OIKOS 92: 297–308. Copenhagen 2001

Short-term versus long-term effects of food intake on reproductive output in a viviparous snake, *Vipera aspis*

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Bonnet, X., Naulleau, G., Shine, R. and Lourdais, O. 2001. Short-term versus long-term effects of food intake on reproductive output in a viviparous snake, *Vipera aspis*. – Oikos 92: 297–308.

Feeding rates influence reproductive output in many kinds of animals, but we need to understand the timescale of this influence before we can compare reproductive energy allocation to energy intake. A central issue is the extent to which reproduction is fuelled by long-term energy stores (''capital'' breeding) versus recently-acquired resources (''income'' breeding). Our data on free-living aspic vipers show that there is no simple answer to this question: reproductive frequency is determined by long-term energy stores, offspring size is influenced by maternal food intake immediately before ovulation, and litter size is influenced by both long-term stores and short-term energy acquisition. Thus, offspring size in free-living vipers reflects the mother's energy balance over the preceding year (via a trade-off between litter size and offspring size) as well as her energy balance in the current breeding season. Hence, different components of a given reproductive output (litter) are not only functionally linked, but also respond to different temporal scales of prey availability. A female's body size has little effect on her reproductive output. Attempts to quantify reproductive energy allocation must take into account the fact that different reproductive traits (such as offspring size versus number) may respond to energy availability over different timespans. Thus, although the aspic viper is a typical ''capital breeder'' in terms of its reliance on stored reserves for maternal ''decisions'' concerning reproductive frequency, it is to some degree a facultative ''income breeder'' with respect to the determination of offspring size and litter size.

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The relative allocation of resources between maintenance, growth, reproduction and storage is a central theme of studies on life-history evolution (e.g., Stearns 1989, 1992, Roff 1992), but we still cannot provide a convincing answer to R. A. Fisher's classic (1930) challenge: ''It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction''. Modelling these kinds of allocation decisions is a relatively straightforward task, and much has been accomplished in this respect (e.g., Charnov 1982). Measuring energy allocation among these pathways, in a form that is directly relevant to those life-history models, has proved to be a more challenging proposition. This is especially true for long-lived organisms living in places where food availability fluctuates on a seasonal or annual basis. Quantifying rates of food intake and various expenditures is logistically feasible, but simply measuring the magnitude of these pathways (although of interest in its own right) does not enable us to answer Fisher's question about the *mechanisms* of allocation. In order to answer the question, we need to

Accepted 17 September 2000

ISSN 0030-1299

understand how fluctuations in food supply influence allocation decisions by the organism.

One central problem in this respect involves the timescale at which those fluctuations occur. Attempts to quantify allocation pathways necessarily invoke a timescale for measurement: for example, we must compare energy gain to energy expenditure over some specified period of time. Clearly, the relevant timescale will differ among taxa: for example, it will be longer for an animal that stores energy for a long period before expending it on reproduction. The timescale will also differ among habitats: for example, it will be longer in a habitat with low food availability, where the animal must forage for longer to gain enough energy to initiate reproduction. Such difficulties may be overcome by choosing the appropriate timescale for the system in question. However, another complication may also arise, which is more difficult to address. For a given reproductive bout by a single animal, some aspects of reproductive output may be governed by energy availability over a long timescale whereas other aspects are determined by short-term energy intake. In this paper we document such a case: a female aspic viper's "decision" as to whether or not to reproduce, and how large a litter to produce, are largely governed by long-term energy stores; but her "decision" as to offspring size is driven by short-term rates of food intake. Unless we know about such relationships, we cannot meaningfully compare resource availability to reproductive output, or apply concepts such as "capital" versus "income" breeding to biological systems.

The division between "capital" and "income" breeders refers to the source of nutrients used to support reproductive expenditure (Drent and Daan 1980, Jönsson 1997). Income breeders drive these resources directly from food consumed during the reproductive season, whereas capital breeders derive these resources from reserves that are developed before the reproductive season. This concept has proved to be useful in studies on birds (e.g., Chastel et al. 1995), but has been rarely explored in other vertebrates (Jönsson 1997, Doughty and Shine 1998). Several features of ectothermy preadapt reptiles to reliance upon capital breeding (Bonnet et al. 1998). Among reptiles, snakes are excellent models to study such strategies because most species provide no parental care (Shine 1988a) and embryonic development is primarily lecithotrophic, with minimal placental transfer of energy (Stewart 1992). Thus, the resources allocated to offspring are fully committed before ovulation, rather than being provided over a long period during gestation or after hatching (or birth). Because the number and size of offspring in snakes are determined during vitellogenesis, it is easier to quantify maternal investment than would be the case in many other kinds of animals. Furthermore, the wide range in body-sizes of adult females within a single snake population (Andrews 1982) provides an opportunity to examine the influence of maternal size on reproductive output.

Previous studies suggest that two main factors are likely to play an important role in determining reproductive output in these animals: (1) maternal body size, because space to hold the clutch depends upon female size (Vitt and Congdon 1978, Seigel and Ford 1987, Shine 1988b, Ford and Seigel 1989a); and (2) energy availability (Ford and Seigel 1989b, Seigel and Ford 1991). In turn, the latter factor can be separated into two components: food intake during follicular growth ("income") versus maternal reserves at the onset of vitellogenesis ("capital"). Long-term energy stores are likely to influence reproductive decisions in some snake species (Diller and Wallace 1984, Blem and Blem 1990, Brown 1991, Bonnet et al. 1994, Naulleau and Bonnet 1996), but not in others (Plummer 1983, Ford and Seigel 1989b, Whittier and Crews 1990, Naulleau and Bonnet 1995). For example, preliminary studies report a positive correlation between maternal reserves and offspring number in *Vipera aspis*, but no such relationship in *Elaphe longissima* (Bonnet and Naulleau 1994, Naulleau and Bonnet 1995).

