# MATING ISOLATION

Contents

I only published one pair of papers on this [4] [5], which had minimal impact. However I still rather like the analysis, and the account here also describes an experiment to try to verify the theory that never got published.

## 1. A MODEL FOR MATING ISOLATION

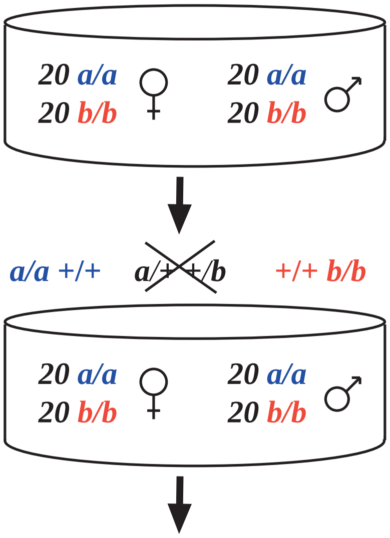

Figure 1. Mating chamber selection for mating isolation

### 1.1. **Introduction.**

When I was at the Rockefeller University, or maybe on a visit shortly afterwards, Francisco Ayala got me interested in an experiment that he and Dobzhansky had been doing for a number of years. The basic outline of the experiment is shown in Figure 1. It involves two recessive mutant strains, labeled $a/a$ and $b/b$. Females and males of the two strains are collected, aged, and then introduced all together into a 'mating chamber'. Offspring are then collected, hybrid offspring discarded, and the two pure strains introduced into the next mating chamber. The procedure is repeated over a number of generations.

Any genes for mating choice that predispose $a/a$ females to mate with $a/a$ males, and vice versa for $b/b$, should be selected. Gradually one ought to see mating isolation developing. Although it may seem surprising that such genes would exist, it seems possible to select Drosophila for most measurable characters such as size, phototaxis (moving towards or away from light), geotaxis (moving up or down). Why not for mating choice?

Experiments such as this have been only partially successful. One experiment in *D.melanogaster* in the 1950s in Edinburgh produced a small amount of isolation [2]. Francisco was also partially successful at increasing isolation between different crossmating species other than *D.melanogaster*, as were Koopman [3] and Kessler [1].

The experiment is an attempt to simulate in the laboratory what is usually referred to as 'reinforcement of mating isolation'. There are many examples where closely related species in contact with each other, ie in sympatry, exercise more precise mating choice than the same species in allopatry. This is sometimes known as the 'Wallace effect', after AR Wallace, Darwin's contemporary.

### 1.2. **The model.**

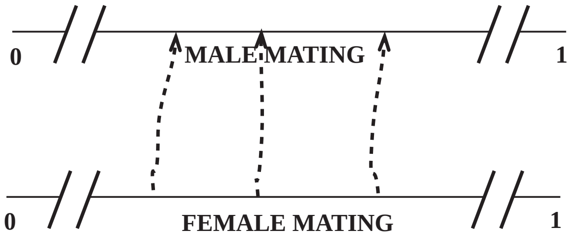

FIGURE 2. Model for mating preference

In an attempt to see why it might be so difficult to change mating behaviour in the laboratory, I set up a model as in Figure 2. The essence of the model is that female and male mating characters are separate and controlled by different sets of genes. It might be easiest to think of the model as a female choice model, with the male character being some form of behaviour, eg speed of wing beat, and the female character being preference for a particular wing beat speed. The two scales are defined to be between 0 and 1. The female scale is defined such the females prefer males at the same point along the scale. The preference is, as indicated, not totally precise.

The model also needs to indicate where current populations lie on the scale. The next diagram shows the frequencies in males and females of the different mating behaviours. One would expect that the two would line up, at least approximately, as shown in Figure 3.

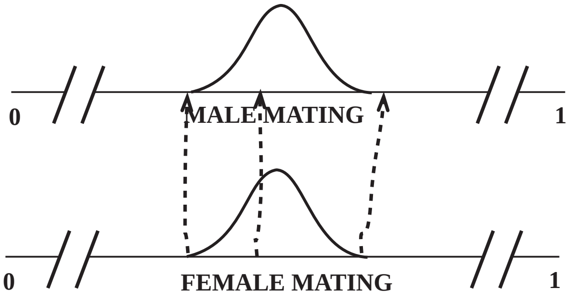

FIGURE 3. A single population on the mating scales

All distributions are assumed to be normal distributions. The model also needs to specify the strength of attraction. It is convenient to do this by assuming a normal distribution as shown in green in the next diagram (Figure 4). The variance of this distribution is given the symbol $W$. It is pictured as being smaller than the variance of female and male scores in the population, V and V' respectively.

