (monthly, seasonal) variation in biological attributes of three snake species: water pythons (*Liasis fuscus*, Pythonidae), keelbacks (*Tropidonophis mairii*, Colubridae) and slatey-grey snakes (*Stegonotus cucullatus*, Colubridae). Adults of all three taxa were encountered more frequently during the dry season than the wet season, whereas juveniles were more commonly encountered in the wet season. The sex ratio among adult snakes also shifted seasonally, but in different ways in different species. These sex-ratio shifts probably reflect reproductive activity (mate-searching by males, oviposition migrations by females) and were accompanied by increased encounter rates. Feeding rates and body condition of keelbacks (a frog specialist) were highest during the wet season when frogs were most abundant. Rats migrated away from Fogg Dam during the wet season, and most pythons (rat specialists) left this area to follow their prey. The pythons that remained at Fogg Dam exhibited low feeding rates and poor body condition. Slatey-grey snakes (a generalist predator) showed less seasonal variation in feeding rates or body condition. Our data show that tropical seasonality induces strong fluctuations in many attributes of snake populations, and that patterns of response differ both among and within species.

KEY WORDS: activity, ecology, feeding, sex ratio, tropics

INTRODUCTION

Tropical zones have often been viewed as aseasonal because, relative to temperate latitudes, annual variation in photoperiod and temperature is low (Wikelski *et al.* 2000). Precipitation, though, is often strongly seasonal in tropical areas, with all or most of the annual rainfall occurring in one or more discrete wet seasons each year. Seasonally inundated areas such as floodplains may consist primarily of freshwater habitat during rainy periods but transform

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to xeric habitats characterized by lack of vegetation and deep soil cracks during the dry season. Although intuition and available data both suggest that climatic conditions in the tropics may exert substantial effects on abiotic and biotic environments, there are surprisingly few detailed studies of the nature of such effects. This dearth of study on tropical systems is especially lamentable when one considers that most species of animals and plants live in the tropics (Vitt 1987).

How do seasonal schedules of precipitation affect the ecology of tropical organisms? The wet season brings about an immense change in resource availability. The abundance of available water and burst of vegetation growth after monsoonal rains may provide food and shelter for many animal taxa, as well as modifying the range of hydric and thermal microhabitats that are available. Plausibly, we might expect to see seasonality in biological aspects such as reproduction and activity levels. Indeed, reproductive seasonality has been reported in diverse tropical taxa (Lemen & Voris 1981, Voris & Jayne 1979), with several studies trying to identify the proximate cues used to synchronize reproduction (Barone 1998, Burns 1985, Gorman & Licht 1974, Sexton *et al.* 1971, Wikelski *et al.* 2000, Wright & Cornejo 1990).

Activity cycles also appear to be seasonal among diverse animal taxa in the tropics. Highly mobile species often migrate seasonally to follow resources or to avoid unfavourable conditions. This phenomenon has been reported in fishes (Bishop & Forbes 1992), reptiles (Madsen & Shine 1996*a*, Webb 1992), birds (Develey & Peres 2000, Morton & Brennan 1992) and mammals (Bodmer 1990, Williams & Newsome 1992). Less mobile species often dramatically decrease activity during unfavourable periods, sometimes aestivating for long periods (e.g. frogs (Tyler 1994); crocodiles, turtles (Morris 1996); lizards (Christian & Bedford 1995, Christian & Weavers 1996, Christian *et al.* 1995); small mammals (Williams & Newsome 1992)). Such behavioural modifications suggest that remaining active and in the same place can be costly. Thus, the seasonal ecology of tropical animals that remain active year-round is of interest.

Here we study the effects of tropical wet–dry seasonality on a combination of sympatric snakes. All three species remain active throughout the year, but differ dramatically in dietary habits. One species specializes on prey that exhibits seasonal migration (rats). Rats are most abundant at the study site during the dry season but migrate to drier areas of the floodplain during the wet season (Madsen & Shine 1996*a*). Another snake species specializes on prey mainly available during the wet season (frogs). The third snake species is a generalist and feeds on both frogs and rats as well as various other prey. Thus, we might expect that these three snake taxa will respond very differently to variation in weather conditions over the course of a year.

We monitored activity levels, feeding rates, body condition and the age structure and adult sex ratios of the populations over the course of several wet and dry seasons. In addition to describing seasonal trends within the three species we asked the following questions: (1) Do feeding rates, body condition and activity levels of the prey-specialist species follow seasonal patterns of prey availability? (2) Are feeding rates, body condition and activity levels of the prey-generalist more aseasonal than those of the prey-specialists? (3) Do sex ratios and age structures of the populations reflect seasonal differences in the timing of reproduction among the three snake species?

METHODS

Study area

Fogg Dam is an artificial waterbody on the Adelaide River floodplain (12°55′S, 131°31′E) 60 km south-east of the city of Darwin. The site lies within Australia's wet–dry tropics. Mean monthly temperatures are > 25 °C throughout the year, but based on 30-y averages, 78% of rainfall occurs during a 4-mo period (December to March 'wet season', see Figure 1). Our study area was the wall of the dam itself (1.3 km long), with permanent water on one side and an annually inundated floodplain on the other. For most of the year the floodplain below Fogg Dam is dry, with deep cracks in the soil. The landscape is flat and virtually treeless, and wildfires often strip the ground surface of any vegetation by midway through the dry season. Wet-season rains stimulate lush growth by ephemeral vegetation (Cowie *et al.* 2000). The site has been described in detail and illustrated in previous papers (e.g. Madsen & Shine 1996*a*).

Study species

The three species of snake encountered most frequently on Fogg Dam are water pythons (*Liasis fuscus* Peters, Pythonidae), keelbacks (*Tropidonophis mairii* Jan, Colubridae) and slatey-grey snakes (*Stegonotus cucullatus* Duméril, Bibron & Duméril, Colubridae). All are non-venomous, oviparous and active foragers, but they differ considerably in body sizes and dietary habits. Water pythons are large (to 2.5 m snout–vent length (SVL), 5 kg) heavy-bodied constrictors that feed almost exclusively on a single species of native rodent (dusky rat, *Rattus colletti*: Madsen & Shine 1996*a*). Keelbacks are natricine snakes, of the same lineage as the well-studied garter snakes and grass snakes of North America and Europe. They are medium-sized, moderately heavy-bodied snakes (to 0.8 m SVL, 300 g) that feed primarily on frogs (Shine 1991, unpubl. data). Slatey-grey snakes reach a snout–vent length of up to 1.5 m (900 g) and are thus of an intermediate size compared with the keelbacks and the water pythons. Slatey-grey snakes have extremely broad diets. Stomachs of museum specimens contained reptile eggs, frogs, small mammals and lizards (Shine 1991). In our study area, slatey-grey snakes feed on frogs during the wet season (15 of 25 prey items, 60%) but take mostly reptile eggs (13 of 51 items, 26%) and small mammals (15 items, 29%) as well as frogs (20 items, 39%) during the dry season (unpubl. data).

