PREY ABUNDANCE AND PREDATOR REPRODUCTION: RATS AND PYTHONS ON A TROPICAL AUSTRALIAN FLOODPLAIN

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Abstract. A 5-yr field study examined the ways in which prey abundance can influence the reproductive rates of predators. Water pythons (*Liasis fuscus*) on the Adelaide River floodplain in tropical Australia prey almost exclusively on dusky rats (*Rattus colletti*). Rat numbers varied dramatically among years of the study. Feeding rates of pythons were highest when rats were abundant, and the snakes were in good condition (mass relative to body length) at these times. The proportion of adult female pythons that reproduced in a given year was also tightly linked to rat abundances. However, reproductive output per litter (offspring size, and fecundity relative to maternal body size) was unaffected by prey availability, perhaps because of high fecundity-independent costs of reproduction. Instead, female pythons reproducing in "good" years were in better condition after oviposition.

These data support an energy-limitation model for snake reproduction, whereby prey availability determines predator reproductive output, but the relationship between the two variables is complex. The degree to which prey availability influences feeding rates of pythons and the degree to which feeding rates influence body condition depend crucially on snake body size (due to size-related shifts in foraging abilities and metabolic costs). Thus, a given prey abundance translates into different energy reserves for different-sized predators. Also, females delay reproduction until they can gain enough energy for a large clutch of eggs, and reproductive output per litter does not then increase with additional energy availability. Such nonlinearities in predator responses to prey availability may be widespread.

Key words: costs of reproduction; energy limitation; Liasis fuscus; predation; Rattus colletti; reptile; Pythonidae; snake.

INTRODUCTION

Rates of reproduction vary enormously from time to time and from place to place. Even within a single population, females may vary considerably in the number and size of offspring they produce per clutch, and in the number of clutches they produce per unit time. This variation has important consequences. The implications for population ecology are obvious, because spatial and temporal variations in reproductive output may be primary determinants of variation in the rate of recruitment of new individuals to the population (e.g., Caughley and Sinclair 1994). Variation in reproductive rates is also the raw material upon which microevolutionary processes depend, and is tightly linked to selection pressures on both females and males (the latter via shifts in operational sex ratio: Emlen and Oring 1977, Madsen and Shine 1992).

Thus, the question as to what drives differences in reproductive rates is a central issue both for ecology and for microevolution. Food supply is widely believed to be a crucial determinant of reproductive output in animal populations, based on results from experimental manipulation (food supplementation) as well as correlational evidence (e.g., Brand and Keith 1979, Ford

and Pitelka 1984, Hochachka and Boag 1987, Arcese and Smith 1988, Korpimaki and Hakkarainen 1991, Caughley and Sinclair 1994, Pons and Migot 1995). However, studies on this question suffer from a strong taxonomic and geographic bias: the overwhelming majority involve birds and mammals in the temperate zone. Hence, the generality of their results remains unclear. Reproductive rates may show little influence of food supply if temporal variation in prey availability is low (as may be true in many tropical habitats; Wilbur et al. 1974), or if species rely upon stored energy for breeding, rather than upon energy gained during the current reproductive season (Drent and Daan 1980). Because reproductive rates are also influenced by a host of other factors (e.g., inbreeding, sociality, predation risk), it is not necessarily true that an increase in prey availability will increase reproductive rates of a predator (Caughley and Sinclair 1994, Chastel et al. 1995, Duquette and Millar 1995). Also, even if reproductive rates *are* driven by prey availability in many systems, the relationship between these two variables may differ. For example, if the mechanistic links between prey abundance and predator reproduction involve threshold effects rather than gradual shifts, there may be significant nonlinearities in the response observed to an increase in prey abundance. Given these uncertainties, we need studies on different types of animals, in different types of habitats, to assess the ways in which

fluctuations in prey availability influence reproductive rates of predators.

Snakes may be excellent model organisms with which to investigate the determinants of variation in rates of reproduction. Previous studies on snakes have revealed that reproductive rates are highly variable both among and within populations, and through time. There may be an order-of-magnitude difference in clutch sizes among females even within the same population (Fitch 1970), and reproductive frequency varies through time and space. In many snake species, high proportions of the adult females skip opportunities for reproduction, and are likely to be nonreproductive in any given year (e.g., Glissmeyer 1951, Seigel and Ford 1987, Brown 1991). Is this variation in reproductive rates driven by variation in food availability? Such a link can be demonstrated in the laboratory (Ford and Seigel 1989), but is more difficult to quantify in the field. Food supplementation in field enclosures did not affect reproductive frequencies in female rattlesnakes, perhaps because of artifacts associated with small enclosure size (Charland and Gregory 1989). To document a link between prey abundance and snake reproduction, we report on a study system in which prey numbers and snake reproductive rates fluctuate from year to year, and in which both of these variables are amenable to accurate measurement. This system occurs on the Adelaide River floodplain in tropical Australia. We have been studying the native rats on this floodplain, and the pythons that eat them, for >5 yr. Here, we assess the linkage between prey availability and predator (snake) reproduction within this system.

