PS + GN

THE QUEST FOR LINKAGES

by W. J. Miller and W. F. Hollander

Characters which do not assort independently in F_2 are in violation of one of Mendel's great principles, and are said to show linkage. By 1920 independent assortment was recognized to indicate that characters were controlled by genes on different sets of chromosomes, while linkage indicated that genes on the same chromosome (pair) were involved. Further, since some genes seemed tightly linked but others not, linkage maps of the chromosomes could be deduced. That is, the tighter the linkage, the closer the genes are to each other on the chromosome map. For pigeons we have so far only rather sketchy maps of two chromosomes, one of which is the sex chromosome:

sex chromosome	first autosome
d r b St	S C o

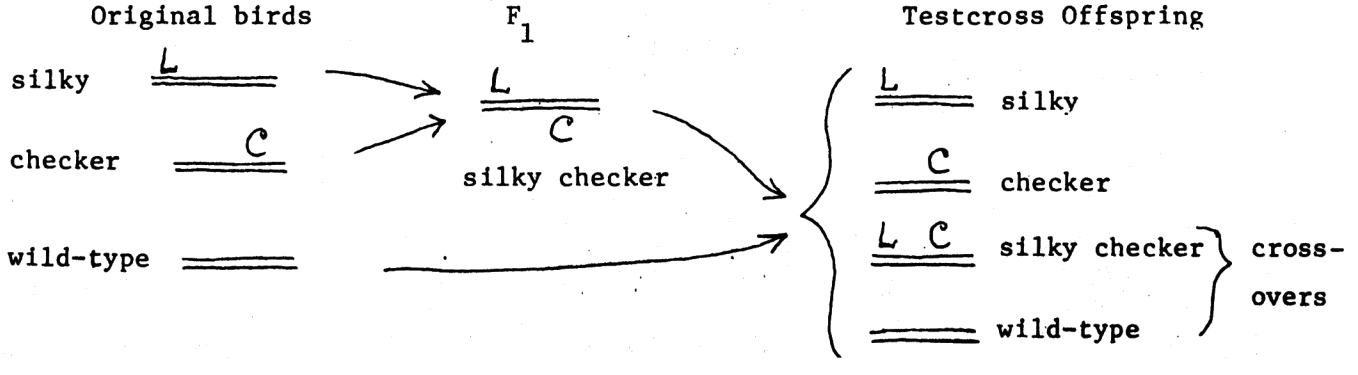
Discovery of a new linkage is an exhilarating experience, but along with such success usually there are many vain searches and bad luck. To hunt for years without finding anything exciting is discouraging, for sure, but some of us deluded souls keep trying. Anyway, by accumulating data we get more and more "feel" of the genetic machinery.

If you are gambling-minded and care to take a chance in this numbers game, how do you start? Let's assume that you are equipped with "facilities"--breeding coops (preferably one per pair birds), a record book (with at least one page for each pair of birds), some cash for expenses, a good eye, common sense, patience, and a touch of insanity. Next you choose two characters (mutants) whose genes seem adequately established, and start to get F_1.

Right there already problems arise: Why not three or more characters? Well, O.K.-fine, but remember that the project is basically a search for linkage between any two. And how about the best way to cross? It can be done in more than one way. For example, one mutant may be in the cock, the other in the hen, or both may be in one parent and neither in the other. Sometimes there is a preference, but usually not. And then the question hits you: How many F_1 should be raised? (Answer: It depends; maybe a couple, maybe a dozen?)

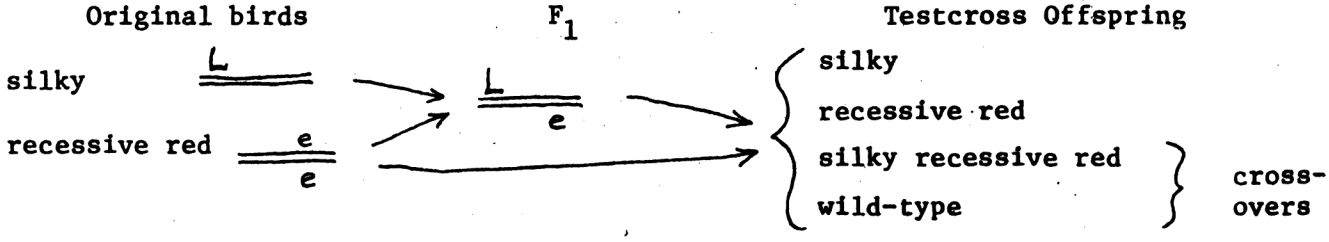
After getting some F_1 birds, the obvious next step is to go for F_2--obvious, but often inefficient. It is much better to get "testcross" matings where possible. Let's examine some examples.

