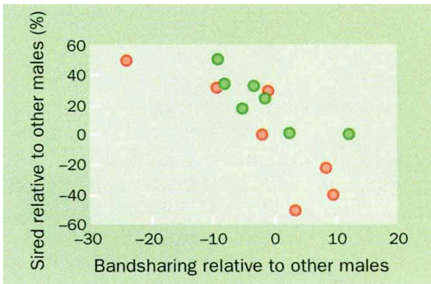
Sperm selection by females

SIR — The history of sexual-selection studies reveals an increasing recognition of the active role of females in determining microevolutionary trajectories. Early studies emphasized male tactics such as combat and scramble competition, and doubted the evolutionary significance of female choice[1]. Even after female choice was convincingly documented, its role was believed to be restricted to pre-copulatory phenomena[1–3]. Despite an increased recent focus on sperm competition within a female's reproductive tract, the female has typically been viewed as providing the arena of competition, rather than being an active participant in the selective process[4]. Our studies on lizards provide the first clear evidence of active selection of sperm by females, in ways that enhance female fitness.

In the Swedish sand lizards (*Lacerta agilis*) we have studied, brother–sister matings reduce offspring viability (and hence maternal fitness)[5]. However, female sand lizards accept copulations from virtually every male that courts them; thus, they often mate with close relatives[5,6]. Most females mate with more than one male, so natural selection should favour females (or eggs) with the ability to discriminate among the sperm of these competing males, and preferentially use the sperm of distantly related males for fertilization. Observations that multiple copulations with different partners enhance the viability of a female's offspring are consistent with such a mechanism, but are controversial[7–10], and have not demonstrated selective use of sperm by females. To do this, we need to know paternity for each offspring.

Our behavioural and DNA fingerprinting studies of a natural population of sand lizards confirm that more closely related males sire fewer offspring per copulation than do more distantly related males. At our study population on the west coast of Sweden, these small lizards (up to 90 mm body length, 20 g) mate in spring; females produce a single clutch of 4 to 15 eggs each year[5]. We observed mating directly in the field, and used the proportion of shared DNA fingerprint bands as an index of genetic similarity[6].

We found that males with a higher genetic similarity to their partner sire a lower proportion of her offspring than do more distantly related males. This effect is most easily seen if the data are standardized, such that each clutch has the same mean value for relatedness of males to the female, and paternity is calculated in relative terms (the observed proportion of offspring sired by a given male minus the proportion expected from chance, based on the number of males involved: $r = -0.85$, $n = 7$, $P < 0.02$; see figure). This result is corroborated by staged matings between pedigree-unrelated lizards in the laboratory. Again, we find a strong negative correlation between a male's genetic similarity to his partner (proportion bandsharing) and the proportion of her offspring that he sires ($r = -0.84$, $n = 7$, $P < 0.02$; see figure). Analysis of covariance shows that the relationship between a male's genetic similarity to his mate versus his proportional paternity of the resulting clutch is similar in matings conducted in the laboratory versus the field (slopes $F_{1,9} = 0.30$, $P = 0.60$; intercepts $F_{1,10} = 4.92$, $P = 0.06$; see figure), with a strong overall effect of the degree of bandsharing on the proportional paternity of the clutch ($F_{1,10} = 23.10$, $P < 0.0008$).



The proportion of offspring fathered by a male sand lizard, within a multiply sired clutch, depends on the degree of his genetic similarity with the female parent. Males that are genetically more similar to their partners (relative to other males) father a lower proportion of offspring, both in natural matings in the field (green circles) and in controlled matings in the laboratory (red circles). The proportion of offspring sired is calculated as the observed proportion minus that expected if paternity was random (50% if two males contributed to the clutch; 33% if three males contributed). The index of bandsharing is calculated as the male's genetic similarity with the female, minus the mean genetic similarity of the female with all males mating with her. We use information from only one male per clutch, to avoid pseudoreplication.

This result might also arise if males that produce more sperm fertilize higher numbers of offspring per copulation[4,11]. However, proportional paternity is not correlated with either the male's body size (and hence testis size), nor the duration he has for sperm replenishment since his last copulation[4,11] ($P > 0.40$ for both variables for both laboratory and field data), and remains correlated with male–female relatedness in a partial correlation analysis in which both of these variables are held constant ($r = -0.64$, $n = 16$, $P < 0.03$). Hence, we conclude that female sand lizards actively select the sperm from distantly related males. Even if they are unable to avoid mating with close relatives, females 'choose' not to use sperm from these matings.

This kind of cryptic female choice via intrauterine sperm competition has important implications. Estimates of inbreeding frequency based on behavioural data (numbers of copulations) may be in significant error, for example. More generally, female sand lizards can exert significant mate choice irrespective of their copulatory behaviour. If such abilities are widespread, they may substantially modify our understanding of the determinants of variance in reproductive success in natural populations, and the degree to which female animals can control male reproductive success. Our data suggest that female organisms are capable of subtle discrimination among potential mates, even after copulation, and hence may control microevolutionary phenomena to a greater degree than has heretofore been suspected.

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CO_2 fluctuation at high latitudes

SIR — Keeling *et al.*[1] recently showed that an increased seasonal amplitude of atmospheric CO_2 concentration in northern latitudes is correlated with increasing land temperature, with this correlation being strongest at high latitudes. Because atmospheric CO_2 has been drawn down by plant photosynthesis earlier in the spring in recent years, and because most high-latitude warming has occurred in winter and spring, rather than in summer[2], Keeling *et al.*[1] suggest that a temperature-driven increased length of growing season accounts for the increased seasonal amplitude of atmospheric CO_2. Here we provide evidence from field measurements that