To take into account the full complexity, the model needs to set separate populations for the two strains involved in the experiment. This is shown in Figure 6, with the two populations coloured as previously for the $a/a$ and $b/b$ strains. The strains are pictured as being very close to each other, at least initially.

It is now possible to calculate the expected change in female and male mating scores. The female score of strain $a$ is expected to change by

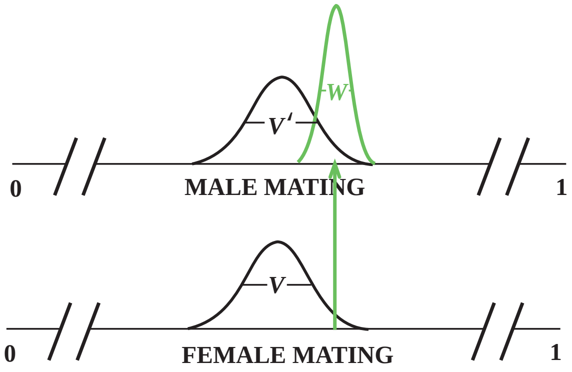

FIGURE 4. Distribution of mating preferences for a single female, shown in green

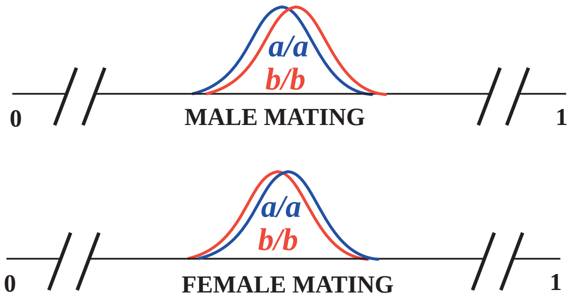

FIGURE 5. Two populations on the mating scales

amount

$$\Delta F_a = \alpha(M_a - M_b)\frac{V}{V + V' + W}$$

where $M$ values represent mean male mating scores, and $\alpha$ is a quantity that depends on the frequency with which strain $a$ females encounter $a$ rather than $b$ males, what they lose by mating with the latter, and what proportion of females mate.

The model predicts that if the males of strains $a$ and $b$ are differentiated, females will evolve towards mating with the correct strain. The endpoint of this process is not clear, since the equations predict that the females may 'overshoot', minimising mating with the wrong strain at the cost of reducing mating with the correct strain.

The situation with males is the converse:

$$\Delta M_a = \beta(F_a - F_b)\frac{V'}{V + V' + W}$$

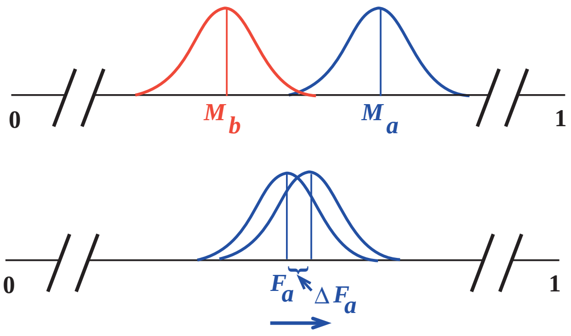

Figure 6. Change in female mating score of strain $a$

The quantity $\beta$ is influenced by the reduction in fitness produced by mating with the wrong strain of females. It is likely that the penalty is not as high in this case, perhaps just a loss of time. In the experimental situation, however, it is possible to physically remove interstrain mating pairs, as done in some of the previous experiments, thereby exacting the same penalty for males as for females.

### 1.3. **An unstable equilibrium?**

The conclusion from the equations is that female differentiation depends on differentiation in males, and vice versa. In theory, if the populations start off at the same point on the scale, this situation cannot be maintained, ie it is an unstable equilibrium. A chance deviation in one direction or the other is enough to set the process off.