MATERIALS AND METHODS

The floodplain, 60 km southeast of Darwin in the Northern Territory of Australia, consists of a relatively flat, treeless plain formed by silt deposition from a major tidal river, the Adelaide River. The area lies within the wet–dry tropics, and has consistently high temperatures that vary little from month to month or year to year (Madsen and Shine 1996b, Shine and Madsen 1996). However, precipitation is far more variable. Most of the annual rainfall is concentrated in a brief wet season, and the amount and timing of wet-season rainfall varies dramatically from year to year (Taylor and Tulloch 1985). Even minor differences in annual rainfall engender massive year-to-year variation in the abundance of a native rat species, *Rattus colletti* (Redhead 1979, Williams and Newsome 1991). This rat is the major prey of the water python (*Liasis fuscus*), a medium-sized (to 3 m total length, 5-kg body mass), nonvenomous snake (Shine 1993).

Over the period 1989–1995, we routinely patrolled roads within 5 km of Fogg Dam, on the Adelaide River floodplain, in the two hours after dusk. All pythons seen were captured and individually marked (scale-clipped), measured, weighed, and sexed (by probing hemipenal sacs) prior to release the following day.

Snout–vent length (SVL) was used as the measure of body length. We dissected road-killed pythons, removed their abdominal fat bodies, and weighed fat bodies and carcasses separately to estimate the proportion of body mass represented by the fat bodies.

We palpated all captured snakes to check for recently ingested prey; all such items were removed by forced regurgitation or defecation. Even well-digested prey could usually be identified to species by characteristic features of fur, scales, or feathers. We classified all snakes <140-cm SVL as juveniles (Madsen and Shine 1996a). The reproductive status of adult female snakes was assessed by palpation of the abdomen; in reproductive females, the enlarged ovarian follicles or oviductal eggs were readily discernible for >2 mo in a female's reproductive cycle. Nonreproductive females were characterised by an absence of these enlarged follicles or eggs during the breeding period, and immediately postovipositional females were recognized by their extreme emaciation and flaccid abdomens. Because reproduction is highly seasonal in this population, we could confidently determine the reproductive status of all adult female pythons captured over the period from July to October.

At monthly or two-monthly intervals from July 1990 to August 1995 (except for April to June each year, when we were absent on other studies), we used live traps to monitor abundances of dusky rats in three sites on the floodplain (Madsen and Shine 1996b). Thus, throughout this period we have indirect (index) estimates of population densities of rats (number of rats trapped per 50 traps along a 500-m transect), feeding rates of snakes (proportion of snakes containing identifiable prey when captured), body condition of snakes (residual scores from the general linear regression of log-transformed mass vs. SVL), and the proportion of adult female pythons that were reproductive. In four years of the study (1991, 1992, 1993, 1995), we kept gravid females until they oviposited, to quantify egg and clutch sizes. Data on snake body lengths and masses were log-transformed prior to analysis, to normalize variances. Further details on the study area, the snakes, the rats, and the methods we used, may be found in our earlier papers from this study (Shine 1993, Madsen and Shine 1996a, b, Shine and Madsen 1996).