Published data suggest that the aspic viper, *Vipera aspis*, offers a classic example of a typical "capital breeder". In snakes, body-condition (mass scaled by size) reflects their long-term foraging success during the preceding year(s) (Forsman 1996, Shine and Madsen 1997). Adult female aspic vipers need to accumulate very large body reserves to reach the body-condition threshold necessary for the induction of vitellogenesis, and hence postpone reproduction for a long period (up to 4 yr) while they are accumulating those reserves (Naulleau and Bonnet 1996). Vitellogenesis in this species involves an intensive mobilisation of maternal reserves (Bonnet et al. 1994) and maternal energy reserves dictate whether or not a female will reproduce in a given year (Naulleau and Bonnet 1996). Captive female vipers can reproduce without feeding during the whole reproductive period (i.e., vitellogenesis plus gestation), demonstrating that reproduction can be entirely supported by the energetic "capital" stored before reproduction.

The aim of our study is to examine the influences of maternal size, energy stores and current energy intake, on the number and size of offspring in a natural population of aspic vipers. How is the very large capital of stored energy invested (packaged) during vitellogenesis? Because female aspic vipers continue to feed during vitellogenesis, we can also examine whether the energy thus obtained has any influence on reproductive output. Does vitellogenesis rely only on maternal reserves, or does this snake adopt a more flexible strategy using supplementary "income" to improve the quality of the litter? In other words, is the aspic viper a "strict" capital breeder with respect to offspring size and litter size as well as reproductive frequency?

Materials and methods

Study site and animals

Over a period of seven years (1992–1998), we studied a large (more than 1000 adults individually marked) population of aspic vipers, *Vipera aspis*, at Les Moutiers en Retz in western central France near the Atlantic Ocean (47°03′N; 02°00′W). This population is near the northern limit of the geographic range of the species. The study area of approximately 33 ha consists of fields and paths bordered by hedges. In fields not used for farming, brambles, brushwood and small trees are common. The study population is separated from adjacent populations by several roads and a village (see Bonnet and Naulleau 1996 for a more detailed description).

The aspic viper is a medium-sized (typically to 55 cm body length, 100 g), slow-moving, terrestrial, venomous snake species (Naulleau et al. 1996). Autopsies and NMR imaging confirm that in this species, good body condition (high mass relative to body length) is related to large body reserves (abdominal fat bodies: Bonnet and Naulleau 1994, 1995, Naulleau and Bonnet 1996, Villevieille 1997). Females more than 41 cm snout-vent length (= 47 cm total body length, the minimal body size where parturition has been observed) were considered sexually mature (henceforth referred to as adult).

Procedures and measurements

Any study to investigate the influence of maternal reserves on reproduction in free-living animals must meet the following criteria:

(1) maternal condition must be recorded at the onset of vitellogenesis; this requires precise information about the timing and kinetics of follicular growth, ideally in relation to mobilisation of maternal reserves;
(2) relationships between maternal size, body condition and energy reserves must be quantified, so that we can estimate the amount of reserves a female can devote to her clutch;
(3) quantitative data about food intake during follicular growth would be useful; failing this, we need a index of food consumption over this period,
(4) we need to recapture the monitored females before laying or parturition (which typically occurs 2 to 6 months after the start of vitellogenesis in snakes: Seigel and Ford 1987), in order to obtain data on reproductive output.

In the present study, snakes were caught by hand and individually marked by scale clipping or (later in the study:1993) with electronic tags (11 ± 1 mm length [mean $\pm$ 1 S.D. as in all subsequent results]; 2.1 ± 0.1 mm diameter; 0.25 ± 0.1 g total mass; 125 KH, sterile transponder TX 1400L, Rhône Mérieux, Destron/IDI INC). The study area was intensively searched almost every day throughout the active season (early February to October) by one to three people; the total searching effort represents more than 3500 h in the field.

More than 500 adult female vipers have been marked since 1992, and their snout-vent lengths, total body lengths (± 0.5 cm), and masses (± 1 g with an electronic scale) recorded in the field. Body condition was calculated as the residual scores from the regression of the natural logarithm of body mass against that of body length (Jayne and Bennett 1990, Madsen and Shine 1992, Naulleau and Bonnet 1996). The snakes were released at the exact point of capture within 15 min, and more rapidly after subsequent recaptures (except before parturition, see below). Measurements were made at three stages during the reproductive season: (1) at the onset of vitellogenesis, (2) at the end of vitellogenesis (late May, i.e., close to ovulation), and (3) before parturition (Fig. 1). In the aspic viper in western central France, vitellogenesis begins in March (Bonnet et al. 1994), but a major increase in follicular size does not occur until late April (Saint Girons 1957, Saint Girons and Duguy 1992; unpublished data from nuclear magnetic resonance; Fig. 1). Vipers are easier to catch at the beginning of the reproductive season, and many females were caught in March or April. Feeding activity is reduced during this first period of vitellogenesis, and there is generally a slight decrease in body mass. Thus, data gathered in March and April were pooled. Body masses obtained during the periods of rapid follicular growth (May and June) and pregnancy (July–August), or from individuals with a prey item in the stomach, were not used to calculate body condition.

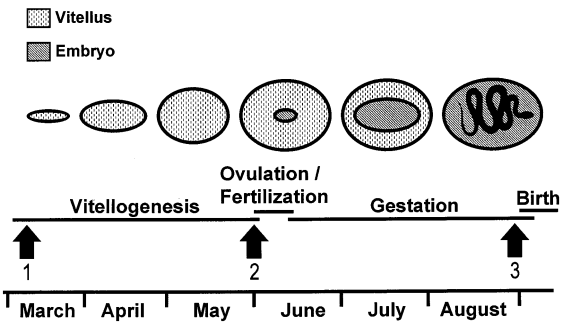

Fig. 1. In the aspic viper (*Vipera aspis*), vitellogenesis begins in early March, with ovulation occurring three months later in early June. Follicular growth (yolk deposition) accelerates in late April and is complete in early June. Embryonic development and egg hydration (dashed zones) occur later, from June to August during gestation until parturition three months later. In the present study, 44 reproductive females were captured at three different physiological states: (1) at the onset of vitellogenesis (arrow 1), (2) at the end of vitellogenesis (arrow 2), and (3) before parturition (arrow 3). Maternal body condition index (an estimate of previtellogenic body reserves) was calculated at the onset of vitellogenesis.

