Low costs, high output: reproduction in an insular pit-viper (*Gloydius shedaoensis*, Viperidae) from north-eastern China

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Abstract

Current life-history paradigms predict that an organism's total reproductive output is determined by its intrinsic level of 'reproductive effort' (RE), interacting with local resource availability. In turn, RE is driven by 'costs of reproduction'. Within the total allocation, selective forces on offspring size ultimately determine both the number and size of offspring (because of a trade-off between these two traits). Although patterns of life-history variation are broadly consistent with this scenario, the evidence is weak: it is generally difficult to measure 'costs' or selective forces on offspring size. To test this paradigm, we need a study organism which differs in these respects from related taxa, so that we can unequivocally generate predictions about life-history traits. A remarkable island population of Asian pit-vipers *Gloydius shedaoensis* was studied for which (unlike mainland conspecifics) 'costs of reproduction' are low, food availability is high, and there is intense selection for large offspring size. Maternal body sizes and condition, and offspring numbers and sizes were quantified for 79 litters over 2 years. As predicted, the snakes display high reproductive output per female (relative to maternal body mass, litter mass is about twice as high as in related taxa), large offspring size (about three times the mass of related taxa) and a strong trade-off between offspring size and litter size. Reproductive output was only weakly correlated with maternal body size, and output was adjusted mostly by manipulating litter size rather than offspring size. Reproductive output varied between years, but maternal body condition after parturition did not. Measures of reproductive output (such as the mass or energy content of the litter) bear little relationship to 'costs of reproduction' in this system.

Key words: cost of reproduction, life-history, reptile, reproductive effort, snake, *Gloydius shedaoensis*

INTRODUCTION

Organisms display extraordinary diversity in reproductive output, both in absolute terms (e.g. litter mass) and also in the way in which that reproductive output is partitioned into a few large offspring *vs* many small offspring (e.g. Roff, 1992). Part of this variation in reproductive output is engendered by proximate variation in resource levels, but only within the broad patterns set by life-history adaptation (e.g. Seigel & Ford, 1987, 1991). Mathematical models suggest that an organism's allocation of resources to reproduction (*vs* maintenance, storage and growth) should be shaped by selection arising from 'costs of reproduction' (e.g. Williams, 1966; Shine & Schwarzkopf, 1992). Similarly, the evolution of offspring size should be sensitive to factors

that affect the probable viability consequences of offspring-size variation, such as the spectrum of prey sizes available to neonates (e.g. Nussbaum, 1981).

Unfortunately, these ideas are difficult to test in any rigorous fashion. Documenting patterns of reproductive output (e.g. litter sizes, offspring sizes, reproductive timing) in wild populations is relatively straightforward, but comparing variation in these traits to variation in putative selective forces is more difficult. The measurement of selective intensities is far from simple, especially given strong spatial and temporal variation in such processes, and complications arising from inter-relations among traits (e.g. Arnold, 1986; Endler, 1986). Because of these logistical problems, current paradigms in the evolution of reproductive output have relatively weak empirical support. Is it really true that total reproductive output by an organism is determined by some intrinsic level of 'reproductive effort' (RE), in combination with local resource availability? In turn, has that

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level of RE evolved in response to 'costs of reproduction', i.e. the degree to which investment in current reproduction will compromise the organism's reproductive output in future seasons (Williams, 1966)? Given some finite sum of resource allocation to reproduction, how should that amount be divided – into a few large offspring or many small ones? Theory suggests that the effects of body size on offspring viability will drive this trade-off such that, mean litter sizes will be secondary consequences of selection for optimal offspring size (e.g. Roff, 1992).

These problems are not intractable, but require the use of appropriate study systems. To clarify the ways in which selective forces have modified reproductive traits, systems that are exposed to strong and clearly identifiable selective pressures on reproductive output can be chosen. The three most important parameters in this respect are the magnitude of reproductive 'costs', the level of local resource availability, and the intensity of selection on offspring size. All are difficult to quantify. However, precise quantification may not be needed. If we can find a study system in which these parameters adopt extreme values very different from those experienced by closely-related taxa, strong qualitative predictions about the ways in which reproductive output in such a system will differ from that in 'normal' situations can be made. In the present paper, data are provided on a system that fulfils these conditions.

Pit-vipers were studied on a small island (Shedao) in north-eastern China. The island lies on a major migration route for passerine birds that spend summer in northern Asia, and hence is a 'stepping-stone' for migrant birds in both spring and autumn. Pit-vipers of the genus *Gloydius* (= *Agkistrodon* of earlier workers: see Parkinson, Moody & Ahlquist, 1997) live in high densities on the island, and feed almost exclusively on these migrating birds (Koba, 1938; Gloyd & Conant, 1990; Li, 1995). The island does not contain any significant predators on the snakes (Li, 1995). Thus, compared to mainland conspecifics, the Shedao pit-vipers are exposed to a very different schedule of selective forces. Massive numbers of prey items are available, albeit only briefly (twice each year, for *c.* 4 weeks each time: De Schauensee, 1984). Predation risk of gravid females is reduced, probably to zero. Gestation occurs during a season when birds are not available, so there is no conflict between reproduction and feeding (e.g. Shine, 1980). In combination, the high prey availability and low 'costs' probably favour high reproductive output. The large body size of prey is expected to provide strong selection for increased offspring size (and thus, decreased litter size: Seigel & Ford, 1987; King, 1993) in this gape-limited predator. Lastly, year-to-year variation in the numbers of migrating birds (because of weather conditions) will generate annual variation in resource availability, enabling us to compare patterns of reproductive output in 'good' and 'bad' years.

Shedao (or 'snake island': *she* = snake; *dao* = island) has been the focus of a major research and conservation effort by Chinese scientists for > 20 years (e.g. Li, 1995). In the course of those studies, Sun, Zhao & Tang gathered data on reproductive output of the endemic pit-vipers, and published a summary of their results in a Chinese journal (Sun, Zhao & Tang, 1993). The present paper analyses these data in more detail.

