

Reproductive versus ecological advantages to larger body size in female snakes, *Vipera aspis*

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Body size can influence an organism's microevolutionary fitness either via ecological factors (ecological selection) or changes in reproductive output (sexual or fecundity selection). Published studies on sexual dimorphism in reptiles have generally focussed on sexual-selective forces on males, under the implicit assumption that the intensity of fecundity selection in females (and hence, overall selection on female body size) is likely to be relatively consistent among lineages. In this paper, we explore the degree to which larger body size enhances ecological attributes (e.g., food intake, growth, survival) and reproductive output (reproductive frequency, litter size, offspring size, offspring viability) in free-ranging female asp viper, *Vipera aspis*. The less-than-annual reproductive frequency of these animals allows us to make a direct comparison between females in years during which they concentrate on "ecological" challenges (especially building energy reserves) versus reproductive challenges (producing a litter). Because female snakes have limited abdominal space to hold the clutch (litter), we expect that fecundity should depend on body size. However, our data show that larger body size had a more consistent effect on ecological attributes (such as feeding rates and "costs of reproduction") than on reproductive output per se. Indeed, total reproductive output was maximised at intermediate body sizes. These results suggest that variation in female body size among and within species (and hence, in the degree of sexual dimorphism) may be driven by the ecological as well as reproductive consequences of body size variation in both sexes.

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The body size of an organism determines many aspects of its biology. Often, body size influences reproductive success (Reiss 1989, Andersson 1994, Bennett and Hoffmann 1998, Witte and Ryan 1998, Kölliker et al. 1999) as well as the animal's interactions with the physical and biological world (e.g., Pough 1980, Peters 1983, Wikelski et al. 1997, Brown and Bomberger Brown 1998, Thompson and Russell 1998, Tracy 1999). At the same time, body size is extraordinarily variable, at almost every level at which one investigates. Mean size typically varies among congeneric species, among conspecific populations, and between the sexes within a single population (e.g., Fitch 1981, Harvey and Ralls

1985). Also, many populations of ectothermic species include independently functioning individuals over a massive range of body sizes (often, over at least an order of magnitude: e.g., Fitch 1970). This wide range of intrapopulational variation in body size provides a great opportunity to tease apart the microevolutionary influences that act on the body size of an organism (Shuster 1989, Preziosi and Fairbairn 1997, Wikelski and Trillmich 1997).

Ever since Darwin (1871), these influences have been broadly separated into two categories: ecological versus reproductive. Ecological selection (sometimes viewed as a type of natural selection; see Darwin 1871, Arnold

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1994) results in the evolution of traits that maximise organismal survival and optimise growth trajectories, etc (Arnold and Wade 1984, Arnold 1994). Reproduction-related processes fall into two broad types: sexual selection and fecundity selection. Sexual selection is traditionally defined to include cases where traits evolve to enhance mating success in interactions with conspecifics (rivals or potential mates). Fecundity selection involves the evolution of traits that enhance reproductive output directly (e.g. through an increase of body size to accommodate large clutches), rather than via such interactions. The distinction between these three processes (ecological, sexual and fecundity selection) is not always clear. For example, both fecundity and survival may covary with increasing foraging abilities (Madsen and Shine 1992, Forsman and Lindell 1993), and their respective influences are thus inextricably mixed. Nonetheless, such classificatory systems may be helpful to better understand how traits have evolved (Arnold 1994). Some traits are clearly attributable to sexual selection (e.g., sex-specific weaponry, bright colours, chemosensory organs: Andersson 1994, Wilkinson et al. 1998). Just as clearly, other traits have been fashioned by ecological selection (e.g., most types of camouflage coloration, body shapes of larvae in holometabolous insects: Darwin 1871, Arnold 1994) and fecundity selection (e.g., sex differences in body size and shape: Bonnet et al. 1998a). Reproductive and ecological selection can work on traits independently, or in synergy, or in opposition.

Organisms may benefit (or suffer) from larger body size either because of reproductive advantages (such as higher fecundity in females, or greater copulatory rates in males) or because of ecological factors (such as an ability to ingest larger prey or to better withstand predator attacks or thermal extremes: Grigg et al. 1979, Magnhagen 1991, Arnold 1993). In practice, the two kinds of processes are tightly linked, with both types of selection simultaneously operating on the range of body sizes within a population (e.g., Shine 1988, Preziosi and Fairbairn 1997). In most cases it is difficult to distinguish between these two processes because of this strong confounding in space and time. For example, in many species individuals generally feed at approximately the same times and often in the same places as they reproduce (e.g., most herbivorous mammals and passerine birds). The problem persists even in species where reproductive and feeding activities are spatially and/or temporally separated. Several taxa of molluscs, fishes, marine birds and mammals provide good examples of this situation, because the parents cease feeding during certain periods of the reproductive cycle. Although feeding and reproduction are decoupled, reproduction in such cases generally involves profound shifts in habitat use, behaviour and/or physiology (e.g., semelparous cephalopods which

die when spawning, catadromic as well as anadromic fishes, or emperor penguins). Because these shifts concern only reproductive individuals, there is no simple way to compare individuals involved in sexual (reproductive) versus ecological (non-reproductive) tasks.

Our ability to distinguish between the reproductive (sexual selection) versus ecological (natural selection) consequences of different body sizes is enhanced if we can find an organism in which reproductive and non-reproductive phases are separated into discrete individual categories. Ideally, this separation should occur without major modifications of the habitat exploited, either in terms of space (e.g., no great variation in predatory pressures or diet) or time (e.g., seasons). Such a situation will allow us to explore the consequences of body-size variation independently for these two major categories of selective forces.

One major characteristic in a species' ecology facilitates such a separation: less-than-annual reproductive cycles. But it is also necessary to restrict attention to species in which reproduction does not entail drastic shifts in the habitats exploited. This criterion excludes organisms such as marine birds or marine turtles. Finally, a considerable intra-population range of adult body sizes is needed to provide enough variation for quantitative analysis. In species that show these features, we can compare organisms over a wide range of body sizes, under similar ecological circumstances (e.g., season, weather, habitat structure) but with one category of animals focussing almost entirely on reproduction and the other group focussing on the accumulation of energy reserves.

