

Costs of Anorexia During Pregnancy in a Viviparous Snake (*Vipera aspis*)

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ABSTRACT Spontaneous anorexia has been documented in various animal species and is usually associated with activities competing with food intake. In natural conditions, most female aspic vipers (*Vipera aspis*) stop feeding during the two months of pregnancy. We carried out a simple experiment on 40 pregnant females to determine whether anorexia was obligatory or facultative, and to investigate the energetic consequence of fasting on post-partum body condition and litter traits. Three diet treatments were applied during gestation: no food, one feeding occasion, and two feeding occasions. Twelve nonpregnant, unfed females were used as a control group. Most gravid females accepted captive mice during gestation, suggesting that anorexia reported in the field was a side effect of the tremendous changes in activity pattern associated with pregnancy. Mass loss was high for unfed reproductive females, indicating high energy expenditure associated with embryo maintenance. Prey consumption allowed compensation for metabolic expenditure and enhanced post-partum female body condition, but had no effects on litter characteristics. The magnitude of the metabolic expenditure during gestation appeared to be independent of fecundity. *J. Exp. Zool.* 292:487–493, 2002. © 2002 Wiley-Liss, Inc.

Life history theory has been largely influenced by the concept of cost of reproduction based on a possible trade-off between current reproduction and future reproductive success (Williams, '66). This notion is supported by a substantial amount of theoretical study suggesting that the form of the relationship between reproductive investment and the magnitude of associated costs influences the evolution of reproductive strategies (Williams, '66; Bull and Shine, '79; Shine and Schwarzkopf, '92).

Identification of proximate mechanisms by which costs are mediated is an important empirical challenge, and two major categories of reproductive costs are classically distinguished (Calow, '79). The first component is ecological and linked to a reduction of survival probabilities associated with reproduction. The second component, recognized as a "fecundity" cost, involves an energy allocation trade-off: The investment in current reproduction affects the residual reproductive value through a depletion of body reserves or growth rate reduction (Williams, '66; Shine, '80). Such a classification is somewhat artificial as the two major forms of costs are interconnected; for example, low body reserves may also affect survival. In addition, there is growing evidence that

organisms can change the relative magnitude of the different components through behavioural modifications (Bauwens and Thoen, '81; Brodie, '89). Costs based on allocation trade-offs can take a diversity of forms. Most studies have been carried out on the effects of direct energy investment into reproduction (Anguiletta and Sears, 2000). However, substantial expenditure may also arise indirectly from cessation or reduction of feeding during all or part of reproduction. Empirical studies indicate that feeding cessation or reduction during reproduction is a widespread phenomenon (Engelmann and Rau, '65; Batholomew, '70; Mrosovsky and Sherry, '80; Weeks, '96). Cessation of feeding when food is available is superficially paradoxical and needs explanation. Furthermore, this indirect component of reproductive effort may translate into a substantial energetic cost of reproduction.

Anorexia is associated with hibernation, migration, or incubation in various endotherm vertebrates (Mrosovsky and Sherry, '80). Although less

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studied, ectotherm vertebrates may also serve as a good model group for the study of feeding cessation. Endothermy is tightly linked with parental cares (Farmer, 2000), and the lack of such cares among numerous ectotherm species leads to a substantial simplification as reproductive effort is sealed prior to oviposition or parturition. Such situations will facilitate the assessment of the relationship between reproductive effort, reproductive output (fecundity), and associated costs. Among squamate reptiles (lizards and snakes), reproduction entails major behavioural changes, notably decrease or cessation of food intake during gestation (Shine, '80; Madsen and Shine, '93; Gregory and Skebo, '98; Gregory et al., '99). Such phenomena are particularly obvious for "capital breeding" species in which long-term energy storage constitutes the primary source of energy for reproduction (Bonnet et al., '98).

The aspic viper (*Vipera aspis*) is a medium size (50 cm) viperid snake that displays those characteristics. In females, energy stores permit them to fuel the entire energetic requirements of reproduction. Depending upon prey availability, food intake may occur during the egg production phase in spring (Saint Girons and Naulleau, '81; Bonnet et al., 2001a). However, field data clearly indicate that many females virtually stop feeding during the two months of pregnancy. Three hypotheses about the proximate factors involved in gestational anorexia can be proposed: 1) anorexia could be a consequence of abdominal space limitation to accommodate both embryos and prey items (Saint Girons, '79); 2) cessation of feeding may be related to a loss of appetite intrinsically associated with gestation (i.e., due to changes in hormonal balance (Bonnet et al., 2001b); and 3) fasting may simply be the result of low foraging success due to behavioural changes in gravid individuals (i.e., thermal needs or predator avoidance).