MATERIALS AND METHODS

Study species and area

Shedao is a small (0.73 km^2) steep-sided rocky island in the Bohai Sea 10 km off the coast of Liaoding Peninsula in north-eastern China (38°57′N, 120°59′E). Details of the island environment and the snakes are given by Li (1995). Monthly mean air temperatures range from -8 °C in January to 26 °C in August. Most of the island is covered in shrubs and bushes. The reptile fauna of the island consists of a single species of pit-viper, *Gloydius s. shedaoensis* (Zhao, 1979), closely related to other *Gloydius* populations in mainland China (Parkinson *et al.*, 1997). Migrating passerine birds visit the island in spring (May) and autumn (September), and provide the main food for the snakes. Examination of gut contents has also detected occasional predation on small rodents and centipedes (Li, 1995). The snakes ambush birds from shrubs and the ground. Activity of the pit-vipers is strongly seasonal, with little activity outside the times when birds are present (Huang, 1984, 1989). Females are viviparous, producing young about once every 4 years (Li, 1995). Mark–recapture studies reveal a population of *c.* 10 000–20 000 snakes on this small island (Huang, 1984; L.-X. Sun, pers. obs.).

Methods

In 1990 and 1991, gravid snakes were captured by hand on 20 August, weighed and measured (snout–vent length (SVL) and tail length), and then placed individually in outdoor cages consisting of circular pots 30 cm in diameter and 30 cm high. The top of each pot was open, but covered with nylon mesh. The cages were placed in the shade and checked daily for evidence of parturition. Neonates were measured (total length) and weighed; it was not possible to determine sex of the offspring. Females were re-weighed < 24 h after parturition. Both the mothers and their offspring were then released.

Data were checked for normality before analysis. Because most patterns were similar among years, regressions based on the entire data set (i.e. combining the 2 years) are reported. However, data are shown separately for each year in the Figures and in Table 1. Statistical analyses of between-year differences are given at the end of Results.

Table 1. Year-to-year variation in traits associated with reproductive output in Shedao pit-vipers *Gloydius shedaoensis*; mean values (SD). Body-condition scores are residual values from the general linear regression of ln-transformed mass *vs* snout–vent length. Relative clutch mass was calculated as the female's mass loss at parturition, divided by her post-partum body mass. The statistical significance of differences between 1990 and 1991 was assessed using one-factor ANOVA. Bold, $P < 0.05$

Trait	1990	1991	Statistical test
Female total body length	71.54 (5.34)	72.42 (4.25)	$F_{1,74} = 0.64$, $P = 0.43$
Female snout–vent length	62.60 (4.96)	64.24 (3.73)	$F_{1,74} = 2.76$, $P = 0.10$
Female condition pre-partum	0.06 (0.13)	−0.06 (0.14)	**$F_{1,74} = 15.49$, $P = 0.0002$**
Female condition post-partum	0.02 (0.13	−0.02 (0.13)	$F_{1,74} = 2.13$, $P = 0.15$
Relative clutch mass	0.88 (0.18)	0.74 (0.20)	**$F_{1,74} = 10.11$, $P = 0.002$**
No. of live offspring	4.66 (1.30)	3.95 (1.29)	**$F_{1,74} = 5.70$, $P = 0.02$**
Proportion of stillborn offspring	0.05 (0.10)	0.03 (0.08)	$F_{1,74} = 1.31$, $P = 0.26$
Neonate total body length	26.34 (0.90)	26.98 (0.99)	**$F_{1,74} = 8.64$, $P = 0.004$**
Neonate mass	14.18 (2.10)	13.73 (1.94)	$F_{1,74} = 0.28$, $P = 0.60$
Date of birth (days from 1 Sep)	23.17 (11.12)	11.35 (6.67)	**$F_{1,74} = 33.52$, $P = 0.0001$**

RESULTS

Data were obtained on 79 litters: 39 in 1990 and 40 in 1991. Table 1 shows mean values for relevant traits in both years, and the results of statistical comparisons between years. Overall (combining data from both years), the female snakes averaged 63.4 cm SVL, and weighed an average of 220 g pre-partum and 124 g post-partum. They gave birth to an average of 4.2 live neonates plus 0.2 stillborn offspring per litter. Most females gave birth in September, but earlier in 1991 than in 1990 (Table 1). Our analysis focuses on inter-relationships among traits such as maternal size, maternal body condition, offspring size and offspring number, and on the ways in which these traits (and the relationships among them) differed between the 2 years of our study. Air temperatures measured on the island were slightly higher in 1991 than in 1990 (based on daily records of minima and maxima, mean air temperatures in
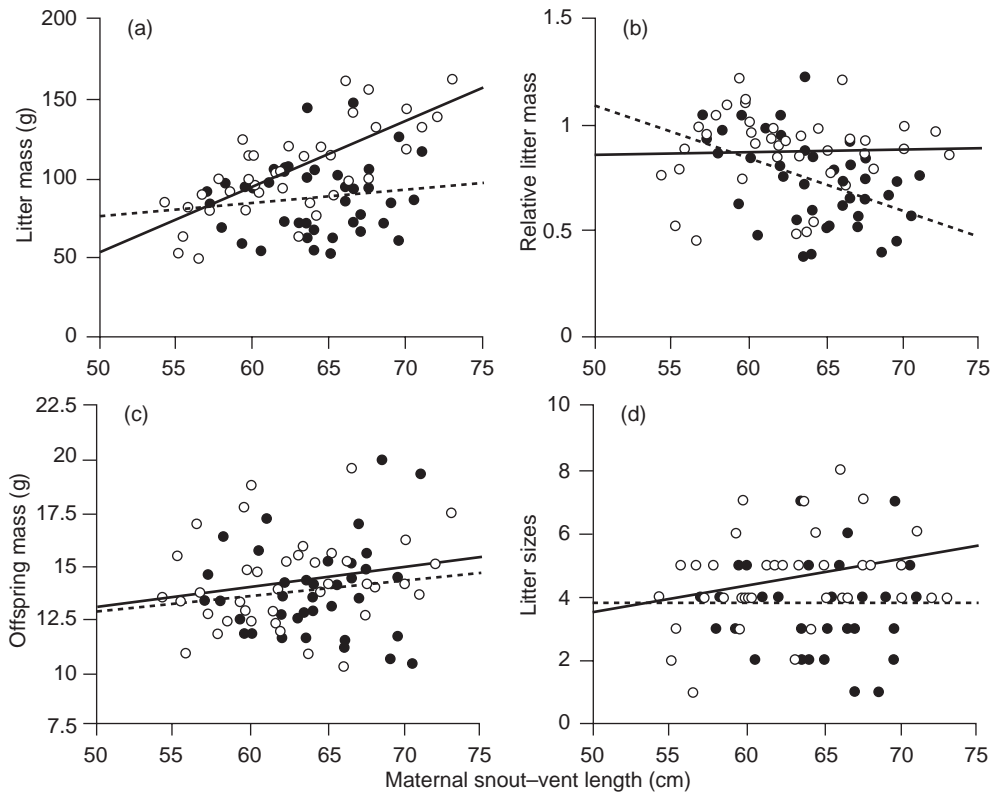