Many kinds of organisms, particularly "capital breeders" provide this kind of opportunity (e.g., Bull and Shine 1979, Clutton-Brock 1991, Jönsson 1997, Bonnet et al. 1998b), but some of the most logistically tractable systems involve temperate-zone snakes (e.g., Duvall et al. 1993, Seigel 1993). Natural populations of snakes typically exhibit large variations in adult body sizes, low vagility, relatively simple morphology and no parental care (hence relatively simple mating systems): all these attributes greatly facilitate interindividual comparisons. Another advantage linked to snake biology is that increasing body size provides more space to hold the clutch (litter) in females, and hence, should be positively linked to fecundity in a relatively straightforward way (Seigel and Ford 1987, Ford and Seigel 1989). Because male snakes do not contribute to the care of their offspring, we expect that females will not compete for mates – and hence, female body size should be subject to fecundity but not sexual selection. Herein, we provide data from a six-year field study on such a snake species, *Vipera aspis*, from central France, and explore the reproductive and ecological consequences of body size for females of this species.

Materials and methods

Sample details and measurements

We studied the aspic viper (*Vipera aspis*) in central western France (close to the village of Les Moutiers en Retz, district 44). This medium-sized (mean adult snout-vent length 48.5 cm, mass 85.5 g) species is abundant (more than 16 adults per hectare – Naulleau and Bonnet 1995) in the mosaic of meadows and regenerating shrubland of our 33-hectare study area. We patrolled the site on almost every sunny day during the vipers' annual activity period (from late February to late October; total searching effort more than 3500 h), captured the snakes by hand, and individually marked them (PIT-Tags) for future identification. All captured snakes were weighed (to the nearest 1 g with an electronic scale), measured (total length and snout-vent length to the nearest 0.5 cm), and the presence of prey items or oviductal embryos was determined via palpation of the abdomen (Fitch 1981). In all sizes of snakes, palpation enabled us to detect small object (as light as 2 g). The snakes ($N = 451$ adult females) were then released at their site of capture.

Because this species is highly philopatric (Naulleau et al. 1996) and the study site is surrounded by habitat unsuitable for vipers (Bonnet and Naulleau 1996), we are confident that any snake not captured over a long period (> 2 yr) had almost certainly died rather than emigrated or avoided capture. Radio-tracking conducted on more than 80 adults (60 females, 20 males) over long periods of time (6 months per year, 1993 to 1997) never revealed any case of emigration. Despite the high population density, we found road-killed individuals in the vicinity of the study zone (which is contained by roads and the ocean) only rarely (three cases in 8 yr), indicating the markedly sedentary habits of these snakes (Bonnet et al. 1999). Gravid female vipers ($N = 139$) were captured 1 d to 3 weeks before parturition (i.e., after the first parturition was recorded in the field each year, generally in late August). These females were maintained in separate cages in the laboratory until they gave birth. We weighed the females every second day during this period, and both the female and her offspring were weighed immediately after parturition.

Analyses

Our analyses deal entirely with female snakes because of the much greater difficulty of quantifying reproductive success in males. This difficulty is particularly great in systems that involve multiple mating by females and the consequent possibility that the number of matings by a male may not translate perfectly into the number of offspring that he sires (e.g., Birkhead et al. 1988, Olsson et al. 1996).

Although snakes are morphologically simple, we have to choose the most useful indicator of size. In our study case, the best measure of body size is snout-vent length (SVL). Body mass may offer a better measure of overall size for some types of animals, particularly for interspecific comparisons because unlike body length, the weight of an organism is less dependent on its shape (Western and Ssemakula 1982, Lindstedt and Calder 1984, Hedges 1985). But in the present study, all the females have the same body plan. Furthermore, although body mass is highly correlated with body length ($r = 0.61$, $N = 387$, $P < 0.0001$), mass is a highly fluctuating, and somewhat imprecise measure. Fat reserves, developing follicles, embryos, and gut contents can account for more than 50% of a snake's "total mass" and all are subject to rapid changes (e.g., at parturition). Thus, body mass is a very labile measure, and a poor descriptor of body size at the intra-population level.

To analyse the effects of body size, we regressed the relevant descriptor of reproductive output or ecological parameters against maternal body size (SVL). In a parallel set of analyses, we divided the range of maternal body lengths (41.5-cm SVL [47-cm total length] to 60 cm SVL [68.5-cm total length]) into nine classes of 2-cm intervals. The smallest (< 44 cm SVL) and largest (> 58 cm SVL) classes encompassed larger size ranges, in order to maintain similar sample sizes within each interval. We calculated means and standard deviations for each reproductive trait over each of these intervals. This system was used for plotting the form of the relationships and was tested statistically as well. In practice, none of the statistical results were changed for analyses based on the full data set, versus on the means for each size category (in all tests, the significance level was very similar). Our rationale for this approach, rather than simply regressing reproductive output measures against body length, was twofold: 1) to graphically reveal patterns more clearly; 2) to prevent undue bias from body-size intervals containing very large numbers of individuals. Statistical analyses were performed with Statistica 5.1 computer software. Each individual was represented only once in the analyses.

Results

Reproductive consequences of body size

The overall result from our analyses was that body size influenced reproductive output, but in rather complex ways: it is not simply an issue of "greater output from larger females".