The three snake taxa show very different life histories and different seasonal schedules of egg-laying (and thus, hatching). Water pythons mate during late-June to mid-August and produce a single clutch in September with hatching in December (Madsen & Shine 1996*b*). Female water pythons mature at about 3 y of age, and males a year earlier (Madsen & Shine 2000*a*, Shine 1991). In contrast, male keelbacks contain active sperm throughout the year and females produce multiple clutches of eggs during the dry season. Eggs incubate for 6–8 wk and hatchlings can mature in less than 1 y (unpubl. data). Lastly, *Stegonotus* mate during August–September and females may produce one clutch of eggs in the late dry season and another in the wet season. Eggs incubate for 3 mo and hatchlings require 2–3 y to mature (unpubl. data).

Survey methods

We have been studying water pythons on the Adelaide River floodplain for >15 y (Madsen & Shine 1996*a*, *b*; Shine 1991, 1993), but intensive studies on the two colubrid species only commenced in 1998. Because our main aim in this paper is to compare the three taxa, we concentrate on data gathered since that time. Between 20 May 1998 and 31 December 2000, we searched for snakes on Fogg Dam by car and on foot during 862 nights. On average, each visit began at 19h00 and lasted 73 min (SD = 25.8). We counted and attempted to capture all keelbacks and slatey-grey snakes seen, and counted all water pythons. Captured snakes were returned to the laboratory and sexed, measured, marked and palpated for the presence of food, eggs or faeces. The next night, they were released at their point of capture. We supplemented observational data on encounter rates of water pythons with information from captures during earlier years of the study (1989–1994). Data on seasonal patterns of rat abundance are also taken from a previous study (Madsen & Shine 1996*a*).

Since March 1999, we have also monitored the abundance of frogs on the Fogg Dam wall. To do so, we established 10 permanent survey grids in which we counted and identified frogs on each visit to the dam. Each grid enclosed a 2-m section of the bitumen road along the top of the dam wall. The road itself is approximately 3 m wide. The 10 grids were spaced 130 m apart across the 1300-m length of the dam wall, and were marked on the road surface with paint. Thus, we sampled approximately 1.5% of the road surface area for frogs each visit.

Predictions

The variables of snake biology that we selected for analysis were activity levels (numbers encountered per hour), age composition (% juveniles), adult sex ratio, feeding frequency (proportion of animals containing food or faeces when captured) and body condition (residual score from the general linear regression of ln-transformed mass versus ln-transformed SVL). Because the three species of snake feed on prey that are likely to show different patterns of availability over the course of a year, we can generate predictions about the responses of each snake species to seasonality.

Encounter rates, feeding rates and body condition would be expected to be maximal at the time of year when food is most abundant. Thus, water pythons should be more common at Fogg Dam during the dry season. Keelbacks should be more common, in better body condition and contain food more often during the wet season. Activity, feeding and condition of slatey-grey snakes should show less seasonality than in the other two species. The age structure (proportion of the sample consisting of juvenile vs. adult snakes) should largely depend on the seasonality of reproduction: juveniles may be most numerous shortly after hatching (e.g. Bonnet *et al.* 1999, Gibbons & Semlitsch 1987). The adult sex ratio should also depend upon the seasonal timing of reproduction: males may be more active (and hence, more frequently encountered) during mate-searching activities, whereas females might be more obvious during egg-laying migrations (Bonnet *et al.* 1999).

Overall, we expect the generalist feeder (*Stegonotus*) to show less monthly or seasonal variation in most attributes than the other two taxa, because its food supply is likely to remain more stable through the year. We also expect that correlations between snake biology and prey abundance should be more clear-cut for keelbacks and pythons than for slatey-grey snakes, given the broader diet of the latter species.

Analyses

We show monthly trends in figures, but to investigate seasonal differences statistically we conduct comparisons between wet season (Dec–Mar inclusive) and dry season (Jun–Sept inclusive) values using t-tests or chi-square tests. This analytical technique is simpler and more powerful than comparing among months. Some individual snakes appear more than once in capture samples. We treated each observation for an individual as independent, thus artificially inflating degrees of freedom in statistical tests. Simulations show that this kind of pseudoreplication should not compromise the conclusions from our statistical tests as long as variation among individuals within a season is similar in magnitude to variation within an individual between seasons (Leger & Didrichson 1994). Our data conform to this assumption. However, we have also adopted a conservative significance level of 0.01. Statistical tests were performed using the software programs Statview 5 and JMP 2.0.4.

RESULTS

Our data reveal strong temporal (monthly, seasonal) variation in most of the traits that we examined.

Prey availability

Frogs The seasonal abundance of frogs varied considerably through time (Figure 1, Table 1). Frog abundance peaked soon after the commencement of

