

$V_g$  from inbred strain mean difference =  $0.5[((\text{Mean}_1 - \text{Mean}_2)/2)^2] = 0.357$ ;

$V_g$  from  $(V_p - V_e)/2 = 0.373$ ;

Heritability ( $h^2$ ) =  $V_g/V_p$  from estimating  $V_g$  as  $0.5[((\text{Mean}_1 - \text{Mean}_2)/2)^2] = 0.94$ ;

Heritability ( $h^2$ ) =  $V_g/V_p$  from estimating  $V_g$  as  $(V_p - V_e)/2 = 0.94$ .

## Discussion

The lab permits an introduction to the analysis and genetic basis of quantitative traits, with no more investment of time or resources than that required to teach Mendelian genetic lab exercises using *Drosophila*. It is inexpensive, concept-rich and investigative, permits the introduction of parametric statistical methods for genetic analysis, and lends itself to collaborative work within groups, class presentations and formal lab reports. The availability of multiple inbred strains for class use will increase the likelihood that some students will select two strains with different mean values for the assayed trait. The lab can also be made incrementally more complex at the discretion of the instructor with respect to genetic concepts, experimental designs, and statistical methods. Limitations of the methods can also be examined, such as inability to identify specific genetic loci, the absence of dominance effects, the absence of epistasis other than additive by additive interactions (Mackay and Falconer, 1996), the limited number of genotypes represented, and potential for confounding genetic differences with maternal effects or epigenetic mechanisms. We present this exercise to facilitate the inclusion of quantitative genetic analysis in undergraduate courses so that students at this level may acquire a more comprehensive and realistic understanding of genetic concepts and analysis.

References: Falconer, D.S., and T.F.C. Mackay 1996, *Introduction to Quantitative Genetics*, 4<sup>th</sup> ed., Benjamin Cummings, New York; Hegmann, J.P., and B. Possidente 1981, *Behav. Genet.* 11(2): 103-114; Lefranc, A., and J. Bundgaard 2000, *Dros. Inf. Serv.* 83: 171-174; Mackay, T.F.C., and R.R.H. Anholt 2006, *Ann. Rev. Genomics Hum. Genet.* 7: 339-367; Mackay, T.F.C., *et al.*, 2012, *Nature* 482: 173-178.



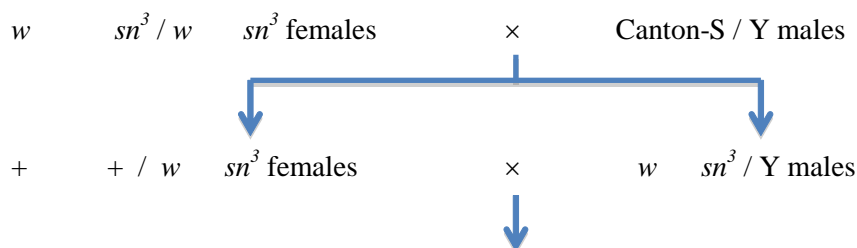
## Can selection alter the frequency of recombination of *Drosophila melanogaster*?

**Knackstedt, Kathryn A., Henry B. Thorpe, Constance R. Santangelo, Michael A. Balinski, and R.C. Woodruff.** Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403.

It has been observed that recombination can increase the amount of new multi-gene genetic variation, which in turn can influence adaptive evolution (Muller, 1964; Maynard Smith, 1978, 1988; Michod, 1995). What is not completely understood is how selection influences frequencies of recombination. In *Drosophila melanogaster* there are three reports that recombination is increased for the autosomes in selection experiments for DDT resistance (Flexon and Rodell, 1982), resistance to daily temperature fluctuations (Zuchenko *et al.*, 1985), and geotaxis (Korol and Liliad, 1994). The influence of selection on the frequency of recombination, however, has only been estimated for the sex chromosomes in one *Drosophila melanogaster* experiment (Korol and Liliad, 1994), and no study has combined selection for bristle number with recombination.

To measure the influence of natural selection on the rate of recombination, we selected for increased sternopleural bristle numbers on the thorax of *Drosophila melanogaster* and determined if there was a concomitant change in the frequency of recombination for two X-linked genes (white eyes, *w*, and singed bristles, *sn*<sup>3</sup>). It is our hypothesis that selection will increase the frequency of recombination for X-linked genes.

As a non-selection control, we measured the frequency of recombination between *w* and *sn*<sup>3</sup> in the Canton-S wild-type stock background before selecting for increased bristle numbers by the following crosses.



The progeny were screened for the frequency of recombinants:  $w +$  (white-eyed long bristles) and  $+ sn^3$  (red eyes and singed bristle), and non-recombinants:  $+ +$  (red eyes and long bristles) and  $w sn^3$  (white eyes and singed bristles). The frequency of recombination was then determined as the number of recombinants out of the total. It is reported that the frequency of recombination between the white and singed loci is about 20.5 map units (Lindsley and Zimm, 1992).

Next we selected for increased bristle numbers in females and males of the Canton-S wild-type stock by selecting for five virgin females and five males with the largest number of bristles, among 40 flies (20 females and 20 males), and mated them for the next generation for a total of three generations of selection (Woodruff and Thompson, 2005).