For hypotheses one and two, gestational anorexia is supposed to be obligatory. In the case of hypothesis three, this phenomenon is expected to be facultative. In the present study, we conducted a simple experiment to test whether gestational anorexia is obligatory or facultative and to examine to what extent feeding cessation during pregnancy translated into energetic costs.

MATERIALS AND METHODS

Study species

The aspic viper (*V. aspis*) is a small viviparous snake, abundant in central western France. In

this area, females typically reproduce on a less-than-annual schedule (Saint Girons, '57a,b; Bonnet and Naulleau, '96; Naulleau and Bonnet, '96; Naulleau et al., '99). Ovulation occurs during the first two weeks of June (Naulleau, '81), and parturition occurs two to three months later, from late August to late September.

Captures and housing

Forty reproductive females were collected in June 2000 from three localities: Château d'Olonnes, Les Sables d'Olonnes (both in Vendée district) and Rochefort (Charentes Maritimes district). Individuals were given a unique scale clip number, measured to the nearest 0.5 cm and weighed to the nearest 1g. Females were placed in six outdoor enclosures (5 × 3 m, mean density: five snakes/enclosure) broadly recreating the natural habitat, and they were exposed to the climatic conditions of the field research station of Chizé (Forêt de Chizé, Deux-Sèvres, 46°07' N, 00°25' W). Each enclosure was equipped with numerous external dens to serve as hiding places. Water was provided ad libitum and vegetation mainly composed of annual Poaceae was kept high (20–40 cm) to provide shade and shelter.

Experimental design

Females were randomly assigned to one of the three feeding treatments during gestation: Group 1 (nine individuals), never fed; Group 2 (17 individuals), one prey item offered in July; and Group 3 (14 individuals), two prey were presented in July and early August. Snakes of both feeding treatment groups were fed by placing a recently killed mouse (average mass 20 g) close to their dens. Prey consumption was recorded by direct observation of feeding, or by less direct means if feeding was not observed (by palpation of mice inside the snake and by a sudden increase in body mass).

As a control group, 12 nonpregnant females (unfed during one month in captivity, in the same conditions as the pregnant females) were weighed to measure mass loss during fasting, independently of gestation.

Records of body mass and reproductive output

The snakes were all weighed at the onset of the experiment in early July (i.e., after ovulation). At this time, the number of eggs was assessed via abdominal palpation (Fitch, '87; Bonnet et al., 2001a for further details on the accuracy of the method). Females were all recaptured at the end

of gestation (late August) and weighed again to determine absolute mass changes between early July and late August. Daily mass change during gestation was calculated using absolute mass change (g) and time elapsed (days) between the two mass records. Snakes were then brought into the laboratory until parturition. We recorded post-partum female body mass and the number, mass (± 0.1 g), and length (± 0.5 cm) of healthy offspring. The number of unfertilized eggs and still-born were also recorded. We made a distinction between the total litter size including healthy neonates, still born offspring, and undeveloped eggs (Farr and Gregory, '91; Gregory et al., '92), and "fit" litter size where only viable neonates were considered. Five females (one in Group 2 and two each in Groups 1 and 3) produced only unfertile eggs. Because snakes were caught after the mating season (Naulleau, '97), those individuals were removed from analysis of reproductive output.

In this species, post-partum female body condition (mass adjusted by size) positively influences survival the year following reproduction and hence residual reproductive success (Bonnet et al., 2000). We calculated body condition as the residual score from the general linear regression of log-transformed body mass value versus log-transformed snout-vent length value for all females (Jayne and Benett, '90; Bonnet et al., 2000). Such an index provides an accurate estimation of body reserves (Bonnet, '96).

RESULTS

Prey consumption

Pregnant females accepted prey most of the time (41 of 45 feeding occasions). Among the 17 snakes fed once, 15 (88%) ate the prey offered, and among the 14 snakes fed twice, 12 (86%) ate both prey offered; two females ate only one mouse each.