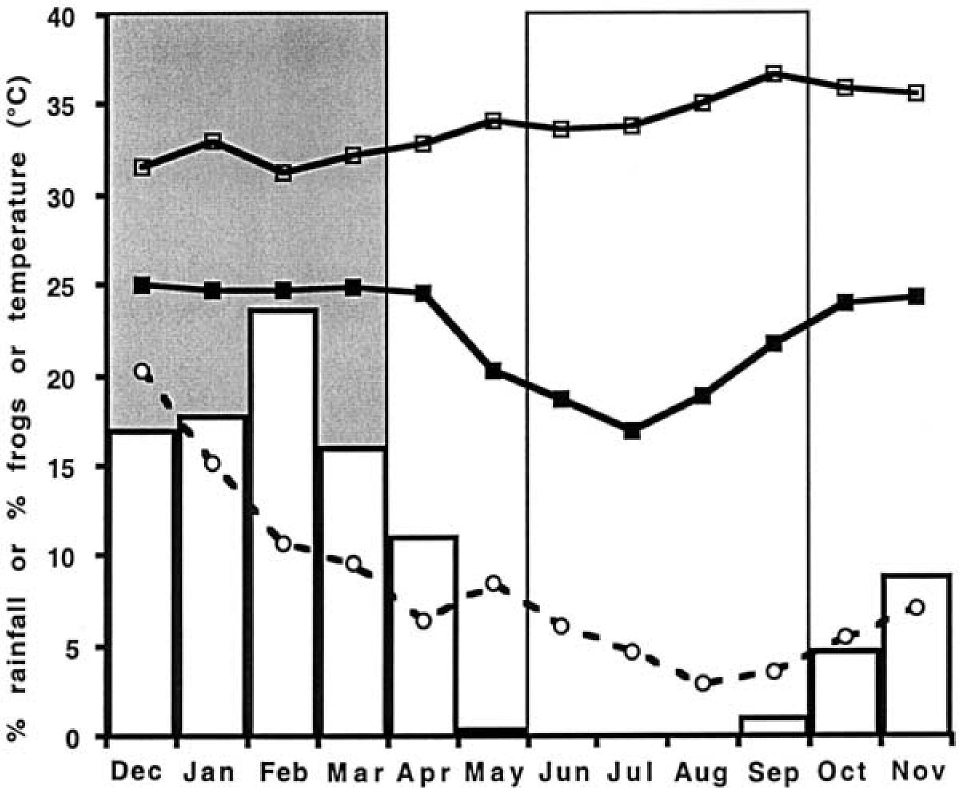

Figure 1. Mean monthly rainfall (bars, as % of annual rainfall) and mean monthly maximum (open squares) and minimum (filled squares) air temperatures (°C) as measured at Middle Point village during 1999–2001. Frog abundances are monthly means of the number counted in 10 survey grids along Fogg Dam expressed as % of total frogs counted (dashed line with open circles). The shaded bar of the graph represents the wet season; unshaded bar represents the dry season.

the rainy season. On average, more than twice as many frogs were encountered during the wet months (Dec–Mar) than during the dry months (Jun–Sept), and this difference was highly significant (Table 1). Although we did not gather data on the topic, it is clear that body-size distributions of frogs also changed through time. The initial wet season peak in numbers involved adult frogs commencing breeding activity, but many of the individuals counted on our transects later in the wet season were metamorphs. The occurrence of frogs throughout even the driest months of the year reflects the presence of permanent water in Fogg Dam.

Reptile eggs Reptile eggs are an important prey item for slatey-grey snakes and are likely to be available throughout the year. Keelbacks lay their eggs throughout the dry season (unpubl. data), whereas wet-season oviposition characterizes the most abundant local lizard taxa: the agamid *Lophognathus* and the scincid *Glaphryomorphus* (James & Shine 1985).

Table 1. Seasonal differences in precipitation, frog abundance and snake abundance, feeding and body condition at Fogg Dam. Weather variables were measured at Middle Point Village (1.5 km from Fogg Dam) throughout the study. The table shows mean values with standard deviation in parentheses and sample size below.

	Wet season (Dec–Mar)	Dry season (Jun–Sep)	Test statistic	P
Minimum air temperature (°C)	24.8 (0.57) 182	18.9 (2.71) 220		
Mean air temperature (°C)	27.4 (1.03) 182	25.5 (1.93) 220		
Maximum air temperature (°C)	32.0 (2.33) 182	34.8 (1.95) 220		
Rainfall (mm d^{-1})	12.0 (20.3) 270	0.16 (2.60) 360		
Number of frogs in survey grids	1.43 (1.95) 239	0.43 (0.73) 300	t = 6.5	< 0.0001
Tropidonophis mairii				
Age structure (% juvenile)	0.39 426	0.01 538	χ^2= 229	< 0.0001
Sex ratio (%male)	0.38 260	0.28 531	χ^2 = 8.1	0.004
Encounter rate (snakes h^{-1})	1.28 (1.36) 277	1.81 (1.78) 350	t = 4.07	< 0.0001
Proportion with food or faeces	0.22 426	0.06 538	χ^2 = 50.0	< 0.0001
Body condition	0.022 (0.14) 422	0.016 (0.16) 524	t = 0.58	0.56
Stegonotus cucullatus				
Age structure (% juvenile)	0.44 99	0.20 190	χ^2 = 20.1	< 0.0001
Sex ratio (% male)	0.69 55	0.81 153	χ^2 = 3.36	0.07
Encounter rate (snakes h^{-1})	0.32 (0.47) 277	0.50 (0.64) 350	t = 3.92	< 0.0001
Proportion with food or faeces	0.16 99	0.20 190	χ^2 = 0.63	0.43
Body condition	−0.037 (0.12) 96	0.022 (0.14) 190	t = 3.51	0.0005
Liasis fuscus				
Age structure (% juvenile)	0.39 810	0.32 1647	χ^2 = 13.4	0.0003
Sex ratio (% male)	0.50 493	0.66 1125	χ^2 = 40.8	< 0.0001
Encounter rate (snakes h^{-1})	1.47 (2.27) 277	3.68 (3.37) 439	t = 9.61	< 0.0001
Proportion with food or faeces	0.16 810	0.28 1647	χ^2 = 40.0	< 0.0001
Body condition	−0.044 (0.16) 807	0.027 (0.14) 1645	t = 11.23	< 0.0001

Rats Dusky rats show strong seasonal shifts in abundance, although there is also massive year-to-year variation in rat numbers (Madsen & Shine 1999). Reproduction occurs during the dry season, so that rat numbers can increase dramatically in the course of a single dry season (Madsen & Shine 1999). Rat numbers near the dam wall then fall precipitously with the advent of wet season flooding, when the rats migrate from the low-lying floodplain (near the dam wall) to higher ground several kilometres away (Madsen & Shine 1996*a*).

Snake activity

Keelbacks showed peak encounter rates during the transitional period between the wet and dry seasons and during the early dry season (Figure 2). Slatey-grey snakes also increased in number during the early stages of the dry season (Figure 2). Python numbers showed an increase throughout the dry season, with a slight decrease during August (Figure 2). The colubrids also showed a minor peak in encounter rate during the wet season (in Dec–Jan), but these peaks were small in comparison to numbers encountered during drier months (Apr–Jun for keelbacks and May–Jul for *Stegonotus*). Encounter rates for all three species were significantly higher during the dry season than the wet season (Table 1).