Food intake and mass gain during vitellogenesis

We do not have data on actual prey masses from female in the field, because we were unwilling to stress these animals by forced regurgitation. Thus, we used the increase in female body mass during vitellogenesis as an index of food intake. The validity of this method was tested using two data sets:

(1) food consumption versus change in body mass for 30 captive female vipers (collected from a variety of locations in France). The captive females were kept in individual cages ($40 \times 40 \times 40$ cm, an electric bulb [60 W] provided a thermal gradient, water was ad libitum). The snakes were offered laboratory mice (weighed to the nearest 0.1 g) each week, and were weighed and palpated regularly. Ovulation date was determined from palpation, radiography (Naulleau and Bidaut 1981) and parturition dates. The changes in body mass recorded during vitellogenesis were of the same order of magnitude in captive (9.1 ± 25.0; range -33.0 to 56 g) versus free-ranging female vipers (see Results).

(2) meals records versus change in body mass in free-living snakes. Recent meals in snakes can be detected by palpation (e.g., Fitch 1987). Although we could not quantify precisely prey consumption in the field, we can compare mass change in snakes recorded to feed during vitellogenesis compared to those that were not recorded to feed over this period.

Reproductive output

One hundred and forty six gravid females were caught one to 21 d before parturition, in late August–early September (Fig. 1), and placed in individual cages in the laboratory until they gave birth. To avoid a selection towards obviously gravid females during capture (distended body, and well-developed embryos easily detected by palpation), all females with identifiable items in the abdomen (detected by palpation, excluding the stomach region) were also collected. Palpation enabled us to detect objects as small as 2 g (corroborated by dissection, unpublished data). Captive females were monitored every day until parturition, and weighed (± 0.1 g) every two days and immediately after parturition.

We recorded the number, mass (± 0.1 g), and length (± 0.5 cm) of healthy offspring, stillborn and relatively undeveloped embryos, and the number and mass of unfertilised eggs (± 0.1 g). To analyse reproductive output, we made a distinction between the "classical" measures of total litter size (henceforth LS) or total litter mass by including healthy neonates, stillborn offspring and undeveloped eggs as well (Farr and Gregory 1991, Gregory et al. 1992); whilst we included only viable neonates in our measures of "effective" reproductive output. Thus, fourteen females that did not produce any healthy offspring were excluded from several analyses. The other 132 females gave birth to 699 healthy offspring. The mean body mass of healthy offspring per litter was used to test the predicted negative relationship between offspring number and size. To control for the effect of female body length, we used partial correlation analyses (Ford and Seigel 1989a).

Statistics

Data gathered in 1992 were excluded from several analyses on reproductive output because we selected five obviously gravid, and large, females this year. This bias should be important for inter-annual comparisons, but probably did not influence other analyses. Estimates of population size were obtained using the program CAPTURE (see Bonnet and Naulleau 1996 for further details on methods). In every case, the first models suggested by the goodness-of-fit tests were Mth (population estimate under individual heterogeneity in capture probabilities) or Mh (population estimate under time variation and individual heterogeneity in capture probabilities; Chao et al. 1992), and they were systematically adopted. The differences between the two estimates were small, and we conserved the first selected model.

Snakes are very secretive animals (Seigel 1993), and the breeding frequency of female aspic vipers is low in western central France (Bonnet and Naulleau 1996). Thus, despite a large initial sample size (> 300) and relatively high recapture rates, we obtained complete data for only 44 females.

In this complete data set, each of these animals was captured at least three times during the 6 months reproductive period: early in vitellogenesis (before 15 April for any given year), close to the time of ovulation (from 15 May to 15 June), and close to parturition (3 weeks to one day before; Fig. 1). The low probability of recapturing a snake at three precise occasions separated by long time intervals combined with the exclusion of individuals caught with prey in the stomach were excluded from analyses, explains why only 44 females were included in the "complete" data set. These females did not differ from other females in mean snout vent length or reproductive characteristics (Table 1). However, this sub-sample of females tended to overrepresent particular years particularly those with high proportions of reproductive animals, and a low feeding rate because we did not use data on body masses of animals containing recently-ingested prey.

To ensure that these biases did not substantially affect our conclusions, we also analysed the larger data set ($N = 146$) in which many more animals were incorporated, but with incomplete data for some individuals. We used these data to examine annual variation in reproductive output. Fourteen of these 146 reproduc-

Table 1. Characteristics of 146 reproductive female aspic vipers (*Vipera aspis*) and their litters. SVL = snout-vent length, Fit litter size = number of healthy neonates, Offspring mass = mean mass of healthy neonates (calculated as the mean of the means gathered on 132 litters). * df = 113 for mean offspring body mass. "Complete" = females monitored throughout the entire reproductive year, from the onset of vitellogenesis until parturition. "Others" = females caught after the onset of vitellogenesis. There was no difference between the two subsets of data ("complete" versus "others") in maternal size or in the reproductive characteristics that we measured.

	SVL (cm)	Total litter size	Fit litter size	Total litter mass (g)	Offspring mass (g)
Complete; $N = 44$	49.1 ± 3.2	5.8 ± 1.6	4.7 ± 2.3	32.0 ± 12.9	6.3 ± 0.9
Others; $N = 102$	48.7 ± 3.3	6.3 ± 2.2	4.9 ± 2.9	35.6 ± 16.2	6.3 ± 1.1
$F_{1,144}$*	0.45	2.0	0.10	1.64	0.15
P	0.50	0.16	0.75	0.20	0.69

tive females were represented twice (at intervals of 2 to 4 yr, due to the low breeding frequency), raising the possibility of pseudoreplication. However, none of our results were modified when we randomly excluded duplicate records from these animals. In the complete data set ($N = 44$), every female was represented only once. The following results are derived from analyses on these two data sets. All the tests were performed using STATISTICA 5.1.

Results

Relationship between food intake, growth and weight gain

Females did not increase in body length during reproductive years, except for a slight increase (1–2 cm) in a few individuals in one year when food availability was exceptionally high (1996, see below). However, females gained appreciably in mass during vitellogenesis (mean mass change was $+11.7 \pm 15.3$ g, $+12 \pm 16\%$ of initial mass, $N = 44$), with considerable variation among individuals (range -12 to $+51$ g, -12 to $+61\%$ of initial mass). Such body mass variations were not related to the female's SVL ($r = 0.08$, $P = 0.58$, $N = 44$), nor to her pre-vitellogenic body mass ($r = -0.13$, $P = 0.41$, $N = 44$) or initial body condition ($r = -0.14$, $P = 0.54$, $N = 44$).