Fig. 1. Reproductive output of Shedao pit-vipers *Gloydius shedaoensis* relative to maternal body size. Compared to small females, larger individuals produced a greater total mass of offspring (a), but a lower mass relative to their own carcass (post-partum) mass (b). Larger females also tended to produce larger offspring (c), but litter sizes did not increase with maternal body size (d). Each data point represents one litter. See text for statistical analyses. ○, data from 1990; ●, data from 1991; solid line, least-squares regression fitted to 1990 data; dotted line, regression from the 1991 data.
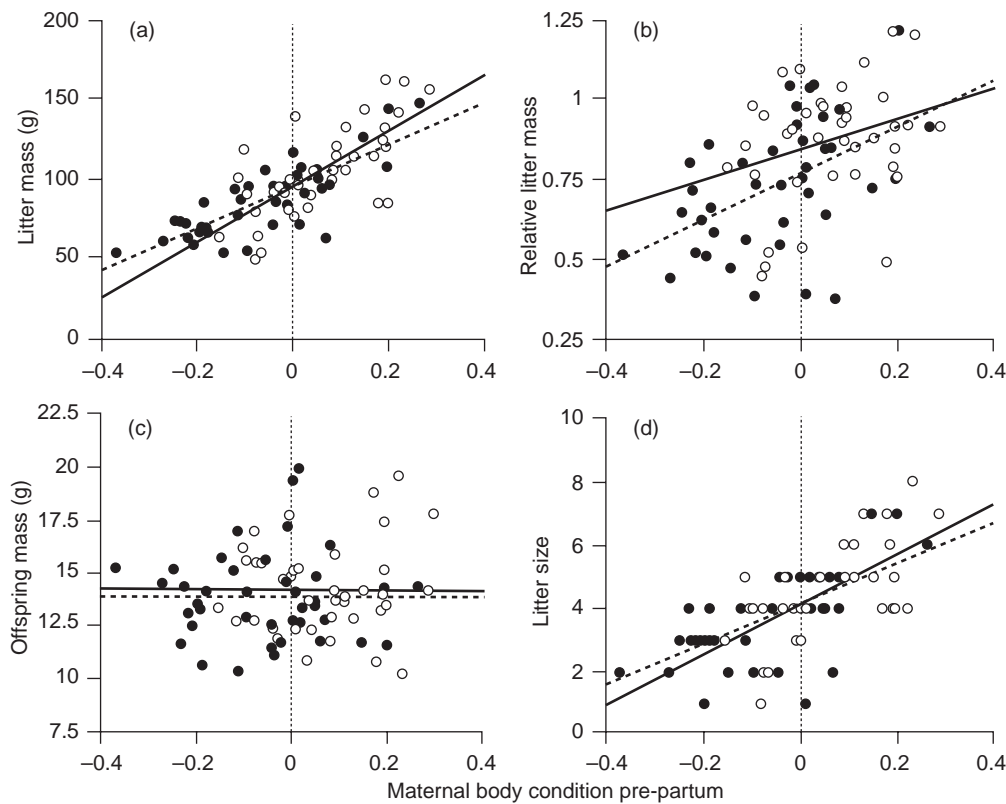
Fig. 2. Reproductive output of Shedao pit-vipers *Gloydius shedaoensis* relative to the body condition of gravid females (residual scores of ln pre-partum mass *vs* snout–vent length). Females that were heavier-bodied before parturition produced a greater total mass of offspring (a), a greater mass relative to their own carcass (post-partum) mass (b), and a greater number of offspring (d). However, the mass of individual offspring was not significantly correlated with maternal pre-partum body condition (c). Each data point represents one litter. See text for statistical analyses. ○, data from 1990; ●, data from 1991; solid line, least-squares regression fitted to 1990 data; dotted line, regression from the 1991 data.

1990–91 averaged 14.9–15.5 °C in May; 20.2–21.0 °C in June; 23.7–24.1 °C in July; 24.8–24.8 °C in August; and 20.3–20.6 °C in September).

Influences on total reproductive output

First, we consider factors that correlate with (and hence, may influence) a female viper's total expenditure on reproduction. The simplest measure of output is total litter mass, but difficulties in comparing output across females with a wide range of body sizes have stimulated many workers to use a size-corrected measure of output: relative clutch mass (RCM: e.g. Seigel & Fitch, 1984). We calculated RCM as the mass lost at parturition divided by the female's post-partum mass.

Published studies on snakes have generally revealed a strong influence of maternal body size on reproductive output (e.g. Seigel & Ford, 1987), so this relationship was examined within *G. shedaoensis*. Analysis shows that both of our measures of reproductive output were related to maternal body size, but in different ways. Larger females produced a greater total mass of offspring, but litter mass relative to maternal body mass actually decreased in larger animals (Fig. 1). In both cases, these relationships were statistically significant (for total litter mass *vs* SVL, $n = 79$, $r = 0.41$, $P = 0.0002$; for RCM *vs* SVL, $n = 79$, $r = -0.25$, $P = 0.03$).

Females may differ in the magnitude of their energy reserves, as well as in body size (length). Plausibly, females in better condition might be able to produce more offspring. We have no measure of maternal energy resources before ovulation, but can use maternal body condition near the end of gestation as an index of this parameter. Because a female cannot feed during pregnancy (there are no birds during this period), her condition late in gestation (residual score from the general linear regression of log-transformed pre-partum mass against SVL) should provide an approximate measure of the total resources that she accumulated before ovulation. In both years of the study, females in better-than-average body condition before parturition produced larger-than-average litter masses, and had larger-than-average RCMs (Fig. 2a,b; total litter mass *vs* maternal pre-partum condition, $n = 79$, $r = 0.77$, $P = 0.0001$; for RCM *vs* maternal pre-partum condition, $n = 79$, $r = 0.49$, $P = 0.0001$). However, much of the mass contributing to high 'maternal condition' is actually composed of the litter, and thus a strong relationship between these variables would be expected.
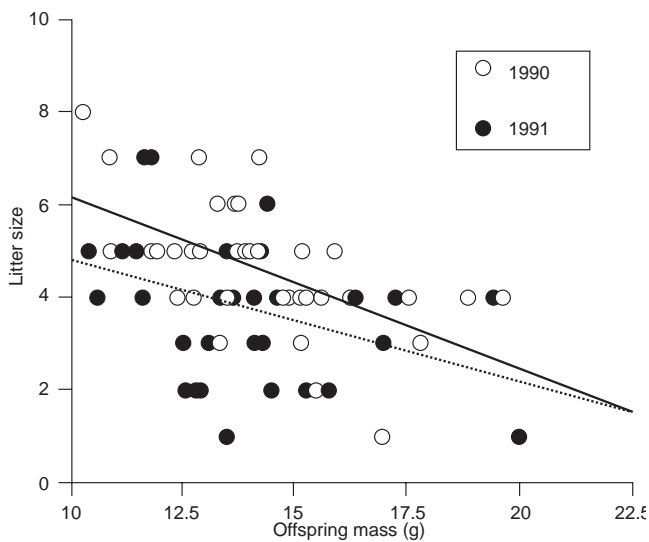
Fig. 3. The trade-off between litter size and offspring size in Shedao pit-vipers *Gloydius shedaoensis*. Each data point represents one litter. See text for statistical analyses. ○, data from 1990; ●, data from 1991; solid line, least-squares regression fitted to 1990 data; dotted line, regression from the 1991 data. See text for statistical analyses.

