



Quantity or quality? Determinants of maternal reproductive success in tropical pythons (*Liasis fuscus*)

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A female's reproductive output (size and number of offspring) may say little about her reproductive success; the 'quality' of her progeny and the time that they are produced may be more important in this respect. We marked and released 1224 hatchling water pythons (*Liasis fuscus*) from 116 clutches of laboratory-incubated eggs, in a study site in tropical Australia. Clutches varied widely in the number of eggs, mean offspring sizes, the proportion of eggs that hatched, and recapture rates of offspring. Clutch size was not significantly correlated with the number of recaptured hatchlings in either year, nor was mean offspring size related to recapture probability. Instead, offspring recapture rates varied as a function of the time of hatching. Recapture rates were higher for hatchlings released in a year with high prey availability than in a year with few prey. In addition, recapture rates were higher for earlier-hatching clutches in the year with few prey. The other significant effect on recapture rates involved offspring viability: some clutches had a much higher proportion of surviving offspring than did others, and recapture rates were higher from clutches with higher hatching success (i.e. proportion of eggs hatching). Hence, the usual measures of reproductive output (clutch size and offspring size) offer only a poor index of a female's reproductive success in this system.

Keywords: natural selection; life history; offspring phenotype; reptiles; snakes; stochasticity

1. INTRODUCTION

Variation in reproductive success (RS) among individuals lies at the heart of Darwinian theory, and yet most empirical work on life-history variation relies on simple measures of offspring size and number as the measure of RS. This 'shortcut' invokes significant assumptions. Offspring size and number are excellent measures of reproductive output, and hence are well suited to testing ideas about the determinants of variance in output (e.g. reproductive effort, costs of reproduction). However, these measures may bear little relationship to maternal RS, unless (i) the number of offspring produced is broadly proportional to the number that survive to reproduce, and (ii) larger offspring size enhances eventual RS, presumably via higher rates of survival and/or growth. For most biological systems, we have little evidence that either of these statements is true.

Although phenotypic variation and differential fitness are the cornerstones of Darwinian natural selection, detailed field studies of the determinants of offspring traits, and the consequences of those traits for subsequent survival and RS, are available for only a few kinds of organisms (e.g. Endler 1986; Clutton-Brock 1988, 1991; Sinervo *et al.* 1992). It is easy to measure offspring phenotypes and demonstrate that they vary, and to model the ways in which that variation might influence organismal

fitness (e.g. Smith & Fretwell 1974; Shine 1978; Schluter 1988). Actually measuring differential survival relative to such phenotypes is a much more difficult task (e.g. Endler 1986).

Nonetheless, many field biologists have responded to this challenge. Reptiles have been the study organisms for a number of these studies (e.g. Fox 1975; Ferguson *et al.* 1982; Ferguson & Fox 1984; Volkl 1989; Jayne & Bennett 1990; Laurie & Brown 1990; Brodie 1992; Janzen 1993; Sinervo & Huey 1990; Sinervo *et al.* 1992; Sinervo & Doughty 1996; Olsson *et al.* 1996). In combination, these studies suggest that phenotypic traits such as hatchling size, colour and locomotor performance can influence survival rates of free-living reptiles. Our focus in this paper is somewhat different. Rather than examining fitness effects of variation among offspring within a population, we consider determinants of variation among reproducing females. Hence, the unit of replication for our analyses is the female and her clutch, rather than each of her individual offspring. We thus ask what characteristics of a female's reproductive output (clutch size, offspring size, time of hatching and/or viability of offspring) are significantly correlated with her eventual RS.

To do this, we explore determinants of survival among hatchling water pythons (*Liasis fuscus*) from wild-caught gravid females in tropical Australia. Our analysis is based on hatchlings from eggs deposited in captivity and incubated under controlled conditions in the laboratory and subsequently released in our study area.