A causal link between maternal mass gain and feeding was suggested by the data set on captive snakes: female viper's food intake during vitellogenesis was highly correlated with her change in body mass over this period ($r = 0.83$, $N = 30$, $P < 0.0001$; Fig. 2). This result was also supported by the data gathered on the 44 free-ranging snakes. Using palpation, we recorded prey in 13 reproductive females in late April–May. All of these animals increased in body mass during vitellogenesis (mean mass change was $+20.7 \pm 15.0$ g, $+24 \pm 17\%$ of initial mass; range $+2$ g to $+51$ g, $+2$ to $+60\%$ of initial mass), whereas the other 31 females in which we found no evidence of feeding showed a lower gain in body mass (mean mass change $+8.0 \pm 14.0$ g, $+8 \pm 14\%$ of initial mass; range -12 g to $+51$ g, -11 to $+54\%$ of initial mass; comparing the two groups, $F_{1,42} = 7.28$, $P = 0.01$). Although many of these 31 females probably fed at some time during vitellogenesis, the difference in mass change is consistent with the hypothesis that mass change reflects feeding rate. Thus we conclude that the increase in body mass constitutes a simple and reliable index of prey consumption over the period of vitellogenesis.

Influence of maternal body length on reproductive output

The first likely correlate (determinant?) of litter size and offspring size is maternal body size; numerous researchers have documented strong allometry in these traits in a wide variety of reptile species (Dunham et al. 1988, Wilbur and Morin 1988). If maternal body size strongly affects reproductive output, then

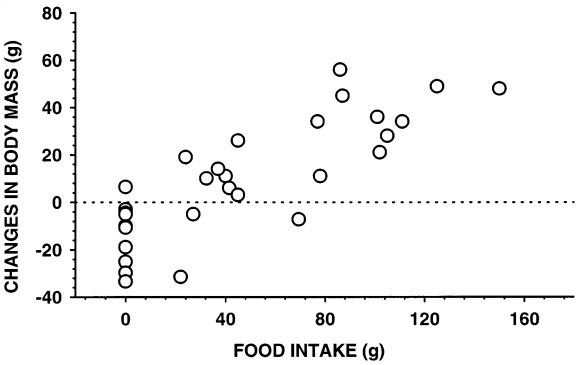

Fig. 2. Relationship between changes in maternal body mass and food intake during vitellogenesis in 30 captive female asp vipers. Food intake was calculated as the sum of the mice consumed during the whole vitellogenic period (3 months). Change in body mass was the difference between the female's mass at ovulation minus her initial mass as recorded at the onset of vitellogenesis. Although change in body mass reflects the influences of complex phenomena (egg hydration + maternal metabolic expenditure + individual physiological differences [e.g., litter size]), food intake strongly influences maternal somatic weight changes (see text for statistics).

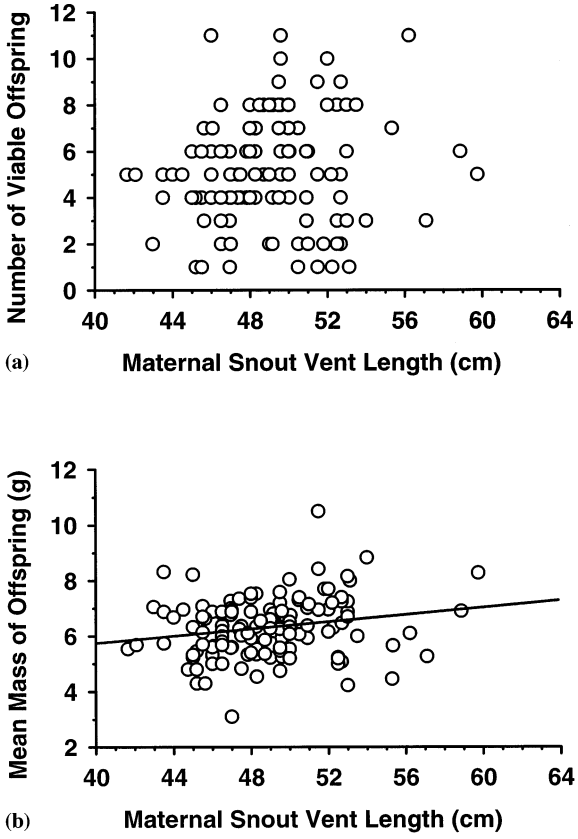

Fig. 3. The relationship between maternal size and reproductive output in *Vipera aspis*. Larger females do not produce more viable offspring (a), but tend to have slightly larger neonates (b).

we need to know this at the outset so that we can factor out allometric effects in all subsequent analyses. We used the entire data set (all females and their litters) for this analysis.

Maternal snout-vent length was weakly correlated with total litter size ($r = 0.17$, $P = 0.036$, $N = 146$), but not with the number of healthy neonates ($r = 0.13$, $P = 0.12$, $N = 146$, Fig. 3a). Hence, maternal body size has little effect on litter size in this population. Larger females tended to produce heavier offspring ($r = 0.22$, $P = 0.01$, $N = 132$, Fig. 3b). The effect was stronger in a partial correlation analysis where we held constant the effect of litter size on offspring size (partial correlation: $r = 0.24$, $P = 0.005$, $N = 132$). Thus, our data suggest that a female's body size influences the mass of her young, but has less effect on the total number of neonates that she produces.

The second plausible influence on offspring size and number is the relationship between these two variables. Given finite resources, an increase in litter size will reduce mean offspring size. We looked for this effect in the entire data set, using mean values for offspring size for each litter.

Trade-off between developing offspring for maternal resources

Offspring snout-vent length and offspring mass were strongly correlated ($r = 0.75$, $N = 699$, $P < 0.0001$); we use body mass to characterise neonatal size, rather than length, because it offers a more direct measure of maternal investment. Stillborn offspring, relatively undeveloped embryos, and unfertilised eggs weigh much less than healthy neonates (mean masses of healthy neonates, stillborn and undeveloped eggs were 6.3 ± 1.1 g [$N = 699$], 4.4 ± 2.0 g [$N = 80$], and 2.0 ± 1.1 g [$N = 103$], respectively), and so were not included in our test of the influence of litter size on offspring size.

