COSTS OF REPRODUCTION INFLUENCE THE EVOLUTION OF SEXUAL SIZE DIMORPHISM IN SNAKES

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Most explanations for sex differences in adult body size have focused on differences between the two sexes in the degree to which larger body size enhances reproductive success. For example, the general tendency for females to grow larger than males has been attributed to production of larger litters by larger females (Darwin 1871; Trivers 1972; but see Shine 1988), and the correlation between large male size and mating systems with male–male competition has led many authors to conclude that larger male size enhances male reproductive success in such systems (Darwin 1871; Clutton-Brock et al. 1977; Shine 1978; Berry and Shine 1980). Because each of these hypotheses deals only with the relationship between body size and reproductive success within one sex, no prediction can be made about the relative sizes of the two sexes (Greenwood and Adams 1987; Shine 1987). The degree of size dimorphism is presumably determined by the relative intensities of selection for large size in the two sexes, as well as the degree of genetic correlation between the sexes for alleles associated with body size (Arnold 1985). It is entirely likely that large size enhances reproductive success in both sexes, but more strongly in one than in the other. In order to predict the actual direction or degree of sexual size dimorphism within a population, we need data on the effects of body size on reproductive success in both sexes. Such data are rarely available (Clutton-Brock 1988), so the balance between selective forces acting on conspecific males and females has rarely been evaluated.

A comparative analysis of sexual size dimorphism and mating systems in snakes reveals that females grow larger than males in most species, but not in species that show male–male combat behavior (Shine 1978). The same pattern has been noted in many other animals, including other reptiles, and generally has been attributed to sexual selection for large male body size in taxa with male–male combat (Shine 1979; Berry and Shine 1980; Fitch 1981). Nonetheless, there are many exceptions to this generalization, and the most puzzling of these are species in which male–male combat occurs but in which females attain larger sizes than males. Species that fail to conform to the usual pattern may tell us a great deal about the factors responsible for those general patterns. In this paper, we use detailed demographic and ecological data on one of these atypical species (the adder *Vipera berus*) to test among potential explanations for female-larger dimorphism in a species with male–male combat. Our analyses suggest that sex differences in costs of reproduction may strongly influence optimal body sizes in each sex, and hence may affect the direction of sexual size dimorphism. We focus here on the potential costs and benefits of larger body size in terms of reproductive success, especially, fecundity selection in females and sexual selection in males.

STUDY ANIMAL AND METHODS

The Biology of Adders

The adder is a relatively small viperid snake widely distributed through Europe (Arnold and Burton 1978). Adders typically occur in small semi-isolated populations and are highly philopatric (Viitanen 1967; Prestt 1971). Both sexes feed primarily on small mammals throughout their lives (Saint Girons and Kramer 1963; Arnold and Burton 1978). During the mating season each spring, males search out reproductive females to court, and they fight with rival males (Viitanen 1967; Andren 1985, 1986). Their

"wrestling matches" involve intertwining of the males but no biting and are almost always won by the larger males (Andren 1986; Madsen 1988).

Females may mate with several different males over the three-week mating period, with subsequent multiple paternity of litters (Stille et al. 1986). Adders are viviparous and give birth to approximately eight offspring (Prestt 1971; Nilson 1981; Andren and Nilson 1983; Madsen 1988). Females usually do not feed during gestation and are emaciated by the time of parturition. They generally require at least one year before their energy stores are sufficiently replenished to enable production of another litter. Hence, many females die before producing a second litter, and surviving females reproduce only once every two years (Prestt 1971; Nilson 1981; Madsen and Shine 1992b). In contrast, adult males court and attempt to mate every year (Viitanen 1967).

Methods of the Present Study

Detailed data on survival rates, growth rates, and reproductive success relative to body size are available for a population of adders in extreme southern Sweden, at Smygehuk (55°20′N, 13°22′E). The habitat and methodology have been described elsewhere (Madsen 1988; Madsen and Shine 1992a,b,c, 1993a,b,c, 1994; Madsen et al. 1992, 1993). Since 1981, one of us (T.M.) has monitored this population every year. All captured snakes are individually marked, and growth and survival rates are determined from recaptures of marked animals. In every year since 1984, reproductive behavior has been observed for every day of the mating season, providing comprehensive information on the success rates of individual males in combat bouts and in mating. Observations on location and behavior of the snakes during the mating season are facilitated by force-feeding miniature radio-transmitters to all reproductive females; most social behavior (including male–male combat) occurs less than 2 m from females (Madsen 1988; Madsen et al. 1993). Gravid females are collected one to two weeks prior to parturition in late summer and are maintained in the laboratory until they give birth. The neonates are measured and marked before being released, with their mothers, in the study area.