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Table 1. *Four putative determinants of maternal reproductive success, the patterns one would predict if each of these was important, and the results of our analyses on two years' reproductive output in water pythons*

trait under selection	prediction	test	
		1991	1992
clutch size	larger clutches will produce more surviving offspring	no	no
offspring size	larger hatchlings will have an increased probability of survival	no	no
time of hatching	earlier hatching will increase the probability of offspring survival	no	yes
'quality' of hatchlings	(i) variation among clutches in offspring survival rates will be greater than expected under the null hypothesis of equal survival probabilities	yes	yes
	(ii) clutches with greater hatching success will also have increased offspring survival	yes	yes

2. MATERIALS AND METHODS

(a) *Study area and species*

The study was conducted in the Fogg Dam conservation reserve, in the lower reaches of the Adelaide River floodplain, 60 km southeast of Darwin in the Northern Territory of Australia. The area lies within the 'wet-dry' tropics; temperatures are high year-round (mean daily maximum air temperature is greater than 30 °C in every month) but precipitation is highly seasonal. More than 75% of the 1300 mm mean annual rainfall occurs during the brief (December–March) 'wet-season'. Rainfall is highly variable among years. During our study, annual rainfall has ranged from 876–2104 mm (data taken at the Coastal Plains Research Station, 2 km from Fogg Dam). The Adelaide River floodplain is a relatively flat, treeless area formed by silt deposition on either side of the river. Most of the floodplain is inundated by monsoonal rains each year, and the vegetation consists of sedges (*Eleocharis*) and grasses (e.g. *Oryza*, *Mnesithea*, *Panicum*). Paperbark (*Melaleuca*) forest fringes the floodplain, giving way to open woodland (dominated by *Eucalyptus*) in higher, drier regions.

Water pythons are large (to 3 m, 5 kg), non-venomous snakes that occur over a wide area of tropical Australia (e.g. Cogger 1992). This species is very abundant on the Adelaide River floodplain. We captured gravid female pythons at night by spotlighting on foot, or from a slowly moving vehicle. The females were collected in three areas less than 5 km from Fogg Dam in August–September, shortly prior to oviposition in 1991 and 1992 (55 females were captured in 1991, and 61 in 1992). The female pythons were maintained in outdoor cages (60 cm × 60 cm × 60 cm) until oviposition. The eggs were removed within 24 h of laying, and incubated in moist (50% water by mass) vermiculite at 29–32 °C. We obtained 697 eggs in 1991, and 806 eggs in 1992. These eggs produced 552 viable hatchlings in 1991, and 672 in 1992 (see Madsen & Shine (1996) for details). Offspring were weighed and measured less than 24 h after hatching, and each hatchling was scale-clipped with a number that identified the clutch from which it came. All hatchlings were released in a single area, 50 m north of Fogg Dam.

In this paper, we use recapture rates as an index of survivorship. Although this technique undoubtedly underestimates survival (because some surviving snakes are not recaptured), differences in recapture rates among clutches and between years are likely to reflect differences in survival rates rather than in dispersal. Only one of the recaptured hatchlings was found at a site other than the Fogg Dam wall; that animal was recaptured 2.5 km from its point of release. The recapture data for each

cohort are based on the subsequent five years (1992–1996 for the 1991 snakes; 1993–1997 for the 1992 cohort). During these two five-year periods, similar numbers of snakes were captured (4064 versus 3990); thus, any difference in recapture rates between the two cohorts is not due to a difference in capture effort.

3. RESULTS

Below, we analyse the numbers and proportions of hatchlings that were recaptured as a function of four different factors that might plausibly influence maternal RS: the number of eggs in the clutch, the mean size of the offspring, the time (year, and season within year) when the offspring hatched, and the 'quality' of the offspring. In each case, we can predict patterns of association among variables based on the hypothesis that the relevant variable is a significant determinant of maternal RS (table 1).

