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The effects of body size, age, and food intake during pregnancy on reproductive traits of a viviparous snake, Thamnophis ordinoides

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The effects of body size, age, and food intake during pregnancy on reproductive traits of a viviparous snake, *Thamnophis ordinoides*[1]

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Abstract: Litter characteristics of viviparous snakes presumably can be influenced by the mother's state (*e.g.,* mass) at the onset of pregnancy, by food acquired during vitellogenesis, or by food eaten by the mother during pregnancy and delivered to the developing embryos via the placenta. Alternatively, food consumed while pregnant could be allocated to the female herself, potentially influencing her future survivorship and/or reproduction. We tested the effects of food consumption during pregnancy on litter traits of the garter snake, *Thamnophis ordinoides*, along with the effects of body size and age of mother. We also measured trade-offs between traits. Age was significantly correlated with body size of female snakes, but it had no direct influence on reproductive traits. Initial body size, by contrast, especially snout-vent length, significantly and positively influenced litter size and mass. Food intake by gravid females declined during pregnancy, and snakes became relatively anorexic prior to giving birth; their appetite resumed following parturition. Snakes offered smaller amounts of food while pregnant ate less than those fed *ad lib*, but had similar postpartum appetites. Higher food intake during pregnancy resulted in higher postpartum mass of females, but not higher litter mass or size of offspring. There was strong evidence of a trade-off between litter size and offspring size and between postpartum mass and litter mass. Overall, our data are consistent with the hypothesis that reproductive traits of viviparous snakes are determined proximately by previously accumulated stores (capital) and/or food consumed during vitellogenesis (income), but not by resources acquired during pregnancy.
Keywords: anorexia, capital *versus* income, demography, life history, snakes, trade-offs.

Résumé : Les caractéristiques des portées des serpents vivipares pourraient être influencées par l'état de la mère (indiqué par exemple par la masse) au début de la gestation, par la nourriture ingérée par la mère pendant la vitellogenèse ou par la nourriture ingérée pendant la gestation et transmise par le placenta aux embryons en formation. Cela dit, la femelle pourrait aussi utiliser la nourriture consommée pendant la gestation de manière à influencer sa survie et sa reproduction future. Nous avons vérifié, chez la couleuvre du Nord-Ouest (*Thamnophis ordinoides*), les effets de la consommation de nourriture pendant la gestation de même que les effets de la taille corporelle et de l'âge de la mère sur les caractéristiques des portées. Nous avons également mesuré les compromis entre ces caractéristiques. L'âge des femelles est significativement corrélé à leur taille, mais n'a aucune influence directe sur les caractéristiques de la reproduction. La taille corporelle initiale, en particulier la longueur entre le museau et le cloaque, influence pour sa part de façon significative et positive la taille et la masse des portées. Les femelles gravides ingèrent de moins en moins de nourriture pendant la gestation et les serpents deviennent en quelque sorte anorexiques avant la naissance des jeunes. Leur appétit revient après la parturition. Les femelles gestantes à qui de petites quantités de nourriture sont offertes mangent moins que celles nourries *ad libitum*, mais leur appétit est similaire en post-partum. Les femelles ayant consommé une plus grande quantité de nourriture pendant la gestation ont une masse plus élevée en post-partum, mais elles ne donnent pas le jour à des portées de masse supérieure ni à un plus grand nombre de petits. Il existe un compromis évident entre la taille de la portée et celle des jeunes, ainsi qu'entre la masse de la femelle en post-partum et celle de la portée. Dans l'ensemble, les résultats corroborent l'hypothèse selon laquelle les caractéristiques de la reproduction chez les serpents vivipares sont déterminées par les réserves accumulées par la femelle (le capital) ou par la nourriture consommée pendant la vitellogenèse (les revenus). Les caractéristiques de la reproduction ne sont toutefois pas liées à la consommation de nourriture pendant la gestation.
Mots-clés : anorexie, capital *versus* revenus, compromis, démographie, histoire de vis, serpents.

Nomenclature: Kirk, 1979.