Importantly, however, the changes may happen very slowly. The fact that divergence in one sex feeds back into divergence in the other, rather than directly into its own divergence, means that it may be very difficult to start the process off. My guess is that this, combined with the likelihood that male divergence is not strongly selected, is enough to account for the failure of experiments to induce much mating divergence. Some computer simulation is given below, showing that this may be the case. The results of the simulation were, however, sensitive to the choice of parameters such as $V$ and $W$.

### 1.4. **Two possible deficiencies of the model and experiment.**

The model is what might be described as a 'facilitation' model. The preference for within strain mating postulated in the model is a positive attraction for the correct strain. There seems another possibility, that in reality the reason for preference of the correct strain is a positive rejection of the incorrect strain. This seems a much more difficult situation to model, even though the net result might be the same under this 'rejection' model.

Another problem, partly with the model and partly with the experiment, is that speed of mating could be an important factor. Particularly in the case where not all females mate, there might be selection pressure for fast mating rather than correct mating.

### 1.5. **Application of the theory to real life.**

As mentioned above, I don't believe that the papers have had any real impact. I recall seeing criticisms that the theory assumed that there was complete overlap of strains rather than the more realistic situation of a partial overlap in a 'hybrid zone' between the two strains. In fact the model is probably reasonably general in this respect, since the parameter *alpha* has a mating probability built in, and as a first approximation partial overlap can be taken into account by just reducing this parameter. The basic conclusion, however, is that if the theory shows that isolation doesn't evolve under complete overlap, then it is even less likely to evolve under a spatially separated model.

The main reason that the paper is never referred to is that Hamish Spencer did some computer simulations, based on the same model but allowing various degrees of overlap, allowing individual mating etc. The conclusions are more or less the same, but whenever anyone refers to the theory of mating reinforcement it is always to this paper. It is true that their simulations were more realistic since they allowed for partial overlap of the species, although as mentioned above this was really taken into account in my model. I have always thought it a bit of a pity that the essential simplicity of the result, the way in which selection for divergence in one sex is dependent on pre-existing divergence in the opposite sex, is lost amongst the numbers of the simulations.

## 2. ANOTHER ATTEMPT TO INDUCE ISOLATION

There might not seem much point in yet another experiment to induce isolation, given that the experiments to date had never been totally successful. The reason for trying again was that I managed to devise other mating procedures which at least showed some improvements on the computer under the assumptions of the mating model. Figure 7 shows some computer simulation runs with a couple of schemes described below. They show that the initial mass-mating scheme in (a) produces rather small and inconsistent isolation. The remaining three graphs, using different mating schemes, show considerable improvements.

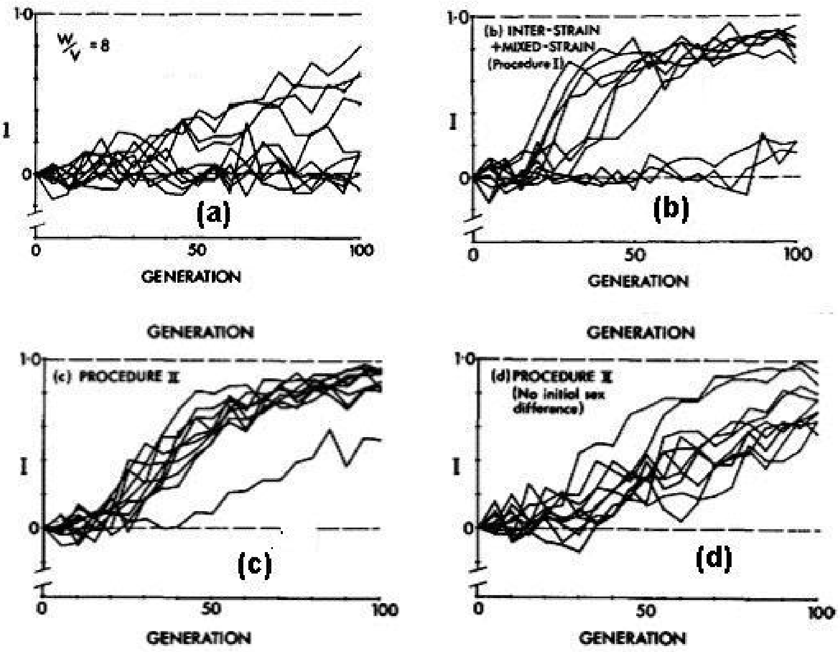

Figure 7. Computer simulation: (a) mass-mating selection, (b) Procedure I, (c) and (d) Procedure II