(a) *Clutch size*

If a larger clutch size enhanced the number of surviving offspring (as intuition suggests), we would expect larger clutches to result in more recaptures. Surprisingly, we saw no evidence of this pattern. No significant correlation between clutch size (total number of eggs laid) and the number of recaptured hatchlings was evident for either cohort (Spearman rank correlation: $n=55$, $r_s=0.06$, $p=0.67$; $n=61$, $r_s=0.22$, $p=0.081$, respectively). Hence, total clutch size was a poor predictor of maternal RS over the two years of our study.

(b) *Hatchling size*

Mean offspring size differed among clutches (range in mean mass of hatchlings = 24.7–49.5 g), but most hatchlings within a single clutch resembled each other in body size. Hence, among-clutch differences in mean offspring size were highly significant in both years of the study (one-factor ANOVA with clutch number as the factor, and hatchling mass as the dependent variable: for 1991, $F_{54,551}=16.7$, $p=0.0001$; for 1992, $F_{60,669}=24.1$, $p=0.0001$). Despite this among-clutch variation, mean hatchling mass was not significantly correlated with the proportion of hatchlings recaptured, in either year of the study (Spearman rank correlation: 1991, $n=55$, $r_s=0.16$, $p=0.25$; 1992, $n=61$, $r_s=0.11$, $p=0.40$). That is, clutches of larger offspring were no more likely to produce survivors than were clutches composed of much smaller hatchlings.

(c) The timing of reproduction

A hatchling's chances of surviving may depend more on when it is produced, rather than its size or any other characteristic. We can examine this possibility at two levels: by comparing hatchling survival rates between the two years of our study, and by comparing survival to hatching dates within each of the two years.

(i) Comparison between years

We recaptured 80 of the 552 (14.5%) hatchlings from the 1991 cohort over their first five years of life (1992–1996), but recaptured only 14 of the 672 (2.1%) hatchlings from the 1992 cohort over the analogous interval (1993–1997). The proportion of hatchling snakes that we recaptured thus differed significantly between the two cohorts ($\chi^2=64.1$, 1 d.f., $p<0.0001$).

(ii) Comparisons within each year

The date of hatching of the first brood laid by our captive females was set to zero, and subsequent broods were assigned a relative date accordingly. In 1991 there was no significant difference in relative hatching date of broods from which we recaptured at least one hatchling compared with broods where no hatchlings were recaptured (mean relative hatching dates were 20.9, s.d.=11.9, and 23.0, s.d.=12.2, respectively; unpaired two-tailed $t_{53}=0.57$, $p=0.57$). However, in 1992 the recaptured hatchlings originated from broods that hatched significantly earlier than broods from which no hatchlings were recaptured (mean relative hatching dates were 17.0, s.d.=13.8, and 25.7, s.d.=10.1, respectively; unpaired two-tailed $t_{59}=2.71$, $p=0.009$).

(d) Offspring 'quality'

The fourth potential determinant of offspring survival is the 'quality' of the hatchlings, independent of their body size. For example, hatchlings from some clutches might display higher survival rates because of genetic superiority or maternal effects. Although 'quality' is an elusive concept, we can test this proposition in two different ways.

(i) Among-clutch variance in survival rates

If some clutches consist of 'better' offspring than others, we expect that the surviving offspring will come disproportionately from a few 'good' clutches, rather than being randomly drawn from among all clutches. In keeping with this prediction, there were large differences among clutches in the proportions of hatchlings that were recaptured: from 0–57% in the 1991 cohort and 0–24% in the 1992 cohort. We used contingency-table analyses to compare the relative numbers of hatchlings that were or were not recaptured among clutches. In both years, the differences in recapture rates among clutches were greater than expected under the null hypothesis of equal recapture probabilities of hatchlings from each clutch (1991, $\chi^2=73.9$, 54 d.f., $p=0.037$; 1992, $\chi^2=93.6$, 60 d.f., $p=0.004$).