The Smygehuk adders are unusually well suited to detailed behavioral study (Madsen et al. 1993), so each year we can monitor virtually all adult adders in the study area (which measures

1 km by 20 to 200 m). For example, we have no records of a male reproductive in one year, not recorded the next year, and then reappearing the following year (as would be expected if we occasionally failed to record some males). Thus, the disappearance of a mature male from the breeding population means that he has died or emigrated, and the latter possibility is extremely unlikely (Madsen and Shine 1992a). Females are more difficult to monitor because (a) they are more cryptic than males except during gestation, and (b) they reproduce only in alternate years. Hence a year when a female is not recorded might represent a year when we have failed to find her rather than when she has failed to reproduce. However, the possibility is very low. Females are relatively obvious during gestation because of their prolonged basking behavior at this time, and gravid adders tend to aggregate in favorable sites prior to parturition (Viitanen 1967). Hence, we are likely to see these snakes during gestation, or close to parturition, when we collect all of the telemetered reproductive females. Because virtually all females reproduce on a two-year cycle (Madsen and Shine 1992b), a female missed during an entire reproductive episode would be likely to appear in our records as apparently reproducing on a 4-yr cycle. We have only recorded 2 such instances in 29 documented female cycles (Madsen and Shine 1992b).

We defined the age at sexual maturation for males as the time they were first recorded courting females, and for females as the time they produced their first litters. Survival rates were determined for immature snakes, adult males, and adult females in years when they reproduced, and adult females during years when they did not reproduce. The number of offspring produced was used as a measure of reproductive success in females. The numbers of matings obtained by males served as an index of their reproductive success. The numbers of progeny fathered would be a better measure (and more directly analogous to our measure of reproductive success in females), but are difficult to determine because of multiple mating by females and the resulting uncertainty regarding paternity (Madsen et al. 1992). Mating success might be a poor predictor of fitness if some matings resulted in considerably more fertilizations than did others. As far as we can tell from electrophoretic evidence, however, most matings result in paternity of some offspring. Thus, there is no clear tendency for most paternity to result from either
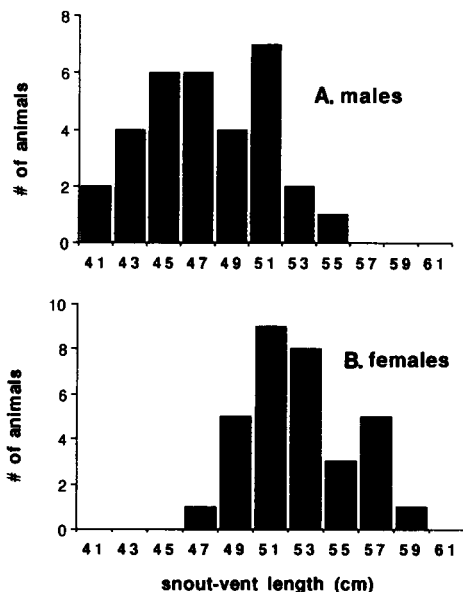
FIG. 1. Frequency distributions of snout–vent length (cm) of adult male and female adders from Smygehuk in southern Sweden.

FIG. 2. Mean growth curves for male and female adders at Smygehuk, based on snout–vent length (cm) of known-age animals at yearly intervals. Bars around mean values show standard deviations, and arrows show mean age and size at maturation in each sex. Data for males (squares) and females (circles) are slightly offset on the horizontal axis to avoid overlap of symbols.

the first or the last mating (Stille et al. 1986). Our analyses also indicate that there is no significant tendency for larger males to mate with larger or more fecund females (Madsen et al. 1993), so matings by large and small males should result in approximately the same numbers of offspring. Although these results suggest that our use of mating success as a substitute for paternity may not introduce major error, we nonetheless recognize that this is an important caveat, and we are currently carrying out paternity analysis in this population. To ensure statistical independence, we have randomly discarded data so that each adult adder is only represented by data from a single mating season.