The predicted negative relationship between offspring number and the mean mass of healthy neonates was not evident from our raw data (Fig. 4a). Using total litter size rather than the number of healthy neonates did not change the significance of this result ($r = -0.15$, $P = 0.09$, $N = 132$). However, when female body length was held constant, mean offspring mass was negatively correlated with offspring number (Fig. 4b). Thus, our data

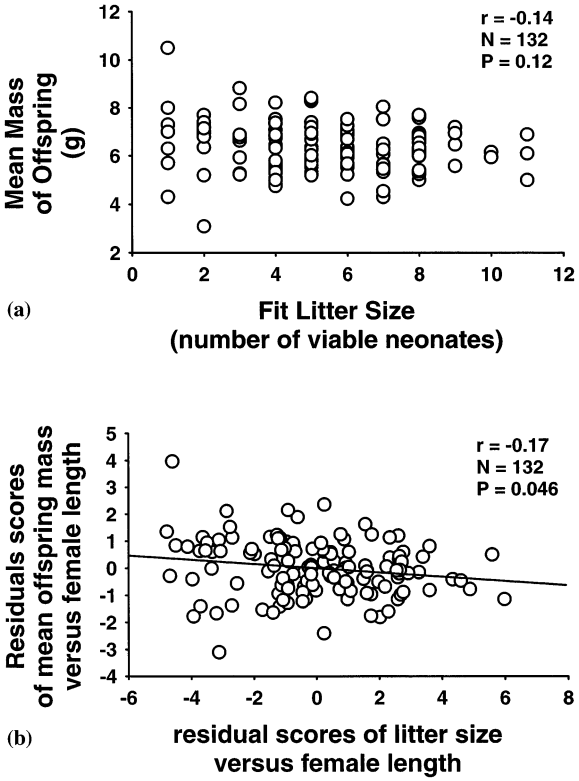

Fig. 4. The relationship between litter size and offspring size in *Vipera aspis*. a) The number of viable offspring produced by a female viper is not significantly correlated with the mean mass of her offspring, unless the analysis factors out the effects of maternal body size on reproductive output (see Fig. 3). If the effect of maternal size is removed (by using a partial correlation analysis), the underlying tradeoff between offspring size and litter size is revealed (b).

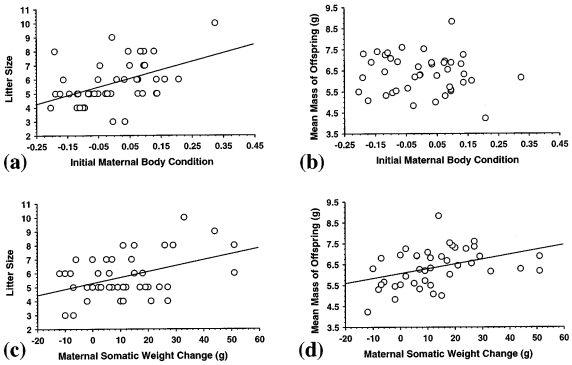

Fig. 5. The relationship between previtellogenic maternal reserves (initial body condition) (a, b), maternal somatic weight change during vitellogenesis (an indication of food intake; see text) (c, d), and reproductive output in *Vipera aspis*. Females with high initial body condition produce larger litters (a) but do not have larger offspring (b). Females that increase substantially in body mass during the vitellogenic period produce larger litters (c) of larger neonates (d).

demonstrate a weak trade-off between offspring size and number in aspic vipers.

We now turn to the relationship between energy balance and viper reproduction. First, we use the data on the 44 females measured at each stage of their reproductive cycles (the ''complete data'' females) to assess relationships between energy stores, food intake, and reproductive output.

Influence of pre-vitellogenic body condition on reproductive output

Female vipers that were in good body condition early in vitellogenesis, tended to produce large litters ($r = 0.47$, $N = 44$, $P = 0.001$; Fig. 5a). In contrast, early body condition had no influence on offspring size ($r = 0.09$, $N = 42$, $P = 0.56$, note that sample size was reduced because two females did not produce any living offspring; Fig. 5b) even when female snout-vent length was held constant ($r = -0.09$, $N = 42$, $P = 0.57$).

Influence of food intake on reproductive output

The change in maternal body mass during vitellogenesis (food intake) was correlated with litter size ($r = 0.42$, $N = 44$, $P = 0.005$, Fig. 5c), even when female snout-vent length was held constant ($r = 0.44$, $N = 44$, $P = 0.002$). Similarly, mass gain during follicular growth strongly influenced offspring size ($r = 0.39$, $N = 42$, $P = 0.01$, Fig. 5d). Controlling for the influence of maternal snout-vent length on offspring mass did not change this result ($r = 0.40$, $N = 42$, $P = 0.01$). When the number of neonates was included as a correcting factor, the influence of maternal mass change on offspring size was strengthened ($r = 0.47$, $N = 42$, $P = 0.002$; and $r = 0.50$, $N = 42$, $P = 0.001$ including maternal snout-vent length as an additional correcting factor). These latter results presumably reflect the fact that litter size influences the amount of energy from a given prey item that can be allocated to each offspring.

The rank correlation between number and size of offspring in the ''complete data'' set ($r = -0.20$, $N = 42$, using number of healthy offspring) was similar to that from the larger data set ($r = -0.14$, $N = 132$). Because offspring size was positively correlated with changes in maternal mass during vitellogenesis, we tested for the presence of this trade-off including change in maternal body mass as a correcting factor. These analyses confirmed the underlying negative relationship between offspring mass and number of healthy neonates ($r = -0.35$, $N = 42$, $P = 0.025$; and $r = -0.40$, $N = 42$, $P = 0.01$ with female snout-vent length held constant).

The body condition of a post-parturient female was affected by her change in body mass during vitellogenesis ($r = 0.43$, $N = 44$, $P = 0.004$). Thus, energy and materials obtained from the prey during vitellogenesis were not exclusively allocated to growing follicles, but were also directed to maternal reserves.