(ii) Correlation between hatching success and survival rate

Offspring viability can be expressed in the egg stage as well as later in life. If some clutches consist of 'better' offspring, we expect to see a positive correlation between

survival rates at these two life-history stages: clutches with high hatching success (proportion of eggs that hatch successfully) should also have a high proportion of survivors as free-living juveniles. Analysis supports this prediction in both years of the study, with significant correlations between hatching success per clutch and the proportion of hatchlings recaptured (Spearman rank correlation: 1991, $n=55$, $r_s=0.38$, $p=0.005$; 1992, $n=61$, $r_s=0.33$, $p=0.01$).

4. DISCUSSION

First, we address the relationship between reproductive output and RS. Intuition suggests that maternal RS should be increased by producing more eggs (because, all else being equal, this should generate more surviving offspring) and larger eggs (because larger offspring 'should' have a higher probability of survival). These two assumptions underpin a high proportion of life-history theory (see, for example, reviews by Stearns (1976, 1980), Roff (1992) and McNamara & Houston (1996)). However, empirical support for both propositions is meagre. There is a large literature on birds, stimulated by Lack's famous hypothesis, showing that the largest clutch size is not necessarily the one that results in the greatest number of offspring surviving to the point of fledging (for examples, see papers in review edited by Clutton-Brock (1988)). Nonetheless, even bird studies generally are forced to estimate maternal RS in terms of numbers and sizes of offspring at the time of termination of parental care. Non-random mortality after this time is often not included in estimates of maternal RS, because of the difficulty of measuring survival in free-living juveniles (but see, for example, Spear & Nur (1994) and Svensson (1997)). In contrast to birds and mammals, most reptiles do not exhibit parental care (Shine 1988); thus, variation in offspring survival is not caused by differential post-hatching parental effort. For these kinds of organisms, Lack (1954) predicted that natural selection should favour a compromise between offspring size and offspring number; that is, we should see a positive correlation between offspring survival and offspring size and a negative correlation between offspring number and offspring size.

However, there are only a few reptilian field studies that reveal a survival advantage to larger body size at hatching (e.g. Fox 1975; Ferguson *et al.* 1982; Ferguson & Fox 1984; Olsson 1992; Janzen 1993). In our study no such effect was detected (table 1), whereas other studies suggest that the putative advantages of larger offspring size apply only in some places (e.g. Sinervo & Huey 1990) at some times (Ferguson & Fox 1984; Laurie & Brown 1990; Sinervo *et al.* 1992; Sinervo & Doughty 1996).

Surprisingly, very few studies have focused on the relationship between clutch size and the number of surviving offspring. Clutch sizes were correlated with the numbers of surviving offspring in one study on small desert lizards (Sinervo *et al.* 1992), whereas no such correlation was detected in our water python population (table 1). Thus, despite their ease of measurement and their value as components of reproductive output measures, there is no certainty that clutch sizes and

offspring sizes offer valid 'shorthand' indices for maternal RS. Indeed, our data challenge this assumption (table 1).

Instead, reproductive timing may be more important, at least in systems with strong temporal variation in prey availability. The pythons in our study area feed almost exclusively on dusky rats, *Rattus colletti* (Shine & Madsen 1997). Dusky rats grow rapidly (reaching more than 60 g at 8 weeks of age) and exhibit pronounced year-to-year fluctuations in abundance (Madsen & Shine 1998). Owing to gape limitation, hatchling pythons cannot ingest rats larger than 30 g (T. Madsen and R. Shine, unpublished data). The scarcity of alternative prey in our study area means that hatchling pythons rely on juvenile rats for their first few meals. However, during the two years of our study, prey availability for the hatchling pythons differed markedly. In 1991, the rats were still breeding when the hatchling pythons emerged in November–December (Madsen & Shine 1998). Thus, small prey were readily available for the neonate pythons. However, the 1992 dry-season was preceded by an extremely 'dry' wet-season. In consequence, rat reproduction ceased in August, with the result that very few ingestible-sized rats were available for the hatchling pythons in that year (Madsen & Shine 1998). The higher survival of 1991 hatchlings compared with the 1992 cohort thus appears to have been mediated via the higher availability of small prey. Similarly, the enhanced survival of early-hatching pythons in 1992 (relative to their later-hatching conspecifics) may be due to greater numbers of ingestible-sized prey earlier in the season.

