

Determinants of mating success in male adders, *Vipera berus*

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Abstract. Seven years' detailed behavioural observations on a small population of adders in southern Sweden provided data for a quantitative analysis of the behavioural determinants of male mating success. Male adders are subject to strong intra-sexual selection. The number of matings obtained by a male adder was enhanced by higher male mobility (distance travelled during the breeding season), mate-finding ability (females located per metre travelled), and ability to defeat rival males in combat bouts (proportions of bouts won). In combination, variation among males in these three abilities accounted for more than half of the variation documented in male mating success. Male success rates in combat bouts were strongly dependent on body size (and hence, age), and reproductive tactics shifted concomitantly. Small males fought other males (especially, large males) only rarely, and achieved the majority of their matings in the absence of other males. Larger males fought other males more frequently, and displayed mate-guarding behaviour on some occasions. Although mating success of male adders was strongly enhanced by larger body size, age per se appeared to exert no independent influence on mating success. Overall, the mating system of adders imposes strong sexual selection on a male's ability to locate females and to conquer rival males in battle.

A recent resurgence of scientific interest in sexual selection (e.g. Bradbury & Andersson 1987) has stimulated a wide range of field studies on the determinants of reproductive success. In particular, there has been a rapid increase in the amount of information available on the ways in which phenotypic traits influence reproductive success in males (e.g. Blum & Blum 1979; Howard 1981; Clutton-Brock et al. 1982; Clutton-Brock 1988). This work has revealed a hitherto-unsuspected diversity in male mating tactics, including numerous examples of size-related (usually, ontogenetic) shifts between alternative reproductive 'strategies' within single populations. Mathematical models for such 'phenotype-limited strategies' have been developed (e.g. Parker 1982). Many examples of both epigamic and intra-sexual selection have been documented, and a complex interplay between these two processes has been revealed. Although much has been learned, there are many types of animals for

which data on determinants of male reproductive success are as yet unavailable. The uneven phylogenetic focus of such studies is well illustrated by Clutton-Brock's recent (1988) compendium of studies on lifetime reproductive success: of the 26 species discussed, the only terrestrial ectothermic vertebrates were two amphibian species.

This paper is part of a series derived from long-term field studies by one of us (T.M.) on a small isolated population of adders in southern Sweden. Elsewhere, we have documented the influence of male body sizes and growth patterns on male mating success, and examined temporal variation in the mating system (Madsen & Shine 1992a, in press). However, we have not previously considered the question of why larger body size enhances male mating success. To do this, we describe behavioural tactics of reproducing males, and the dependence of alternative male mating tactics on body size. Our data show that male adders vary considerably in their abilities to find receptive females and vanquish rival males, that these characteristics influence mating success of males, and that male mating tactics vary with body size.

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Adders are small venomous snakes, with males growing to 55 cm snout-vent length (SVL) and females to 65 cm. They are widely distributed through Europe (Arnold & Burton 1978), and their general ecology and reproductive biology have been extensively studied in several parts of the species' range (e.g. Saint Girons & Kramer 1963; Viitanen 1967; Prestt 1971; Andren & Nilson 1981; Nilson 1981; Andren 1985, 1986; Stille et al. 1986; Madsen 1988; Madsen & Stille 1988; Forsman 1991; Madsen et al. 1992; Madsen & Shine 1992a, in press). These studies reveal the following general features of adder mating systems. Adult males emerge from winter inactivity approximately 3 weeks before females, and bask on sunny days until they are ready to shed their skins and begin active mate-searching. Reproductive females are relatively sedentary, and sometimes widely dispersed. Males encountering females engage in vigorous courtship, and will fight with other males if they appear. These battles are highly ritualized, with the two combatants intertwining and each attempting to force down the other's head with his own. Biting has not been recorded in these combat bouts. Females produce litters only once every 2 years, on average, but may mate several times (often, with several different males) within a single mating season. Multiple mating may enhance the viability of a female's offspring (Madsen et al. 1992).