Population structure

The proportion of the data-sets made up of repeat measures on the same individuals varied among species. For water pythons, 46% of individuals were

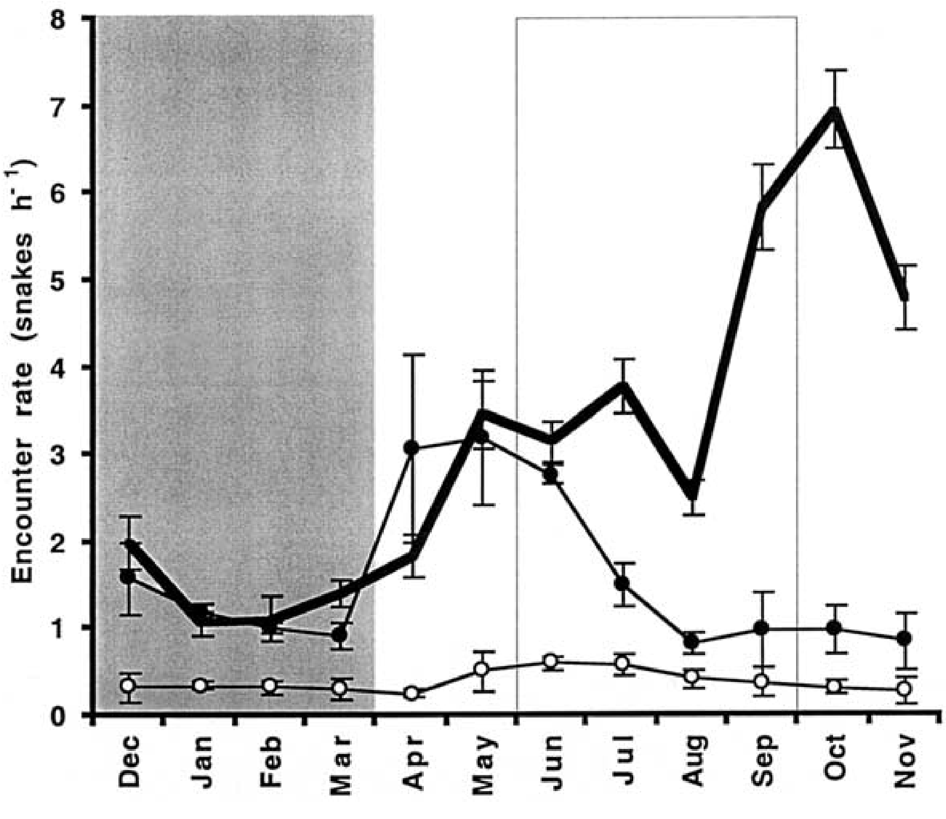

Figure 2. Rates at which snakes of three species were encountered on the wall of Fogg Dam over the period May 1998 to December 2000. Keelbacks (*Tropidonophis mairii*) are shown by filled circles; slatey-grey snakes (*Stegonotus cucullatus*) by open circles, and water pythons (*Liasis fuscus*) by a thick line. The graph shows mean values and associated standard errors for each month. The shaded bar of the graph represents the wet season; unshaded bar represents the dry season.

measured more than once and the mean number of measurements per individual was 1.6. For keelbacks, 26% of individuals were measured more than once; the mean number of captures per individual was 1.4. Slatey-grey snakes were recaptured more often, with 77% of individuals measured more than once (mean of 4.0 measures per individual).

In all three snake species, age structure shifted seasonally (Figure 3). In each case, the proportion of juvenile animals was higher in the wet season than the dry season (Figure 3, Table 1).

Adult sex ratio differed among species: collections of adult keelbacks were always female biased, whereas the reverse was true for *Stegonotus* and *Liasis* (Figure 3). Sex ratio also shifted among months in all three species (Figure 3) and differed significantly between wet and dry seasons for keelbacks and pythons. The difference was only marginally significant for slatey-grey snakes (Table 1).

Proportion containing food/faeces

Our predictions regarding the relationships between seasonal patterns of prey abundance and feeding rates were met for all three species when all individuals (male plus female, juvenile plus adult) were considered together. Keelbacks fed more often during the wet season. Pythons captured at Fogg Dam fed more often during the dry season compared to the wet season, but no such difference in feeding rate was detected in pythons that migrated out on the floodplain during the wet season. Slatey-grey snakes showed no seasonal difference in rates of feeding (Figure 4, Table 1). Analysing sexes and age classes separately revealed that the predictions were met in each class only for slatey-grey snakes (Table 2). For water pythons at Fogg Dam, adult females and juveniles fed more often during the dry season but adult males showed no seasonal difference in feeding rate (Table 2). In keelbacks only adult females met the prediction of feeding more often during the wet season (Table 2). Juveniles and adult male keelbacks showed no significant seasonality in feeding rate (Table 2).

Body condition

Our predictions regarding the relationships between body condition (mass relative to body length) and seasonal patterns of prey abundance were only met for water pythons when all individuals were considered as a whole (Table 1). However, there was strong spatial variation in this trait. We also sampled water pythons on the floodplain, where most of the animals move to follow the migrating rat population (Madsen & Shine 1996*a*). These snakes were in better condition during the wet season than the dry season, although the difference did not attain statistical significance ($t = 1.67$, $df = 37$, $P = 0.10$). A two-factor ANCOVA with season and location (Fogg Dam vs. floodplain) as independent variables, ln-transformed SVL as covariate and ln-transformed mass as the dependent variable, indicated a marginally significant interaction term ($F_{1, 1909} = 3.44$, $P = 0.06$). That is, the way in which body condition shifted