Thus, our study suggests a strong link between prey availability and offspring survival (see, also, Volkl 1989). Although the reliance of hatchling water pythons on juvenile rats may impose strong selection on the predator to synchronize its reproductive cycle with that of its prey, the duration of dusky rat reproduction in the Fogg Dam area fluctuates stochastically (Redhead 1979; Madsen & Shine 1998). Hence, ovipositing pythons may be unable to predict prey abundances for their hatchlings. As in many long-lived organisms (e.g. Congdon *et al.* 1982; Clutton-Brock 1988), recruitment to the adult population may come disproportionately from offspring produced during an occasional 'good' season.

The strong effect of hatching success and the non-random recaptures among our water python clutches suggest that an important determinant of maternal RS involves some aspect of offspring viability. A similar relationship between clutch viability and offspring survival has been reported in Swedish sand lizards, *Lacerta agilis* (Olsson *et al.* 1996). In the Swedish study, apparently 'normal' offspring with malformed siblings had lower survival rates than did offspring from broods with no malformed young. Olsson *et al.* (1996) suggested that the malformations were probably the outcome of matings between close kin, and that the 'normal-looking' offspring from these broods harboured non-detected detrimental alleles. We have no direct evidence that the non-random survival of water pythons is caused by genetic factors, but two of our results (the significantly non-random recapture rates among clutches, and the correlation between hatching success and recapture rate) point in this direction.

The field of life-history evolution is blessed with numerous theoretical models that seek to explain and predict variation in egg size and clutch size under a variety of selective regimes (e.g. Smith & Fretwell 1974; Shine 1978; Winkler & Wallin 1987). These models are useful, but are almost impossible to test given the limitations of current data. In particular, we need more work to see why clutches differ so dramatically in offspring viability. If factors such as reproductive timing or offspring viability are more important determinants of maternal RS than are the number and size of offspring (as is suggested by our results, as well as by analyses of lifetime RS in an array of other organisms (Clutton-Brock 1988)), then theoretical models will need to consider these variables more explicitly.

We thank E. Cox and P. Fisher for assistance in python husbandry, G. Bedford, B. Cantle, P. Harlow, M. Stephens, P. Osterkamp and J. Osterkamp for field assistance, and K. Levy for logistical support. The work was funded by the Australian Research Council and the National Geographic Society (Research and Exploration Fund).

REFERENCES

- Brodie, E. D. III 1992 Correlational selection for color pattern and antipredator behavior in the garter snake, *Thamnophis ordinoides*. *Evolution* **46**, 1284–1298.
- Clutton-Brock, T. H. 1988 *Reproductive success. Studies of individual variation in contrasting breeding systems*. University of Chicago Press.
- Clutton-Brock, T. H. 1991 *The evolution of parental care*. Princeton University Press.
- Cogger, H. 1992 *Reptiles and amphibians of Australia*. Sydney: Reed Books.
- Congdon, J. D., Dunham, A. E. & Tinkle, D. W. 1982 Energy budgets and life histories of reptiles. In *Biology of the Reptilia*, vol. 13 (ed. C. Gans & F. H. Pough), pp. 233–271. New York: Academic Press.
- Endler, J. A. 1986 *Natural selection in the wild*. Princeton University Press.
- Ferguson, G. W. & Fox, S. F. 1984 Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. *Evolution* **38**, 342–349.
- Ferguson, G. W., Brown, K. L. & DeMarco, V. 1982 Selective basis for the evolution of variable egg and hatchling size in some iguanid lizards. *Herpetologica* **38**, 178–188.
- Fox, S. F. 1975 Natural selection on morphological phenotypes of the lizard *Uta stansburiana*. *Evolution* **29**, 95–107.
- Janzen, F. J. 1993 An experimental analysis of natural selection on body size of hatchling turtles. *Ecology* **74**, 332–341.
- Jayne, B. C. & Bennett, A. F. 1990 Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* **44**, 1204–1229.
- Lack, D. 1954 *The natural regulation of animal numbers*. Oxford: Clarendon Press.
- Laurie, W. A. & Brown, D. 1990 Population biology of marine iguanas (*Amblyrhynchus cristatus*). II. Changes in annual survival rates and the effects of size, sex, age and fecundity in a population crash. *J. Anim. Ecol.* **59**, 529–544.
- McNamara, J. M. & Houston, A. I. 1996 State-dependent life histories. *Nature* **380**, 215–221.
- Madsen, T. R. & Shine, R. 1996 Determinants of reproductive output in female water pythons (*Liasis fuscus*, Pythonidae). *Herpetologica* **52**, 146–159.

