in the progenote. As information from other genes of similar antiquity becomes available, more clarity should ensue. It is the data, rather than arguments, that are lacking.

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# Can female adders multiply?

SIR --- Madsen et al.<sup>1</sup> conclude from a field study on an adder (Vipera berus) population from southern Sweden that most of the females mated multiple times in a season, and that those females that copulate more frequently than others also produce a higher mean number of viable offspring. These findings suggested to the authors that the increase in viability of fertilized eggs is due to sperm competition, in which the 'best' sperm compete for the chance to effect fertilization. But in an adder population from northeastern Italy (Sella Nevea, Carnic Alps, 1,100 m high), we find that only about 18% of the females mated multiple times in a season, and those females copulating multiple times very often do so with the same male<sup>2</sup>.

In the reproductive period of 1993, we captured 20 free-living adders (belonging to the population studied by Luiselli<sup>2</sup>) immediately after the end of hibernation (before the start of the mating period). and placed them in a outdoor enclosure (in the adder habitat) to monitor the exact number of copulations of each female. Receptive males from the same population were introduced into the enclosure. Ten female individuals were mated only once (group A), and ten were mated multiple times (from 3 to 8, group B). We used differently sized males, but there were no mean size differences between adders that copulated with female groups A or B. After the end of the experiments, we measured clutch parameters of the two groups of females by using methods as described in refs 3 and 4.

As in the study by Madsen et al.<sup>1</sup>, we found that the number of copulations was not significantly correlated with litter size or with female fecundity relative to body size (in either case, r < 0.3, P > 0.1), and that the number of matings by a female did not affect her mean offspring mass, her total mass or her proportional body mass loss during gestation (in all cases, r < 0.3, P > 0.1). But our data did differ from those of Madsen *et al.*<sup>1</sup> in that multiple matings did not reduce the proportions of offspring that were dead at birth. In fact, the proportion of dead offspring per litter was not significantly different in the two groups of females ( $\overline{x} = 12.0 \pm [s.d.]$ )

16.52% of female group B versus 14.0  $\pm$ 17.66% of female group A: two-tailed t = -0.19, d.f. = 18, P > 0.8), and the correlation between proportion of stillborn young and number of different males mated with was not significant (r = 0.53, ANOVA: mean square = 0.069, F = 3.17,P = 0.1). Thus, at least in the population we studied, the number of different males mated with does not seem to be the primary determinant of the proportion of viable offspring produced by a female adder. Thus, although the arguments of Madsen et al.<sup>1</sup> are interesting, we suspect their results may not apply to all adder populations. On the other hand, it could be claimed that the mating pattern is adaptive in each case, and that female adders mate multiply with different males only when there is a positive benefit from doing so.

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SIR — Females of many animal species mate frequently, with several different males. This 'promiscuous' female behaviour is unexpected from simple Darwinian theory because the number of offspring produced by a female does not increase if she has more sexual partners. In an earlier paper<sup>1</sup>, some of us suggested that by this behaviour, females promote sperm competition among males, and their offspring are thereby sired by males with 'better' genes. We found that female adders (Vipera berus) that mated with several males produced a higher proportion of viable offspring than did 'monogamous' females<sup>1</sup>. Parker<sup>5</sup> suggested that judgement of this hypothesis should be suspended until further evidence was accumulated. Here we report a study of lizards that strongly supports the earlier hypothesis<sup>1</sup>. Not only does multiple mating of lizards with different partners increase hatching success and lower the incidence of deformities, but it also enhances survivorship of free-living iuveniles.

We studied a population of marked, blood-sampled sand lizards (Lacerta agilis) 50 km south of Gothenburg on the Swedish west coast<sup>6,7</sup>. Matings were directly observed (n=32) or were inferred from the post-copulatory mate guarding (n=108) that characteristically follows the 2-4-min-long copulation7. In 1989 and 1990, we incubated eggs from the female lizards under identical conditions in the laboratory. Hatchlings were marked by toe-clipping and were blood sampled before being released at random sites at the Asketunnan study area. We used DNA fingerprinting<sup>7</sup> to establish paternity and to assess the degree of genetic variation in

the population. After one year we recaptured the survivors to determine whether offspring from multiply-mating females were more likely to survive as free-living juveniles.

Genetic variation in the population was low (mean band sharing among individuals was 66%, range, 63-68, n=30). Despite the low genetic variation, we could identify male-specific bands in five broods; four had mixed paternity (our unpublished data). Females mated on average 3.7 times with 1-5 different males (mean, 1.7). The resulting clutches varied in hatching success (mean, 81%; range, 38-100). We recaptured 42 of the 516 released hatchlings, with some clutches being much more highly represented than others (mean, 9.5%; range, 0-43%). As some of us predicted (one-tailed tests), a female's number of sexual partners was: (1) positively correlated with the hatching success of her eggs ( $r_s=0.59$ , P=0.0003, n=31; (2) negatively correlated with the proportion of hatched young that exhibited malformations ( $r_s=0.33$ , P=0.035, n=31); and (3) positively correlated with the proportion of her offspring that were recaptured after 1 year ( $r_s=0.37$ , P=0.020, n=31). This result remained significant when clutch size was controlled for in a partial correlation analysis  $(r_s=0.41, P=0.014, n=31).$ 

Could these differences in offspring viability be caused by nutrients in the ejaculate, rather than by genetic enhancement of offspring? Probably not. Some females mated more than once with the same male, enabling us to examine the effects of number of copulations independently of the number of partners. Increased copulations with the same male did not increase a female's offspring viability (number of matings versus hatching success:  $r_s = -0.19$ , P = 0.502; versus % deformities:  $r_s=0.42$ , P=0.136; versus offspring survival:  $r_s=0.41$ , P=0.143, n = 15).

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