(1) *Frequency of reproduction* – The proportion of reproductive animals varied significantly among the different size classes of adult females ($\chi^2 = 27.1$, 8 df,

$P < 0.001$). The proportion of reproducing females was highest at intermediate body sizes, and declined at both smaller and larger sizes, but was not positively correlated with body size ($r = 0.30$, $N = 9$, $P = 0.43$; Fig. 1a). These estimates provide only an approximation of actual reproductive frequencies because a viper's reproductive status and its body size influence its catchability through thermoregulatory (basking) requirements (Bonnet and Naulleau 1996). Thus, the actual frequency of reproduction is lower than suggested by the proportion of reproductive animals in our samples because reproductive snakes are more easily captured, and this will be especially true of larger snakes (which are easier to catch). Thus, the decrease in reproductive frequency in larger snakes will be greater than indicated by our data, due to the catchability bias that leads to an over representation of large reproductive snakes.

(2) *Litter size* – The number of offspring in a litter was not significantly correlated with maternal body length ($r = 0.16$, $N = 125$, $P = 0.07$ using the full data set; and $P = 0.43$ using the means for each of the nine size categories). However, the relationship was close to statistical significance (full data set), and the number of ova ovulated (as detected by palpation on females around ovulation time in May–June [3 months before parturition]) was significantly associated with maternal SVL ($r = 0.24$, $N = 154$, $P < 0.005$, full data set; and $P = 0.042$ using the nine size categories). The difference between these two results reflects the fact that some ova are unfertilised, and others are fertilised but die before birth (such ova may disappear during gestation; XB et al. unpubl.). The consequence of these effects is that litter size changes between ovulation and birth in some females, and the magnitude of this change was great enough to obscure the underlying correlation between

maternal SVL and litter size. Nonetheless, the clear pattern is that a female's reproductive output in terms of viable offspring is only very weakly linked to her body size. Even for the “significant” correlation noted above, the relationship was very weak (explaining only 5% of the variance in litter sizes) and the slope was low (a mean increase of only 30% [5.3 to 7.7] in litter size for an increase of 25 cm in maternal SVL).

(3) *Offspring size* – Mean neonatal mass showed a marginally significant positive relationship with maternal body size ($r = 0.19$, $N = 116$, $P < 0.045$, full data set; and $P = 0.06$ using the nine size categories; Fig. 1c). As for the relationship involving litter size (above), the regression explained only a very small proportion (3.5%) of the variance in neonatal size.

(4) *Offspring viability* – The proportion of viable neonates was relatively low overall ($75 \pm 33\%$ of total litter size; range 0 to 100% viability). Stillborn offspring or non-fertilised oocytes were no more frequent in the litters of smaller females than larger animals ($r = 0.10$, $N = 125$, $P = 0.27$, full data set; and $P = 0.88$ using the nine size categories; Fig. 1d). Because ratio measures can introduce statistical artefacts, we repeated this analysis using residual scores from the linear regression between the number of viable offspring and the total litter size as our measure of offspring viability. This analysis yielded the same result as the previous one based on the ratio ($r = 0.08$, $N = 125$, $P = 0.38$, full data set; and $P = 0.55$ using the nine size categories).

(5) *Overall reproductive output* – The most straightforward index of total reproductive output (the combination of litter size and offspring size) is total litter mass; this index positively correlates with body size ($r = 0.24$,

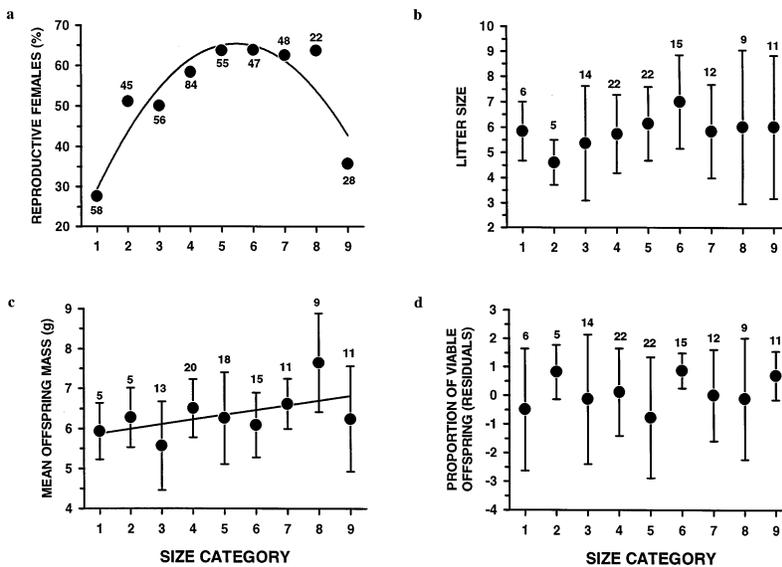


Fig. 1. Reproductive correlates of maternal body size in aspic vipers, *Vipera aspis*. The proportion of reproductive animals is maximized at intermediate body sizes (a). Larger females tend to produce slightly larger litters (b; $P = 0.43$; but $P = 0.07$ with full data set [$N = 125$]) and larger offspring (c; $P = 0.06$; $P = 0.045$ with full data set [$N = 116$]), but the trends are weak. There is no obvious relationship between maternal body size and offspring viability (d). Each symbol represents the mean (\pm S.D. when calculable, as in subsequent graphs) for a 2-cm size class (see Materials and methods), numbers give sample size. See text for statistics.

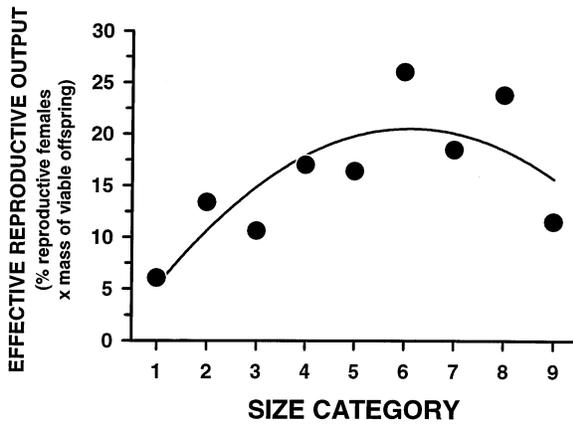


Fig. 2. Total reproductive output (a product of mean reproductive frequency, litter size, offspring size and offspring viability), expressed in terms of mean mass of viable (live-born) offspring per female per year, for each 2-cm snout-vent length interval over the range of adult female body sizes in asp viper, *Vipera aspis*. This index of reproductive fitness is not correlated to body size ($P = 0.14$). See text for statistics.