(1) Suppose we want to work with two dominant (or partially dominant) mutants, such as silky and checker. If we start with a silky bar X checker, some of the F_1 birds will be desired silky checkers. To make a testcross, we simply mate these with wild-type birds (that is, having neither mutant). To diagram the project, let's assume that there is really linkage -- only one pair of chromosomes involved:

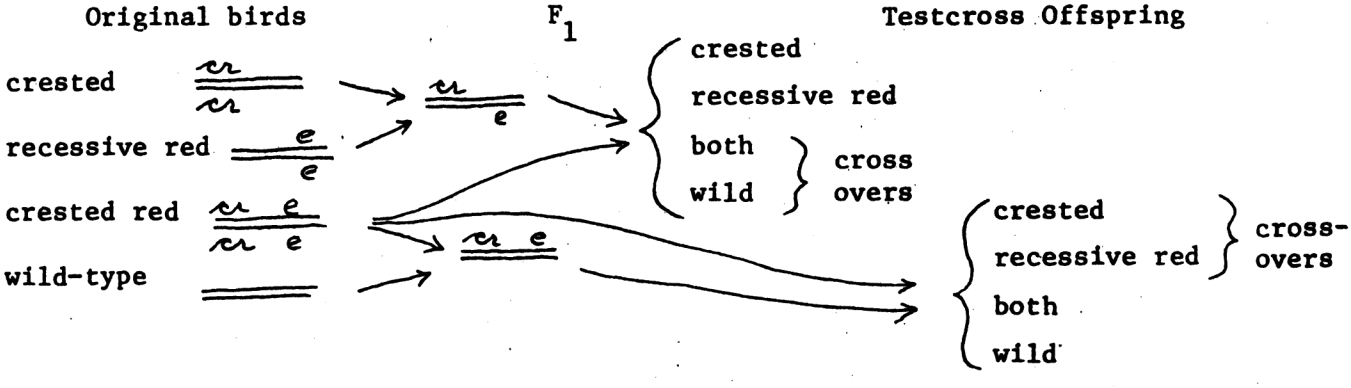


Crossing over of the chromosomes in meiosis of the F_1 bird is necessary for production of silky checker and of wild-type progeny in the testcross. If linkage is very tight, there will be few or no crossovers. Therefore, we count. Suppose we get a dozen squabs and find that only one is a crossover. That is good grounds for believing we have linkage (8% crossing over). But no proof -- we might have simply had a statistical fluke. So, more testing is needed. However, if the first result had been the reverse -- only one "non-crossover" in the dozen squabs -- there would be no good reason to suspect linkage any more, and we could consider the test complete; independence indicated. Of course, usually the counts are not so clear as that. After some 50 squabs have been classified, and recorded, we may sometimes still be undecided. Anyway, make a report! (See a similar example by Miller, 1964, "First linkage of a species antigen in the genus Streptopelia," Science 143: 1179-1180.)

(2) Suppose we want to work with one dominant or partial dominant character and one recessive. In this case the testcross can be a back-cross:



(3) Suppose we want to work with two recessive mutants, say crest and recessive red. Either or both of two procedures can be used here:



In the above examples the double-recessive (crested recessive red) can be obtained readily, maybe by purchase. But for some other example, the double recessive may not yet exist anywhere, such as crested albino. For such birds we have to obtain F_2. If these mutants are independent we can expect approximately 1/16 of the F_2 squabs to be the double recessive type. If we don't get any in say 50 squabs, suspicion of linkage is strong, and testing would be worth continuation. If any double recessive young appear, they can then be used for testcrosses.

Sometimes linkage tests are not so simple. If one of the mutants is lethal or sterile when homozygous, or if both mutants are affecting related phenotypes, serious difficulties face us. Testing linkage of albino with any other color pattern mutant, for example, gives only half the testcross progeny classifiable as crossovers or non-cross-overs, and F_2 is hopeless.

Considering all the headaches, and the rare delights, it would seem sensible for such projects to be run in a coordinated, cooperative way. So who will join us?