Combined effects of maternal length, maternal reserves, food intake and offspring competition for energy on reproductive output

Our data allow us to quantify the four main factors that seem likely to influence reproductive output (number and size of offspring) in female vipers. These factors are independent of each other; for example, two of them (maternal length and maternal body condition) are independent by definition. The third variable, change in maternal body mass during the vitellogenic period (food intake), was not influenced by either of these variables (see above). The fourth independent variable is the trade-off between number versus size of growing follicles, given the finite amount of energy allocated for vitellogenesis.

Stepwise multiple regression analyses were performed on the ''complete data'' set ($N = 44$) with these four independent variables, and the number or size of offspring as the dependent variables. The highest proportion of the variation in litter size was explained when all four predictor variables were included in the analyses ($r^2 = 0.61$, $N = 42$, $P < 0.00001$). However, variation in mean offspring mass was largely explained by maternal weight change and litter size in the regression model ($r^2 = 0.25$, $N = 42$, $P = 0.003$), with no further significant increase in explained variance by including the other variables ($r^2 = 0.30$, $N = 42$, $P = 0.008$ with the four variables). Hence, we conclude that the reproductive output of a female aspic viper is determined by the

Table 2. Annual variation in the body sizes and reproductive output of female aspic vipers (*Vipera aspis*). SVL = snout-vent length, Fit litter size = number of healthy neonates, Litter mass = total litter mass, Offspring mass = mean mass of healthy neonates. Data for the first four variables (columns) were analysed by one way ANOVAs with year of the study (1992–1998) as the factor. For the final trait (mean offspring mass), we used a two-factor ANOVA with litter number nested within year (so df = 6, 557 for offspring mass). These ANOVAs reveal no significant variation in maternal body size (SVL) of 146 reproductive female aspic vipers, but significant variation in some of the characteristics of their litters. Significant values are indicated in bold faces. Note that excluding 1992 from analyses (see text) did not change any results.

	SVL (cm)	Total litter size	Fit litter size	Litter mass (g)	Offspring mass (g)
$F_{6,139}$*	0.44	3.42	1.58	2.36	7.14
P	0.85	**0.01**	0.16	**0.03**	**0.0001**

combined effects of at least four factors: her body length, her pre-existing energy reserves, her food intake during vitellogenesis (as estimated by her weight change over this period) and the trade-off between offspring size versus number (i.e., competition among the offspring for energy).

Annual variation in energy availability and viper reproduction

In order to evaluate the generality of our results on 44 females, we can also examine patterns of annual variation in the traits of interest in the all females. If our results from the "complete data" sample are robust, they should enable us to understand the ways in which annual variation in prey availability influences the reproductive output of vipers.

Mean maternal body size remained consistent among years, but significant annual variation occurred in some of the reproductive traits (Table 2). The consistency in maternal body size, combined with the lack of strong body-size effects on reproduction (Table 2, Fig. 3), substantially simplifies the analysis of correlates of annual variation in reproductive biology. It also supports the notion that factors other than maternal size influence reproductive output in our study population.

Prey availability varied substantially over the course of our study (see Bonnet et al. 2000a). Vipers feed mainly on voles, whose populations typically fluctuate in this region in a 3- to 4-yr cycle (Krebs and Myers 1974, Delattre et al. 1992). Such fluctuations directly influence feeding rates of the snakes (as revealed by the proportion of snakes with a prey in the stomach, Bonnet et al. 2000a). Restricting the analyses to the vitellogenesis period and to adult females, we can divide the years of our study into three categories in this respect. Two years (1994 and 1998) were poor (9% [$N = 228$] and 10% [$N = 81$], respectively, of the snakes with a prey in the stomach), three were "medium" (1993, 1995 and 1997 with 14% to 21% [$99 < N < 180$] of the snakes with a prey in the stomach) and one was extremely high (1996, when 40% [$N = 131$] of captured snakes contained prey). Given this inter-annual variations in feeding rates, we expect to find substantial variation in reproductive traits like reproductive frequency, litter sizes or offspring size. Our data on annual variation broadly support these hypotheses.

(1) Reproductive frequency showed substantial variation, but is difficult to quantify precisely because population sizes also varied (Fig. 6; $\chi^2 = 99.9$, df = 5, $P < 0.0001$). The number of reproductive females strongly decreased after a low food year (1994), and increased after a good year (1996). The proportion of reproductive females in comparison to the total number of adult females also varied significantly among years ($\chi^2 = 46.3$, df = 5, $P < 0.0001$), and was apparently related to prey availability in the preceding year (Fig. 6).

(2) Litter sizes varied among years (Table 2), with an increase of mean litter size during the "high-food"

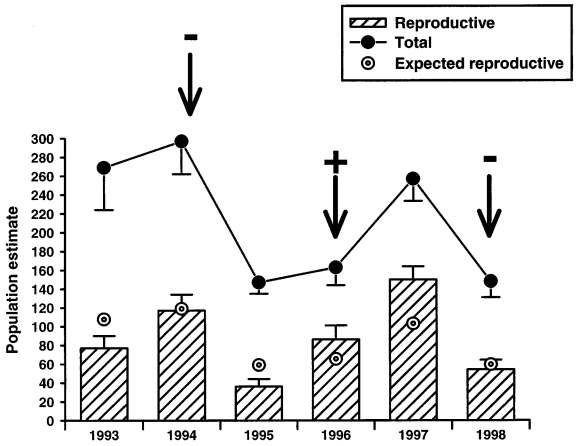

Fig. 6. Annual variation in the total number of adult females in a closed population of asp vipers (black dots − S.D., black line). The observed number of reproductive females (a subset of the total number of adult females) is represented with hatched bars (+ S.D). The expected number of reproductive females (dotted circles), simply calculated as a constant proportion (33%; see Bonnet and Naulleau 1996) of the total number of adult females, is indicated to better visualise the annual fluctuations in the relative number of reproductive females in comparison to the total number of adult females. The arrows with the sign " − " indicates a low food availability year, the arrow with the sign " + " indicates an exceptionally high food availability year. Population estimates (± S.D.) were calculated using the program CAPTURE (see text for statistics).