Introduction

A prime concern of life-history theory is how the costs incurred in allocating time and energy to one activity *versus* another (*i.e.,* "trade-offs", such as reproducing *versus* growing; Reznick, Nunney & Tessier, 2000) shape the evolution of schedules of demographic events in a lifetime (Roff, 1992; Stearns, 1992). Broad patterns of life-history evolution are necessarily studied at higher taxonomic levels, and there is some debate as to whether meaningful life-history "tactics" can be discerned at the intraspecific level (Stearns, 1980; Brown, 1983). However, the study of intraspecific or intrapopulation variation in life-history traits can tell us what proximate factors are involved in influencing variance of expression (Brown, 1983), including phenotypic plasticity (Brown, 1985); traits within populations ultimately are the source of adap-

tive change (Bennett, 1987). Furthermore, individual variation in resource acquisition (and thereby life-history traits) has important consequences for population dynamics (Lomnicki, 1988).

In recent years, research on squamate reptiles, including snakes, has made important contributions to our understanding of the evolution of life histories and demographic traits (Shine, 1980; Ford & Seigel, 1989; Shine, 1995; Schwarzkopf, 1996; Doughty & Shine, 1997). Many species of snakes and other reptiles are considered to be classic examples of "capital" breeders (Doughty & Shine, 1997; Bonnet, Bradshaw & Shine, 1998; Doughty & Shine, 1998). In rattlesnakes, for example, reproductive frequency of individual females depends on a female's ability to garner resources in the year(s) prior to reproducing (Macartney & Gregory, 1988). However, snakes also would be "income" breeders, at least partly, if they directed resources acquired during vitellogenesis or, in the case of viviparous species, also during gestation, towards producing more or larger progeny. The latter would be possible only if placentotrophy is well developed and food intake during pregnancy can influence offspring size (Shine & Downes, 1999). Gregory and Skebo (1998) showed that food intake by garter snakes (*Thamnophis elegans*) during pregnancy did not influence size or number of offspring. Although they did not test the effect of food intake during vitellogenesis, their data do help explain why food intake can be low in pregnant snakes (Gregory, Crampton & Skebo, 1999).

In this study, we tested how variation in characteristics of female northwestern garter snakes (*Thamnophis ordinoides*) early in pregnancy and in their feeding behaviour during pregnancy influence reproductive traits. Given what we knew about limited placental function in *T. ordinoides* (Stewart *et al.,* 1990), plus data from a congener (Gregory & Skebo, 1998), we predicted that food consumed during pregnancy would contribute to postpartum size of the mother rather than to litter mass. Thus, we anticipated that variation among females in litter characteristics would result from initial variation in female size or condition rather than from variation in food consumption while gravid. A novel feature of our study is that we also estimated the ages of females, via skeletochronology of tail vertebrae (Waye, 1999; Waye & Gregory, 1998), and tested the effect of age on reproductive traits. Although body size and age are likely to be correlated, they also might have separate and independent effects on other life-history traits (Bronikowski & Arnold, 1999). Finally, given that resources available for growth and reproduction are finite, we expected to find evidence of trade-offs between competing traits (*e.g.,* litter size *versus* offspring size, litter mass *versus* postpartum mass).

Methods

We collected 31 apparently pregnant *Thamnophis ordinoides* in May 1999 from six sites on southern Vancouver Island, British Columbia. All snakes were measured (snout-vent length, SVL), by stretching them along a metre stick, and weighed on an electronic balance. They were housed in individual plastic cages (41 × 28 × 15 cm), with newspaper substrate and water *ad lib*, in an air-conditioned room with a constant temperature of 16 °C. A heat strip under one end of each cage provided a temperature gradient of about 18-30 °C (see Gregory, Crampton & Skebo, 1999; Gregory, 2001). Unlike Gregory, Crampton, and Skebo (1999) and Gregory (2001), we did not record positions of snakes in cages on a regular basis. Furthermore, because the cage racks were against a wall, the warm end of each cage also was the darker end.

We randomly divided the snakes into two groups, with the constraint that we attempted to ensure equal size distribution in each. One group was fed dew worms (which this species eats in the field) *ad lib* twice a week for the duration of the experiment; the other was offered about half of what an "*ad lib*" snake of similar body mass would eat. The main purpose of dividing the snakes into two feeding groups was to help generate variance in the amount of food consumed among snakes. We recorded the amount eaten (mass of worms) at each meal. Following parturition, all snakes in both groups were fed *ad lib*. Snakes were weighed once a week until they were close to parturition; then they were weighed twice a week. The last weighing before parturition provided an estimate of prepartum mass.