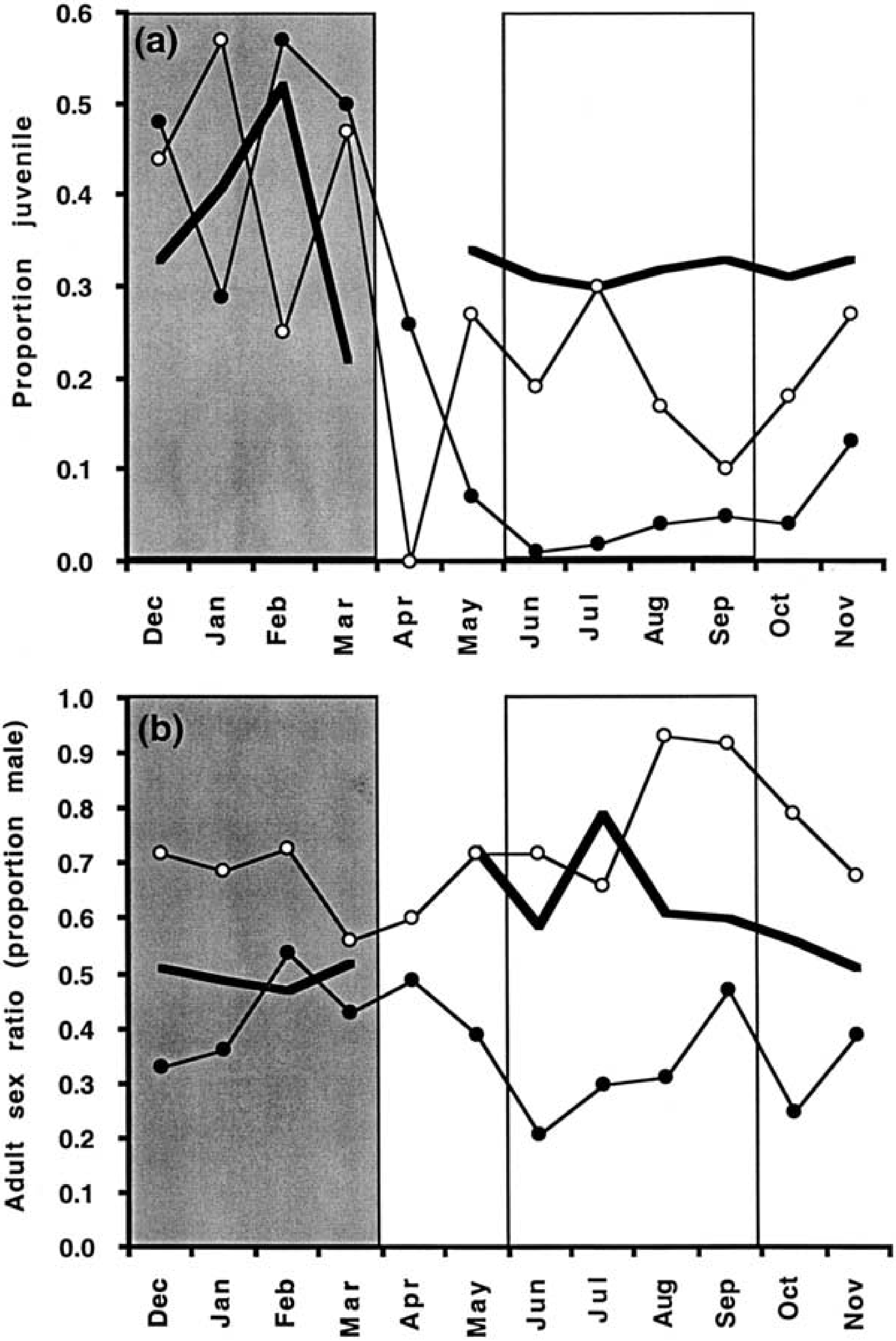

Figure 3. Monthly variation in age structure (proportion juveniles (a)) and adult sex ratio (proportion males (b)) of three species of snakes on the wall of Fogg Dam. Keelbacks (*Tropidonophis mairii*) are shown by filled circles; slatey-grey snakes (*Stegonotus cucullatus*) by open circles, and water pythons (*Liasis fuscus*) by a thick line. The shaded bar of the graph represents the wet season; unshaded bar represents the dry season.