Because we were interested in the mechanism by which prey availability might influence python reproduction, we investigated variables related to food intake (feeding rate) and energy storage (body condition), as well as rat abundance and snake reproduction. For these "intermediate" variables, we analyzed correlations using monthly (rather than annual) means, to increase the power of our tests. Presumably, the linkages between prey availability, food intake, and energy storage are similar among months as among years. However, we also examined annual variation in all of these traits, for comparison with annual variation in reproductive output of the pythons.
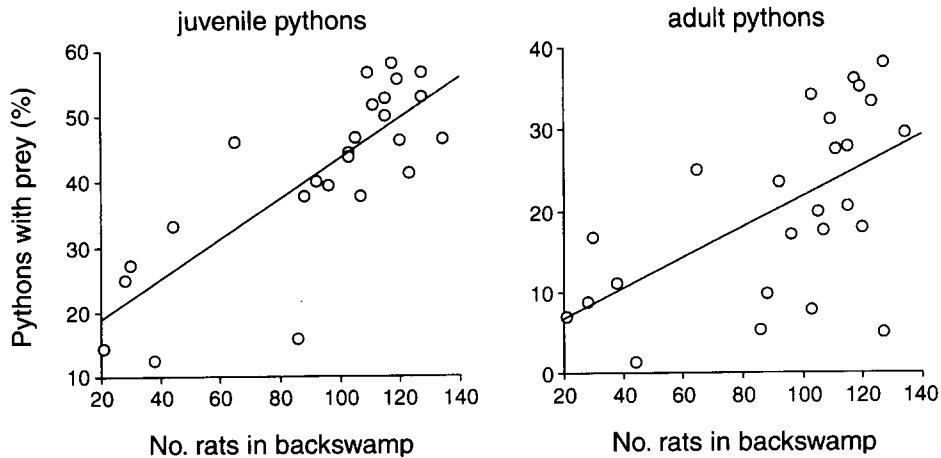
FIG. 1. Relationships between feeding rate (percentage of captured snakes containing recently ingested prey) and prey availability (abundance of dusky rats in the backswamp, a low-lying area of the floodplain; Madsen and Shine 1996b) in juvenile (<140-cm snout–vent length, SVL) and adult water pythons. Each data point represents the mean for one month. See *Results* for statistical analyses.

RESULTS

In total, we captured 4758 pythons (for a total of 7397 captures, including snakes caught on more than one occasion) and 4409 rats. Our data revealed considerable temporal variation in most of the characteristics that we studied. For example, rat population densities ranged from 21 to 140 rats/500-m transect, and the proportions of adult female pythons that were reproductive ranged from 9% to 87% over the five years of our intensive study.

Prey availability vs. python feeding rate

The proportion of snakes containing prey when captured varied among years. This variation was statistically significant for juvenile pythons ($n = 1533$, $\chi^2 = 28.38$, df = 5, $P < 0.0001$), as well as for adults of
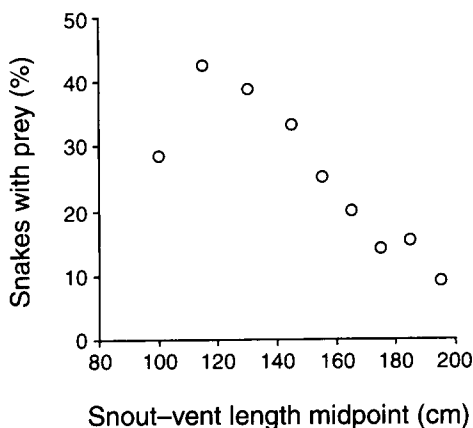

FIG. 2. Feeding rates of water pythons tend to decline with increasing body size. This graph is based on overall mean values for the percentage of captured snakes containing freshly ingested prey. Each data point shows the value for all snakes within a 10-cm SVL interval, plotted against the midpoint of this interval. See *Results* for statistical analysis.

both sexes (males: $n = 1834$, $\chi^2 = 79.08$, df = 5, $P < 0.0001$; nonreproductive females: $n = 525$, $\chi^2 = 13.62$, df = 5, $P < 0.02$). Gravid females ($n = 184$) did not contain prey in any year. Comparisons among monthly mean values for traits allowed us to test the hypothesis that prey availability influences the feeding rates of pythons. As expected, feeding rates were higher in months when the rats were abundant. This trend was particularly clear in juvenile pythons ($n = 25$ months, $r = 0.80$, $P < 0.0001$; Fig. 1). Feeding rates of adult pythons are affected by reproductive activities (both sexes reduce food intake during breeding: T. Madsen and R. Shine, *unpublished data*). Nonetheless, a link between rat abundance and adult python feeding rate was still clear ($n = 25$ months, $r = 0.58$, $P < 0.003$; Fig. 1).