Within 24 h of parturition, we counted all offspring (including dead and undeveloped young: Farr & Gregory, 1991; Gregory, Larsen & Farr, 1992) and weighed the complete litter. Although we appreciate the argument that number of young, perhaps including stillborns (Bronikowski & Arnold, 1999), is a more meaningful measure of litter size from the point of view of population dynamics, undeveloped eggs do represent energetic investment by the female. They thus are important from a life-history perspective. Furthermore, inclusion of such eggs allows comparison with snakes dissected in an early stage of embryonic development (*e.g.,* we used dissection to determine litter size of two snakes that died before they gave birth). We also measured the SVL and mass of each live neonate and weighed the mother. Unlike Gregory and Skebo (1998), we also measured SVL of the mother following parturition, in order to obtain an estimate of growth during pregnancy.

Immediately after parturition, we cut off the distal portion of the mother's tail (usually about 5 mm) with scissors cleaned in alcohol. We fixed, dehydrated, and mounted tail tips according to Waye and Gregory (1998). We cut sections 15 μm thick on an AO Spencer "820" microtome and mounted them on slides coated with Haupts' solution. These were stained in 1% toluidine blue. Counting of growth rings in these samples was preceded by practice counts on a collection of tail sections from known-age snakes. We also took tail samples from dead snakes and from snakes that did not give birth.

We performed statistical analyses using SPSS 9.0 (SPSS Inc., Chicago, Illinois) and SAS 8.0 (SAS Institute Inc., Cary, North Carolina). Analyses consisted of regression/correlation, analysis of variance (ANOVA), and analysis of covariance (ANCOVA). Because of non-orthogonality of data, we used Type II or Type III sums

of squares in calculating F-values. We assessed the assumptions of parametric tests by examining plots of residuals. To better satisfy those assumptions, we used logarithmically (base e) transformed data in all analyses.

We used ANOVA or ANCOVA to compare mean variable values between feeding treatment groups. However, although straightforward, this approach masked considerable variation in food consumption among individuals within each group. In all remaining analyses, therefore, we pooled the two feeding groups and treated feeding level as a continuous, rather than categorical, variable.

We initially examined simple correlations among variables in search of patterns. However, we derived our major conclusions from multiple regression analyses. We first divided our variables into two sets: predictors, either initial characteristics of female snakes (age, SVL, mass) or characteristics of pregnancy (amount of food eaten), and responses (litter size, offspring size, litter mass, postpartum mass, and SVL). Thus, predictors were treated initially as independent variables and responses as dependent on them. We then separately regressed each of the response variables against the full set of predictor variables. All of these regressions ignore the influences of reproductive traits on each other; those effects are considered in the regressions exploring trade-offs below.

To avoid problems stemming from collinearity among predictor variables (Graham, 2003), we calculated tolerance values in each analysis to ensure that no independent variable would be retained in a regression if its tolerance fell below 0.15 (slightly more conservative than the cutoff of 0.10 suggested by Quinn & Keough, 2002). No variables were dropped from analyses on this basis. We then tested all possible subsets of independent variables and chose the simplest (*i.e.,* fewest predictors) regression model that best "explained" variation in the response variable, based on minimization of Akaike's Information Criterion (AIC, corrected for small sample size; Johnson & Omland, 2004). We found strong agreement between AIC and other criteria for choosing the "best" model (*e.g.,* BIC, adjusted R^2; Quinn & Keough, 2002; Johnson & Omland, 2004). We also used unadjusted R^2 as an indicator of overall fit of each final regression model (but see Anderson-Sprecher, 1994).

Trade-offs between traits usually cannot be assessed using simple correlations between those traits because of the influence of other variables on either or both; thus, a multiple regression approach is again appropriate. However, which of the two variables of interest should be treated as predictor and which as response is not so clear. We used a path model in Gregory and Skebo (1998) to designate predictor and response variables in regressions for testing trade-offs. We then summarized the trade-off using the partial correlation between the two variables of interest, with other relevant variable(s) held constant. This contrasts slightly with Gregory and Skebo's focus on semi-partial correlations.

In multiple regression, semi-partial and partial correlation are best viewed as expressing two different aspects of the same problem. The squared semi-partial correlation (not just the semi-partial correlation as noted incorrectly by Gregory and Skebo, 1998) represents the absolute increment in overall R^2 attributable to adding X_i after all the other independent (or X-) variables are already in the equation. The squared partial correlation, by contrast, is the proportional reduction of the remaining variation in Y (dependent variable) not accounted for by the other X-variables, but accounted for by X_i (Nie *et al.,* 1975).