- Madsen, T. & Shine, R. 1998 Rainfall and rats on a tropical floodplain: climatically-driven dynamics of an Australian rodent population. *Aust. J. Ecol.* (In the press.)
- Olsson, M. 1992 Sexual selection and reproductive strategies in the sand lizard (*Lacerta agilis*). PhD thesis, University of Gothenburg, Sweden.
- Olsson, M., Gullberg, A. & Tegelström, H. 1996 Malformed offspring, sibling matings, and selection against inbreeding in the sand lizard (*Lacerta agilis*). *J. Evol. Biol.* **9**, 229–242.
- Redhead, T. D. 1979 On the demography of *Rattus sordidus colletti* in monsoonal Australia. *Aust. J. Ecol.* **4**, 115–136.
- Roff, D. A. 1992 *The evolution of life histories*. New York: Chapman & Hall.
- Schluter, D. 1988 Estimating the form of natural selection on a quantitative trait. *Evolution* **42**, 849–861.
- Shine, R. 1978 Propagule size and parental care: the 'safe harbor' hypothesis. *J. Theor. Biol.* **75**, 417–424.
- Shine, R. 1988 Parental care in reptiles. In *Biology of the Reptilia*, vol. 16 (ed. C. Gans & R. B. Huey), pp. 275–330. New York: Alan R. Liss, Inc.
- Shine, R. & Madsen, T. 1997 Prey abundance and predator reproduction: rats and pythons on a tropical Australian floodplain. *Ecology* **78**, 1078–1086.
- Sinervo, B. & Doughty, P. 1996 Interactive effects of offspring size and timing of reproduction on offspring reproduction: experimental, maternal, and quantitative genetic aspects. *Evolution* **50**, 1314–1327.
- Sinervo, B. & Huey, R. B. 1990 Allometric engineering: an experimental test of the causes of interpopulational differences in locomotor performance. *Science* **248**, 1106–1109.
- Sinervo, B., Doughty, P., Huey, R. B. & Zamudio, K. 1992 Allometric engineering: a causal analysis of natural selection on offspring size. *Science* **258**, 1927–1930.
- Smith, C. C. & Fretwell, S. D. 1974 The optimal balance between size and number of offspring. *Am. Nat.* **108**, 499–506.
- Spear, L. & Nur, N. 1994 Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. *J. Anim. Ecol.* **63**, 283–289.
- Stearns, S. C. 1976 Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51**, 3–47.
- Stearns, S. C. 1980 A new view of life-history evolution. *Oikos* **35**, 266–281.
- Svensson, E. 1997 Natural selection on avian breeding time: causality, fecundity-dependent, and fecundity-independent selection. *Evolution* **51**, 1276–1283.
- Volkl, W. 1989 Prey density and growth: factors limiting the hibernation success in neonate adders (*Vipera berus* L.) (Reptilia: Serpentes, Viperidae). *Zool. Anz.* **222**, 75–82.
- Winkler, D. W. & Wallin, K. 1987 Offspring size and number: a life history model linking effort per offspring and total effort. *Am. Nat.* **129**, 708–720.