Interestingly, however, this relationship differed between snakes of different body sizes. At equivalent rat densities, juvenile snakes fed more often than did adults, as shown in Fig. 1 (one-factor ANCOVA with snake maturity/immaturity as the factor, rat abundance as the covariate, and the proportion of pythons with prey as the dependent variable: slopes $F_{1,46} = 2.82$, $P = 0.10$; intercepts $F_{1,47} = 44.90$, $P < 0.0001$; and more generally, using 10-cm SVL intervals, with snake size group as the factor: slopes $F_{8,49} = 1.92$, $P = 0.08$; intercepts $F_{8,57} = 13.69$, $P < 0.0001$). Mean feeding rates declined with body size ($n = 9$ size classes, mean SVL vs. percentage of snakes with prey: $r_s = -0.88$, $P < 0.013$; see Fig. 2), as did the rate at which feeding rates increased with increases in rat abundance (SVL group rank vs. slope of the regression equation linking rat numbers to python feeding rates: $n = 9$ classes, $r = 0.73$, $P < 0.03$). This result indicates that food "availability" is not a simple function of prey abundance, because feeding rates depend on predator body sizes as well as on rat abundances.
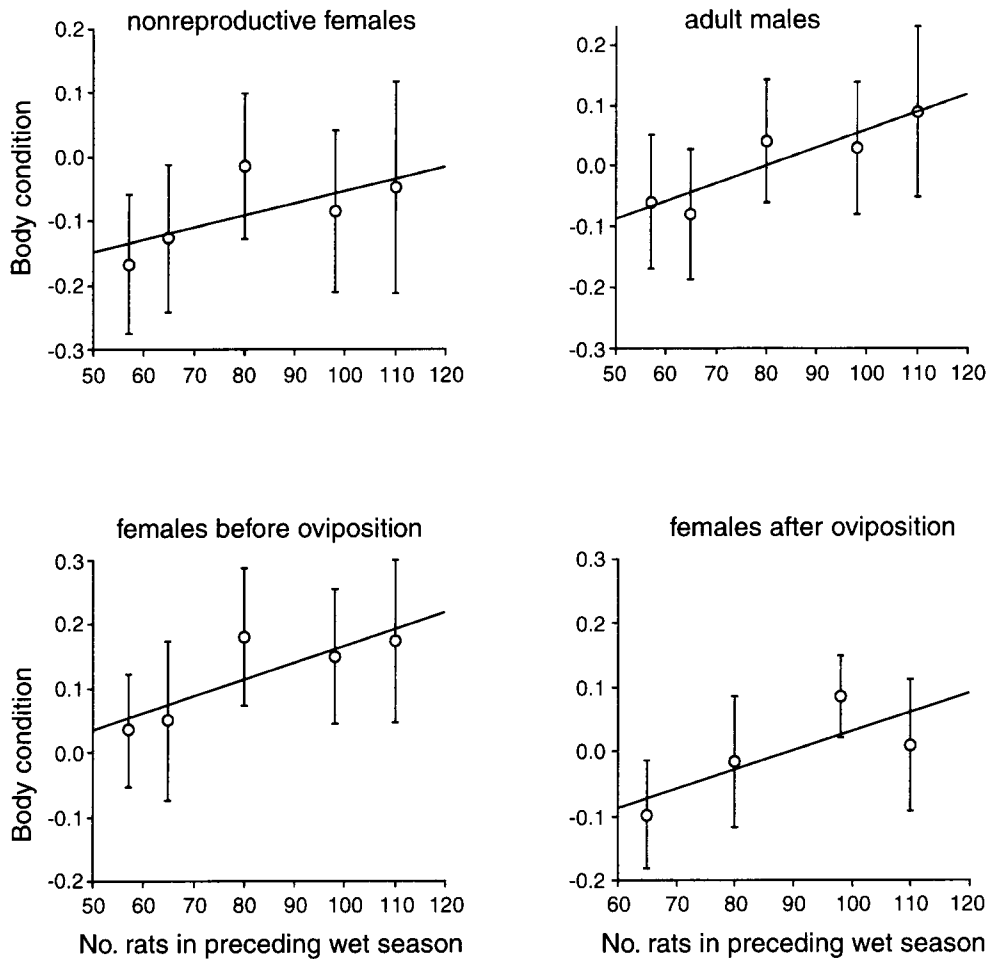
FIG. 3. The body condition of water pythons (graphed separately by gender and reproductive status), compared to the abundance of dusky rats in the preceding wet season. "Body condition" indexes are residual scores from the linear regression of log-transformed mass vs. snout–vent length. Each point shows the mean value ($\pm$ 1 SD) for one group for one year. Correlation statistics are as follows: nonreproductive females, $r = 0.68$, $P = 0.20$; males, $r = 0.91$, $P = 0.033$; prereproductive females, $r = 0.84$, $P = 0.08$; postreproductive females, $r = 0.77$, $P = 0.24$.