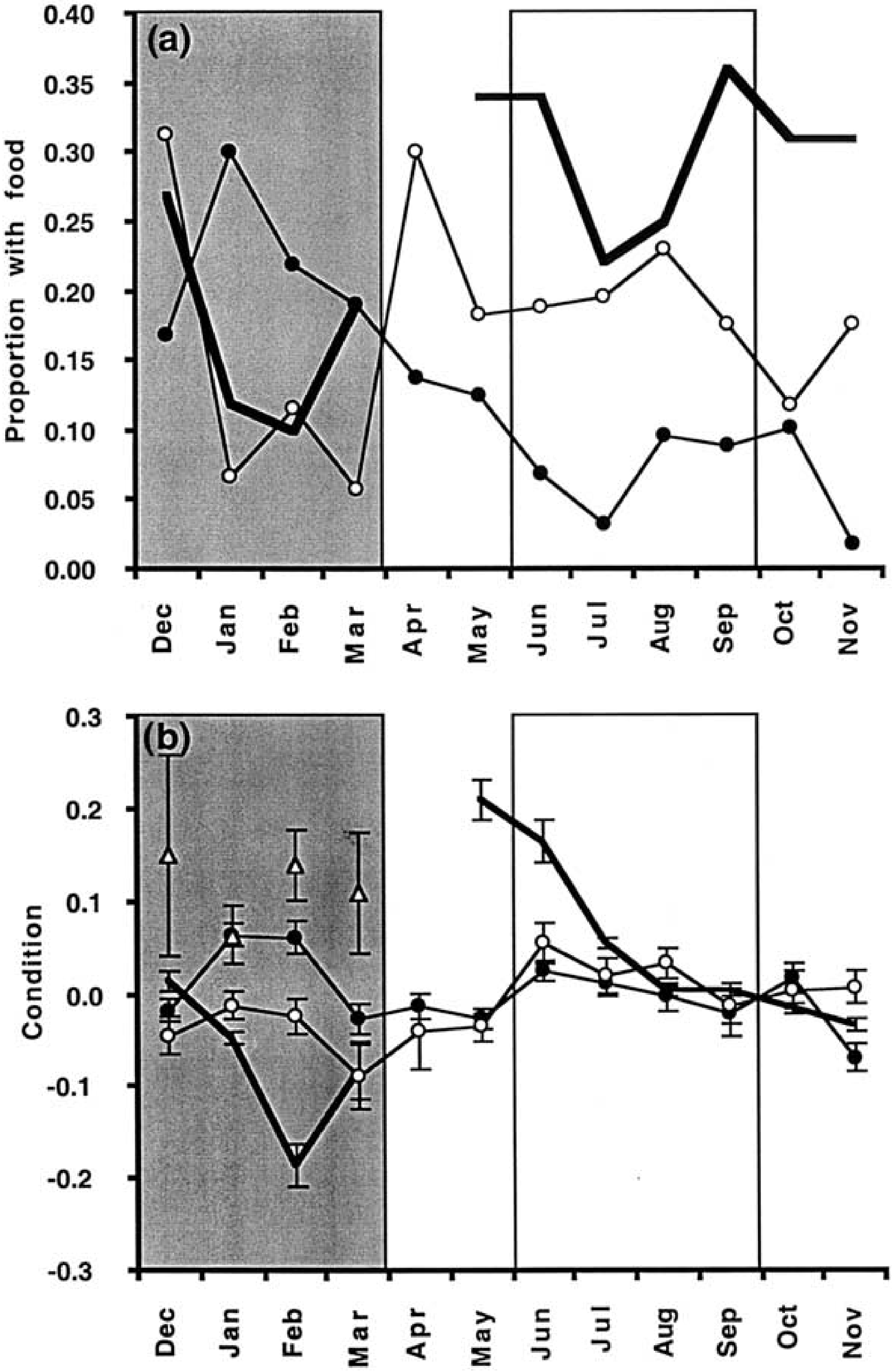

Figure 4. Monthly variation in the proportion of snakes that contained faeces or freshly ingested prey items at the time of their collection (a) and body condition of snakes (b) on the wall of Fogg Dam. Body condition values are means with associated standard errors for each month. Keelbacks (*Tropidonophis mairii*) are shown by filled circles; slatey-grey snakes (*Stegonotus cucullatus*) by open circles, and water pythons (*Liasis fuscus*) by a thick line. Water pythons captured on the floodplain during the wet season are shown as open triangles. The shaded bar of the graph represents the wet season; unshaded bar represents the dry season.

Table 2. Seasonal differences in numbers, feeding and body condition of three species of snake at Fogg Dam. Data are analysed separately for juveniles, adult males and adult females for each of the three taxa. For continuous variables, the Table shows mean values with standard deviation in parentheses and sample size below.

	Wet season (Dec–Mar)	Dry season (Jun–Sep)	Test statistic	P
Tropidonophis mairii				
Number captured				
Juvenile	166	7	$\chi^2 = 129$	< 0.0001
Adult male	99	149	$\chi^2 = 10.1$	0.001
Adult female	161	382	$\chi^2 = 89.9$	< 0.0001
Proportion with food or faeces				
Juvenile	0.19	0.00	$\chi^2 = 1.66$	0.20
	166	7		
Adult male	0.16	0.11	$\chi^2 = 1.16$	0.28
	99	149		
Adult female	0.28	0.05	$\chi^2 = 61.8$	< 0.0001
	161	382		
Body condition				
Juvenile	0.02 (0.158)	−0.10 (0.114)	t = 1.86	0.07
	164	6		
Adult male	0.086 (0.128)	0.001 (0.123)	t = 5.24	< 0.0001
	99	148		
Adult female	−0.026 (0.139)	0.021 (0.164)	t = 3.16	0.0017
	159	370		
Stegonotus cucullatus				
Number captured				
Juvenile	44	37	$\chi^2 = 0.61$	0.44
Adult male	38	124	$\chi^2 = 45.7$	< 0.0001
Adult female	17	29	$\chi^2 = 3.13$	0.08
Proportion with food or faeces				
Juvenile	0.14	0.11	$\chi^2 = 0.15$	0.70
	44	37		
Adult male	0.13	0.23	$\chi^2 = 1.84$	0.18
	38	124		
Adult female	0.29	0.17	$\chi^2 = 0.93$	0.33
	17	29		
Body condition				
Juvenile	−0.062 (0.128)	0.015 (0.133)	t = 2.63	0.01
	43	37		
Adult male	−0.05 (0.079)	0.003 (0.121)	t = 2.52	0.013
	36	124		
Adult female	0.056 (0.130)	0.109 (0.183)	t = 1.04	0.31
	17	29		
Liasis fuscus				
Number captured				
Juvenile	317	522	$\chi^2 = 50.1$	< 0.0001
Adult male	245	748	$\chi^2 = 255$	< 0.0001
Adult female	248	377	$\chi^2 = 97.5$	< 0.0001
Proportion with food or faeces				
Juvenile	0.22	0.43	$\chi^2 = 35.8$	< 0.0001
	317	522		
Adult male	0.13	0.16	$\chi^2 = 1.6$	0.21
	245	748		
Adult female	0.12	0.31	$\chi^2 = 29.1$	< 0.0001
	248	377		
Body condition				
Juvenile	−0.065 (0.171)	0.045 (0.138)	t = 10.15	< 0.0001
	316	521		
Adult male	0.004 (0.121)	0.000 (0.130)	t = 0.41	0.69
	245	747		
Adult female	−0.064 (0.176)	0.056 (0.144)	t = 9.28	< 0.0001
	246	377		

from dry season to wet season tended to differ between Fogg Dam pythons (which became thinner) and floodplain pythons (which became fatter) (Figure 4b).

Contrary to prediction, keelbacks showed no seasonal difference in body condition (Table 1). Slatey-grey snakes (the prey generalist) did not show aseasonality in body condition as expected. Instead, they were in better condition during the dry season (Table 1).

When our samples are broken into age/sex classes, however, the results were less clear-cut. In keelbacks, adult males were in better condition during the wet season and adult females were in significantly better condition during the dry season. Body condition of juvenile keelbacks did not differ between seasons (Table 2). This contrast produces an absence of apparent seasonality in the pooled analysis. In slatey-grey snakes, breaking the analyses into age/sex classes revealed that although the overall tendency to be in higher condition during the dry season was apparent among all classes, it was only statistically significant in juveniles and marginally significant in adult males. Condition of adult females did not differ significantly between seasons (Table 2). Seasonal differences in body condition of water pythons mirrored the results for feeding rates. Juveniles and adult females that remained at Fogg Dam met prediction and were in better condition during the dry season, but condition of adult males did not differ between seasons (Table 2).

DISCUSSION

Previous studies on seasonal patterns in tropical snakes have often been based on museum specimens collected over a wide area, or on relatively small samples of live snakes. Unless one is able to differentiate trends among adult males, adult females and juveniles, data on activity patterns may be of limited ecological value (Dalrymple *et al.* 1991). Our data set is much larger than those previously available, facilitating the attempt to discriminate trends among sexes and age classes. The importance of this latter point is apparent from the numerous differences found in seasonal responses among juveniles, adult males and adult females in each species.