The reproductive behaviour of male adders can be separated into four components, all of which may play a role in determining mating success. First, males move long distances, on a daily basis, in search of receptive females. Second, males must be able to locate these females, presumably by the pheromonal trails they deposit on the substrate during their relatively limited movements (e.g. Ford & Low 1984). Third, unless they can find an unaccompanied female, males must be able to defeat other males in combat before they can court the female uninterrupted. Lastly, males must be able to court effectively, so that the female is willing to mate. Male snakes appear to be unable to inseminate females forcibly, and female cooperation is thus essential for mating to occur (e.g. Devine 1984). Below, we consider each of these phases of male reproductive activity in turn. Although there is significant annual variation in the operational sex ratio, and hence in some aspects of the mating system (Madsen & Shine, in press), the broad outlines remain the same from year to year and we have thus combined data from all 7 years for the following

analysis. To ensure statistical independence, however, we have randomly discarded data such that each adult adder is represented only by data from a single mating season. A total of 48 males and 39 females is represented, although we lack information on some variables for some of these animals.

MATERIALS AND METHODS

We studied the determinants of male mating success in a small population of adders (mean \pm SD number of reproducing adults per annum = 28.7 ± 5.37 , range 21–34 over the 7 years of this study) living in grassy coastal meadows at the extreme southern tip of Sweden (Smygehuk, $55^{\circ}20'N$, $13^{\circ}22'E$). The population is separated by 20 km from other adder populations, and our mark-recapture and radiotelemetric studies have provided no evidence of immigration or emigration. The study area is approximately 1 km long, and 20–200 m wide. A more detailed description of the study area and the methodology have been given elsewhere (Madsen 1988). Information gathered from 1984 to 1990 is used in the present paper.

All adders captured in the study area are given an individual permanent mark by clipping ventral scales. Each spring prior to the commencement of mating activity, all adult males are captured, measured and paint-marked so that they can be identified at a distance, and all reproductive females are force-fed miniature radiotransmitters so that their subsequent positions can be determined easily. The small size and open habitat of the study area, together with the bright colours and active behaviour of reproductive males, mean that all reproductive adults can be located and captured prior to mating each year. Most social behaviour occurs close to these females, so that we could monitor male-male and male-female interactions in the population by observing these females, and any males in their vicinity, at intervals of ca 45 min over the period 0900–1800 hours on sunny days during the 3-week mating period each spring. Because female adders usually mate with more than one male each season, most broods have multiple paternity (Stille et al. 1986). Thus, we cannot allocate paternity precisely, and so must use mating success (number of matings obtained) as an index of male reproductive success. Throughout this paper, mean values are given with their standard deviations.