Influences on litter size and offspring size

Given a finite investment into the litter, a trade-off between the number and size of offspring is expected, i.e. a fixed amount of energy can be partitioned into either a few large offspring or many small ones. Our data provide clear evidence of such a trade-off in *G. shedaoensis*: larger litters consisted of smaller offspring ($n = 79$, $r = -0.44$, $P = 0.0001$; Fig. 3).

This trade-off had more effect on litter sizes and offspring sizes than did maternal body size or condition. Maternal body size was not significantly correlated with either offspring size ($n = 79$, $r = 0.16$, $P = 0.16$; Fig. 1c) or litter size ($n = 79$, $r = 0.10$, $P = 0.38$; Fig. 1d). Females with higher body-condition indices before parturition gave birth to more offspring ($n = 79$, $r = 0.66$, $P = 0.0001$; Fig. 2d), but mean neonatal mass was not significantly correlated with maternal body condition before parturition ($n = 79$, $r = 0.03$, $P = 0.78$; see Fig. 2c).

Because of the complex inter-relationships among maternal body size, maternal body condition, offspring size and litter size (Figs 1–3), however, univariate tests may fail to disentangle causal relationships. Multivariate path analysis is well-suited to such data sets, because it can clarify indirect as well as direct causal connections (e.g. King, 1993). Path coefficients (standardized partial-regression coefficients) can be used to predict the amount of change in a dependent variable (in units of standard deviations of that variable) caused by a change of one standard deviation in another (independent) variable. A simple path diagram incorporating the following links was used: (1) maternal SVL and body condition can affect both litter size and offspring size; (2) litter size can affect offspring size

(because litter size is determined before offspring size in the process of female reproduction in snakes: King, 1993); (3) all four of these traits affect RCM; (4) a female viper's body condition after parturition is affected by her condition before giving birth, as well as by her RCM (Fig. 4). Path coefficients were calculated separately from the data gathered in each year of the study. The coefficients were similar in these two analyses (Fig. 4), despite differences between years in mean values of some traits (Table 1).

The path analysis supports the conclusion (above) that female SVL had little influence on reproductive output. Instead, female condition pre-partum was a significant predictor of offspring size as well as offspring number (Fig. 4). The influence of maternal condition on offspring size was not evident in the univariate analyses (above, and see Fig. 2c), because of the strong negative trade-off between offspring size and offspring number. This trade-off is also evident in the path analysis (Fig. 4), but is incorporated into the multiple regressions for calculating path coefficients. Thus, the relationship between maternal body condition and offspring mass is revealed by the multivariate technique whereas it was masked in the univariate analysis.

The path analysis also suggests that variation in RCM may be driven primarily by variation in litter sizes. In turn, a female's body condition after parturition was influenced equally (although in opposite directions) by her prior body condition and her reproductive expenditure (Fig. 4). Overall, a female pit-viper's reproductive output was more highly correlated with her body condition than with her body size.

Timing of parturition

Traits such as litter size and offspring size may be linked to the seasonal timing of reproduction (e.g. Weatherhead *et al.*, 1999). Both effects are seen in the Shedao pit-vipers. Average offspring mass (but not body length) was larger for litters born later in the year (Fig. 5; for offspring mass, $n = 79$, $r = 0.34$, $P = 0.002$; for length, $n = 79$, $r = -0.01$, $P = 0.95$). Females that gave birth relatively early in the year also tended to produce larger litters. The correlation between order of the litter and number of offspring was highly significant in 1991 ($n = 40$, $r = -0.47$, $P = 0.002$) but not in 1990 ($n = 38$, $r = -0.12$, $P = 0.49$; see Fig. 5).

Costs of reproduction

Maternal body condition after parturition may provide an index of a female's ability to survive a long period without feeding (e.g. Madsen & Shine, 1993). What factors determine the body condition of a post-parturient female Shedao pit-viper? Females with higher-than-average RCMs were thinner-than-average after giving birth (RCM *vs* condition, $n = 79$, $r = -0.35$, $P = 0.002$; see Fig. 6a). Maternal body condition after
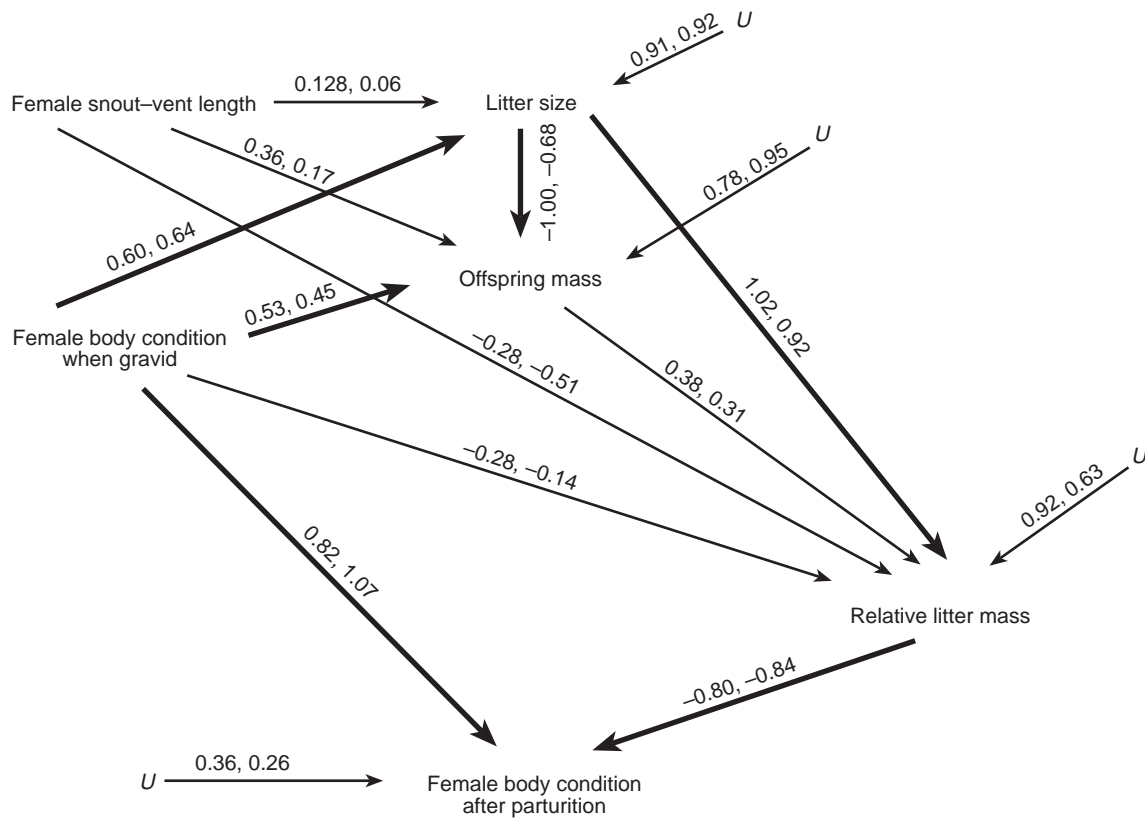
Fig. 4. Path analysis of reproductive output in Shedao pit-vipers *Gloydius shedaoensis*. Two path coefficients are given for each pathway; the first is based on analyses for 1990 data and the second for analyses on 1991 data. All pathways have *P* values < 0.05. The proportion of unexplained variance (U) is calculated as described in King (1993). Pathways with high values are shown in thicker lines.