Prey availability vs. body condition of pythons

Dissections of 46 road-killed pythons indicated that most of the variance in body condition was due to the size of the abdominal fat stores. These were virtually absent in emaciated snakes, but constituted 15–20% of body mass in robust (presumably, well-fed) snakes. Our statistical tests revealed significant annual variation in body condition in all of the groups tested (heterogeneity of slopes test, with year as the factor, SVL as the covariate, and body mass as the dependent variable: juveniles, $F_{5, 1633} = 6.56$, $P < 0.0001$; adult males, $F_{5, 1811} = 7.05$, $P < 0.0001$; nonreproductive adult females, $F_{5, 515} = 3.42$, $P < 0.005$; preoviposition reproductive females, $F_{5, 442} = 26.17$, $P < 0.0001$). For postoviposition reproductive females, slopes of the mass vs. length regression were homogeneous among years ($F_{3, 131} = 0.47$, $P = 0.70$), but intercepts differed (ANCOVA: $F_{3, 134} = 7.82$, $P < 0.0001$; see Fig. 3). We also calculated residuals from log-transformed mass vs.

length regressions, to compare body condition with other variables. These condition scores varied significantly among years (one-factor ANOVA with year as the factor and condition score as the dependent variable: juveniles, $F_{5, 1348} = 7.70$, $P < 0.0001$; adult males, $F_{5, 1817} = 112.18$, $P < 0.0001$; nonreproductive adult females, $F_{5, 521} = 20.97$, $P < 0.0001$; preoviposition reproductive females, $F_{5, 436} = 3.65$, $P < 0.003$; postoviposition reproductive females, $F_{3, 135} = 7.23$, $P < 0.0003$).

Our analyses support the hypothesis that the observed temporal variation in body condition results from variation in food supply, and thus in feeding rates. The pythons were generally fatter (i.e., greater mass relative to SVL) following months with high feeding rates. As before, this pattern was clearest for juvenile snakes (regressing condition indices vs. feeding rates in the prior month: $n = 18$ months, $r = 0.74$, $P < 0.0005$), but the same pattern was also seen in both
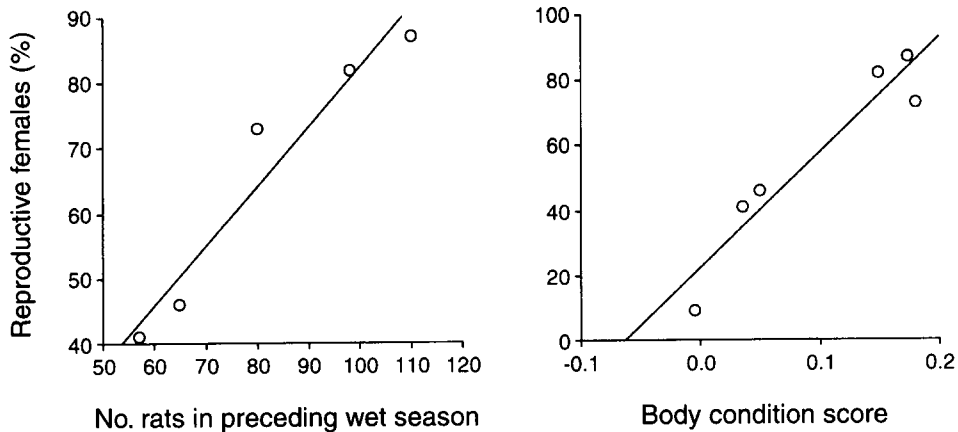
FIG. 4. The percentage of adult female water pythons that reproduce in a given year, compared to the abundance of dusky rats during the preceding wet season, and to the mean body condition of the snakes (residual scores from the mass vs. length regression). Each data point is based on all data from a single year. See *Results* for statistical analyses.

adult females ($n = 18$ months, $r = 0.54$, $P < 0.03$) and adult males ($n = 18$ months, $r = 0.44$, $P = 0.076$; however, for condition index 2 mo after the feeding-rate estimate, $n = 17$ months, $r = 0.76$, $P < 0.002$). A more detailed analysis shows that the way in which feeding rates translated into changes in body condition was affected by the body size of the snakes. To investigate this effect, we divided snakes into size groupings (10-cm SVL intervals) and used one-factor ANCOVA within each sex (with body-size interval as the factor, percentage of snakes with prey the preceding month as the covariate, and body condition as the dependent variable). For both sexes, different-sized snakes differed significantly in the form of the relationship between feeding rate and body condition (for males: slopes $F_{8,42} = 6.26$, $P < 0.0001$; for nonreproductive females: slopes $F_{8,45} = 1.26$, $P = 0.29$, but intercepts $F_{8,53} = 5.62$, $P < 0.0001$).