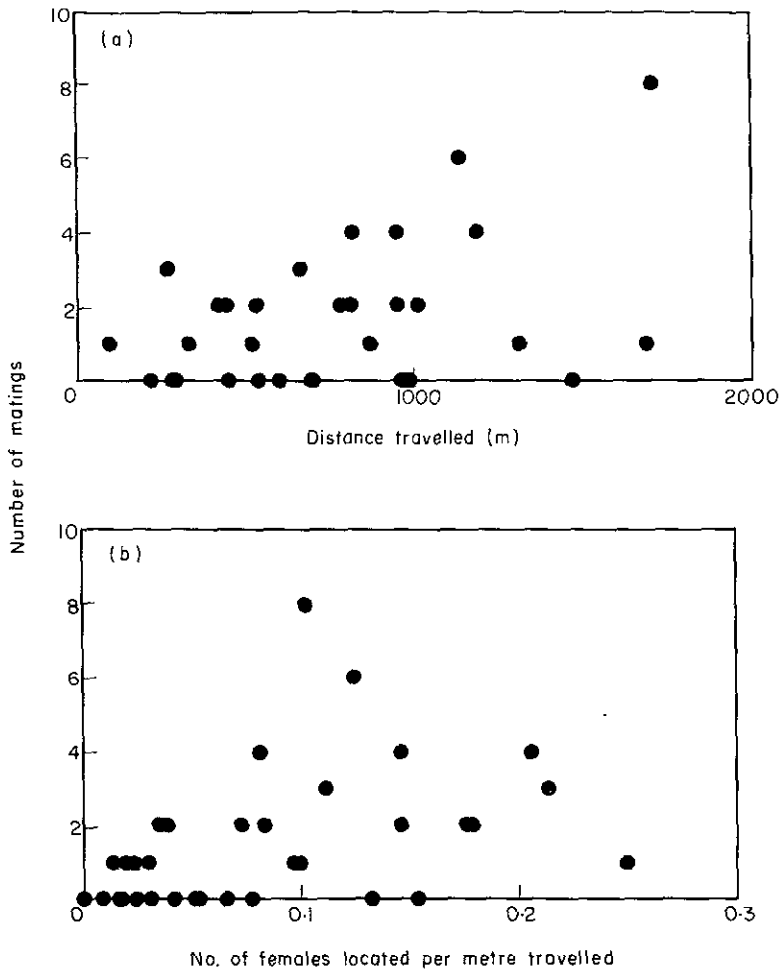


Figure 1. The number of matings obtained by a male adder in relation to (a) the total distance that he travels during the mating season, and (b) his efficiency in locating receptive females (number of females located per metre travelled per day).

RESULTS

Distances Moved in Mate-searching

Adult male adders moved about very little during the basking phase preceding their springtime slough ($\bar{X}=7.0 \pm 6.4$ m/day, $N=34$ males), but commenced long-distance movements as soon as the skin had been shed. They travelled an average of 47.7 ± 25.9 m/day during the mating season ($N=34$ males), and males that showed greater overall movements during the mating season also obtained more matings ($r=0.37$, $N=34$, $P<0.03$; Fig. 1a). This enhanced mating success was not attributable to any trend for larger males to be more mobile.

Larger males did not move significantly further than did smaller males (correlating SVL with mean distance travelled daily, $r=0.14$, $N=34$, $P=0.42$). Partial correlation analysis confirmed that male body size was significantly correlated with mating success even when mobility (total distance moved) was held constant in the analysis ($r=0.36$, $N=34$, $P<0.05$).

Ability to Find Females

Receptive females are widely dispersed through a complex habitat, with the exact locations of females differing between years. Females move relatively little during the mating period ($\bar{X}=8.5$ m/day:

Madsen & Shine 1992b). These sedentary habits make females more difficult for males to locate because snake pheromones are large molecules, unsuited to aerial dispersal, and males must rely on encountering a trail laid on the ground (e.g. Ford & Low 1984). Each reproductive female was courted by an average of 7.24 ± 2.48 males ($N=38$), out of the average of 21 adult males in the population each year (range = 17–25, $N=7$ years). The body sizes of females did not influence the frequency with which they were courted (correlation of female SVL with the proportion of sampling times when a male was within 2 m of a female: $r=0.10$, $N=39$ females, $P=0.49$). The number of females visited by a male was significantly correlated with the number of matings he obtained ($r=0.76$, $N=48$ males, $P<0.001$), but there was no significant tendency for larger males to locate more females (correlating male SVL with number of females located: $r=0.22$, $N=48$, $P=0.15$). When male SVL was held constant, the partial correlation between the number of females visited by a male and the number of matings he obtained was still significant ($r=0.75$, $N=48$, $P<0.001$).

These data can also be examined in terms of a male's efficiency in mate-searching: i.e. the number of females he locates relative to the extent of his mean daily movements. Do males that locate more females per metre they travel experience a higher reproductive success? This measure assesses a male's efficiency in finding mates, reflecting variation among males in factors such as trail-following ability. Males that were more efficient at finding females obtained more matings ($r=0.41$, $N=34$, $P<0.02$; Fig. 1b) regardless of their body size (the partial correlation between mate-finding ability and mating success was still significant when male SVL was held constant: $r=0.47$, $N=34$, $P<0.01$). Indeed, larger males were no better at locating females than were their smaller rivals (correlating male SVL with mate-finding ability, $r=0.10$, $N=34$, $P=0.53$).