parturition was not significantly correlated with total litter mass ($n = 79$, $r = 0.12$, $P = 0.30$; see Fig. 6b), litter size ($n = 79$, $r = 0.07$, $P = 0.56$; Fig. 6c) or mean offspring mass ($n = 79$, $r = 0.13$, $P = 0.26$; Fig. 6d).

Annual variation in reproductive traits

Many of the traits that we studied differed significantly in mean values between the 2 years (Table 1). Females were similar in overall body length, but were in better physical condition (i.e. weighed more relative to SVL) in 1990 than in 1991. This result is tested using residual scores in Table 1, for comparability with the other variables tested. A more robust test involves one-factor ANCOVA with year as the factor, SVL as the covariate and log mass as the dependent variable. This test confirms that pre-partum mass relative to SVL was higher in 1990 than in 1991 (slopes equivalent $F_{1,72} = 1.71$, $P = 0.19$, but intercepts differ $F_{1,73} = 15.52$, $P = 0.0002$). Maternal body condition post-partum did not differ between the 2 years in tests using either residual scores (Table 1) or one-factor ANCOVA (same design as above; slopes equivalent $F_{1,72} = 0.12$, $P = 0.73$, intercepts $F_{1,73} = 2.36$, $P = 0.13$).

For offspring traits, the comparisons between years in Table 1 were based on mean values per litter. A more robust statistical approach for this comparison is to use nested ANOVA, with factors being year, and female ID no. nested within year. Then, differences between years can be tested against the nested factor rather than against the residual error term (Sokal & Rohlf, 1981). As before, the more sophisticated analysis generates the same result as the simpler one in Table 1. Samples from the 2 years did not differ in mean offspring mass ($F_{1,77} = 0.27$, $P = 0.60$), but differed in neonatal total body length ($F_{1,77} = 6.82$, $P = 0.01$) and body shape (residual scores from log mass relative to length: $F_{1,77} = 12.27$, $P = 0.001$).

As well as examining the shifts in mean values of traits between years, the relationships among traits documented in the above analyses can be examined. Relationships among maternal body size, body condition, offspring size, and offspring number remained fairly similar between years (see coefficients in Fig. 4), but in four cases relationships among traits differed between 1990 and 1991.

(1) *The relationship between female body length and reproductive output*. ANCOVA (with year as the factor, female SVL as the covariate and RCM as the dependent variable) confirms that RCM decreased in larger females in both years, but the rate of this decrease was greater in 1991 than in 1990 (slopes $F_{1,72} = 4.15$, $P = 0.045$; see Fig. 1b). Similarly, total litter mass was
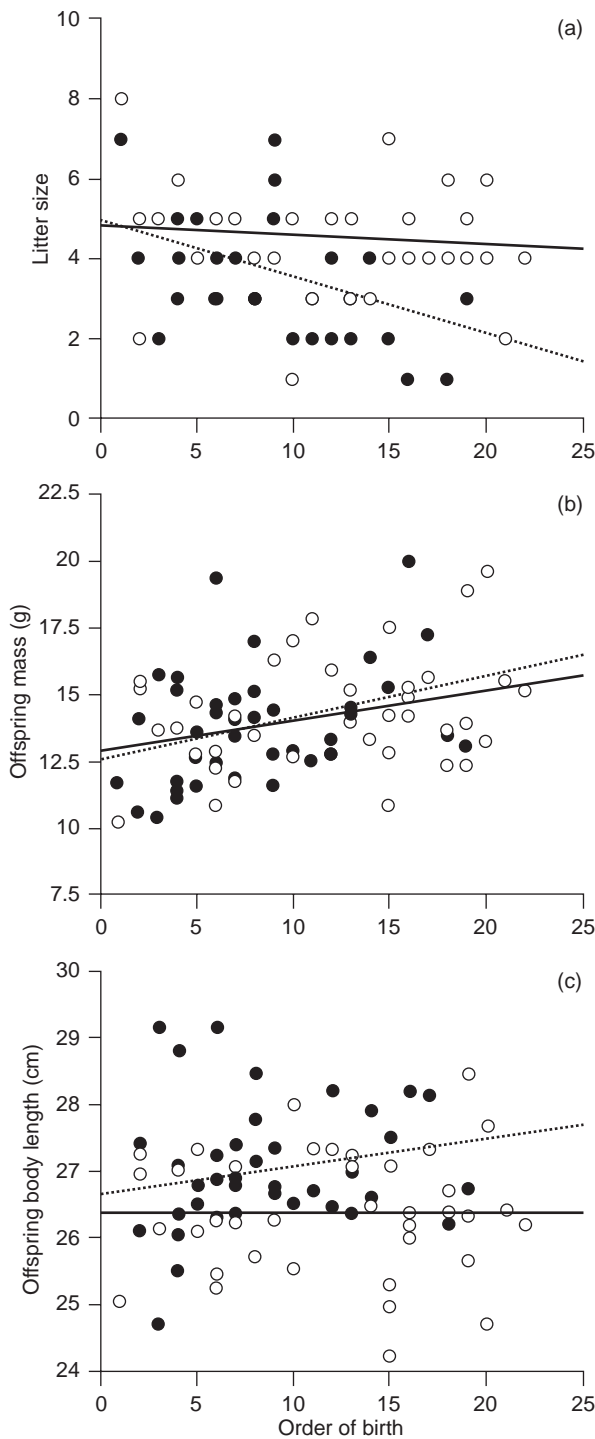
Fig. 5. The temporal order in which parturition occurred in Shedao pit-vipers *Gloydius shedaoensis*, compared to (a) the number of offspring per litter, (b) the mean mass of offspring in each litter, and (c) the mean body length of those offspring. Each data point represents one litter. Open circles show data from 1990, dots show data from 1991. Solid line shows least-squares regression fitted to 1990 data; dotted line shows regression from the 1991 data. See text for statistical analyses.