Proximate Causes of Sexual Dimorphism in Adders

As in all other adder populations studied (Forsman 1991), females attain larger sizes than do males at Smygehuk (fig. 1B: $t_{78} = 6.54$, $P < 0.001$). We have data on growth patterns for 24 known-age females and 14 known-age males. This sex bias in sample sizes is due to the greater numbers of females initially captured as small juveniles, when their ages can be reliably inferred from their body sizes. The larger mean adult body size of female adders is due to a combination of delayed maturation and higher growth rates in
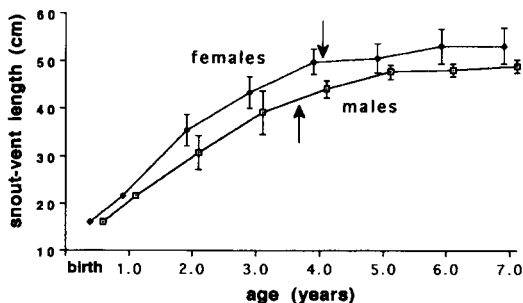
females than in males. Growth rates slowed dramatically after maturity in each sex (fig. 2), and analysis of data on these known-age animals showed that this effect was due to maturation rather than simply a general slowing of growth with age. For males, the growth increment in SVL from the third year to the fourth year of life was higher in snakes delaying maturity than in same-age animals that matured at 3 yr [means $= 3.25 \pm 1.71$ cm ($n = 4$) vs. 7.86 ± 0.90 cm ($n = 7$), $t_9 = 5.98$, $P < 0.0003$]. Similarly, female adders maturing at 4 yr grew less in the next year than did same-age snakes that delayed maturation for an additional year [means $= 0.33 \pm 0.52$ cm ($n = 6$) vs. 4.50 ± 0.71 cm ($n = 2$), $t_6 = 9.23$, $P < 0.0001$]. Juvenile growth rates differed between the sexes, with females exceeding males in mean growth rates over the first 3 yr (one-factor ANCOVA with sex as the factor, age as the covariate, and SVL as the dependent variable: slopes $F = 10.04$, df $= 1$, 76; $P < 0.001$). Hence, adult males were smaller than females for two reasons: they grew more slowly (especially as juveniles) and matured at 3 to 4 yr (of 14 known-age males, 7 matured at 3 yr and the other 7 at 4 yr). Most females did not produce their first litter until their fourth or fifth year (2 at 3 yr, 16 at 4 yr, 5 at 5 yr, and 1 at 6 yr). The mean age and size at maturation were thus higher in females than in males ($t_{43} = 3.45$, $P < 0.001$ for age; $t_{43} = 8.02$, $P < 0.001$ for size).

In both sexes, maturation was more closely linked to body size than to age: late-maturing animals were those with lower growth rates as juveniles. There was no significant difference in mean SVL at maturity between male snakes ma-
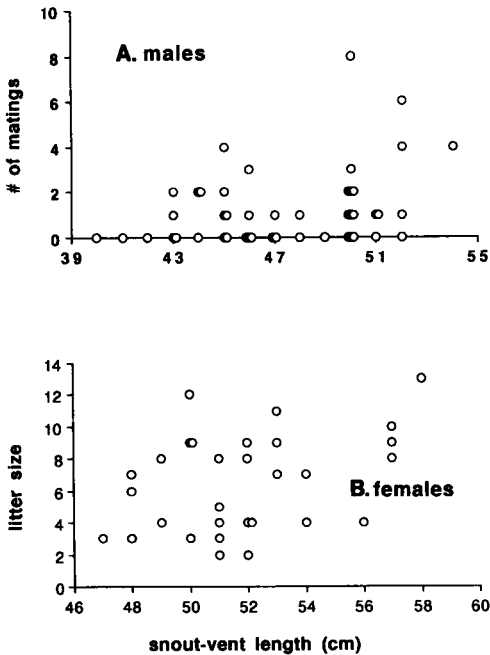
FIG. 3. The relationship between snout–vent length (cm) and reproductive success per season in Smygehuk adders: (A) number of matings as a function of body size in males (polynomial regression: number of matings = $50.53 - 2.41 \cdot SVL + 0.03 \cdot SVL^2$); (B) litter size as a function of maternal body size in females (linear regression: litter size = $0.29 \cdot SVL - 8.06$).

turing at 3 yr versus 4 yr ($t_{12} = 0.35$, $P = 0.73$). Although females maturing at different ages varied slightly in SVL, mean body lengths at maturity for each age-class ranged only between 48.5 and 51.0 cm (Madsen and Shine 1992b).