$N = 115$, $P = 0.011$, full data set; and $r = 0.76$, $N = 9$, $P = 0.017$ using the size categories). Restricting measurements to the mass of viable offspring leads to similar results ($r = 0.23$, $N = 115$, $P = 0.012$, full data set; and $r = 0.72$, $N = 9$, $P = 0.028$ with size categories). The mean total mass of viable offspring produced by a female viper (the product of the probability of reproduction, mean litter size, mean neonatal mass, and offspring viability) provides a measure of total effective reproductive output per female per year for each size class. This index of annual reproductive output aims to reflect the average amounts of energy and materials transformed into viable offspring, and thus provides a

simple estimate of reproductive fitness for a given size class per year. Because litter size and offspring size increased only slightly with maternal SVL, whereas the proportion of reproductive animals declined at the largest size, this overall measure of reproductive output was not significantly correlated with maternal SVL ($r = 0.53$, $N = 9$, $P = 0.14$; see Fig. 2).

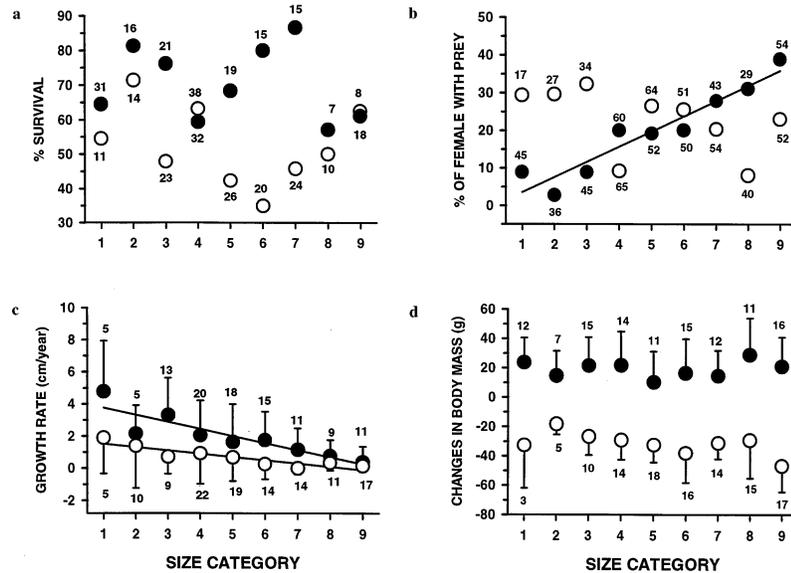
Ecological consequences of body size

The body size of an animal can influence the rate at which it feeds, grows, stores energy reserves, or escapes various potential sources of mortality (Peters 1983, Sinervo and Huey 1990, Sinervo et al. 1992, Brown and Bomberger Brown 1998). Thus, we can investigate the effects of body size on all these traits, and can compare reproductive and non-reproductive animals in terms of these allometries. Differences between these two groups of animals can reveal “costs of reproduction” – that is, effects of reproductive activity on the animal’s survival and energy balance.

(1) *Survival* – Body size did not affect a female viper’s probability of survival, either in reproductive years or in non-reproductive years ($P > 0.5$; Fig. 3a). Contingency-table analysis of snakes in each of the 2-cm SVL intervals detected no significant differences among size classes in survival probabilities (for non-reproductive snakes, $\chi^2 = 6.16$, 8 df, $P = 0.63$; for reproductive snakes, $\chi^2 = 7.16$, 8 df, $P = 0.52$).

(2) *Food intake* – Recently ingested prey items can be accurately detected by palpation, and the proportion of animals containing prey offers an index of the rate of

Fig. 3. Ecological correlates of female body size in asp viper (*Vipera aspis*), with data plotted separately for females in reproductive (open circles) and non-reproductive (filled circles) years of their cycles. Body size had little effect on survival rates (a), but strongly influenced feeding rates of non-reproductive snakes (as indexed by the proportion of freshly captured snakes containing prey ($P < 0.0001$), b) and growth rates of both groups of animals (c; $P < 0.0001$). Rates of annual change in body mass differed between reproductive and non-reproductive females, but were relatively unaffected by maternal body size (d; $P = 0.07$ in reproductive females, and $P = 0.80$ in non-reproductive females). See text for statistics.



prey consumption. Fig. 3b shows that the proportion of snakes with food increased markedly with body size in non-reproductive females ($r = 0.95$, $N = 9$, $P < 0.0001$), but was not associated with body size in reproductive females ($r = 0.41$, $N = 9$, $P = 0.28$). Single-factor ANCOVA (with reproductive status as the factor, SVL interval as the covariate and percentage of specimens with food as the dependent variable) showed that the two groups of snakes differed significantly in the way in which SVL affected feeding rates (interaction between reproductive status and size class: $F_{1,14} = 25.44$, $P < 0.0002$). This result is mainly explained by a behavioural shift during pregnancy: reproductive females concentrate on thermoregulatory activity at the expense of foraging trips (Naulleau et al. 1996). Thus, larger females skip opportunities to take advantage of their greater swallowing capacities, and thus pay a higher “cost of reproduction” in this respect because reproduction entails a greater reduction in food intake for these animals.

(3) *Growth rate* – Fig. 3c illustrates the mean increment in body size (cm SVL/year) against the midpoint of each of the 2-cm SVL intervals, and shows that growth rate strongly decreased with size (as expected for such organisms: Andrews 1982). This reduction in the rate of growth at larger body sizes was evident both in non-reproductive and reproductive females ($r = -0.89$, $N = 9$, $P = 0.001$, and $r = -0.90$, $N = 9$, $P < 0.001$, respectively). However, the slope of the relationship between body size and growth rate was lower for reproductive females than for non-reproductive ones (from the ANCOVA on these data, interaction $F_{1,14} = 6.44$, $P < 0.025$). This difference in slopes reflected the fact that reproductive females of all size classes showed very little growth, whereas small non-reproductive females grew much faster than larger animals (Fig. 3c). Thus, the “cost of reproduction” in terms of reduced body growth during a reproductive year was much greater for a small female than for a large one.