If prey abundance influences feeding rates, and feeding rates influence body condition, we would expect that prey abundance is also positively correlated with body condition. Our analyses support this prediction. The body condition of juvenile pythons was highest following months of high prey abundance (for juvenile snakes, $n = 18$ months, $r = 0.60$, $P < 0.009$). Adult snakes may take longer to change body condition in response to increased prey availability, as previously noted. The body condition of adult male pythons was not significantly correlated with prey availability in the preceding month ($n = 17$ months, $r = 0.25$, $P = 0.33$), but was significantly correlated with prey availability 2 mo earlier ($n = 15$ months, $r = 0.59$, $P < 0.022$). We did not examine adult females for this pattern, because the analysis would be complicated by the facts that gravid females do not feed, that reproduction profoundly influences maternal body condition, and that we could not reliably distinguish postreproductive vs. nonreproductive females in the months following oviposition.

Although strong links among prey availability, feeding rates, and body condition were evident in these comparisons based on monthly means, the lower sample sizes for comparisons among years greatly reduces statistical power. Hence, although mean body condition of all groups of pythons was positively correlated with prey availability in annual comparisons (Fig. 3), these relationships were not statistically significant in most comparisons (see Fig. 3 legend). Nonetheless, the data are consistent with the hypothesis that temporal variations in prey availability (whether at the monthly or annual level) drive variation in feeding rates and body condition of the pythons.

Prey availability vs. python reproduction

Does rat abundance influence python reproduction? Three such effects are conceivable: prey availability might influence (1) the frequency of reproduction (i.e., the percentage of adult females that reproduce in a given year); (2) the reproductive output per clutch (through shifts in either egg size or clutch size or both); and/or (3) the size at maturation and, consequently, the number of adult females in the population. Our data suggest that the first of these effects occurs, but the second and third do not.

1. *Percentage of reproductive females.*—In years when rats were abundant, a high percentage of female pythons reproduced ($n = 5$ years, $r = 0.96$, $P < 0.01$; see Fig. 4). As would be expected from the relationship between prey availability and body condition, these were also years when prereproductive females were in unusually good body condition (using residual scores from the mass vs. length regressions to assess condition; body condition vs. percentage of reproductive females: $n = 6$ years, $r = 0.95$, $P < 0.004$; Fig. 4).

2. *Reproductive output per clutch.*—We have shown that years of high prey availability coincided with relatively fat snakes and a high percentage of reproductive females. Are reproductive females also fatter than usual

in such years (such that one might expect their reproductive output to be higher than usual), or is it simply that higher percentages of females reach some threshold level of energy storage sufficient for reproduction? In the latter case, there may be no effect of prey availability on python body condition *among reproductive females.* Our data show that prey abundance *does* affect body condition of reproductive, as well as nonreproductive, females. In "good" rat years, females that reproduced were in unusually good condition: that is, prior to oviposition, they were heavy relative to their body length.

Nonetheless, this year-to-year variation in body condition of reproductive females did not translate into year-to-year differences in reproductive output per clutch. Mean egg sizes were similar for the the three years for which we have detailed data (Fig. 5; one-factor ANOVA with year as the factor and mean egg size per clutch as the dependent variable: ($F_{2, 114} = 1.32$, $P = 0.27$). Also, clutch sizes relative to maternal body sizes did not differ significantly among the four years in which we recorded clutch sizes (Fig. 5; one-factor ANCOVA with year as the factor, maternal snout–vent length as the covariate, and clutch size as the dependent variable: slopes $F_{3, 131} = 0.89$, $P = 0.45$; intercepts $F_{3, 134} = 2.31$, $P = 0.08$). Similarly, relative clutch mass (RCM) did not vary among years (one-factor ANCOVA with year as the factor, maternal postoviposition mass as the covariate, and total clutch mass as the dependent variable: slopes $F_{3, 127} = 0.93$, $P = 0.43$; intercepts $F_{3, 130} = 0.73$, $P = 0.54$).

3. *Body size at maturation.*—The size at maturation (SVL of the smallest reproductive female) showed little variation among the five years of our study (range 148–154 cm). Although size at maturation tended to be lower following years of high rat abundance, this trend did not attain statistical significance ($n = 5$ years, $r = -0.39$, $P = 0.52$).