Competition with Other Males

There are more male than female adders in the population of reproductive adults at Smygehek every year, because of the lower reproductive frequency and lower adult survival rates of the females (Madsen & Shine 1992). The operational sex ratio (ratio of fertilizable females to sexually active males: Emlen & Oring 1977) varied between 0.04

and 0.79 from 1984 to 1990 (Madsen & Shine, in press). Because courtship is prolonged (see below), most females are attended by males for most of the mating season, and it is likely that a male finding a reproductive female will simultaneously encounter a rival male. Females were unaccompanied by males on $58.7 \pm 20.0\%$ of the occasions on which they were located during the mating season ($N=39$ females, monitored ca once per 45 min). Successful courtship required an average of 96.4 ± 61.1 min prior to copulation ($N=148$ courtship sequences). Hence, females were rarely unattended by males for periods as long as those required for successful courtship.

We recorded 178 matings, in 30 of which the female was not observed prior to copulation. We have classified the remaining 148 matings into three categories, as follows. Only a single male attended the female prior to copulation in 79 (53%) of the 148 matings, and we call these 'solitary matings'. Another 54 (36%) were preceded by male-male combat (henceforth termed 'combat matings'). Of these 54 matings, 10 were by large males (\bar{X} SVL = 49.9 ± 3.5 cm, $N=9$ males) that remained with females after their initial mating, and mated again with the same female after 2–5 days. In all other cases, the successful male left after mating to search for other females. The remaining 15 matings (10%) were 'waiting matings' by small males that had been driven away from the female by larger rivals, but had waited nearby and later returned to court the female successfully after their rival had departed.

Because smaller males never won combat bouts, and usually retreated from larger males, small individuals rarely figured in matings preceded by combat. Thus, mean body sizes of successful males varied among the three types of matings (after randomly deleting data so that each male is represented only once: one-factor ANOVA, with mating type as the factor, $F_{2,36}=3.75$, $P<0.03$). Males engaging in 'combat matings' were significantly larger than males participating in either 'waiting matings' or 'solitary matings' (a posteriori Tukey-Kramer tests: $P<0.05$; Fig. 2). Body sizes of females did not vary significantly among the three types of matings ($F_{2,36}=0.32$, $P=0.73$).

Male-male combat plays a central role in the mating system of the adder. Generally only two males are involved, but we recorded three cases of combat bouts involving three males simultaneously, and one case where four males fought together. When two males encounter each other in the vicinity