higher for larger females in both years, but increased more rapidly with increasing SVL in 1990 than in 1991 (slopes $F_{1,75} = 8.11$, $P = 0.006$);

(2) *The trade-off between litter size and offspring size.* In both years of the study, larger litters consisted of smaller offspring (Fig. 3). ANCOVA (with year as the factor, number of offspring as the covariate, and mean offspring mass as the dependent variable) detected a difference between years in the position of this trade-off line. The trade-off was present in both years, but for any given offspring mass, litter sizes were larger in 1990 than in 1991 (slopes equivalent $F_{1,75} = 0.56$, $P = 0.46$, but intercepts differ $F_{1,76} = 4.33$, $P = 0.048$);

(3) *Costs of reproduction.* Females with high RCMs tended to be very heavy-bodied before giving birth, and very thin after giving birth (see Figs 2b & 6a). ANCOVA (with year as the factor, RCM as the covariate, and maternal body condition score as the dependent variable) showed that the 2 years differed in the relationships between RCM and maternal condition both pre-partum and post-partum. For any given RCM, females were heavier-bodied in 1990 than in 1991. This was true for condition pre-partum (slopes equivalent $F_{1,75} = 1.34$, $P = 0.25$, but intercepts differ $F_{1,76} = 7.30$, $P = 0.01$; Fig. 2b), as well as post-partum (slopes equivalent $F_{1,75} = 2.01$, $P = 0.16$, but intercepts differ $F_{1,76} = 17.68$, $P = 0.0001$; Fig. 6a);

(4) *Timing of reproduction vs litter size.* As noted above, litters produced earlier in the year were larger, in 1991 but not 1990. A heterogeneity of slopes test confirms the statistical significance of this difference between years (year as the factor, order of birth as the covariate, litter size as the dependent variable: $F_{1,75} = 3.99$, $P = 0.049$).

DISCUSSION

The ecological context for reproduction in *G. shedaoensis* is very different from that experienced by most snakes, and indeed from that experienced by closely-related taxa on the Chinese mainland. The primary differences relevant to reproductive output are that food is abundant, 'costs' of reproduction are minimal, and there is intense selection for large off-spring size.

(1) *Abundant food.* During the main bird-migration periods, food is super-abundant on the island. Thousands of birds arrive on Shedao each week, and many snakes feed every day (based on palpation of multiple prey items from recently captured animals: Li, 1995; R. Shine, pers. obs.). Because food intake influences reproductive output (e.g. Andren, 1982; Ford & Seigel, 1989), we predict high litter masses and RCMs in the Shedao pit-vipers.

(2) *Low 'costs' of pregnancy.* These 'costs' are low, for three reasons:

(i) Predators of adult snakes are absent from Shedao (Li, 1995), so that lowered mobility of reproductive females will not increase their vulnerability (Shine, 1980; Seigel, Huggins & Ford, 1987).

(ii) The snakes on Shedao are active only during the seasons of bird migration; they remain under cover
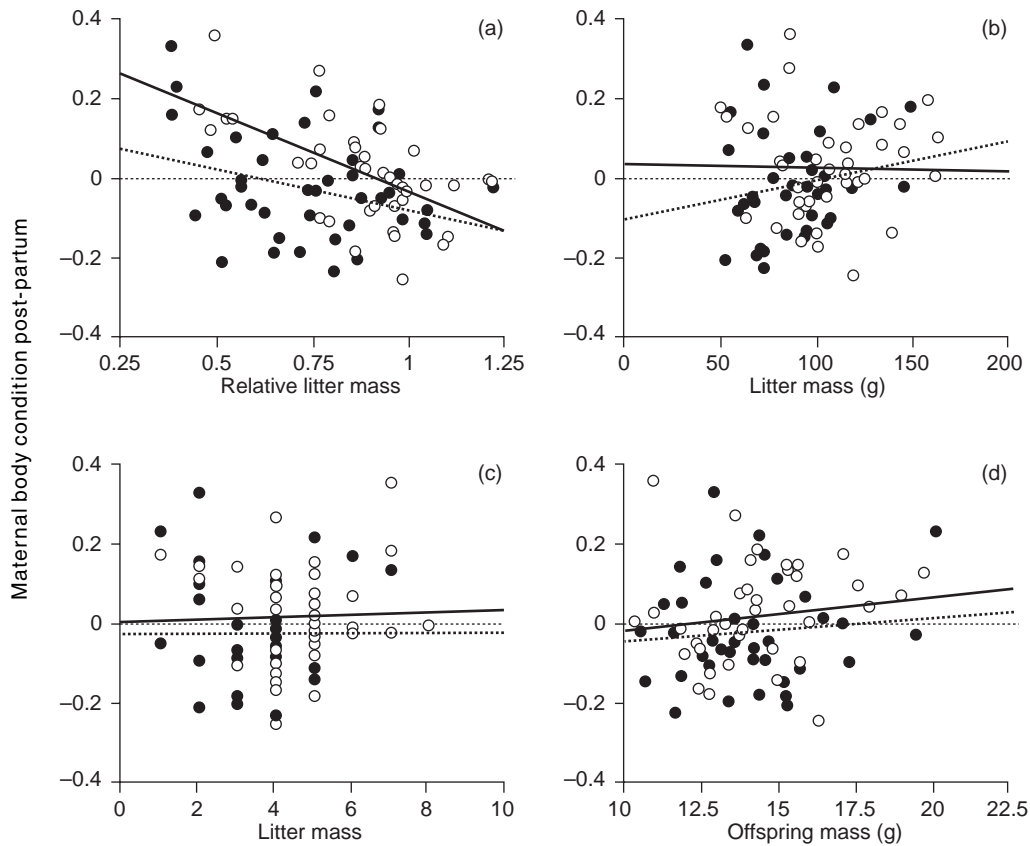
Fig. 6. Body condition of female Shedao pit-vipers *Gloydius shedaoensis* following parturition (residual scores of ln post-partum mass *vs* snout–vent length) was lower for females with high RCMs (a), but was not significantly correlated with the animal's total litter mass (b), litter size (c) or mean offspring size (d). Each data point represents one litter. ○, data from 1990; ●, data from 1991; solid line, least-squares regression fitted to 1990 data; dotted line, regression from the 1991 data. See text for statistical analyses.