REPRODUCTIVE ADVANTAGES OF LARGER BODY SIZE

Our approach is to compare male and female adders with respect to the consequences of different body sizes for reproductive success. Life-history theory (Bell 1980) suggests two plausible explanations why selection may favor larger body sizes in female adders than in conspecific males: (1) Reproductive success increases more rapidly with body size in females than in males, because a given increment in body size yields a greater increment in litter size for females than in mating success for males (as suggested by Forsman [1991], for adders); or (2) reproductive success increases no more rapidly with body size in females than in males, but females face higher fecundity-independent costs of reproduction. If this

is true, females may maximize their lifetime fitness by delaying reproduction until they attain a large body size, whereas males may benefit from early maturation as long as they do not experience such high costs of reproduction.

Although these two hypotheses are superficially similar, they rely on different life-history stages as targets of selection. The former hypothesis (advantage to larger size) assumes that selection has acted to optimize mean adult body size, whereas the second hypothesis invokes optimization of the body size at maturation. We can use our data on Smygehuk adders to test between these alternative hypotheses.

Effects of Body Size on Reproductive Success within a Season

(1) Litter sizes increase with larger female body size in adders (fig. 3B; $r = 0.39$, $n = 32$, $P < 0.04$). This fecundity advantage could favor continued growth in females resulting in females growing larger than males.

(2) The degree to which larger size enhances male mating success in the Smygehuk population varies considerably among years, depending upon the operational sex ratio (Madsen and Shine 1993a). Nonetheless, larger males obtained consistently more matings in each year, and this size effect remains evident when the data for the seven years are combined. Larger males were more likely to win combat bouts (true in all 143 bouts observed) and hence obtained more matings (using only one season's data for each individual male: fig. 3A; $r = 0.48$, $n = 48$, $P < 0.01$).

In each of the seven years of the study, the correlation coefficient linking maternal body size to litter size was lower than the analogous coefficient linking male body size to mating success. Using a sign test for paired comparisons, this sex difference is statistically significant ($P = 0.008$). Thus, within any given breeding season, reproductive success was more highly correlated with body size in male adders than in conspecific females. Although this comparison necessarily confounds age with body size, it suggests that body size enhances reproductive success to a greater degree in males than in females. We therefore doubt the hypothesis (Forsman 1991) that the small size of male adders relative to females results from a lack of selective advantage to large body size in males within a single reproductive season. We turn to our second hypothesis: the idea that selection has operated on the body size at sexual maturation, so that high

costs of reproduction favor delayed maturation in females.

Costs of Reproduction and Lifetime Reproductive Success

The degree of sexual size dimorphism at maturation in reptiles is highly correlated with the degree of dimorphism at mean adult size (Shine 1990). For the Smygehuk adders, the SVL of an individual at maturation is significantly correlated with the maximum SVL it will attain (males, $r = 0.38$, $n = 48$, $P < 0.01$; females, $r = 0.39$, $n = 34$, $P < 0.05$). Thus, patterns of sexual differences in mean adult size may reflect selection on size at maturation rather than on mean adult size per se (Gibbons and Lovich 1990). We therefore investigate possible evolutionary determinants of relative sizes at maturation in male and female adders.

Annual survival probabilities of the Smygehuk adders are lower for adult males (0.75) and reproductive adult females (0.60) than for adult females in years when they do not reproduce (0.80) or for subadults (in both sexes, 0.85 to 0.88 in the year before maturation). Survival rates of adult males decrease with body size (Madsen and Shine 1993b). Because most females reproduce every second year (24 of 29 documented cycles), the mean probability of survival of females from one reproductive year to the next is the product of survival rate in a reproductive year multiplied by that in a nonreproductive year ($0.60 \times 0.80 = 0.48$). From these data we infer: (a) there is a higher survival cost of reproduction in females than in males; (b) the number of reproductive events per lifetime is lower in females than in males (mean = 1.35, SD = 0.49 for 34 females; mean = 3.14, SD = 1.74 for 48 males; comparing sexes, $t_{80} = 5.82$, $P < 0.001$; Madsen and Shine 1993b); and (c) thus, the first year of reproduction makes a larger contribution to lifetime reproductive success in females (mean = 85%, SD = 15%, $n = 34$) than in males (mean = 14%, SD = 27%, $n = 16$; $t_{48} = 13.80$, $P < 0.0001$). It follows that the reversed dimorphism may be a consequence of selection for delayed maturity in females, larger body size at maturity, and higher reproductive success in this first year of reproduction. In contrast, the relatively low costs experienced by reproducing males mean that there is little disadvantage in maturation at a small size, even if reproductive success in the first breeding season is low, because subsequent opportunities for reproduction are reduced only