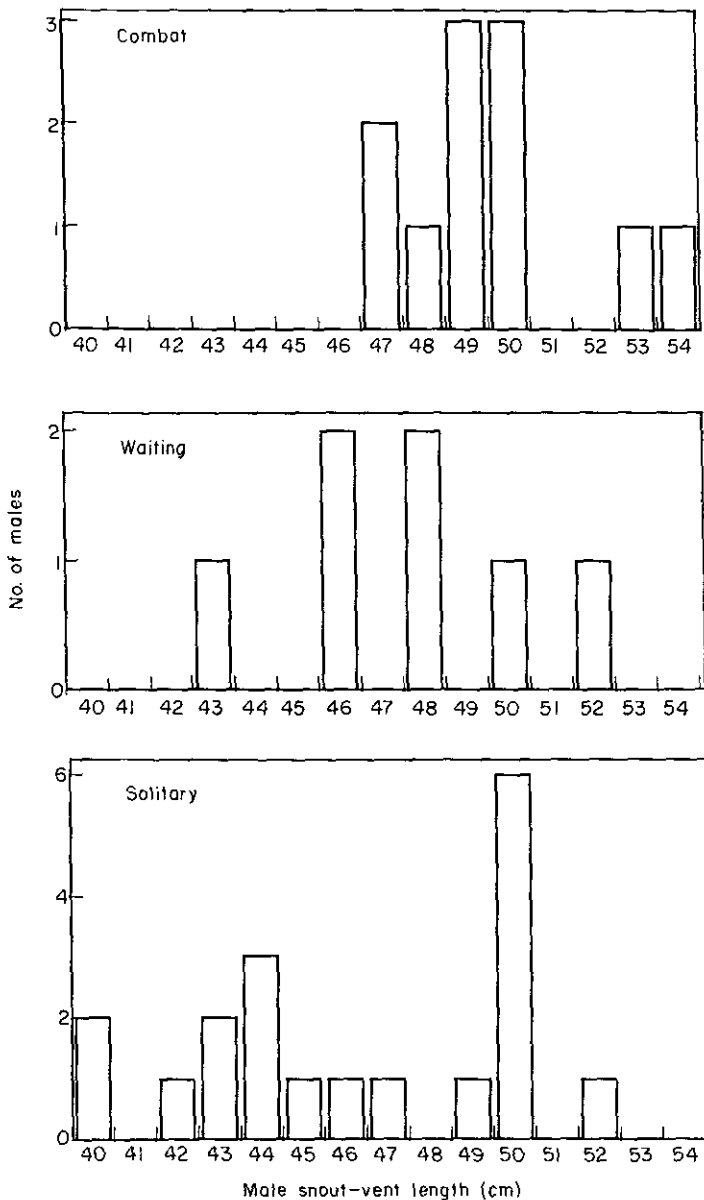


Figure 2. Distributions of body sizes (snout-vent lengths, in cm) of copulating male adders in three different types of matings: (a) those preceded by male-male combat; (b) those by males that were driven away from a female by another male, but then returned and copulated after the other male had departed; and (c) those by solitary males, with no male-male interaction prior to copulation.

of a reproductive female, either combat will ensue or the smaller male will flee. Having retreated, the smaller male may then either leave the female and search for another, or wait within 2 m of the female and attempt to court her again once the larger male has departed. The behaviour employed by the male

depends on his body size in each of these cases. The tendency for smaller males to retreat rather than fight larger males presumably reflects the advantages of larger body size in these combat bouts: larger males won every one of the 143 bouts that we observed. If two males of equal size engaged in

combat ($N=20$ cases), often no clear victor was apparent, with the result that both would eventually stop fighting and begin courting the female simultaneously. No matings were observed from these multiple courtings.

The frequency with which a male participated in combat bouts influenced his mating success. Males that fought more often also obtained more matings (correlating number of fights with number of matings, $r=0.28$, $N=48$, $P=0.05$). However, this effect was closely tied to body size. Larger males fought more often (correlating SVL with number of combat bouts: $r=0.36$, $N=48$, $P<0.02$), and the higher mating success of more combative males was attributable to their larger body size rather than variance in combative tendencies among males of the same body size. The frequency of combat bouts was not significantly correlated with male mating success ($r=0.18$, $N=48$, $P>0.10$) if the effects of variation in body size were removed in a partial correlation analysis. Thus, males that fought frequently did not attain any more matings than did males of the same size that fought less frequently.

The number of matings obtained by a male was influenced by his success rate in combat bouts, as well as his participation rate. Males that won a higher proportion of their combat bouts obtained more matings ($r=0.36$, $N=48$, $P<0.02$). Again, body size was the main determinant of this effect. Larger males won a higher proportion of bouts overall ($r=0.54$, $N=48$, $P<0.01$), and because of this success, obtained more matings per combat bout ($r=0.28$, $N=48$, $P<0.05$) and per female visited ($r=0.28$, $N=48$, $P<0.05$). However, the number of matings obtained by a male was independent of his prowess in combat if the effects of body size were removed from the analysis (using partial correlations as above, $r=0.07$, $N=48$, $P=0.70$). Overall, these data suggest that male-male combat plays an important role in determining male mating success, and that variation in a male's rates of participation and success in combat are tightly linked to his body size.

