preferences in order to conform to such a result, and his model would need to include components for each type of female. Our explanation based on relative mating receptivities for females and courtship activities for males seems simpler and less hypothetical.

O'Donald¹ cited a paper in press⁸, not available to us, where possible behavioural events were proposed which should follow from his preference model. He predicted that "The proportion of preferential matings would therefore decline with increasing density", so that in the double chamber experiments⁷ with a minority ratio in the upper chamber, when extra males were added to the lower chamber, the minority advantage would disappear. O'Donald did not discuss a prediction for the opposite result, namely the induction of a minority advantage with double chamber technique by initiating the experiments with equal numbers of types in the upper chamber, which Ehrman⁹ demonstrated later. In both cases, addition of flies to the lower chamber increased density.

Furthermore, O'Donald considered "A similar result would follow if different male genotypes determined different levels of courtship activity . . . A less responsive female would mate readily with one or more active males and would therefore tend to show a preference that decreased at higher levels of stimulation". These assumptions are not borne out by recent experiments of Spiess and Schwer¹⁰, which have demonstrated that, in spite of courtship intensity differences between two genotypes of male *D. melanogaster*, females displayed no bias toward either type at control frequencies, whether flies were tested as groups of 20 pairs or as single virgin females confined with six males. But when two types of males were introduced at unequal frequencies, the females accepted minority males without alteration in the average time to acceptance; nor did minority males court with any change in their intensity. In fact, Spiess and Schwer¹⁰ found by analysing the sequence of individual courtships that females are less inclined to mate with the type of male which courts them first; Ehrman's observations agree. We have interpreted these results as lending support to the behavioural hypothesis⁴ that a female samples males and their courtship cues, becoming habituated to the majority (or alternatively avoiding the cue of the first male to court) but accepting a male with cue different from that she first detected. Thus behavioural tests lend no evidence for a female preference parameter.

The establishment of either argument as the mechanism to account for rare male mating advantage can only follow more extensive empirical behavioural testing¹⁰⁻¹².

A more substantive proof for a behavioural basis of the male minority

advantage in mating will be published elsewhere by E.B.S.

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O'DONALD REPLIES—In restating their own behavioural interpretation of the rare-male advantage in *Drosophila*, Spiess and Ehrman argue that because no evidence of preferential mating has been found at 'control frequencies' when genotypic frequencies are equal, therefore only a small fraction of females could display no more than "some negligible amount of preference". This conclusion does not follow, however. If equal proportions of females prefer two genotypes, then in my model any magnitude of such preferences will give equal expectations of numbers of matings at the control frequencies. In the data, deviations from equal expectations occur at the control frequencies. These deviations, although not significant by themselves in the small sample sizes at these frequencies, are nevertheless much reduced after fitting of the preferences estimated from the data obtained at all frequencies. This is shown in the expectations of the matings in Table 1a of ref. 1.

It is certainly true, as Spiess and Ehrman state, that in fitting their data I assumed equal expression of preference among the female genotypes. If preferences were expressed at different levels in different genotypes, this would produce assortative mating which has not been observed. Spiess and Ehrman's own explanation, which, they say, seems simpler and less hypothetical also depends on the same assumption. Both explanations would become less simple if the assumption were removed from the models.

Spiess and Ehrman then refer to some data of Spiess and Schwer, still in the press. It seems to me that these data clearly refute Spiess and Ehrman's own model, but not the model of female

preference. If males differ in the intensity of their courtship and females become habituated to the courtship cues provided by the males, then at the control frequencies we should expect a bias in favour of the males with the less intense courtship giving fewer cues to which the females would be less likely to become habituated. The absence of bias favouring one or other type of male therefore refutes both my own model based on differences in courtship intensities and Spiess and Ehrman's model, leaving the model of female preference. If females have preferences for one or other of the males, regardless of differences in courtship intensity, then no bias should be found in the matings at the control frequencies.

On evolutionary grounds, Spiess and Ehrman's theory is implausible: a general tendency to mate with the more unusual phenotypes would be maladaptive.

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Population dynamics and the length of food chains

PIMM and Lawton¹ have claimed that increasing the number of trophic levels tends to increase the time taken for a stable ecosystem to return to equilibrium after a perturbation, and they have suggested that this is the chief reason why food chains are typically short. I show here that the first of these claims is not necessarily true, and that even if it were, the second does not follow from it.

Pimm and Lawton based their conclusions on investigations of the eigenvalues of matrices whose elements were chosen randomly subject to certain constraints on magnitude and sign. Their key finding was that as the number of trophic levels increased, so did the reciprocal of the largest eigenvalue. In fact it is quite easy to see how this came about. In all the models that were considered, of the diagonal elements only those associated with the primary producers were allowed to be non-zero, and these were all chosen within the interval (0, -1). The expected value of the trace of the stability matrix was thus proportional to the number of primary producers. Since the trace of a matrix is equal to the sum of the eigenvalues, and since the probability that at least one eigenvalue of a 4×4 stable matrix will have a real part greater than a certain fixed value clearly decreases as the sum of the eigenvalues decreases, we would expect that the six models would fall into three classes and that in order of increasing stability (in the sense of Pimm and Lawton) these would be (a, b), (c, d, f), (e). This is precisely what was found.