slightly. Annual variation in the operational sex ratio in the Smygehuk population means that in some years, reproductive females are too numerous and too widely dispersed for larger males to monopolize matings (Madsen and Shine 1993a). Thus, in years with a relatively low intensity of male–male competition, a small male may obtain several matings (Madsen and Shine 1993a) and the payoff to early maturation will be high.

SIMULATION MODELS OF LIFETIME REPRODUCTIVE SUCCESS

The role played by costs of reproduction can be clarified by constructing simple simulation models of the adder's life history, following Madsen (1987). We combined the data on growth rates and survival rates with those on the relationship between reproductive success and body size in each sex (fig. 3; see caption for equations) to calculate the probable lifetime reproductive success of an adder. To do this, we estimated the total number of offspring produced by adders of each sex at each age (table 1), discounted by the probability of mortality prior to reproduction at each age. Because growth is very slow in older adders (fig. 2), we assumed zero growth after age 6 (table 1). We used average survival rates for subadults (0.87), adult males (0.84, 0.80, 0.76, 0.71, 0.67, 0.63 in successive annual size classes, and 0.63 thereafter), and reproductive (0.60) and non-reproductive (0.80) adult females [see Madsen and Shine (1993b) for detailed analyses of these costs] to construct the simulation model. The values for probable reproductive success at each age were then summed over an arbitrary potential adult life span of 20 yr to estimate the overall lifetime production of progeny by an adder of that sex. This life span is much greater than the usual adult longevity (3.14 yr in males, 2.29 in females; Madsen and Shine 1993b) to avoid artifacts from artificial truncation of the life span. In practice, survival rates are low enough that ages greater than 7 yr contribute very little to the probable total of lifetime reproductive success. In populations that are relatively stable in numbers, lifetime reproductive success should give a reasonable estimate of fitness in terms of natural selection (Charlesworth 1980).

The simulation can then be modified to examine the fitness consequences of changes in size at maturity. For example, suppose we assume a female matured at a body size that she would normally reach at 3 yr (= 43.7 cm, a year earlier

TABLE 1. Mean snout–vent length (SVL, in cm) and predicted reproductive success of male and female adders at each age. These figures are calculated from observed growth rates of reproductive and nonreproductive animals, and litter sizes and mating success relative to body size. Note that females reproduce only once every 2 yr but values are given for each year to enable calculation of probable litter sizes for females initially reproducing at different ages. Values for SVL and litter sizes for females at 5 and 6 yr are for females that have reproduced previously (†) and those that have not (*), calculated from the growth costs measured in the field (see the text).

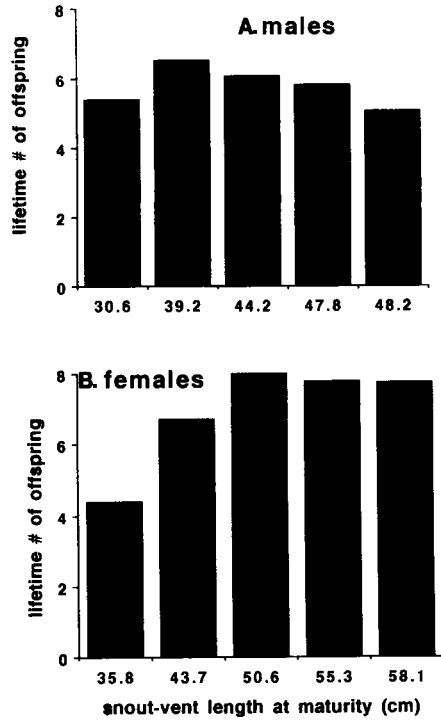| Age (yr)	Males		Females	
	SVL	No. of matings	SVL	No. of offspring
1	21.5	0	21.5	0
2	30.6	0	35.8	2.32
3	39.2	0.70	43.7	4.61
4	44.2	0.75	50.6	6.61
5	47.8	1.69	53.0†/55.3*	7.31†/7.97*
6	48.2	1.84	55.3†/58.1*	7.97†/8.78*