We do not present data on body condition (residuals from a regression of mass on SVL) in this study. Body condition of capital breeders prior to vitellogenesis can influence whether or not a female breeds in a given year (Bonnet *et al.,* 2001), but all the snakes we used were already pregnant when we collected them. Similarly, in income breeders, reproductive status should depend on resources acquired during vitellogenesis, not on body condition later in pregnancy. Furthermore, traits that we measured (*e.g.,* litter mass) should be related to absolute mass of mother rather than relative mass (*i.e.,* all else being equal, a larger, heavier snake should have a heavier litter than a smaller snake of equivalent condition).

Results

For various reasons (snakes that were either not pregnant or resorbed their eggs, mortality, or otherwise incomplete records), only 24 snakes (13 "*ad lib*" and 11 "less fed"), all evidently in good health throughout the experiment, completed pregnancy. Most of our statistical analyses are restricted to these 24 snakes, except for simple correlations where we had some data from other snakes (adding these animals to analyses did not affect the conclusions). The age of all but two snakes could be estimated; thus, sample size for most of our multiple regression analyses was reduced to 22. One neonate escaped before we could determine which litter it came from; we did our analyses several times, successively adding this neonate to litters born around the same time as we discovered it, but this had no influence on any conclusions, so we left it out. Although we did not record positions of snakes in cages, most snakes usually were seen at the warm ends of their cages.

Age was significantly correlated with initial SVL ($r = 0.46$, $P = 0.01$, $n = 29$, Figure 1). Initial SVL was positively correlated with litter size ($r = 0.43$, $P = 0.03$, $n = 26$) and with litter mass ($r = 0.55$, $P = 0.02$, $n = 24$). When we partialled out age, the relationship between SVL and litter size changed little in strength ($r = 0.49$, $P = 0.02$, $n = 22$). Age by itself was unrelated to litter size ($r = 0.21$, $P = 0.33$, $n = 24$) or litter mass ($r = 0.18$, $P = 0.42$, $n = 22$). Neither SVL nor age was significantly correlated with average offspring mass.

There were very strong correlations between the two measurements of SVL and the three measurements of mass (*e.g.,* initial SVL and initial mass, $r = 0.92$, $P < 0.0001$, $n = 30$; postpartum SVL and postpartum mass, $r = 0.84$, $P < 0.0001$, $n = 24$). However, age was correlated only with initial mass ($r = 0.53$, $P = 0.004$, $n = 28$). Litter mass also was positively correlated with various measures of female mass (*e.g.,* prepartum mass, $r = 0.80$, $P < 0.0001$, $n = 24$).

Snakes in the two feeding regimes were not significantly different, on average, in prepartum characteristics (Table I), whether or not SVL was included as a covari-

ate. The snakes that were offered lower amounts of food usually ate somewhat less than half of what "*ad lib*" snakes would eat (Figure 2); two of the former group did not eat at all while pregnant (although only one of these was used in our main analyses). The lower diet did not seem to affect the snakes negatively, and there was no difference in litter size, offspring size, or number of dead or undeveloped young between the two groups (Table I; SVL used as a covariate, slopes equal). However, postpartum mass did differ significantly between the two groups (ANCOVA, $F_{1, 21} = 8.14$, $P = 0.01$, SVL covariate, slopes equal). All snakes stopped feeding 1 to 5 weeks before parturition (Figure 2). After parturition, when all snakes were fed *ad lib*, feeding increased dramatically in every individual; by two weeks after parturition, there was no difference in food consumption between the two groups, but neither fed as much as prepartum "*ad lib*" snakes at peak consumption (Figure 2).
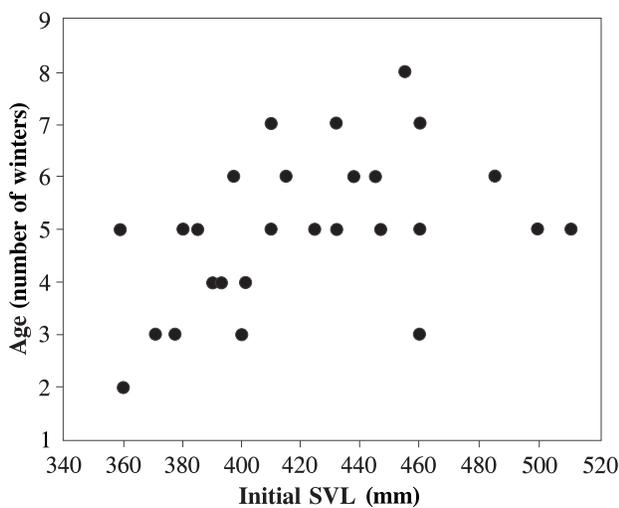

FIGURE 1. Age *versus* initial SVL for female *Thamnophis ordinoides*; two points are coincident and another is hidden. Plot includes data from dissected snakes that died before parturition, although exclusion of these animals does not change strength of relationship (see text).