What I argued in the papers is that a possible problem with the mass-mating procedure of Figure 1 is that there is too much going on. The procedure combines selection for selecting for correct intra-strain matings, and simultaneously selecting against incorrect inter-strain matings. It seemed that one could separate these out. For example, strain *a* females could be put into a mating chamber with just strain *b* males. Then the females that failed to mate could be introduced to strain *a* males. There are various combinations of this sort of approach. Two are given below (Figure 8 and Figure 9).

### 2.1. Selection against inter-strain matings.

I managed to get a small grant from the Australian Research Council to try the experiments. We (Mick Murphy and I) worked hard to set up the initial strains, even isolating naturally occurring recessive markers in order to avoid crossing laboratory markers into the strains.

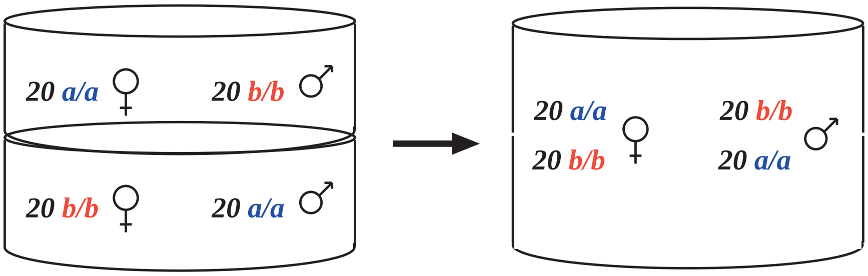

Figure 8. Procedure I. Both strains are selected for avoiding inter-strain mating

We constructed a special type of double mating chamber that allowed us to test Procedure I, one of the two recommended procedures that produced the divergence in (b) of Figure 7. Strain *a* females were introduced to strain *b* males in the top half, and the reciprocal females and males in the bottom half. Only after a measured period of time was the separation between the two chambers pulled out, allowing the possibility of intra-strain matings.

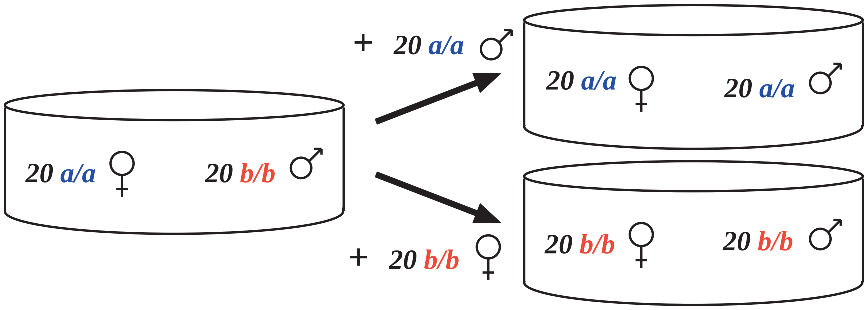

Figure 9. Procedure II. One pair selected for avoiding inter-strain mating, then the opposite sex selected for intra-strain mating.

Unfortunately the experiment produced no lasting isolation. I recall one generation when it looked as if significant isolation was developing, but in the next generation it had disappeared. Because of the negative results we never got around to writing up the experiment. Because of this, the details of the experiment have been lost, although they may still exist in old lab note books.

### 2.2. **Conclusions.**

Where some isolation has been induced in laboratory experiments with Drosophila, it has been from inter-specific matings such as between *D. persimilis* and *D. pseudoobscura* (Kessler, 1966 [1]). Interestingly Kessler used a mating scheme quite similar to that of Procedure II above. So maybe there is some reason for ignoring our failures and trying again.

## References

[1] S. Kessler. Selection for and against ethological isolation between drosophila pseudoobscura and drosophila persimilis. *Evolution*, 20:634–645, 1966.

[2] GR Knight, A Robertson, and CH Waddington. Selection for sexual isolation within a species. *Evolution*, 10:14–22, 1956.

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