throughout the (bird-less) summer (e.g. Li, 1995). Thus, gestation does not reduce food intake, because non-reproductive animals also do not feed at this time of year. Hence, the 'opportunity cost' of reproduction (the decrement in food intake of reproductive snakes compared to that of non-reproductive conspecifics) will be trivial.

(iii) In other snake species, females that are emaciated after parturition may be unlikely to survive: they die either of starvation (depletion of energy reserves) or because predators kill them as soon as they begin to move about and forage (e.g. Madsen & Shine, 1993; Luiselli, Capula & Shine, 1996). This major 'cost' is not experienced by the Shedao snakes. First, the major peak of bird migration occurs in September–October, immediately after the female pit-vipers have given birth. They thus have the opportunity to rapidly recoup their energy stores. Second, the females do not need to expend energy in order to forage: they simply wait in ambush for the birds to arrive (e.g. Li, 1995).

(3) *Selection for larger body size of neonates*. Most prey items are large relative to snake size, so that gape-limitation restricts feeding rate. The snakes often seize but fail to ingest relatively large birds; snakes < 24 cm SVL cannot swallow even the smallest passerine species

(Li, 1995; pers. obs.). Neonatal snakes thus feed primarily on centipedes, which are more difficult to capture, and have less nutritional value, than avian prey items (Li, 1995). Also, larger body size may enhance neonatal survival probabilities by enabling the young snakes to withstand prolonged starvation. In keeping with this idea, eight experimentally starved neonatal *G. shedaoensis* survived for an average of 274 days (Wu, 1977).

These three characteristics should favour the evolution of distinctive patterns in reproductive output, as follows.

(1) *Abundant food*. Overall levels of reproductive output should be higher than in most other snakes.

(2) *Low 'costs' of pregnancy*. These should reduce selection against high levels of output. There should be less selection against low output also, because reproduction does not entail fixed (fecundity-independent) costs (Naulleau & Bonnet, 1996). We might expect highly variable litter sizes and RCMs in the Shedao snakes, with little correlation between female body size and fecundity.

(3) *Selection for larger body size of neonates*. We expect intense selection for increased offspring size in Shedao, relative to mainland pit-viper populations that

are exposed to a wider range of potential prey types and sizes.

A comparison of our results with published literature on snake reproduction provides broad support for these predictions.

Total reproductive output. Shedao pit-vipers produce a remarkably large litter relative to maternal mass, compared to other snake species of similar adult body size. The relative litter mass of snakes in our sample averaged 80% of maternal carcass mass, compared to a mean of 39% in other viviparous snakes (Seigel & Fitch, 1984; note that these authors included litter mass in the numerator as well as the denominator, so their values have been converted to be consistent with our method of calculating RCM). Values for 14 samples of viviparous viperid species in their review ranged from 16% to 71%, all less than *G. shedaoensis*. More recent studies on viviparous viperids also report lower RCMs than those shown by the Shedao pit-vipers; for example, non-gravid female *Crotalus horridus* weighed 60% less than gravid individuals (Brown, 1991); *Sistrurus miliarius* lost an average of 45% of their pre-birth mass at parturition (Farrell, May & Pilgrim, 1995), and females in two populations of *Crotalus viridis* had average RCMs of 37% and 42% (Macartney & Gregory, 1988). These comparisons suggest that RCM is substantially higher in *G. shedaoensis* than in most other snakes.

Based on low costs of reproduction, we predicted that Shedao pit-vipers would show variable, as well as high, levels of reproductive investment (above). Our data confirm high variation in RCMs (range = 0.37–1.22). The coefficient of variation (CV) of RCM for *G. shedaoensis* averaged 26.2 (21.6 in 1990, 28.5 in 1991). Only a few published data sets on viviparous viperid snakes are available for comparison. For the copperhead *Agkistrodon contortrix*, CVs calculated each year over a 5-year period averaged 13.7 (range from 8.0 to 23.9: Seigel & Fitch, 1984). For the western rattlesnake *Crotalus viridis*, CV averaged 16.2 (Macartney & Gregory, 1988). The European adder *Vipera berus* had a low CV of RCMs in a year when prey were plentiful (11.4) but a high CV when prey were scarce (36.1; Andren & Nilson, 1983); a highly inbred population of this species also showed a high CV (33.3; Madsen & Shine, 1993). More data are needed to see if *G. shedaoensis* is indeed distinctive in its degree of variation in RCM.

Our analyses help to identify some of the factors that generate variation in RCMs. Maternal body size was not important in this respect (Fig. 4). Studies on other snakes have generally found that RCMs remain fairly constant across a wide range of maternal SVLs (e.g. Seigel & Ford, 1987), but some exceptions do occur. For example, RCMs decreased with increasing maternal body size in 1 of 2 years within European adders *Vipera berus* (Andren & Nilson, 1983), as in the Chinese pit-vipers. However, the opposite pattern was detected in the European colubrid *Coronella austriaca* (Luiselli *et al.*, 1996).

Offspring size. Neonatal body size is also distinctive

in the snakes from Shedao. Most Asian *Gloydius* species produce small offspring, averaging 15–23 cm long and weighing 5–10 g (based on 13 taxa reviewed by Gloyd & Conant, 1990). Studies on a mainland population of *G. shedaoensis* reveal a similar situation (mean offspring mass 5 to 6 g: J.-L. Li, pers. comm.). In contrast, the offspring of our island population of *G. shedaoensis* averaged 26 cm and 14 g (Table 1). A similar shift to fewer larger offspring may be common in island populations of snakes (Wharton, 1966).