Thus, the main effect of variation in food consumption during pregnancy was on postpartum mass.

Despite significant differences in postpartum mass, the two groups of snakes did not differ significantly in average increase in SVL during pregnancy, although "less fed" snakes actually grew more on average (Table I); this difference bordered on significance when tested by simple ANOVA ($F_{1, 22} = 3.42$, $P = 0.08$), but was clearly nonsignificant when we included initial SVL as a covariate ($F_{1, 21} = 1.50$, $P = 0.23$; slopes equal). Overall, change in SVL was negatively correlated with initial SVL ($r = -0.57$, $P = 0.004$, $n = 24$); that is, larger snakes grew less. To test for a possible trade-off between change in mass *versus* change in SVL, we regressed postpartum mass against initial mass and postpartum SVL against initial SVL and then tested the correlation between the residuals ($r = -0.19$, $P = 0.37$, $n = 24$).

Of variables characterizing initial conditions and pregnancy, initial SVL had by far the major influence on litter characteristics and postpartum variables; in fact, in most cases, it was the only independent variable retained in the "best" regression model (Table II). As above, amount eaten figured only in the analysis of postpartum mass and again had a highly significant positive effect. Age was retained in one of the final models and had a strong negative effect on postpartum mass, all other factors held constant. We detected no significant effects of any variables on neonate mass.

Presumably, prepartum mass represents the cumulative effect of initial conditions, food eaten during pregnancy, and the mass of the full-term litter. When we regressed prepartum mass against initial SVL, amount eaten, and litter mass, the "best" model retained all three variables and was highly significant ($F_{3, 20} = 84.81$, $P < 0.0001$; $R^2 = 0.93$); all three independent variables had highly significant positive effects (all Ps < 0.002; all tolerance values high). We thus used prepartum mass in assessing trade-offs between life-history traits.

The simple correlation between litter size and average neonate mass was negative, but nonsignificant ($r = -0.22$, $P = 0.31$, $n = 24$). However, when we regressed average

TABLE I. Summary of characteristics of two groups of pregnant *Thamnophis ordinoides*. Values are mean (SD, range). Females that did not complete parturition ($n = 6$) are excluded (see text). The largest female in the "*ad lib*" group is an outlier (see text); exclusion of this individual changed means presented here very little, but reduced SD for several variables. "Litter" and "progeny" include live and dead young, plus undeveloped yolks, except where indicated otherwise. Sample sizes are 11 for "less fed" snakes and 13 for "*ad lib*" snakes (except for age, for which $n = 11$, and average SVL of live littermates, for which $n = 12$). Untransformed data are presented here, but analyses were done on $\log_e$-transformed data, as indicated in text.

Variable	"Less Fed" group	"*Ad Lib*" group
Age (number of winters)	5.4 (1.36, 3-7)	5.3 (1.42, 3-8)
Initial SVL (mm)	402.5 (27.51, 359-460)	423.0 (40.19, 371-510)
Postpartum SVL (mm)	413.4 (27.23, 366-466)	429.1 (36.48, 380-510)
Initial mass (g)	38.8 (9.37, 24.5-54.5)	42.8 (14.69, 27.0-79.0)
Prepartum mass (g)	40.7 (10.23, 26.3-56.3)	53.2 (21.44, 26.4-111.1)
Postpartum mass (g)	25.4 (5.98, 16.5-35.9)	33.7 (9.64, 23.8-60.4)
Litter mass (g)	9.1 (3.68, 2.8-14.0)	11.1 (6.03, 2.6-28.7)
Average mass of progeny in litter (g)	1.3 (0.45, 0.3-1.8)	1.3 (0.27, 0.7-1.7)
Average SVL of live littermates (g)	129.8 (6.04, 117.0-139.9)	133.7 (6.36, 117.7-143.3)
Litter size	7.4 (2.11, 3-11)	8.8 (4.15, 2-19)
Number of dead young in litter	0.4 (0.51, 0-1)	1.8 (2.09, 0-7)
Number of undeveloped eggs in litter	1.2 (2.64, 0-7)	0.7 (1.55, 0-5)
Amount eaten prepartum (g)	35.4 (20.36, 0.0-69.9)	96.8 (36.17, 52.6-176.2)