Hence, at the end of gestation, it was possible to classify females by the actual number of prey eaten: no prey (11 individuals); one prey consumed (17 individuals); two prey consumed (12 individuals). In the following analysis, we considered both group treatments and actual number of prey eaten.

Changes in body mass during gestation

The three groups did not differ in snout-vent length (one factor ANOVA, $F(2,37) = 1.74$; $P = 0.20$), size-adjusted initial body mass (ANCOVA, $F(2,36) = 1.39$; $P = 0.26$), or size-adjusted number of eggs (ANCOVA, $F(2,36) = 0.45$; $P = 0.63$; Table 1).

Group 1 females showed a significantly higher daily mass loss during gestation compared to the control group (0.22 g/d versus 0.11 g/d; $F(1,18) = 12.58$; $P < 0.0019$), using an ANCOVA with treatment as factors, daily mass change as dependent variable, and initial body mass as the covariate.

The feeding regime significantly influenced the change in body mass during gestation (ANCOVA, $F(2,36) = 41.12$; $P < 0.00001$ considering treatment groups, and $F(2,36) = 66.41$; $P < 0.00001$ considering number of prey consumed). Daily mass loss pre-partum was less marked in Group 2 females than those in Group 1 (adjusted mass change -0.04 g/day versus -0.22 g/day). An average mass gain of 0.07 g/day was observed in Group 3 females. Reconducting the analysis by considering the actual number of prey eaten rather than treatment groups did not change those results (daily mass change: -0.21 g/d for snakes fasting during pregnancy, -0.03 g/d for snakes that consumed one prey, and 0.09g/d for snakes that consumed two preys) (Fig. 1).

Hence, using either initial group treatments or the number of prey actually consumed led to similar results. In the following analysis, we only present calculations based on the number of prey ingested during pregnancy, because it should more directly bear upon the influence of energy intake on reproductive output and post-partum female body condition.

Litter characteristics and females' post-partum condition

The number of prey consumed during pregnancy did not influence litter size (ANCOVA, $F(2,32) = 0.21$; $P = 0.81$), litter mass ($F(2,32) = 1.67$; $P = 0.23$), fit litter size ($F(2,32) = 1.39$; $P = 0.26$), and fit litter mass ($F(2,32) = 1.84$; $P = 0.21$). Similarly, no differences in mean offspring snout vent

TABLE 1. Characteristics of the pregnant females recorded at the onset of the experiment, for the three treatment groups¹

Traits	Unfed (9)	Fed once (17)	Fed twice (14)	P
Maternal SVL (cm)	50.1 \pm 4.5	51.4 \pm 5.7	47.7 \pm 4.7	0.20
Initial body mass (g)	116.1 \pm 36.0	113.4 \pm 40.3	114.1 \pm 23.1	0.26
Number of palpated eggs	7.3 \pm 2.0	6.6 \pm 1.8	6.5 \pm 1.9	0.63

¹Values are expressed as means \pm SD, sample size is indicated in parentheses. SVL = snout vent length. See text for statistics.

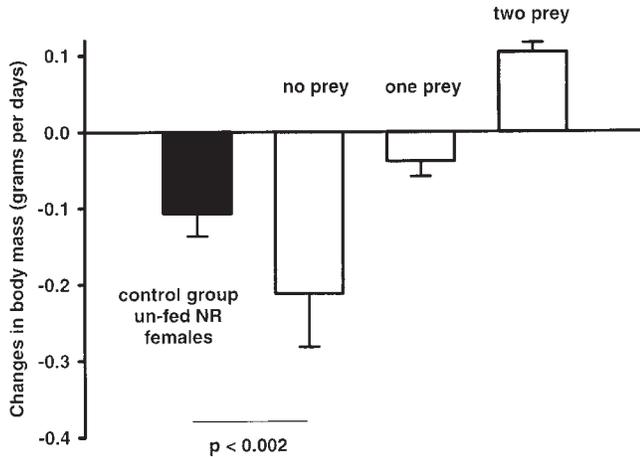


Fig. 1. Effects of diet on female daily mass change (in grams per day scaled with initial body mass) during the course of gestation. Error bars represent standard error. See text for statistics.

length (ANCOVA, $F(2,32) = 0.57$; $P = 0.57$) or mean offspring mass (ANCOVA, $F(2,32) = 0.55$; $P = 0.58$) were detected (Table 2). However, females that ate twice were in higher body condition than females that fasted or ate only one prey (ANOVA, $F(2,32) = 5.54$; $P < 0.008$; Fig. 2).