Relationships between maternal attributes (such as size and condition) and offspring attributes (such as body length, mass and date of parturition) display considerable interspecific and intraspecific variation within snakes (e.g. Madsen & Shine, 1992; King, 1993; Farrell *et al.*, 1995; Weatherhead *et al.*, 1999). Given the high intercorrelations among traits, the causes of such diversity are difficult to identify. Several of the trends seen in *G. shedaoensis* mirror those reported for other snake species. For example, females of larger size, in better body condition, tend to produce larger offspring. This result holds true for North American cottonmouth moccasins (Blem, 1981) and watersnakes *Nerodia sipedon* (Weatherhead *et al.*, 1999), and the same (albeit not statistically significant) trend was seen in European adders (Andren & Nilson, 1983) and smooth snakes (Luiselli *et al.*, 1996). The exact reverse (larger females and females in better condition produce smaller not larger offspring) was seen in the North American colubrid *Storeria dekayi*, because of a strong trade-off between litter size and offspring size (King, 1993).

Neonatal *G. shedaoensis* born later in the year tended to be larger (heavier but not longer-bodied) than those born earlier (Fig. 5). Earlier parturition may provide the opportunity for neonates to feed before winter. Offspring born later may have less opportunity, and thus may benefit from larger energy reserves. In practice, such ideas are difficult to test in any rigorous way: in snakes as in other animals, detailed analyses reveal complex relationships between reproductive seasonality and other traits (e.g. Olsson & Shine, 1977*b*; Newton & Marquiss, 1984; Madsen & Shine, 1998). As in *G. shedaoensis*, larger litters are born earlier in *Storeria dekayi* (King, 1993), *Sistrurus miliarius* (Farrell *et al.*, 1995), and *Coronella austriaca* (Luiselli *et al.*, 1996). Local weather conditions can also influence the timing of parturition, with birth being delayed in cooler years (Blanchard & Blanchard, 1941).

Litter size. The large offspring mass of *G. shedaoensis* is associated with a relatively small mean litter size (mean = 4.2: see Table 1), because of the strong tradeoff between these two traits (Figs 3 & 4). Other *Gloydius* species, although smaller than *G. shedaoensis*, typically produce approximately twice as many offspring per litter (average of seven to 10 offspring for 13 taxa reviewed by Gloyd & Conant, 1990). The same is true of mainland specimens of *G. shedaoensis* (mean = eight to nine offspring: J.-L. Li, pers. comm.). This difference in litter size is presumably not a direct target of selection, but an epiphenomenon of selection on offspring size. In

keeping with this inference, year-to-year variation in maternal body condition generated variation in mean litter size but not in mean offspring mass (Table 1).

A trade-off between offspring size and litter size is widespread in snakes, as in other kinds of animals, but is rarely so obvious as in *G. shedaoensis* (Fig. 3). In most previously studied snakes, the effect of maternal body size on litter size has to be removed statistically before the size–number trade-off is detectable (Madsen & Shine, 1992; King, 1993; Luiselli *et al.*, 1996). Even then, some species show no such trade-off (e.g. Farrell *et al.*, 1995). Because maternal body size has little influence on litter size in our island pit-vipers, allometric effects do not obscure the trade-off between offspring number and size. Interestingly, the position of the trade-off line between these two traits differed significantly between the 2 years of our study (Fig. 3; see statistical test above). Similar variation has been documented in lizards, and provides evidence that the trade-off is enforced by finite energy supply for the litter, rather than finite space within the maternal body cavity (Olsson & Shine, 1997*a*). This conclusion fits well with the weak relationship between body-size and reproductive output in the Shedao pit-vipers (Fig. 1).

Annual variation

Mean values for several reproductive traits differed between the 2 years of our study (Table 1). In the year when females were in higher body condition, the snakes produced larger litters, and heavier litters relative to their own body mass. Offspring were longer-bodied (especially in litters born early in the year) in this 'high maternal body condition' year, but mean offspring mass did not differ between years (Table 1).

As for many of the other issues discussed, comparison with other snake species reveals considerable diversity in responses to annual variation in food supply. Although it is generally true that fluctuations in resources generate fluctuations in reproductive output (e.g. Andren & Nilson, 1983; Seigel & Fitch, 1985), some species of snakes show little year-to-year variation in reproduction under such conditions (e.g. Plummer, 1983). Even when snakes respond, they may do so primarily by modifying the condition threshold for reproduction, rather than output per litter (Shine & Madsen, 1997; Madsen & Shine, 1999). Even when output per litter is modified, this can happen via changes in litter sizes, offspring sizes, or both (see above references). The complexity is well-illustrated by comparing our results on annual variation in offspring size with those of Weatherhead *et al.* (1999) from *Nerodia sipedon*. Their watersnakes showed significant annual variation in offspring mass but not body length, whereas we detected the opposite pattern (Table 1). It seems probable that actual measures of the influence of phenotypic traits on hatchling survival and growth will be needed, before we can understand the adaptive (or other) reasons behind these kinds of puzzling interspecific variations.

Costs of reproduction

Although average values for maternal pre-partum body condition and reproductive output varied between the 2 years of our study, maternal body condition after oviposition did not (Table 1). This latter trait may offer a valuable index of the snake's energy reserves, and thus her ability to tolerate prolonged starvation. In at least two other snake species, maternal body condition post-partum significantly influences a female's probability of surviving to reproduce again (Madsen & Shine, 1993; Luiselli *et al.*, 1996).

The exact level of reproductive output of our Shedao pit-vipers differed among years, without any corresponding change in the magnitude of 'costs' experienced by reproducing snakes. By any measure, female vipers devoted more resources (mass, energy) to reproduction in 1990 than they did in 1991 (Table 1), but we infer that the actual 'costs of reproduction' were similar (i.e. close to zero) in the 2 years. There is no evidence of differences between years in the additional risk due to pregnancy, the degree to which food intake was reduced due to pregnancy, or the degree to which a female's emaciated condition post-partum reduced her probability of surviving to the next feeding bout. There is a clear cautionary tale from these data. Year-to-year variation in resource availability can generate substantial variation in reproductive output, without any corresponding variation in the 'costs' experienced by reproducing animals (i.e. the degree to which current investment in reproduction reduces an individual's probable future reproductive output; Williams, 1966). Thus, we need to understand the ecological context of reproduction before using simple energy- or mass-based measures of reproductive effort as indices of 'costs' or 'reproductive effort'.

The main message from our analysis, however, is encouraging. In this unusual island system, with 'costs' and selective forces very different from those experienced by most snake taxa, the pit-vipers of Shedao display a series of novel features of reproduction (e.g. high output, large offspring size) that are in the directions predicted by current paradigms in life-history theory.

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