neonate mass on litter size and prepartum mass, we obtained a clear demonstration of a trade-off between these two traits ($r_{partial}$ = -0.61, P = 0.002). Similarly, although the simple correlation between litter mass and postpartum mass was positive (r = 0.46, P = 0.02, n = 24), regression of postpartum mass on litter mass and prepartum mass yielded a highly significant negative partial correlation between these two traits, again indicative of a trade-off between them ($r_{partial}$ = -0.71, P = 0.0002).

Discussion

A logical starting point for describing life histories is the age-based schedule of births and deaths, as expressed in standard life tables (Roff, 1992), and indeed, much of life-history theory is age-based (Partridge & Harvey, 1988; Brommer, 2000). For many kinds of organisms, however, demographic traits are measured routinely with respect to body size (or even a life-history "stage") rather than age. Such organisms fall into essentially two categories: 1) those for which both age and size data are available, but size is considered the better predictor of

demography (Charron & Gagnon, 1991; Werner & Caswell, 1977); 2) those for which age data are unavailable and body size is used as a surrogate (Sauer & Slade, 1985). For organisms in the second category, size may in fact be an equal or better predictor of values of life-history traits (Roff, 1992), and hence of population dynamics, than age, but this obviously has not been assessed in such cases. Size-based demographic models are in widespread use (Caswell, 1989), but they may yield different results from age-based models (Babcock, 1991). Furthermore, it is possible that age and size have separate or interacting effects on demographic characteristics. Thus, a complete analysis of demography may require knowledge of both size and age (Law, 1983). Alternatively, age may be included as one component of a more general physiological "state" of a life history (McNamara & Houston, 1996).

In *Thamnophis ordinoides* in this study, age was significantly correlated with body size. This is consistent with data on *T. elegans* (Waye, 1999), but different from *T. sirtalis*, in which there was no relationship (Waye & Gregory, 1998). However, despite this correlation, we could demonstrate no effect of age on reproductive characteristics. Thus, with respect to reproduction at least, the demography of these snakes is better described by size-based models than age-based. Olsson and Shine (1996) reached a similar conclusion in a study of lizards. Nonetheless, several cautions are in order before abandoning the need to determine age.

First, the relationship between age and reproductive traits may vary among populations, even within species (Bronikowski & Arnold, 1999), so the generality to emerge eventually may be that each case needs to be assessed separately; the question then would shift to what factors influence whether age is important. Second, age can affect traits not measured in this study; for example, in some animals, maternal age may have significant effects on physiological characteristics, as well as body size, of offspring (Wang & vom Saal, 2000). Third, even if age does not directly influence reproductive output, age of first reproduction is still a key factor influencing potential rate of population growth (Cole, 1954). Age and size may play variable roles in determining sexual maturity (Policansky, 1983; Gibbons & Greene, 1990) and timing of reproduction (Cuadrado & Loman, 1999). Organisms also have finite lifespans, and age therefore must be taken
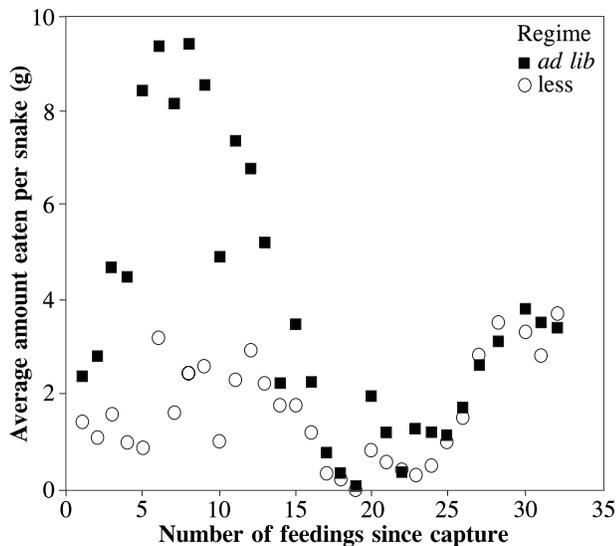

FIGURE 2. Average amount of food eaten per snake at each feeding since capture (including meals at which no food was eaten); n = 24. Most births occurred between feedings 17 and 25, inclusive.