FIG. 4. Calculated values for lifetime reproductive success of male and female adders maturing at different ages (and thus, body sizes). Ages at maturation range from 2 to 6 yr, and are the same on both graphs (see table 1 for the relationship between age and size at maturation in both sexes). The values for lifetime reproductive success, derived from a simple simulation model (see the text), suggest that male adders maximize their lifetime reproductive success by maturing at a smaller size than do female adders.

than the usual age at maturation). We predict that she will be able to produce a litter of 4.6 offspring and will experience an annual probability of survival of 0.60 rather than 0.87 for that year. She will add only 0.35 cm to her SVL during the year, rather than the 2.28 cm growth increment typical of nonreproductive years (Madsen and Shine 1993b). Her body sizes, annual probabilities of survival and litter sizes at subsequent reproductions can be calculated from the mean growth rates, growth costs, survival costs, size and fecundity relationships for this population. The same kinds of calculations can easily be made for males, with size-dependent survival costs (from 4% per annum for small males to 25% in the largest size group) but without growth costs (Madsen and Shine 1993b). For males, we calculated lifetime production of offspring from numbers of matings (based on a mean litter size of 6.17, from an average of 3.65 matings per female per season, = 1.69 offspring fathered per mating). Thus, the reproductive success of a male in each season was calculated by multiplying his expected number of matings by 1.69.

The model suggests that females maximize their lifetime reproductive success by maturing at about 50 to 55 cm SVL, a size usually attained at 4 to 5 yr (figs. 2, 4B). In contrast, males maximize their lifetime fitness by maturing at a smaller size, around 40 to 44 cm in length. This size is usually reached at about 3 to 4 yr (figs. 2, 4A). The model based only on size-related costs

and benefits thus accurately predicts body sizes and ages at maturation in Smygehuk adders of both sexes; the actual mean sizes at maturation are 50.7 cm for females, and 43.4 cm for known-age males. Overall, the snakes are behaving approximately as predicted from the model, under the hypothesis that natural selection would adjust age at maturation in such a way as to maximize lifetime reproductive success. Our model successfully predicted that females should mature at larger sizes than males—and therefore grow to larger mean adult sizes—despite the fact that reproductive success increased more rapidly with increasing size in males than in females within any given season.

The importance of costs of reproduction in determining the optimal body sizes at maturity can be shown most easily by interchanging the costs faced by males and females while leaving

other factors (reproductive frequency, and relationship of body size to reproductive success) unchanged. To do this, we allocated survival rates between successive reproductions of 0.75 to females and 0.48 to males (i.e., swapped rates between the sexes). We removed growth costs from the model because these apply only to females. When this is done, the optimal size at maturity strongly increases in males (to 47.8 cm) and decreases in females (to 35.8 cm). Thus, the predicted optimal size at maturation is reversed when the costs of reproduction are interchanged between the sexes. We also manipulated other variables differing between the sexes (reproductive frequency, growth trajectory, and the relationship between SVL and reproductive success) to see whether the optimal sizes at maturation were affected when the values for these variables were interchanged between the sexes. For example, we investigated the possibility that females would be favored to mature at smaller or larger sizes than those observed in nature if they followed a slower (malelike) growth pattern, or experienced a higher (malelike) increment in reproductive success with increasing body size. Characteristics of males were investigated in the same way. Our tests showed that none of these variables changed the direction of sexual size dimorphism or sex-specific age at maturation.

The results from these simulations suggest that the female adders' larger body sizes may be due to the higher costs faced by reproducing females. These costs take three main forms: the lower survival of reproductive females; the lower growth rates of reproductive females; and the postponement of subsequent reproduction in this sex because of the high energy demands of ovulation and gestation. This lowered reproductive frequency influences optimal size at maturity in the model because it further reduces survival between one reproductive episode and the next in females compared to males. The other important component of reproductive costs in our model is the increase in mortality rates in larger males. Because small males are able to obtain occasional matings even if they devote little effort to reproductive activity (and thus, experience little risk of predation), early maturation does not impose as high a cost in males as it does in females.

DISCUSSION

Our analysis has focused on reproductive biology and has ignored other potential explanations for the evolution of sexual dimorphism. For example, ecological divergence between the sexes may well have been important in the evolution of body sizes of snakes but has probably influenced the degree, rather than the direction, of sexual size dimorphism (Shine 1989, 1991; Forsman 1991). Also, sex differences in adult survival rates (Howard 1981) and energy allocation to reproduction (Woolbright 1983) generally produce only minor changes to the degree of sexual size dimorphism set at maturation (Shine 1990).