Our data provide strong evidence that many traits of tropical snake populations show substantial seasonal variation. This is not surprising, given the strongly seasonal precipitation patterns in the study area (Figure 1), but it reinforces the notion that tropical habitats are far from aseasonal despite their thermal stability. The patterns of variation are complex, differing not only among the three sympatric study species, but also among age/sex classes within each taxon. Multiple causal processes are undoubtedly important in generating these patterns of variation, and a descriptive study such as our own cannot provide rigorous tests among alternative explanations. Nonetheless, the diversity among our three study species in attributes such as prey types and reproductive cycles, means that we can usefully examine the extent to which such factors can predict patterns of seasonal variation in demographic traits.

One clear result from our study is that the three species respond in different ways to varying weather conditions over the course of the annual cycle. The same kind of interspecific diversity has been reported for other traits in tropical snakes (e.g. reproductive seasonality – Jayne *et al.* 1995, Saint Girons 1982, Vitt 1983, Vitt & Vangilder 1983, activity – Dalrymple *et al.* 1991, Henderson & Hoevers 1977). Such observations falsify any simple notion that abiotic (weather) conditions drive snake ecology in any straightforward way. Instead, processes within snake populations depend upon a series of phylogenetically conservative factors (such as breeding systems and foraging modes), in combination with proximate environmental influences. It is impossible to identify seasonal activity peaks from studies treating snakes as a group: instead, data are required on individual species (Gibbons & Semlitsch 1987) and may even be required from age and sex classes within each taxon (Dalrymple *et al.* 1991, present study).

Prey availability and snake feeding rates

Although it is difficult to quantify prey *abundance* (especially for a generalist feeder such as *Stegonotus*), this challenge is trivial compared to quantifying the *availability* of prey for a snake. Specific aspects of the predator's motivation, foraging mode or sensory system may affect 'availability' very dramatically, at any given level of prey abundance. Seasonal shifts in habitat complexity (vegetation density) might similarly modify feeding opportunities. Thus, although we can document seasonal shifts in prey numbers, it is difficult to translate these into prey availability.

This problem is evident for all three snake species that we studied. For keelbacks, frog numbers were highest during the wet season (Figure 1), with a concomitant increase in rates of feeding by the snakes (Figure 3). There was a strong positive correlation between our indices of frog abundance and feeding rates of the snakes ($n = 12$, $r = 0.67$, $P = 0.016$). Nonetheless, a more detailed analysis reveals varying patterns in different age/sex classes of keelbacks. For example, adult female keelbacks feed significantly less often during the dry season (Table 2). We speculate that feeding rates of adult females during the dry season may be suppressed while they are enlarging follicles and forming eggs (reproductive female snakes of many species are anorexic: Brodie 1989, Shine 1980). Thus, the low dry-season feeding rates of adult female keelbacks are likely due not to decreased prey availability (because juveniles and adult males are able to maintain feeding rates during the dry season) but rather are due to anorexia associated with reproduction. The ability of juvenile and adult male keelbacks to maintain feeding rates during the dry season may relate to the permanent presence of water at Fogg Dam. Alternatively, keelbacks may hunt for frogs in their refugia in soil cracks in dry areas adjacent to the dam.

Seasonal shifts in the availability of rats are even more problematic to quantify. Although the rats are abundant during the dry season, they are hidden in deep soil cracks at that time of year (Madsen & Shine 1999). Hence, they may be inaccessible to some types of snake (especially, large pythons) but accessible to others (juvenile pythons and slatey-grey snakes). Although rat densities may decline during the wet season, the rodents might be more vulnerable to snakes at this time because the soil cracks close and thus the rats have nowhere to hide. In consequence, seasonal patterns of rat availability may differ from patterns of rat abundance, and may differ depending upon the body size of the predator. Nonetheless, the low feeding rates of water pythons that remain at Fogg Dam during the wet season indicate a cost associated with not migrating to follow the movements of rats. The apparent lack of seasonality in feeding rates of male pythons appears to be a reflection of anorexia associated with dry-season breeding (see below). During the Jun–Aug mating season, feeding rates of males are much lower than those of females and juveniles (Madsen & Shine 2000*b*).

Lastly, the broad dietary habits of slatey-grey snakes also introduce problems for assessing prey availability. Even if we knew the numbers of frogs and reptile eggs on the dam wall at any point in time, we cannot assess 'availability' without knowing the relative difficulty of locating and ingesting each type of prey. However, the relative stability of feeding rates and body condition of slatey-grey snakes between wet and dry seasons fits our prediction that a generalist feeder will be less sensitive to fluctuations in prey abundance.

Given the complications of relating prey abundance to prey availability, all that we can realistically expect is a broad correlation between the two factors – and hence, that seasonal shifts in snake traits are likely to correlate only loosely with our measures of prey abundance. The problem will be smallest for a taxon which feeds on a single type of prey whose abundance is easily monitored. In our study, keelbacks come closest to this situation, and it is encouraging to see correlations between frog numbers and snake feeding rates in this system. Relations between food abundance and feeding and body condition should also be more apparent among juveniles, whose patterns of feeding should be independent of reproductive activities. In keeping with this notion, our predictions relating feeding rates to prey abundance tend to be better met among juveniles than among adults.

Body condition

Water pythons that remained on the dam wall through the wet season showed a considerable decline in body condition, whereas animals that migrated to the floodplain showed an increase. This difference fits well with the much higher availability of rats on the floodplain at this time of year. The average body condition of dam-wall snakes increased dramatically at the end of the wet season, reflecting the return of the (now well-fed) floodplain animals. Body condition then fell over the course of the dry season, mainly reflecting anorexia and energy expenditure associated with reproduction in both sexes (Madsen & Shine 2000*b*). As with feeding rates, the seasonal trend for condition to be lower during the wet season may represent a cost associated with not migrating to follow the dispersal of rats.

The sharp increase in keelback condition from November to January corresponds well to the initial explosion of frog numbers. The subsequent decline in condition (from March to April) may be due to the fact that most of the animals captured at this time are juvenile snakes (see Figure 3). As noted above, juvenile keelbacks take many newly transformed frogs, but the frogs grow so quickly that they are soon too large to be eaten by the young snakes (pers. obs.). Thus, the juvenile snakes (and perhaps, adult males) may begin to lose condition because many of the frogs that they encounter are too large to be ingested. The timing of high rates of feeding by female keelbacks during the wet season is dissociated from the timing of high body condition (the dry season). This is presumably caused by females storing energy for reproduction rather than allocating it to growth.