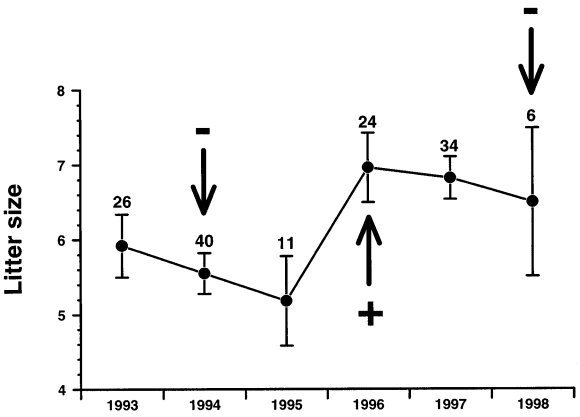

Fig. 7. Annual variation in litter size (annual mean ± S.E.) in a closed population of asp vipers. Numbers above each symbol indicate sample size (number of females). The arrows with the sign " − " indicates a low food availability year, the arrow with the sign " + " indicates an exceptionally high food availability year. See text for statistics.

year (1996) and the next ones as well (Fig. 7). This is what we would predict from the notion that litter sizes are mainly affected by existing energy stores, and by current feeding rates also (see above). Similarly, during a year of low prey availability (1994) we observed a reduction of mean litter size, and in the following year as well (Fig. 7).

(3) Offspring mass was higher in the "good" year (1996) than at any other time in the study, and a nested ANOVA (with litter number nested within years) detected significant variation in offspring body mass among years (Fig. 8, Table 2). Interestingly, during the 1994 "poor" year we did not observe any reduction of offspring sizes, but such effect may have occurred in 1998 (Fig. 8). Thus we speculate that females allocate additional nutrients to offspring only in exceptionally "good" years, and hence that modest annual variation in food supply will not be automatically reflected in detectable changes to mean offspring mass. Instead, changes to offspring mass will be apparent only in occasional very good years (Fig. 8).

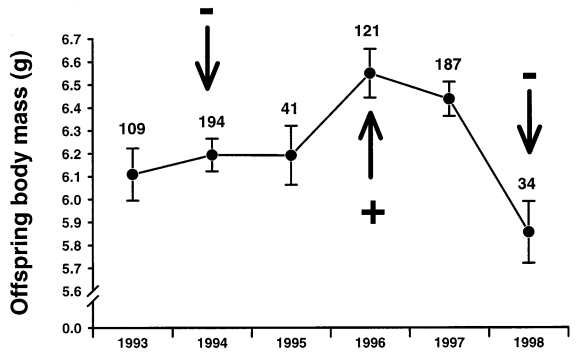

Fig. 8. Annual variation in mean offspring mass (annual mean ± S.E.) in a closed population of asp vipers. Numbers above each symbol indicate sample size (number of neonates). The arrows with the sign " − " indicates a low food availability year, the arrow with the sign " + " indicates an exceptionally high food availability year. See text for statistics.

Discussion

Our data suggest that the reproductive outputs of a female aspic viper (i.e., the size and number of offspring in her litter) are affected in complex ways by her energy acquisition over the months and years preceding the actual birth of the offspring. Her foraging success over an interval of one to three non-reproductive years determines the magnitude of her energy stores, and hence the "decision" as to whether or not she will reproduce in a given year (because reproduction is initiated only after females attain a precise body-condition threshold: Naulleau and Bonnet 1996). Our data show that these energy stores (measured by female body condition before the onset of vitellogenesis) determine litter size: females with larger energy stores initiate vitellogenesis of a greater number of follicles. To our knowledge (see below), this study demonstrates for the first time (using strict methodological criteria to calculate early body condition) that in snakes, *initial* maternal reserves gathered over years before reproduction positively influence reproductive output. Food intake after this time, but before ovulation, also seems to affect the female's reproductive output not only by changing her litter size, but by modifying the mean mass of her offspring.

Recruitment of follicles starts at the initiation of vitellogenesis in early March (Bonnet et al. 1994), feeding activity is rare before April, and vitellogenesis culminates in May–June (see Fig. 1). Thus, we might expect that food intake during vitellogenesis occurs too late to modify the number of growing follicles. However, we found a positive relationship between food intake and litter size. This counterintuitive result may be due to the influence of food intake on follicular atresia. Autopsies (Saint Girons 1957) and nuclear magnetic resonance imaging data (unpubl.) show that undersized follicles, as well as atretic follicles, are common during vitellogenesis. Well-nourished females may proceed with vitellogenesis rather than resorption of some of these smaller follicles.

Importantly, the impact of additional food (= energy) on offspring mass necessarily depends on litter size also, because a larger litter means that a given amount of energy is divided among a greater number of offspring. Thus, offspring size in the aspic viper is affected by the mother's feeding success over the preceding few years (because her accumulated energy

stores will determine litter size) as well as her feeding success in the weeks immediately preceding ovulation. Similarly, litter sizes are affected by feeding rates in this vitellogenic period as well as in previous years. The end result is that the link between food supply and reproductive output is complex. We must understand short-term as well as long-term rates of food intake before we can interpret variation in reproductive output in aspic vipers.

Trade-offs between litter size and offspring size occur in several snake species (Ford and Seigel 1989a, Madsen and Shine 1992), including the aspic viper (see above). Our study also shows that this trade-off (competition among growing follicles during the initial partitioning of energy) can be obscured by subsequent variation in food intake (Lessells 1991). Thus, although large litters should result in small follicles, this trade-off may be obscured by variation among females in the magnitude of additional energy reserves gathered during vitellogenesis (see van Noordwijk and de Jong 1986, Doughty and Shine 1997). Follicles "compete" for resources not only at the initiation of vitellogenesis, but throughout the vitellogenic period (when additional energy from recently-consumed prey becomes available). Thus, sibling ova compete for resources at two distinct levels and for two distinct energetic sources: first at the onset of vitellogenesis for the energy stored by the mother before reproduction, and second during vitellogenesis for the prey caught by the mother.