(4) *Changes in body mass.* – When we plotted the data for changes in maternal body mass in the same way as for changes in maternal body length (above), a very different pattern was apparent (Fig. 3d). Non-reproductive females of all body sizes gained approximately similar amounts of body mass, whereas reproductive females of all sizes lost an approximately similar amount (Fig. 3). Statistical analysis shows a trend for mass loss to be slightly greater in larger females in reproductive years ($r = -0.64$, $n = 9$, $P = 0.07$), but no such trend in non-reproductive years ($r = -0.10$, $N = 9$, $P = 0.80$). ANCOVA revealed no significant difference in slopes between data for reproductive versus non-reproductive animals (interaction $F_{1,14} = 3.11$, $P = 0.10$), but a strong difference in intercepts ($F_{1,15} = 258.3$, $P < 0.0001$; see Fig. 3b). Thus, “costs of

reproduction” in terms of maternal mass change were not affected by body size.

Discussion

The distinction between ecological and reproductive components of selection is a powerful, albeit rarely exploited, approach to understand the evolution of body size within populations (Grant and Grant 1995, Brown and Bomberger Brown 1998, Neems et al. 1998). For example, the relative contributions of these two processes to overall microevolutionary pressures on body size have rarely been documented under field conditions (Wikelski and Trillmich 1997, Larsson et al. 1998). Our work differs from previously published studies because we focussed on a single sex (females), comparing individuals involved in reproductive versus ecological activities, but under identical environmental conditions. The resulting analyses offer a strong challenge to a common paradigm in reptilian reproduction: the notion that body size strongly enhances reproductive output in females, but has less important effects on the organism’s ecological interactions.

A very large literature indicates that increases in maternal body size are tightly linked to increases in reproductive output, mostly via increases in litter sizes (e.g., Fitch 1970, Moll 1979, Seigel and Ford 1987, Cooper-Preston and Jenkins 1993, Wikelski and Trillmich 1997). In a few snake species, offspring sizes and relative clutch masses increase with maternal body size also (Shine 1981, Stewart 1989, Luiselli et al. 1996). In contrast, our data on aspik vipers did not show a consistent increase in reproductive output with increasing maternal body size (Figs 1, 2). Instead, the traits most consistently strongly affected by maternal body size in our population of aspik vipers were “ecological” rather than reproductive characteristics. Non-reproductive larger vipers eat more frequently, but grow much less, than do smaller snakes.

We do not know the mechanistic basis for these effects; they may involve factors such as gape-limitation (so that larger snakes have access to a wider prey resource). Regardless of the mechanisms producing these allometries, however, the end result is that “costs of reproduction” in terms of reduced food intake are higher for large vipers, whereas the “costs” measured in terms of reduced growth rates are lower for these large animals. In combination with these results, the size-independent changes in body mass (Fig. 3) suggest that larger females store this “excess” energy as body reserves rather than growing in length. This latter result supports one prediction from a recent model on size-related energy gain in gape-limited predators (Forsman 1996). Perhaps more importantly, the aspik viper is a typical capital breeder that must accumulate very large

amounts of body reserves before reproduction (Bonnet et al. 1994, Naulleau and Bonnet 1996). Litter size is more strongly influenced by pre-vitellogenic body reserves than by maternal size in this species (XB et al. unpubl.). Thus, in terms of fitness, increase in body size may well be a lower priority than the storage of body reserves.

As a result of these processes, body size affects the biology of female vipers in at least three ways:

(1) Body size has a direct (but weak and non-linear) influence on reproductive output (Fig. 2).

(2) A female's overall energy balance (rate of food intake and relative allocation to body reserves versus growth) is strongly affected by her body size (Fig. 3). Despite their greater foraging abilities, larger females cease growing. Mass-specific metabolic rates also change with body size (e.g., Grigg et al. 1979, Schmidt-Nielsen 1991), further modifying the energy balance. High maintenance requirements of larger individuals may increase their vulnerability to periods of food shortage (Nagy and Shoemaker 1984, Wikelski et al. 1997; but see Forsman 1996). However, our data did not show any effect of size on survival (either on reproductive or non-reproductive individuals).

(3) The way in which reproduction influences food intake and growth rate depends upon body size, so that the "costs of reproduction" will depend upon body size also.

The end result of these three processes is that body size has more effect on a female viper's interactions with the environment than it does on her reproductive output. Even in terms of reproduction, the major effects of body size involve allometry in the "costs of reproduction", rather than in reproductive output per se.

Undoubtedly, other reptile species differ from *Vipera aspis* in these kinds of relationships. Indeed, other populations of vipers (or even the same population studied in other years) might show different patterns. In particular, we suspect that many individuals in our population are energy-limited. In captivity, under artificial and favourable climatic conditions, and when food was provided ad libitum, large females were highly fertile and even reproduced with a less than annual frequency (Naulleau 1973, Naulleau and Saint Girons 1981). By contrast, in our study area, low food availability and unfavourable climatic conditions (which impede digestion of prey) likely explain why many large females cannot fill up their body with energy (fat) reserves during non-reproductive years, and thus cannot reproduce annually (Bonnet and Naulleau 1996). In turn, this difficulty in accumulating energy reserves has the result that females ovulate at a very

wide range of body conditions (Fig. 1 in Naulleau and Bonnet 1996). Such large variations in body reserves may mask the influence of maternal size on reproductive output (XB, GN, RS, and OL unpubl.).