Our field data and simulations suggest that differences in costs of reproduction between the sexes may be significant evolutionary determinants of sexual size dimorphism. Even if the relationship between reproductive success and body size is identical in the two sexes, a higher fecundity-independent cost of reproduction in one sex than in the other may favor a marked disparity in optimal body sizes at maturation, and hence in overall mean adult body sizes. In other words, the greater fecundity that potentially could be realized by larger individuals is put at risk to a greater degree in females than in males because the survival rate of reproductive females is less than that of reproductive males. Thus, it may not be possible to predict the direction or degree of sexual size dimorphism simply from data on the relationship between body sizes and reproductive success within a single season (Trivers 1972; Clutton-Brock 1988; Shine 1988).

High costs of reproduction in females may have been important in other snake species with this same combination of male combat and larger-female-than-male size (Shine 1978). The models developed in this paper are applicable to other animal species, including those in which males are larger than females. The scarcity of published data on costs of reproduction make it difficult to determine the generality of this effect, but we can make broad predictions. For example, reproductive costs in reptiles are likely to be higher for viviparous females than for oviparous females (Seigel et al. 1987) and higher for females with low reproductive frequencies (Bull and Shine 1979). Low frequencies of female reproduction tend to be found in populations living in cold climates (Saint Girons and Kramer 1963; Shine 1981). If costs are indeed higher in such taxa, we predict that female size relative to male size should be greater in viviparous reptiles than in oviparous taxa overall, and greater in temperate-zone than in tropical reptiles. Preliminary analyses reveal both of these patterns (Fitch 1981).

However, general patterns in the influence of reproductive costs on sexual size dimorphism may not exist, because the magnitude of costs of reproduction may vary at a local level in response to temporal and geographic variation in factors such as food supply and predator abundance. A more promising approach may be to repeat our analyses with data on reproductive success and costs of reproduction in other taxa, and hence determine whether male and female sizes at maturation can be accurately predicted from simple models incorporating costs of reproduction. Our success in this regard with adders suggests that such tests would be worthwhile.

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FOOD PROVISIONING IN RELATION TO REPRODUCTIVE STRATEGY IN ALTRICIAL BIRDS: A COMPARISON OF TWO HYPOTHESES

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Among altricial birds, variation in clutch size is enormous (Lack 1968). For instance, many marine seabirds are able to produce only a single egg during a breeding season, whereas the clutch size of small passerines may exceed 10 eggs. Furthermore, there is much interspecific variation in nestling growth rates (Ricklefs 1968a, 1973). Here, I examine how interspecific variation in provisioning rates relates to variation in these two reproductive traits. By using recently developed methods for analyses of comparative data (Harvey and Pagel 1991), a strong association was found between clutch size and food provisioning rate.

Two, not mutually exclusive, hypotheses were summarized by Lack (1968) to explain how parental provisioning rates should relate variation in reproductive traits. The first hypothesis assumes clutch size to be closely adjusted by the amount of food the parents are able to provide during the period when nestlings' food demands are highest (Lack 1947, 1966). Thus, large provisioning rates should be found in species with large clutch sizes. Several studies have demonstrated the importance of food for intraspecific variation in avian reproductive performance (for reviews, see Martin 1987; Boutin 1990). The second hypothesis assumes that rapid growth rates to reduce predation losses influence provisioning rates. Selection for short fledging periods should lead to investment of the available resources into rapid growth rates, rather than increased offspring number. In accordance with this hypothesis, species nesting on the ground, and therefore more susceptible to nest predation, have higher growth rates (Ricklefs 1968a) and smaller clutch sizes (Sæther 1985; Kulesza 1990) than species nesting in concealed nests. Thus, the energetic input into the nests should be independent of clutch size according to this hypothesis.

A problem which is frequently encountered in comparative studies (Harvey and Mace 1982; Pagel and Harvey 1988; Harvey and Pagel 1991) is the confounding effects of body weight. Differences in clutch size and provisioning rate are related to differences in body weight, i.e., large birds lay a smaller number of eggs (Sæther 1987) and have offspring that grow more slowly (Ricklefs 1973) but need more energy (Calder 1984) than those of smaller birds.