

Multiple mating by females: the design and interpretation of selection experiments

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Genetic correlation between the sexes in mating success is still an open empirical issue. Only three critical selection experiments have been performed (Manning 1963; Dunnington & Siegel 1983; Gromko & Newport 1988), and the results are equivocal in each case. Furthermore, the most recent experiments have problems and, in general, selection experiments may not be the best way to detect or estimate the critical genetic correlation. Under these circumstances, it seems premature to argue that the issue is settled. Instead, we see a need for more and better experiments.

We suggested that multiple mating by females (female mating success) might be genetically correlated with mating success in males (Halliday & Arnold 1987; Arnold & Halliday 1988). In both sexes the trait in question would be measured in units of number of mates, preferably over some long time interval but with some correction for differences in lifespan. The variable under scrutiny in Gromko & Newport's (1988) experiment is the elapsed time from a female's first mating to her second mating. Female remating time might be related to female mating success, but Gromko and colleagues have not shown this. Moreover, a genetic correlation between male and female contributions to female remating time, although interesting, is tangential to our argument. Thus, the results of Gromko & Newport (1988), summarized in Fig. 1 of Gromko (1992), suggest that male contribution to female remating time showed a correlated response to selection on female contribution in one experiment, but there was no evidence of a correlated response in a second experiment. The authors set up two selection lines in both experiments. In one line, females with the fastest remating times were selected; in the other, females with the slowest times were selected. Selected females were bred in every generation to males from an unselected base population. After 13–28

generations of selection, the authors compared the remating times of females from the base (control) population when their first and second mates were drawn from the up selection line as opposed to the down (cf. the middle pairs of bars in Gromko 1992, Fig. 1a, b). The results indicate that in one experiment the genetic constitution of the first or (more probably) the second mate affected the female's remating time and that these genetic differences in male contribution evolved as a corollary to selection on females. Note that the male's ability to affect the remating time of females is not the same as male's mate number, although it may very well be a component. In this sense, Gromko & Newport's (1988) results are somewhat distant from our argument.

Cheng & Siegel (1990) argued that a selection experiment in domestic chickens, *Gallus domesticus*, indicates no genetic correlation between male and female mating frequency. The experiment in question (Dunnington & Siegel 1983), however, suffers from two major design faults. (1) Male mating frequency was assessed by putting males in tester flocks of females. The genetic composition of those flocks fluctuated and may have changed progressively over the course of the experiment. The resulting inflation of within-line variance was mitigated somewhat by maintaining an unselected control line, but some statistical power was lost. (2) Both an upward and a downward selection line were maintained, but neither was replicated. This lack of replication and the relatively high inbreeding coefficient after 23 generations (0.41) make the experiment vulnerable to the interpretation that drift may have produced results that are attributed to selection.

Several recommendations for future work emerge from the selection experiments that have been performed so far. More extensive discussions of many of these points can be found in Bohren

(1975) and Hill (1980). (1) In testing for correlated responses in one sex, after selecting on the other sex, it is informative to set up matings between as many different combinations of males and females as are available. Manning (1963) used this technique to tease apart the contributions of males and females to mating speed. (2) In assaying mating speed or frequency, so that one or the other sex can be selected, it is desirable to use mating partners from an unselected base population. The worst procedure would be, for example, to use females from the selected line as mating partners when the intent is to select only on males. Dunnington & Siegel's (1983) protocol was better than this, but still, some of the female birds in their tester flock were from the selected lines. Their protocol was predicated on the assumption that females will not show a correlated response to selection on males. (3) An unselected control line is a desirable design feature. With only one selected line (no control), progressive change can be partly or wholly a result of changes in environmental conditions. With only two selected lines (no control), only the difference between line means can be interpreted as a response to selection. (4) Replicate selection lines in each direction are needed to conclusively discriminate between the effects of selection and drift (Hill 1980). In tests for correlated response, one obtains only one degree of freedom from each additional replicate line. (5) Selected lines begun from different base populations (e.g. Gromko 1992) are not replicates. (6) Standard errors for heritability estimates obtained by regressing means on generation number (e.g. Dunnington & Siegel 1983) may be underestimated unless autocorrelation in the data is taken into account (Bohren 1975; Hill 1980).

Breeding designs may be a better vehicle for estimating genetic correlation between the sexes in natural populations than selection experiments. When the objective is to estimate genetic parameters prevailing in a base (e.g. natural) population, Bohren (1975) has argued that a single generation of selection may give more meaningful estimates than a multigeneration selection experiment because of the cumulative effects of drift and inbreeding

depression, and systematic change in the genetic parameters themselves. Furthermore, for none of the three selection experiments described above, is there a natural reference population (of which the base population is an unbiased sample). Consequently, we still do not have an estimate of the genetic correlation between males and females in mating success or frequency for any natural population of animals. Future attempts at estimation should consider paternal half-sib and other breeding designs (Falconer 1989) in which parents are drawn directly from nature or are only a few generations removed. In the meantime, a genetic correlation between the sexes in mating success remains a hypothesis that has not been conclusively rejected, as well as a phenomenon with potentially interesting evolutionary consequences.

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