A positive relationship was detected between mass change during pregnancy and female post-partum body condition ($r = 0.37$, $n = 35$, $P < 0.02$). Using a repeated measure ANOVA (with diet as the factor and measures of body mass at ovulation, pre-parturition, and post-parturition as dependent variables), we found a significant effect of diet on mass changes over pregnancy (Wilk's lambda = 0.35; $F(6,62) = 13.21$; $P < 0.00001$; specific diet effect, $F(2,33) = 6.67$; $P < 0.003$; Fig. 3).

DISCUSSION

Comparisons were made in the feeding behaviour among three groups of pregnant vipers and with a control group of nonpregnant snakes. Pregnant females accepted prey most of the time (41 of 45 feeding occasions). This observation clearly invalidates the hypothesis of an intrinsic (physiological or anatomical) origin of anorexia during pregnancy. Dramatic reduction of food in-

take reported in the field is thus a facultative phenomenon and appears to be a consequence of modification in the activity pattern. In female viviparous snakes, important behavioural changes are associated with gestation (i.e., increase in basking rate, physical burden, Birchard et al., '84; Seigel et al., '87; Brodie, '89). In female aspik vipers, gestation is accompanied by a drastic reduction of the home range of monitored females from 30 to a few square meters (Naulleau et al., '96). Pregnant females also adopt higher thermal preferences and substantially increase basking time (Saint Girons, '52; Bonnet and Naulleau, '96). Thermal conditions are important to optimize embryonic developmental speed along with many offspring traits in squamate reptiles (Fox et al., '61; Packard and Packard, '88; Shine et al., '97). If changes in gravid female thermal preferences optimize developmental rates of the embryos, interference with other activities may also occur. Most notably, the time devoted to thermoregulation will trade off with the time spent foraging. In this study, we facilitated feeding behaviour by placing prey very close to the snakes. In support of this, anecdotal cases of gravid females with a prey in the stomach (even in late gestation) have been reported in the field (Naulleau, '97). Those females were extremely sedentary (i.e., not engaged in foraging activities) as indicated by extensive radio tracking data (Naulleau et al., '96) and thus were probably "lucky" in catching voles passing very close to the basking site. The same situation has been documented in a closely related species, the adder (*Vipera berus*, Madsen and Shine, '92).

As food was accepted, it was possible to explore the effects of the different diets. Food intake significantly affected the pattern of mass change during gestation (Fig. 1). The higher body mass loss detected among unfed pregnant females in comparison to the control group suggests that metabolic expenditure associated with embryonic development is high. Data on fasting pregnant females allowed us to assess the relationship between daily mass loss during pregnancy (i.e.,

TABLE 2. Characteristics of the offspring produced, considering the number of prey consumed by pregnant females during gestation¹

Offspring trait	No prey (9)	One prey (16)	Two prey (10)	P
Mean offspring mass (g)	5.7 ± 1.3	6.0 ± 1.5	5.5 ± 1.1	0.58
Mean offspring SVL (cm)	17.4 ± 1.4	17.1 ± 1.1	17.2 ± 1.2	0.57

¹Values are expressed as means ± SD, sample size (number of litters per group) is indicated in parentheses. SVL = snout vent length. See text for statistics.