Nonetheless, although our results are based on a single population, they offer a challenge to another paradigm in reptile ecology. An extensive literature on sexual differences in body size puts major emphasis on selective forces affecting males (e.g., Fitch 1981, Stamps 1983, Shine 1994, Sinervo and Lively 1996, Wikelski and Trillmich 1997). The rationale for this emphasis appears to be that (1) the major female-specific force on body-size evolution is fecundity selection (increasing clutch sizes at larger body sizes), and (2) because fecundity selection is driven by "packaging" constraints (a simple increase in abdominal space available for the litter in larger females: e.g., Shine 1992), the strength of this selective force is likely to be similar among lineages. Thus, variation in sexual size dimorphism has generally been attributed to factors acting on males rather than females (e.g., Vitt and Cooper 1985, Madson and Shine 1992, Shine and Fitzgerald 1995).

Our data dispute this scenario on two fronts. First, body-volume constraints clearly cannot explain variation in litter sizes among vipers (Fig. 1); instead, a female's litter size depends upon her energy stores (Naulleau and Bonnet 1995, XB, GN, RS, and OL unpubl.). Second, if the costs and benefits of different body sizes depend upon the allometry of feeding rate or "costs of reproduction" (Fig. 3), then minor shifts in ecological conditions may well modify the resulting optima (Wikelski and Trillmich 1997). In such cases, we might expect that selective forces on female body size, as well as male body size, could vary significantly through space and time. This result suggests that adaptive explanations for sexual size dimorphism may need to look at selective forces on females more carefully than has generally been the case.

Data on other snake species suggest that there may be considerable variation in the form of the relationships explored in this paper. Although litter sizes increase with maternal body size in most species for which sufficient data have been accumulated, there are several species for which this is not the case (e.g., see review by Seigel and Ford 1987, Ford and Seigel 1989). The relationship between offspring size and maternal body size varies even more among populations within a single species (Seigel and Ford 1987). Similarly, reproductive frequency increases with increasing body size in females of several snake species (e.g., Blem 1982, Shine 1986), but attains a maximum value at intermediate body sizes in the Australian python *Liasis fuscus* (Madsen and Shine 1996). This latter pattern is the same as that seen in *V. aspis* (Fig. 2; suggested by Saint Girons 1957). Interestingly, not all females grow to a large size. For example, some female vipers that reproduced in 1993 were still small [SVL < 50 cm] when captured five

years later. The existence of such individual reproductive tactics suggests that life-time reproductive success (the currency by which selection works) may well be optimised in different ways by different individuals. This possibility deserves further analysis. Additional complications occur when taking into account the source of energy necessary for reproduction and growth: the ability to capture prey. The proportion of recently captured snakes containing food increased with increasing SVL in non-reproductive female *V. aspis* (Fig. 3), and the same pattern has been documented in three Asian python taxa (Shine et al. 1998, 1999). However, the reverse situation has been documented in another python species (Shine and Madsen 1997).

This interspecific diversity in the relationships between body size and reproductive versus ecological activities in snakes may provide an excellent opportunity to investigate body-size evolution. There are many reports of variation in body sizes within closely related snake lineages (e.g., Forsman 1991). Some of these cases undoubtedly reflect phenotypic plasticity in growth trajectories (e.g., Madsen and Shine 1993), whereas other instances probably involve adaptive shifts (e.g., Schwaner and Sarre 1988, 1990). It would be instructive to examine the consequences of body-size variation for ecological and reproductive traits within these systems, and see whether observed patterns of variation in body size are more easily explicable in terms of ecological versus reproductive advantages to different body sizes.