Then we determined if the frequency of recombination between the white and singed genes in the selected line was significantly higher than in the control (unselected) Canton-S stock by use of the chi-square test. We predicted that the frequency of recombination in the selected line would be significantly higher than in the control (unselected) line. This would give support to the hypothesis that natural selection can modify the frequency of recombination on all chromosomes, including the sex chromosomes.

#### *Rate of recombination before selection for increased bristle numbers:*

We measured the frequency of recombination between the white and singed loci by the crosses shown above, and the results for five independent estimations are as follows: KAK (115/803 = 14.3%), HBT (31/230 = 13.5%), CRS (117/872 = 13.4%), MAB (51/323 = 15.8%), and RCW (116/790 = 14.7%) for an average recombination rate of 14.3% (431/3,018), which is significantly lower than the reported rate of 20.3 map units (20.3 % recombination) (Lindsley and Zimm, 1992).

#### *Selection for increased bristle number:*

We next selected for increased bristle numbers as discussed above and the average results for five separate selection experiments are shown in Figure 1. The number of bristles in females and males were increased, but neither increase is significant over time (females  $P = 0.33$  and males  $P = 0.06$ ).

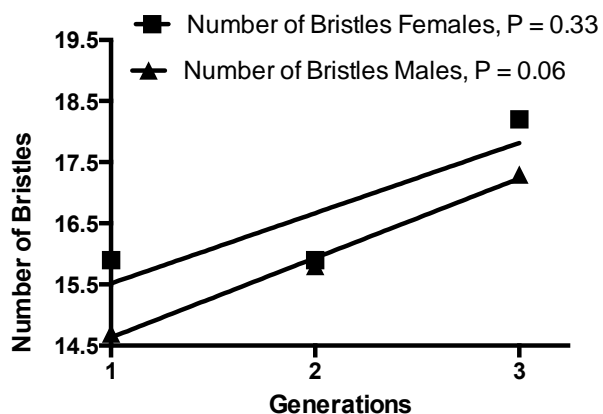


Figure 1. Responses to selection for increased bristle numbers.

The rate of recombination between the white and the singed loci after three generations of selection was: KAK (126/638 = 19.7%), HBT (65/486 = 13.4%), CRS (112/600 = 18.7%), MAB (131/437 = 30.0%), and RCW (123/820 = 15.0%) for an average recombination rate of 18.7% (557/2981), which is significantly different from the recombination rate before selection for increased bristle number ( $P < 0.001$ ).

Comparisons of the rates of recombination between the white locus and the singed locus before and after selection are shown in Table 1 and Figure 2. The chi-square values are for a one-tail test because we predicted that recombination frequencies would go up with selection (using the Prism program).

Table 1. Recombination frequencies before and after selection for increased bristle numbers in five experimental runs and the totals.

	Before Selection	After Selection
KAK	115 / 803 (14.3%) <sup>1</sup>	126 / 638 (19.7%) <sup>1</sup>
HBT	31 / 230 (13.5%) <sup>2</sup>	65 / 486 (13.4%) <sup>2</sup>
CRS	117 / 872 (13.4%) <sup>3</sup>	112 / 600 (18.7%) <sup>3</sup>
MAB	51 / 323 (15.8%) <sup>4</sup>	131 / 437 (30.0%) <sup>4</sup>
RCW	116 / 790 (14.3%) <sup>5</sup>	123 / 820 (15.0%) <sup>5</sup>
Average	431 / 3018 (14.3%) <sup>6</sup>	557 / 2981 (18.7%) <sup>6</sup>

<sup>1</sup>P = 0.003; <sup>2</sup>P = 0.48; <sup>3</sup>P = 0.003; <sup>4</sup>P < 0.0001; <sup>5</sup>P = 0.43; <sup>6</sup>P < 0.0001

decreased in response to selection? There might be times that it is advantageous for closely linked genes to evolve together, as is seen for genes that are found together within inversion heterozygotes (see a discussion of this topic on page 120 in Klug *et al.*, 2013). 2) What are other advantages of recombination? Recombination is important for the removal of deleterious mutations in groups, instead of one at a time in organisms that are asexual (Kondrashov, 1988). Recombination is also essential for the normal segregation of chromosomes during meiosis and for repair of DNA double-strand breaks (Davis and Smith, 2001; Dudas and Chovanec, 2004).

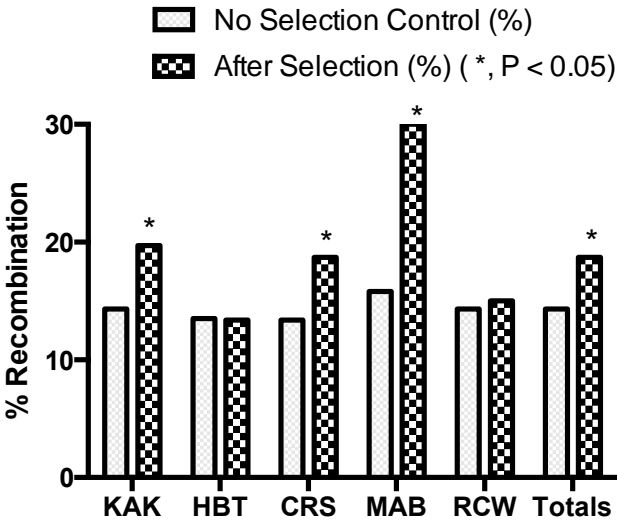


Figure 2. Percent recombination before and after selection for increased bristle numbers.

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