Whether or not two males engage in combat depends not only on their absolute body sizes, but also on the relative disparity in body sizes between the two participants. Males assess the sizes of their opponents very quickly, and retreat rapidly if the other male is much larger than themselves. This behaviour results in a close matching of body sizes between pairs of combative males, as can be seen by comparing the mean disparity in snout-vent lengths

between pairs of fighting males (2.92 ± 2.44 cm, $N=159$ pairs) with those based on comparisons of randomly chosen pairs of males from among those that engaged in male combat in the Smygehuk population (3.44 ± 2.38 cm; $t_{4,75}=2.23$, $P<0.03$).

The relative sizes of the two participating males influence the duration of combat as well as its probability of occurrence. Combat bouts between males of very different body sizes tended to be very brief (often, less than 20 s), whereas bouts between males of similar size sometimes lasted for hours. The duration of a combat bout was correlated with the disparity in body sizes of the participating males (using $\ln[1+X]$ transforms of both variables to normalize variances, in this test and those below: $r=0.45$, $N=37$, $P<0.005$). The absolute body sizes of the snakes also affected the duration of combat, because larger males tended to fight for briefer periods. This can be shown by comparing the mean size of the two participating males to the duration of the bout ($r=0.46$, $N=37$, $P<0.005$).

Courtship Behaviour

Having located a solitary receptive female, or driven away smaller rivals, a male must then court the female and induce her to mate. Because another male is likely to arrive soon and interrupt courtship, there should be a premium on a male's ability to court effectively and induce female cooperation as soon as possible. Under such circumstances, epigamic selection should be intense. However, courtship is prolonged, with most females requiring about 90 min of courtship before they will mate (see above). The determinants of the duration of courtship prior to copulation are thus of interest.

Female body size did not influence the duration of courtship prior to copulation (correlating female SVL with duration: $r=0.032$, $N=35$, $P=0.84$): i.e. larger females were no more or less ready to mate than were smaller individuals. Neither did male body size influence the duration of courtship (correlation of male SVL with duration: $r=0.17$, $N=35$, $P=0.34$). The duration of courtship also did not vary significantly among the three different types of matings ($F_{2,34}=1.63$, $P=0.21$). The body sizes of adult males apparently do not influence their choice of mates (or vice versa). A comparison of body sizes of males and females in mating pairs revealed no significant correlation between the body sizes of the two partners ($r=0.063$, $N=37$, $P=0.70$). Hence, these results provide no evidence

of epigamic selection on male courtship ability in adders.

DISCUSSION

These data enable us to evaluate the influence of various behavioural traits on male mating success. Our primary result is to demonstrate correlations between the mating success of male adders and their performance in a variety of tasks: in the distance they travel in search of mates; their ability to find mates; and their ability to defeat each other in combat bouts. Variation among male adders exists in each of these characteristics, and correlates with male mating success in each case. We interpret these correlations to mean that the abilities to travel further, search more efficiently, and defeat rival males are likely to enhance mating success in male adders. However, we recognize that it is dangerous to infer causation from correlation, especially because traits such as mobility and mate-finding ability may themselves be intercorrelated in occurrence, so that their common correlation with mating success may in fact be due to their correlation with each other. The simplest test of this caveat is to carry out a partial correlation analysis, with male mating success and the various male 'abilities' (distance travelled, females located per metre travelled, and success rates in combat bouts) as the variables of interest. This procedure reveals that all three of these male 'abilities' correlate significantly with male mating success, independent of the effects of the other two variables. In total, these three behavioural variables accounted for 55% of the variance in mating success among our sample of male adders. The square of the partial correlation coefficient represents the proportion of the variance in male mating success that could be predicted in a linear regression sense only by a specific variable and not by either of the other two variables in the analysis. When analysed in this way, male mobility (total distance travelled in mate-searching) explained 19% of the variance in mating success among males, mate-finding efficiency (females located per metre travelled) explained another 19%, and ability to win combats explained a further 10%.

The reproductive abilities of male adders are strongly influenced by body size, primarily because larger males are better able to defeat rivals in battle, and can guard these females against other males.