TABLE II. Summary of multiple regressions testing effects of predictors (initial characteristics of females or characteristics of pregnancy) on reproductive and postpartum traits. Only the "best" model (based on minimizing AIC, as explained in text) is presented in each case. Examination of competing models ($\varnothing$AIC ″ 2) revealed no additional or conflicting effects of any predictor variables. Sign of relationship (+ or) and P-value are given for each independent variable. All analyses were done on log_e-transformed data, using only the 22 snakes for which we had complete records. Note slight difference in P for correlation between litter size and initial SVL from that reported in text (the latter included snakes not incorporated in these analyses because of incomplete data).

Dependent variable	Independent variables in "best" regression	Overall significance	R^2
Average neonate mass	Initial SVL (+, 0.20)	$F_{1, 20}$ = 1.78; P = 0.20	0.08
Litter mass	Initial SVL (+, 0.002)	$F_{1, 20}$ = 12.50; P = 0.002	0.38
Litter size	Initial SVL (+, 0.02)	$F_{1, 20}$ = 6.05; P = 0.02	0.23
Postpartum mass	Amount Eaten (+, < 0.0001)	$F_{4, 17}$ = 46.71; P < 0.0001	0.92
	Initial SVL (+, 0.01)		
	Initial Mass (+, 0.05)		
	Age (, 0.07)		
Postpartum SVL	Initial SVL (+, < 0.0001)	$F_{1, 20}$ = 692.10; P < 0.0001	0.97

explicitly into account in any discussion of, for example, lifetime reproductive success, lifetime changes in reproductive effort, or senescence. Finally, age might influence probability of survivorship (Berkeley, Chapman & Sogard, 2004) and therefore population dynamics.

Two previous long-term studies have examined the influence of age on litter characteristics of snakes. Bronikowski and Arnold (1999) studied six populations of *Thamnophis elegans* for two decades and found age effects in some populations but not others. Populations with annually stable food supplies showed rapid body growth, low survivorship, and no age effects. However, those that were subjected to great annual variation in food supply showed slow growth, high survivorship, and significant age effects on litter characteristics: older females had larger litters. In a 7-y study on a single population of adders (*Vipera berus*), Madsen and Shine (1992) saw no age effect, other than its influence on SVL. Madsen and Shine (1992) also found that between-snake variation can be much greater than between-year variation in individual snakes, which could produce spurious correlations of reproductive traits with age, depending on the age distribution in the population. Only multi-year studies can address this issue.

Presumably, maximum litter size in viviparous snakes is fixed at ovulation and any influence of food intake thereafter on reproductive output could affect (via placentotrophy) only offspring size, but not their number (although it plausibly might affect the number surviving). However, food consumption by pregnant *Thamnophis ordinoides*, like that by pregnant *T. elegans* (Gregory & Skebo, 1998), affected only postpartum mass, not offspring size or litter mass. Therefore, the main effect of feeding during pregnancy in this species is on growth, survivorship, and/or future reproduction of the mother. Placental transport of inorganic nutrients to embryos is known in *T. ordinoides*, but organic nutrients are supplied principally via the yolk (Stewart *et al.,* 1990). Thus, embryos may derive benefits from income during pregnancy, but the majority of their required nutrients have been laid down before development commences (lecithotrophy). Whether those nutrients are "income" during vitellogenesis, "capital" from before vitellogenesis, or a bit of both, is another question.

Even in mainly capital breeders (*e.g., Vipera aspis*, Bonnet *et al.,* 2002), fecundity may be further significantly influenced by income acquired during vitellogenesis (Bonnet *et al.,* 2001; Lourdais *et al.,* 2002; Lourdais *et al.,* 2003). Either way, body mass or condition during pregnancy is almost certain to be correlated with reproductive output and therefore not necessarily reflective of previtellogenic conditions (Bonnet *et al.,* 2001). In this respect, our finding of a strong effect of initial mass on litter mass is not surprising, but only confirmatory. Thus, to determine definitively the extent to which *Thamnophis* are capital breeders, we need to measure parameters such as body mass and condition prior to vitellogenesis and how they are further influenced by food intake until that point.