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References

- Andersson, M. 1994. Sexual selection. – Princeton Univ. Press.
- Andrews, R. M. 1982. Patterns of growth in reptiles. – In: Gans, C. and Pough, H. (eds), *Biology of Reptilia* 13. Academic Press, pp. 273–312.
- Arnold, S. J. 1993. Foraging theory and prey-size-predator-size relations in snakes. – In: Seigel, R. A. and Collins, J. T. (eds), *Snakes: ecology and behavior*. McGraw-Hill, pp. 87–116.
- Arnold, S. J. 1994. Is there a unifying concept of sexual selection that applies to both plants and animals? – *Am. Nat.* 144: S1–S12.
- Arnold, S. J. and Wade, M. J. 1984. On the measurement of natural and sexual selection: theory. – *Evolution* 38: 709–719.
- Bennett, D. M. and Hoffmann, A. A. 1998. Effects of size and fluctuating asymmetry on field fitness of the parasitoid *Trichogramma carverae* (Hymenoptera: Trichogrammatidae). – *J. Anim. Ecol.* 67: 580–591.
- Birkhead, T. R., Pellatt, J. and Hunter, F. M. 1988. Extra-pair copulation and sperm competition in the zebra finch. – *Nature* 334: 60–62.
- Blem, C. R. 1982. Biennial reproduction in snakes: an alternative hypothesis. – *Copeia* 1982: 961–963.
- Bonnet, X. and Naulleau, G. 1996. Catchability in snakes: consequences on breeding frequency estimates. – *Can. J. Zool.* 74: 233–239.
- Bonnet, X., Naulleau, G. and Mauget, R. 1994. The influence of body condition on 17- β estradiol levels in relation to vitellogenesis in female *Vipera aspis* (Reptilia: Viperidae). – *Gen. Comp. Endocrinol.* 93: 424–437.
- Bonnet, X., Bradshaw, S. D. and Shine, R. 1998a. Capital versus income breeding: an ectothermic perspective. – *Oikos* 83: 333–341.
- Bonnet, X., Shine, R., Naulleau, G. and Vacher-Vallas, M. 1998b. Sexual dimorphism in snakes: different reproductive roles favour different body plans. – *Proc. R. Soc. Lond. B* 265: 1–5.
- Bonnet, X., Naulleau, G. and Shine, R. 1999. The dangers of leaving home: dispersal and mortality in snakes. – *Biol. Conserv.* 89: 39–50.
- Brown, C. R. and Bomberger Brown, M. 1998. Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. – *Evolution* 52: 1461–1475.
- Bull, J. J. and Shine, R. 1979. Iteroparous animals that skip opportunities for reproduction. – *Am. Nat.* 114: 296–316.
- Clutton-Brock, T. H. 1991. The evolution of parental care. – Princeton Univ. Press.
- Cooper-Preston, H. and Jenkins, J. W. G. 1993. Natural history of the Crocodylia. – In: Glasby, C. J. Ross, G. J. B. and Beesley, P. L. (eds), *Fauna of Australia* 2A, Amphibia and Reptilia. Australian Government Publishing Service, Canberra, pp. 337–343.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. – Murray.
- Duvall, D., Schuett, G. W. and Arnold, S. A. 1993. Ecology and evolution of snake mating systems. – In: Seigel, R. A. and Collins, J. T. (eds), *Snakes: ecology and behavior*. McGraw-Hill, pp. 165–200.
- Fitch, H. S. 1970. Reproductive cycles in lizards and snakes. – *Misc. Publ. Univ. Kans. Mus. Nat. Hist.* 52: 1–247.
- Fitch, H. S. 1981. Sexual size differences in reptiles. – *Misc. Publ. Univ. Kans. Mus. Nat. Hist.* 70: 1–72.
- Ford, N. B. and Seigel, R. A. 1989. Relationships among body size, clutch size, and egg size in three species of oviparous snakes. – *Herpetologica* 45: 75–83.
- Forsman, A. 1991. Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. – *J. Anim. Ecol.* 60: 253–267.
- Forsman, A. 1996. Body size and net energy gain in gape-limited predators: a model. – *J. Herpetol.* 30: 307–319.
- Forsman, A. and Lindell, L. E. 1993. The advantage of a big head: swallowing performance in adders, *Vipera berus*. – *Funct. Ecol.* 7: 183–189.
- Grant, P. R. and Grant, B. R. 1995. Predicting microevolutionary responses to directional selection on heritable variation. – *Evolution* 49: 241–251.
- Grigg, G. C., Drane, C. R. and Courtice, G. P. 1979. Time constants of heating and cooling in the eastern water dragon, *Physignathus lesueurii* and some generalisations about heating and cooling in reptiles. – *J. Therm. Biol.* 4: 95–103.
- Harvey, P. H. and Ralls, K. 1985. Homage to the null weasel. – In: Greenwood, P. J., Harvey, P. H. and Slatkin, M. (eds), *Evolution: essays in honour of John Maynard Smith*. Cambridge Univ. Press, pp. 155–171.
- Hedges, S. B. 1985. The influence of size and phylogeny on life history variation in reptiles: a response to Stearns. – *Am. Nat.* 126: 258–260.
- Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. – *Oikos* 78: 57–66.
- Kölliker, M., Heeb, P., Werner, I. et al. 1999. Offspring sex ratio is related to male body size in the great tit (*Parus major*). – *Behav. Ecol.* 10: 68–72.