We have interpreted this result as a direct consequence of the importance of large male body size in physical combat, but other interpretations are also possible. For example, larger males might achieve more matings not because of their size, but because of their age (and hence, some benefit from learning or from social consequences of age). The hypothesis that age (as well as size) influences male mating success is best investigated using partial correlations, as explained above. Such an analysis shows that mating success is strongly influenced by body size ($r=0.48$, $N=48$, $P<0.001$) but is independent of age once body size is taken into account ($r=0.06$, $N=48$, $P=0.69$).

The results of a broad comparative analysis suggest that male-male combat imposes strong selection for large body size in male snakes (Shine 1978). The data presented above support this hypothesis, and provide an opportunity to evaluate various plausible alternative hypotheses on the reasons why larger male body size enhances male mating success. Body size apparently does not influence a male adder's choice of mates (at least in terms of their body size, and hence their probable fecundity), nor his abilities in mate-searching or in inducing female receptivity more rapidly during courtship. Neither is the influence of body size on male mating success an indirect consequence of the correlation between a male's age and his body size. Instead, our data suggest that the strong selective advantage to large body size in male adders (Madsen & Shine 1992a, and see above) is due primarily to the important influence of body size in physical combat between rival males. Perhaps because of this size-dependent advantage, smaller males show a distinct shift in reproductive tactics. When displaced by a larger rival, these smaller males tend to rely on waiting near a receptive female and returning frequently to attempt courtship, rather than leaving in search of another female. In contrast, large males depend mostly on male combat and mate guarding to secure copulations.

The size-dependent shifts in mating tactics of male adders result primarily from phenotypic plasticity rather than genetic differentiation within the population (cf. Clutton-Brock et al. 1982). Variation in body sizes among adult male adders at Smygehuk results primarily from variation in age (one-factor ANOVA, with age in years as the factor, $F_{2,25}=13.2$, $P<0.001$; 53.1% of variance in adult size due to age). As in many other organisms ranging from bullfrogs, *Rana catesbeiana*, to red

deer, *Cervus elaphus* (Howard 1981; Clutton-Brock et al. 1982), younger males adopt reproductive behaviour patterns enabling them to obtain occasional matings without coming into direct physical conflict with larger males. This behavioural shift is consistent with predictions from Parker's (1982) mathematical models of 'phenotype-limited strategies', wherein phenotypes differ in their inherent competitive abilities, and individuals adopt strategies that are conditional upon their phenotype. In the case of the Smygehuk adders, the relative success rates of the different phenotypes (body sizes) vary through time. Smaller males may reproduce very successfully in years when the operational sex ratio is high (many fertilizable females per breeding male), because the larger males cannot effectively monopolize all of the available females (Madsen & Shine, in press). Under such circumstances, 'solitary matings' and 'waiting matings' are common, and male body size has relatively little effect on mating success. In contrast, years of low operational sex ratio make it virtually impossible for small males to obtain matings (Madsen & Shine, in press).

The size-dependent shifts in male mating tactics reflect the options open to reproducing males (Parker 1982). Small males, because they are unable to defeat larger rivals, can obtain matings in only two ways: by finding a solitary female and inducing mating before a larger male arrives; or by remaining near a female after a larger male arrives, and then returning to the female after he leaves. The former option is made more difficult by the high visit rate of males to females. The latter option is likely to be effective only if visit rates are relatively low, and if the larger male does not remain and guard his mate after copulation. The lower mating success of smaller males is thus primarily a function of their lower ability to win combat bouts.

The tendency for small males to flee at high speed when they were approached by larger males, or after they were defeated in combat, is puzzling. Even prolonged combat bouts do not result in any obvious physical injury to either participant. Ritualized battles such as these are only likely to be evolutionarily stable strategies if there is some threat of real injury upon escalation of the contest (Maynard Smith 1976; Parker 1982). Although biting by male snakes during combat bouts is rare, it has been reported in several taxa including three viperid species (e.g. Shine et al. 1981; Carpenter 1986; Ross & Marzec 1990). The extraordinarily

long fangs and toxic venom of viperid snakes may mean that even a minute probability of being bitten is enough to induce smaller adders to flee from their larger rivals.

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