DISCUSSION

Because of the sensitivity of dusky rat populations to stochastic climatic variation (Redhead 1979, Williams and Newsome 1991), combined with a high and unpredictable variation in the amount of monsoonal rainfall each wet season (Taylor and Tulloch 1985), rat abundances on the Adelaide River floodplain vary dramatically from year to year. Our data document some of the consequences of this variation for the predators that feed upon the rats. When rats are abundant, the pythons feed frequently and amass large fat stores. In years following high rat abundance, a high proportion of adult females reproduces. In contrast, low rat abundances reduce feeding rates by the pythons, so that most of the snakes are relatively thin and most females are subsequently nonreproductive. Female pythons that do reproduce in such years produce a "normal" reproductive output, in terms of egg sizes and clutch sizes, but are very thin after oviposition.
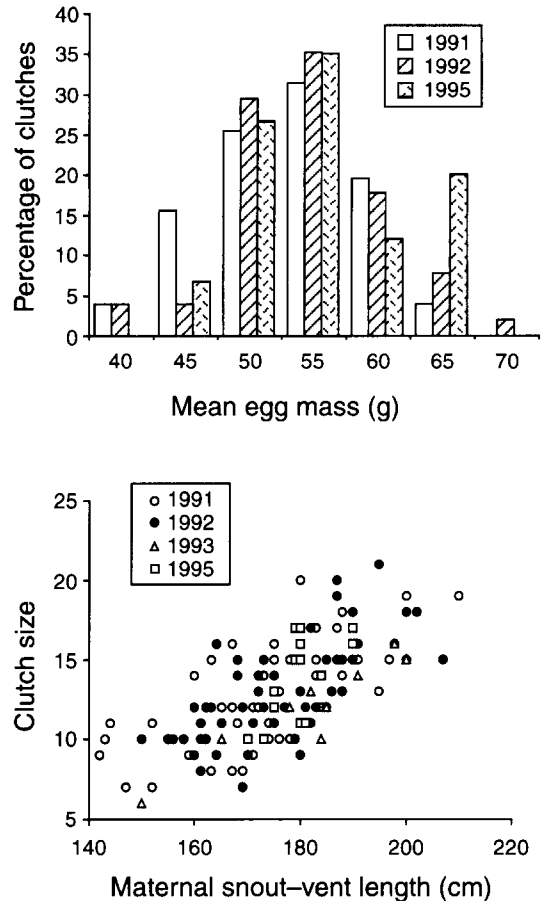

FIG. 5. Year-to-year variation in the reproductive output of water pythons. The upper histograms show the distributions of the mean mass of fertile eggs (one data point per clutch) in three different years. The lower graph shows clutch size relative to maternal SVL in five different years. These data emphasize the temporal consistency of reproductive output per litter, compared to the strong among-year differences in the proportion of reproductive females in the population. See *Results* for statistical analyses.

A link between prey availability and predator reproduction has been documented in many populations of birds (see review by Hochachka and Boag 1987) and mammals (e.g., Brand and Keith 1979, Todd et al. 1981, Ford and Pitelka 1984, Lunn et al. 1994), although data are scarce for most other groups (but see Weisberg and Lotrich 1986, Boersma 1995). Even within birds and mammals, however, patterns are unclear. Manipulative (food supplementation) studies provide the most direct evidence on this topic, but have often produced conflicting results. For example, some species show little reproductive response to increased prey availability (e.g., Duquette and Millar 1995). Other taxa respond by changing reproductive output, but the variable that changes is sometimes litter size, whereas in other cases it is offspring size, reproductive frequency, or some combination of these three variables (e.g., see Ho-

chachka and Boag 1987, Korpimaki and Hakkarainen 1991, Chastel et al. 1995, Pons and Migot 1995).

Although laboratory manipulations demonstrate a functional relationship between food intake and reproductive output in snakes (e.g., Ford and Seigel 1989), ours is the first field study on snakes to quantify such an effect. The linkage between prey availability and predator reproduction is strong, but not simple. Perhaps the most interesting aspects of our results are the significant nonlinearities occurring at three steps in the causal chain that links rat abundance to reproductive output of the pythons. Firstly, snake body size influences the degree to which a given level of prey abundance translates into an increment or decrement in the feeding rate of an individual python. Secondly, snake body size affects the degree to which a given feeding rate influences the python's condition (i.e., its energy stores). And lastly, reproduction appears to be an "all-or-none" phenomenon, whereby the output per clutch is unaffected by the magnitude of a female's energy stores.

There are clear biological reasons for each of these nonlinearities. Firstly, the differences in feeding rate among pythons of different sizes (Fig. 2) reflect two phenomena. The low feeding rates of very small pythons are due to gape limitation: newly hatched snakes are too small to ingest adult dusky rats, the only abundant prey type. Hence, the hatchling pythons rely upon juvenile rats (a much less abundant food resource) until they are large enough (≈80 cm SVL: T. Madsen and R. Shine, *unpublished manuscript*) to ingest adult rats. The subsequent linear decline in feeding rates with body size (Fig. 2) reflects the ability of small pythons to penetrate deep into the soil cracks where the rats live and breed, which larger pythons are unable to do. Hence, the larger snakes must rely on ambushing occasional surface-active rats (*personal observation*). When rats are at low population densities, they are relatively inaccessible to larger snakes. When rats become more common, they spend disproportionately more time in surface activity (because all available crevices are already occupied: Redhead 1979), and so become more accessible to even the largest pythons. Thus, python body sizes determine the rate at which increases in rat abundance cause snake feeding rates to increase.