Capital breeding and/or lecithotrophy allow snakes that are in otherwise good condition to separate feeding and reproduction both spatially and temporally. This is adaptive if food is scarce during the reproductive season, if gravid females move to a safer habitat where food is less abundant, or if foraging endangers the mother or litter (Jönnson, 1997). Many squamates reduce feeding during pregnancy, especially late in gestation (Schwarzkopf, 1996). Gregory, Crampton, and Skebo (1999) found that gravid *T. elegans* fed less than nongravid, even when readily available food was provided *ad lib* with proximate dangers (*e.g.,* predators) removed. Whether pregnant *T. ordinoides* are relatively anorexic throughout pregnancy is unknown because we did not compare them with nongravid females, although they clearly became anorexic towards the end of pregnancy.

Reduced feeding could be a selected trait to prevent the mother from endangering herself or her litter while pregnant. Shine (1980) demonstrated that gravid scincid lizards were slower and preyed upon more often than were males or nongravid conspecifics. Both this study and that of Gregory and Skebo (1998) show that low food intake need not adversely affect the litter, as long as pregnant females thermoregulate (*cf.* Gregory, 2001). However, low food intake during pregnancy does affect postpartum mass and condition of the mother. In some cases, gravid females are fairly emaciated after parturition (Madsen & Shine, 1992) and need to build up reserves either to survive or to reproduce again. In fact, reproduction by the same female may not even be possible in successive years in some cases (Macartney & Gregory, 1988). In garter snakes, reproduction in consecutive years may be the norm, with only occasional seasons skipped by most females, but more field data are needed on this point. Skipping opportunities to reproduce and capital breeding are often associated with similar factors: migration, viviparity, and egg brooding (Bull & Shine, 1979).

A surprising result of this study is that the snakes offered less food did not eat everything offered them (and in two cases not at all), especially considering that the "*ad lib*" snakes ate so much more at a similar stage of pregnancy (Figure 2). What kinds of physiological feedback mechanisms determine whether a gravid snake will feed or not? Can tendency to feed be determined, at least in part, by availability of food? These differences point to plasticity of feeding behaviour in pregnant snakes.

The fact that all snakes, regardless of food intake, ceased feeding well before parturition suggests that anorexia in late pregnancy has little to do with nutritional need. Gregory, Crampton, and Skebo (1999) also observed a decline in food intake to nearly zero before parturition in *T. elegans*, followed by a postpartum increase in consumption, as here (Figure 2). What is additionally surprising in this study is that the "less fed" snakes ate no more than the "*ad lib*" snakes when both groups were fed *ad lib* after parturition and that both ate smaller meals than pregnant "*ad lib*" snakes at peak consumption. Decreases in food intake late in the active season have been observed in the field (Gregory & Stewart, 1975), but this does not explain the difference between our results and those of Gregory, Crampton, and Skebo (1999), in which the postpartum increase in food consumption was more dramatic. Nonetheless, it is possible

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that seasonal variation in tendency to feed influences the postpartum feeding response to some degree.

Trade-offs comprise a central feature of life-history theory (Stearns, 1989; Schluter, Price & Rowe, 1991; Reznick, Nunney & Tessier, 2000), although they can be difficult to measure. For example, if resource acquisition varies among individuals, then two traits may covary positively, even if there actually is a trade-off between them (Tuomi, Hakala & Haukioja, 1983; Doughty & Shine, 1997; Reznick, Nunney & Tessier, 2000). In this study, in which resource acquisition was measured during part of pregnancy, expected negative relationships were revealed between litter size and offspring size and between litter mass and postpartum mass.

Growth in length is important in snakes because body length is often the best predictor of litter size (Seigel & Ford, 1987). Thus, growth in length during pregnancy might partially reduce the impact of current reproduction on future reproduction, provided condition can be regained following parturition. The slight negative relationship between growth in length and mass in our study suggests that growth in length is bought at the expense of mass. Allocation to length *versus* mass may have different implications for life-history traits of snakes and merits more attention.

The results of this study are consistent with similar work on *Thamnophis elegans* (Gregory & Skebo, 1998; Gregory, Crampton & Skebo, 1999) and therefore suggest general patterns within the genus that also likely apply to other viviparous snakes. Food consumed during pregnancy does not increase size or number of offspring, at least not in any gross manner, but does influence body mass following parturition, which has important potential consequences for future reproduction and population dynamics.

Acknowledgements

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