- Larsson, K., van der Jeugd, H. P., van der Veen, I. T. and Forslund, P. 1998. Body size declines despite positive directional selection on heritable size traits in a barnacle goose population. – *Evolution* 52: 1169–1184.
- Lindstedt, S. L. and Calder, W. A. 1984. Body size, physiological time, and longevity of homeothermic animals. – *Q. Rev. Biol.* 56: 1–16.
- Luiselli, L., Capula, M. and Shine, R. 1996. Reproductive output, costs of reproduction, and ecology of the smooth snake, *Coronella austriaca*, in the eastern Italian Alps. – *Oecologia* 106: 100–110.
- Madsen, T. and Shine, R. 1992. Temporal variability in sexual selection acting on reproductive tactics and body size in male snakes. – *Am. Nat.* 141: 167–171.
- Madsen, T. and Shine, R. 1993. Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. – *Evolution* 47: 321–325.
- Madsen, T. and Shine, R. 1996. Determinants of reproductive output in female water pythons (*Liasis fuscus*, Pythonidae). – *Herpetologica* 52: 146–159.
- Magnhagen, C. 1991. Predation risk as a cost of reproduction. – *Trends Ecol. Evol.* 6: 183–186.
- Moll, E. O. 1979. Reproductive cycles and adaptations. — In: Harless, M. and Morlock, H. (eds), *Turtles: perspectives and research*. Wiley and Sons, pp. 305–331.
- Nagy, K. A. and Shoemaker, V. H. 1984. Field energetics and food consumption of the Galapagos marine iguana, *Amblyrhynchus cristatus*. – *Physiol. Zool.* 57: 281–290.
- Naulleau, G. 1973. Reproduction twice in one year in a captive viper (*Vipera aspis*). – *Br. J. Herpetol.* 1: 353–357.
- Naulleau, G. and Saint Girons, H. 1981. Poids des nouveau-nés et reproduction de *Vipera aspis* (Reptilia: Viperidae), dans des conditions naturelles et artificielles. – *Amphibia-Reptilia* 2: 51–62.
- Naulleau, G. and Bonnet, X. 1995. Reproductive ecology, body fat reserves and foraging mode in females of two contrasted snake species: *Vipera aspis* (terrestrial, viviparous) and *Elaphe longissima* (semi-arboreal, oviparous). – *Amphibia-Reptilia* 16: 37–46.
- Naulleau, G. and Bonnet, X. 1996. Body condition threshold for breeding in a viviparous snake. – *Oecologia* 107: 301–306.
- Naulleau, G., Bonnet, X. and Duret, S. 1996. Déplacements et domaines vitaux des femelles reproductrices de vipères aspic *Vipera aspis* (Reptilia, Viperidae) dans le centre ouest de la France. – *Bull. Soc. Herpetol. Fr.* 78: 5–18.
- Neems, R. M., Lazarus, J. and McLachlan, A. J. 1998. Lifetime reproductive success in a swarming midge: trade-offs and stabilizing selection for male body size. – *Behav. Ecol.* 9: 279–286.
- Olsson, M., Shine, R., Gullberg, A. et al. 1996. Female lizards control paternity of their offspring by selective use of sperm. – *Nature* 383: 585.
- Peters, R. H. 1983. *The ecological implications of body size*. – Cambridge Univ. Press.
- Pough, F. H. 1980. The advantages of ectothermy for tetrapods. – *Am. Nat.* 115: 92–112.
- Preziosi, R. F. and Fairbairn, D. J. 1997. Sexual dimorphism and selection in the wild in the waterstrider *Aquarius remigis*: lifetime fecundity selection on female total length and its components. – *Evolution* 51: 467–474.
- Reiss, M. J. 1989. *The allometry of growth and reproduction*. – Cambridge Univ. Press.
- Saint Girons, H. 1957. Croissance et fécondité de *Vipera aspis* (L.). – *Vie Milieu* 8: 265–286.
- Schmidt-Nielsen, K. 1991. *Animal physiology, adaptation and environment*, 4th ed. – Cambridge Univ. Press.
- Schwamer, T. D. and Sarre, S. D. 1988. Body size of tiger snakes in southern Australia, with particular reference to *Notechis ater serventyi* (Elapidae) on Chappell Island. – *J. Herpetol.* 22: 24–33.
- Schwamer, T. D. and Sarre, S. D. 1990. Body size and sexual dimorphism in mainland and island Tiger Snakes. – *J. Herpetol.* 24: 320–322.
- Seigel, R. A. 1993. Summary: future research on snakes, or how to combat “lizard envy”. – In: Seigel, R. A. and Collins, J. T. (eds), *Snakes: ecology and behavior*. McGraw-Hill, pp. 395–402.
- Seigel, R. A. and Ford, N. B. 1987. Reproductive ecology. – In: Seigel, R. A., Collins, J. T. and Novak, S. S. (eds), *Snakes: ecology and evolutionary biology*. Macmillan, pp. 210–252.
- Shine, R. 1981. Venomous snakes in cold climates: ecology of the Australian genus *Drysdalia* (Serpentes: Elapidae). – *Copeia* 1981: 14–25.
- Shine, R. 1986. Ecology of a low-energy specialist: food habits and reproductive biology of the arafura filesnake (Acrochordidae). – *Copeia* 1986: 424–437.
- Shine, R. 1988. The evolution of large body size in females: a critique of Darwin’s “fecundity advantage” model. – *Am. Nat.* 131: 124–131.
- Shine, R. 1992. Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? – *Evolution* 46: 828–833.
- Shine, R. 1994. Sexual size dimorphism in snakes revisited. – *Copeia* 1994: 326–346.
- Shine, R. and Fitzgerald, M. 1995. Variation in mating systems and sexual size dimorphism between populations of the Australian python *Morelia spilota* (Serpentes: Pythonidae). – *Oecologia* 103: 490–498.
- Shine, R. and Madsen, T. 1997. Prey abundance and predator reproduction: rats and pythons on a tropical Australian floodplain. – *Ecology* 78: 1078–1086.
- Shine, R., Harlow, P. S., Keogh, J. S. and Boeadi. 1998. The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. – *Funct. Ecol.* 12: 248–258.
- Shine, R., Ambariyanto, Harlow, P. S. and Mumpuni. 1999. Ecological attributes of two commercially-harvested python species in northern Sumatra. – *J. Herpetol.* 33: 249–257.
- Shuster, S. M. 1989. Male alternative reproductive strategies in a marine isopod crustacean (*Paracerceis sculpta*): the use of genetic markers to measure differences in fertilization success among α -, β -, and γ -males. – *Evolution* 43: 1683–1698.
- Sinervo, B. and Huey, R. 1990. Allometric engineering: an experimental test of the causes of interpopulational differences in performance. – *Science* 248: 1106–1109.
- Sinervo, B. and Lively, C. M. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. – *Nature* 380: 240–243.
- Sinervo, B., Doughty, P., Huey, R. and Zamudio, K. 1992. Allometric engineering: a causal analysis of natural selection on offspring size. – *Science* 258: 1927–1930.
- Stamps, J. A. 1983. Sexual selection, sexual dimorphism, and territoriality. – In: Huey, R. B., Pianka, E. R. and Schoener, T. W. (eds), *Lizard ecology: studies of a model organism*. Harvard Univ. Press, pp. 169–204.
- Stewart, J. R. 1989. Facultative placentotrophy and the evolution of squamate placentation: quality of eggs and neonates in *Virginia striatula*. – *Am. Nat.* 133: 111–137.
- Thompson, M. B. and Russell, K. J. 1998. Metabolic cost of development in one of the world’s smallest lizard eggs: implications for physiological advantages of the amniote egg. – *Copeia* 1998: 1016–1020.
- Tracy, C. R. 1999. Differences in body size among chuck-walla (*Sauromalus obesus*) populations. – *Ecology* 80: 259–271.
- Vitt, L. J. and Cooper, W. E., Jr. 1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. – *Can. J. Zool.* 63: 995–1002.
- Western, D. and Ssemakula, J. 1982. Life history patterns in birds and mammals and their evolutionary interpretation. – *Oecologia* 54: 281–290.

- Wikelski, M. and Trillmich, F. 1997. Body size and sexual size dimorphism in marine iguana fluctuate as a result of opposing natural and sexual selection: an island comparison. – *Evolution* 51: 922–936.
- Wikelski, M., Carrillo, V. and Trillmich, F. 1997. Energy limits to body size in a grazing reptile, the Galapagos marine iguana. – *Ecology* 78: 2204–2217.
- Wilkinson, G. S., Kahler, H. and Baker, R. H. 1998. Evolution of female mating preferences in stalk-eyed flies. – *Behav. Ecol.* 5: 525–533.
- Witte, K. and Ryan, M. J. 1998. Male body length influences mate-choice copying in the sailfin molly *Poecilia latipinna*. – *Behav. Ecol.* 5: 534–539.