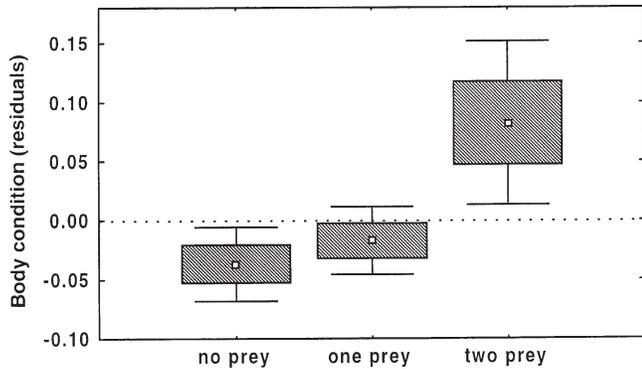


Fig. 2. Effects of diet on female post-partum body condition. Females eating twice differed significantly from females fasting or eating once. White squares represent mean value, hatched squares represent standard error, and error bars represent 1.96 standard error.

metabolic expenditure) and reproductive output characteristics. Interestingly, the magnitude of mass loss was not correlated with total litter size ($n = 9$, $r = 0.06$, $F(1,7) = 0.02$, $P = 0.86$) or, more importantly, fit litter size ($n = 9$, $r = 0.27$, $F(1,7) = 0.56$, $P = 0.48$). Thus, metabolic expenditure during pregnancy appears to be the consequence of an increase in metabolic rate independent of fecundity.

Food intake during gestation did not influence characteristics of the litter but did enhance the post-partum body condition of the females. Energy intake permitted the snakes to compensate for the high metabolic expenditure of gestation. Interestingly, such effects were only detected for females that ate two preys. Perhaps the first prey

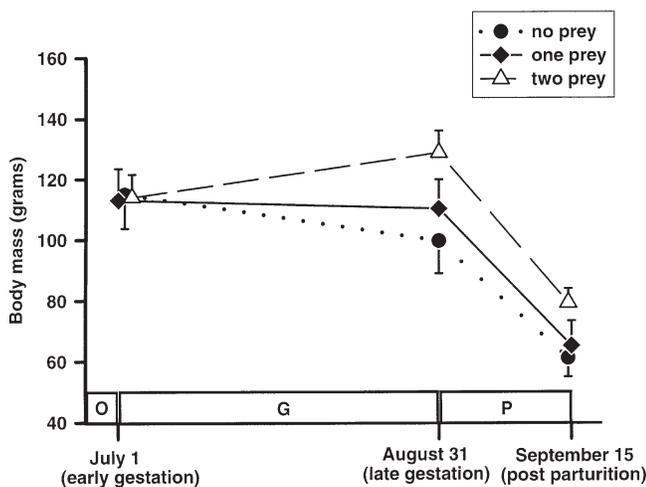


Fig. 3. Influence of diet on pattern of mass changes during the experiment. Symbols represent size-adjusted body mass ± 1 standard error. O: ovulation; G: gestation; P: parturition.

consumed is devoted to the reconstruction of digestive structures, as has been documented in infrequent feeders such as snakes (Secor and Diamond, '95; Cossins and Roberts, '96).

The dramatic reduction of feeding activities during pregnancy constitutes a substantial component of the total energy expenditure of reproduction in female aspik vipers. However, anorexia during pregnancy can only be considered as a cost of reproduction if it entails a reduction of the residual reproductive value. In this species, the female reproductive cycle is largely influenced by fat store recovery. Results gathered in a related work (Bonnet et al., 2000) indicate that post-partum body condition is a reliable predictor of survival and probability of future reproduction. Females that feed during pregnancy should benefit from higher post-partum body condition in terms of survival, and they may also be able to breed again and sooner than unfed females (unpublished data).

This study shows that, if most energy investment into the litter occurs prior to ovulation (Bonnet, '96), gestation also generates significant energy expenditure at two distinct levels: 1) the significant somatic mass loss of fasting pregnant females suggests that energy expense to sustain embryo development is high; and 2) the strong reduction of food intake observed in the field is an additional energetic cost. Due to its indirect origin, the magnitude of this later cost should be driven by current level of food availability, notably by marked year-to-year variation in prey (voles) density reported in the field (Delattre et al., '92; Bonnet et al., 2001a).

Despite the limited sample size ($n = 9$), the fecundity-independent nature of metabolic cost associated with pregnancy agrees with results gathered by Madsen and Shine ('93), who reported significant fixed costs in the adder (*V. berus*). Such fecundity-independent costs are probably a widespread phenomenon influencing the evolution of life history strategies (Bull and Shine, '79). In the case of the aspik viper, the integration of those particular energetic costs will help to further understand the "all or nothing" system of energy allocation displayed by this species (Bonnet and Naulleau, '96; Bonnet et al., 2001c [in press]).

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