In combination with previous work on this species (Naulleau 1965, Naulleau and Bidaut 1981, Naulleau et al. 1996), our data clarify the complex relationship between maternal foraging success and reproductive activity. Non-reproductive individuals accumulate large body reserves over an interval of one to three years, by storing a large proportion of the energy they assimilate from prey consumed over that period. During that time, they remain very secretive (Bonnet and Naulleau 1996) until they exceed the body-condition threshold necessary for reproduction (Naulleau and Bonnet 1996). After this long period of abstinence, vitellogenesis takes the form of an "explosive" investment: almost all maternal reserves are allocated to reproduction to produce the greatest possible number of young. We have recorded several litter masses greater than the mass of the post-parturient female (maximum = 112%). Energy opportunistically obtained by feeding during vitellogenesis is also directed to the developing follicles, and significantly increases offspring size. After reproduction, females are very emaciated and many do not survive until the next year (Bonnet 1996, Bonnet et al. 2000b). Thus, many female aspic vipers are semelparous, producing only one litter in their lifetimes (unpubl.). Given the low probability of breeding again, the "costs" of additional investments to an already high reproductive effort will be low in terms of decrements in future reproductive opportunities (Williams 1966). Consequently, females should be under strong selection to maximise the effective output from any reproductive attempt, rather than conserve resources to invest in subsequent litters. This situation may be widespread in viperid snakes (Madsen and Shine 1993; W. S. Brown, pers. comm.).

Reptiles have increasingly been used as "model organisms" for research in this field (Seigel 1993). However, both our methods and our results provide a contrast to most previous work on these animals. Firstly, we focus on events during vitellogenesis (the period during which most of the variation in litter size and offspring mass is generated) rather than during pregnancy (e.g., Stewart 1989, Shine and Harlow 1993, Baron et al. 1996, Gregory and Skebo 1998). Vitellogenesis may extend for periods as long as pregnancy in many reptile species (including the aspic viper), and is a crucial phase in terms of maternal reproductive "decisions". Vitellogenesis can be viewed as the "explosive" phase of the energetic investment of reproductive females (Bonnet et al. 1994). Secondly, maternal body size has little effect on reproductive output in the aspic viper (Bonnet et al. 2000a), in strong contrast to most other snake species for which similar data are available (e.g., Seigel and Ford 1987). This result is not an artefact of low statistical power; our sample size is larger than in most previous analyses (mean sample size was 32.8 ± 51.3 in 61 studies reviewed by Seigel and Ford [1987]). Other studies on the aspic viper from the same region revealed a positive correlation between maternal size and litter size (Naulleau and Saint Girons 1981). The difference between these studies is probably explained by the particular methodology we employed (collection of all animals that were potentially reproductive). If we had searched only for obviously gravid snakes (e.g., snakes with particularly large litters), we would have ignored many females with small litters relative to their body size.

Another difference between our study and previous analyses is that we have used a very strict criterion as to when in the reproductive cycle we estimate body reserves from overall body condition. Thus if measurements are taken on females during pregnancy or close to the time of ovulation, the reproductive products (follicles, eggs or embryos) constitute a significant proportion of maternal body mass. Hence, body condition at this time is likely to be a direct measure of reproductive output, not an indicator of the magnitude of body reserves such as the fat bodies and liver (Bonnet and Naulleau 1994, 1995). In such a case, a positive correlation between "body condition" and reproductive output is almost inevitable, since the same variable occurs in both sides of the equation. In addition, the origin of the energy invested into the clutch cannot be determined by such a methodology, and the respective influences of food intake and maternal reserves become indistinguishable. Our data constitute a basis for devel-

oping hypotheses that can be tested by rearing snakes in controlled diets from the onset of vitellogenesis to the production of the offspring (e.g., laying or parturition).

Despite these methodological problems, data from other snake species are sufficient to document substantial interspecific differences in the relationship between energy acquisition and reproductive expenditure. For example, experimental studies show that food intake during vitellogenesis affects clutch sizes but not offspring sizes in two American snake taxa (*Thamnophis marcianus* and *Elaphe guttata*: Ford and Seigel 1989b, Seigel and Ford 1991). In both of these "income-breeding" genera, maternal energy reserves may play only a small role in fuelling reproductive expenditure (Whittier and Crews 1990, Naulleau and Bonnet 1995). In contrast, field data on a "capital-breeding" viperid snake, *Vipera berus*, suggest that offspring size may be affected by prey availability in this species (Andrén and Nilson 1983). Our own data suggest that reproductive frequency in the aspic viper is driven by long-term energy stores, but that litter sizes and offspring sizes respond in complex ways to maternal feeding rates over both the short and the long term.

More generally, we predict that broad patterns will be apparent across species, depending on the extent of their reliance upon stored energy for breeding. In "capital" breeders, early body condition will determine reproductive status (Diller and Wallace 1984, Brown 1991, Naulleau and Bonnet 1996) and will largely determine offspring number (present study). In such species, breeding frequencies will often be low because long periods of time are necessary to accumulate energy reserves (Martin 1993, Bonnet and Naulleau 1996). The mass of the clutch relative to maternal mass will often be high, because there is a massive investment of body reserves to reproduction. In contrast, we predict that the reproductive decisions of "income" breeders (which can store only limited body reserves) will be less dependent on maternal body condition prior to vitellogenesis (Plummer 1983, Whittier and Crews 1990, Naulleau and Bonnet 1995). Breeding frequency should be higher, with the number of offspring dependent on maternal foraging success immediately before breeding (Ford and Seigel 1989b). Relative clutch (litter) mass should be relatively low.

There is undoubtedly a continuum between capital and income breeders in snakes, as in other organisms (Chastel et al. 1995), so that there is ample opportunity for robust empirical tests of these predictions. This interspecific diversity in the role of energy reserves for reproduction, and the partial decoupling of control systems that regulate different aspects of reproductive output (offspring size versus number) mean that snakes offer exceptional opportunities to answer Fisher's (1930) challenge about the ways in which animals allocate energy to reproduction.

Acknowledgements – We thank L. Schmidlin, M. A. L. Zuffi, and C. Thiburce for helping to measure, weigh, and mark several hundred neonates. We also thank S. Duret and M. Vacher, who spent many months to catch the snakes. T. Madsen, P. Doughty, D. Reznick, S. J. Hall and S. D. Bradshaw provided helpful comments on the manuscript. Financial support was provided by Centre National de la Recherche Scientifique (France) and the Australian Research Council. Rex Cambag, J. T. Wilmslow and Gisèle Gaboune helped to solve many technical problems.

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