Stegonotus showed a decline in condition during the wet season, but a rapid recovery in the early dry season (March to May: Figure 4). This latter time corresponds to the main oviposition season for keelbacks, and their eggs are a major prey resource for slatey-grey snakes at this time of year (unpubl. data).

Activity patterns

In their review of activity patterns in snakes, Gibbons & Semlitsch (1987) noted that virtually nothing is known about tropical snakes in this respect. In temperate zones, the seasonal and daily timing of activity is usually constrained by ambient temperatures. Peaks in activity levels are associated with migrations to and from hibernation sites and with breeding activity, especially mate searching by males.

Changes in encounter rate might be due to changes in abundance, activity level or dispersal. Both of the latter processes, at least, are important in the species that we studied. The numbers of snakes that we encountered on the dam wall varied substantially through time, but in different ways in the three study species (Figure 2).

The lowest part of the floodplain (the backswamp) is close to the dam wall, and hence the rats continue to breed in this area after other higher parts of the floodplain have become too dry. Thus, the area close to the dam wall may become a better foraging ground for pythons (relative to higher areas) as the dry season progresses (Madsen & Shine 1996*a*). Radiotelemetric monitoring shows that most water pythons move closer to the dam wall as the floodplain dries out, but leave the vicinity of the dam wall at the onset of the wet season as they follow the rat populations back out across the floodplain (Madsen & Shine 1996*a*). Encounter rates of pythons fit well with these telemetric data (Figure 2).

Neither of the colubrids makes such large seasonal movements (unpubl. data from telemetry), but the increase in numbers of adult female keelbacks during the dry season reflects migrations of females to the dam wall for egg-laying (pers. obs.). Thus, dispersal rather than shifting activity levels may generate the seasonal peaks in encounter rates in both keelbacks and water pythons (Figure 2).

In contrast, wet- and dry-season home ranges of slatey-grey snakes overlap considerably (unpubl. data). Slatey-grey snakes were present in similar numbers year-round (Figure 2), but with a significantly higher incidence in the dry season than the wet season (Table 1). The increase in encounter rates during the dry season was largely due to adult male snakes, and our observations of reproductive activity at this time of year suggest that mate-searching behaviour by males is the reason for the increased rate of encounters.

Thus, major peaks in activity level of the two colubrid species at Fogg Dam appear more related to reproduction than to feeding. In contrast, the highest encounter rate of pythons (late dry season) coincides with peak rat numbers.

Population structure

Shifts in age structure were consistent in the three species, despite differences in the seasonal timing of reproduction (Figure 3). The peak in numbers of juvenile water pythons during the wet season reflects the timing of hatching of the single clutch produced each year (Madsen & Shine 1996*b*). The two colubrid species, however, both produce multiple clutches over a prolonged period of the year (unpubl. data). The low numbers of juvenile keelbacks encountered during the early part of the dry season is a reflection of the timing of hatching and their rapid maturity – most of the previous year's hatchlings have reached mature size by May–June. The low numbers of juvenile keelbacks encountered during the later part of the dry season is puzzling, however, because the majority of clutches are laid during May–June and hatch during July–August (Brown & Shine, unpubl. data). Thus, large numbers of hatchling keelbacks enter the population during the dry season but they are not encountered until the onset of the rainy season. Possibly, hatchling keelbacks remain inactive or sequestered until it begins to rain. The low numbers of juvenile pythons and slatey-grey snakes in dry-season samples (Figure 3) suggest that some aspect of the dry season reduces the catchability of these young snakes. In keeping with this inference, the same pattern is seen in both adults and juveniles of other small-bodied snake species as well. For example, we record taxa such as *Dendrelaphis*, *Furina* and *Rhinoplocephalus* much more often in the wet season than the dry season (unpubl. data). The reasons for this pattern are elusive, but might involve direct effects of humidity stimulating activity (e.g. Daltry *et al.* 1998), seasonal changes in the availability of vegetation cover, or the abundance of prey.

Adult sex ratios also showed substantial variation through time (Figure 3). A dry-season peak in the activity of male water pythons coincides with the seasonal timing of mating in this species (mid-June to mid-August – Madsen & Shine 1996*b*; see Figure 3). The same may be true of *Stegonotus*: we have recorded mating and male–male combat in August and September (see above). In keelbacks, most of the adult females that dominate samples during the dry season (Figure 3) were gravid animals that had come to the dam wall for oviposition. Unsurprisingly, therefore, interspecific variation in the seasonal patterns of sex-ratio shifts were apparently driven by interspecific variation in reproductive seasonality. Notably, however, the primary effects involved mate-searching by adult males in two taxa, and egg-laying migrations by adult females in the other.

Overview

Our data on the numbers, feeding rates, body condition and population structure of tropical snakes reveal substantial seasonal variation in every trait that we examined, in each of the three species. It is thus clear that the changing conditions experienced in the wet–dry tropics do indeed affect snake populations in many ways.

The causal mechanisms driving seasonal variations in our study species are complex, and it is notable that different age/sex classes within a population can be affected in different ways. Apart from a higher incidence of juveniles during the wet season, there are few general trends. Indeed, the primary impression from our Figures (2–4) is of interspecific variation, not consistency. Our data on the composition of samples help to explain much of this variation. Essentially, the variation that we have documented in samples taken throughout the year on a single small study area (the wall of Fogg Dam) is the sum total of at least three processes:

(1) Some traits shift throughout the year. For example, keelbacks feed more during the wet season because frogs become more available, and the snakes become heavier-bodied as a result.
(2) Other traits shift in mean values in our samples because different components of the snake population are differentially active at different times of year. Notably, dry-season mating activities shift adult sex ratios and body condition in both water pythons and slatey-grey snakes. The underlying population-wide values for these traits may well be constant year-round, but our samples show strong seasonal variation.
(3) A third set of variables in our samples shifts among seasons because of migration, such that the snakes we sample on the dam wall are a non-random subset of the entire population. For example, the water pythons that remain on the dam during the wet season are in much lower body condition than those that leave, and the shifting sex ratio of dry-season keelbacks reflects migration of egg-laying females to the dam wall.

Even in such an intensively studied system as Fogg Dam, however, there are still many facets of seasonality that are difficult to understand. It is clear that tropical reptiles display complex patterns of seasonal change in a wide variety of attributes, that sympatric species may sometimes differ markedly in such patterns, and that such differences are not simple consequences of interspecific variation in dietary habits. Our data suggest that reproductive activities may often be important determinants of seasonality in other attributes, and override patterns associated with feeding.

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