The rate at which energy stores accumulate at any given feeding rate also depends upon python body size. Larger pythons have higher metabolic costs (in absolute terms) and may expend more energy on reproductive activities. Mean prey sizes do not increase over the range of body sizes of adult pythons, because all feed on the relatively small (≤210 g) dusky rats. Hence, any given level of food intake (feeding rate) sustains a lower level of body condition in larger pythons than in smaller conspecifics. Because of these allometric relationships, any particular level of "prey abundance" has different consequences for the energy balance of

snakes of different body sizes, partly because these animals differ in their ability to acquire prey, and partly because of metabolic costs associated with body size. Thus, the relationship between prey abundance and snake condition is complex, and differs substantially between snakes of different body sizes.

The third nonlinearity is due to another aspect of snake biology. Why don't female pythons adjust their reproductive expenditure per clutch relative to prey availability? Studies on desert lizards have detected flexibility of this kind. For example, annual variation in mean clutch sizes of *Urosaurus ornatus* is correlated with climatic factors (presumably operating via changes in prey availability; Ballinger 1977, Smith et al. 1995), and food supplementation (via irrigation) prevented a seasonal decline in clutch size of *Uta stansburiana* (James and Whitford 1994). Such responses may be most common in relatively short-lived species that rely on energy gathered during the current breeding season to sustain reproduction (e.g., Lack 1968, Hochachka and Boag 1987, Arcese and Smith 1988, Clutton-Brock 1988, Simons and Martin 1990). In relatively long-lived species that are likely to have other chances to breed, selection may favor females that wait until they can produce a large clutch before reproducing at all. This tactic may enhance maternal fitness if there are significant "costs" of reproduction that are independent of the numbers of eggs produced. In such cases, organisms may benefit from reproducing infrequently, but with very large clutches, because they thus minimize the number of times they must pay such "costs" (Bull and Shine 1979). Clearly, this strategy relies upon an ability to accumulate large energy reserves that can support subsequent breeding.

Under this scenario, the reproductive output per clutch is essentially maximized (relative to maternal abdominal volume available to carry the eggs, or to the "costs" of reproduction), so that females cannot increase clutch or offspring sizes even if they encounter unusually "good" years. Instead, females that are exposed to unusually high prey availability can allocate "excess" energy to storage. Such energy reserves may fuel the high costs of shivering thermogenesis to warm the clutch (Harlow and Grigg 1984), enhance maternal survival after reproduction, and reduce the time required to gather enough energy for the next clutch (Madsen and Shine 1993*a*, Luiselli et al. 1996). Comparisons of reproductive output in European adders (*Vipera berus*) during years of high and low prey availability suggested that maternal body condition before and after parturition was affected by energy reserves, whereas relative clutch mass was not (Andrén and Nilson 1983). These results are similar to those for our pythons, although the adders were also reported to display shifts in mean litter sizes and offspring sizes between the two years of the study.

This nonlinear relationship between prey availability and reproductive output per clutch has strong impli-

cations for the measurement of "reproductive effort" (RE). If reproduction by a given female in a given year is essentially "all-or-none" (i.e., represents a virtually constant output relative to maternal body size), then there is no point in attempting to measure that output very precisely and then using minor variations in expenditure per clutch to test ideas about RE. Instead, the crucial variable is the frequency with which a female reproduces relative to her energy intake, rather than her expenditure per clutch. This conclusion reinforces Seigel and Ford's (1987) suggestion that reproductive frequency is the most important, but least understood, axis of interspecific and intraspecific variation in the life histories of snakes.

Our data also suggest that it will be difficult to devise simple measures of prey "availability" to compare with reproductive energy allocation, because of the confounding effects of body size. For example, many wide-ranging snake species show extensive intraspecific variation in body size, often in conjunction with differences in dietary composition (e.g., Kephart 1982, Schwaner and Sarre 1988, Madsen and Shine 1993b). Such variations also occur in endothermic vertebrates, but are typically much less extreme. Our data suggest that intraspecific body-size variation in snakes may have considerable ecological ramifications, because the way in which prey availability translates into predator reproductive output is very sensitive to even minor body-size differences, and is crucially dependent on the details of habitat structure (e.g., crevice size vs. predator body size) and reproductive costs. Hence, the widespread geographic variation in body sizes among snakes may offer an excellent opportunity to identify factors regulating reproductive output in predator populations.

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