than those resulting from traditional lecture/lab classes, yet widespread acceptance by university faculty of new pedagogies and curricular materials still lies in the future (National Research Council, 2003; DeHaan, 2005). Today's undergraduate science classrooms are bursting at the seams. They are tomorrow's innovators, inventors, scientists, and researchers. It's time to blend basic research with teaching for the future, making scientists better teachers and teachers better scientists.

I continue to believe that only a well-informed citizenry will be qualified to create policies and develop programs that will help stem the extensive alteration of our natural world. Publishing data in a tiered peer-review article is important; yet, only a select few can actually read and understand targeted and complex data. Conveying complex data to the level that allows undergraduates to think and ponder real world questions is one of the most worthwhile endeavors that scientists can undertake, for it is in the imperative of the messages, delivered to those who will build on what they learn in their classrooms, that our very futures depend.•

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LETTERS

Recombination Frequency and Linkage Distance

Pamela A. Marshall, in her article "Mapping Linked Genes in *Drosophila melanogaster* Using Data from the F2 Generation of a Dihybrid Cross" (Vol. 70, No. 9, Nov/Dec 2008), incorrectly asserts that we do not show how to calculate recombination frequency and linkage distance between two genes in dihybrid F2 crosses in our book *Genetics Laboratory Investigations*. We actually deal extensively with the estimation of linkage from F2 dihybrid cross data in our Investigation 11 on Linkage and Crossing Over, using the Linkage Intensities Table first published by R.A. Fisher and B. Balmukand in the *Journal of Genetics* in 1928 (Vol. 20 [1928-1929],79-92) and incorrectly attributed to Immer (1930) in the article. In our Investigation 11, botanical data derived from both tomato (*Lycopersicon esculentum*) and from barley are used to demonstrate how this Linkage Intensities Table is used for crosses in either coupled or repulsed orientation.

Drosophila melanogaster has been used extensively for demonstrating linkage and crossing over for genes on the X-chromosome, but usually not for the autosomes, largely for two reasons. First, since the homogametic sex in dipteran insects are female, a cross of X-linked recessive bearing females with wild-type males will produce F1 progeny in which females are heterozygous and phenotypically wild-type and males that are hemizygous for the mutant recessive phenotype. Consequently, the mating of F1 females with F1 males effectively constitutes a testcross for genes on the X-chromosome and provides F2 data that can be fairly easily analyzed by beginning students. The second feature about *Drosophila* that has limited the use of dihybrid linkage studies of genes on the autosomes arises out of the fact that recombination in males of *Drosophila melanogaster* is totally suppressed. Thus, in the case of linked autosomal recessive gene traits, F1 heterozygous males can only produce two types of gametes (the parental types) instead of the four types expected if recombination occurred (two parental types and two recombinant types). Hence, the utilization of R.A. Fisher's Dihybrid Linkage Intensities Table is inappropriate for the analysis of autosomal dihybrid linkage data in *Drosophila*.

However, *Drosophila* dihybrid linkage data can still be used in "open-ended" experiments as we point out in our book and in

published articles but only for linked genes in coupled orientation. For example, a cross of homozygous recessive *sepia* and *ebony* (*se e//se e*) flies with wild-type flies (+ +//+ +) will produce F1 heterozygous females and males (+ +//*se e*). The F1 females will produce four gametic types: both parental types (+ +/ and *se e/*) and two recombinant types (*se* +/ and + *e/*), but F1 males will produce only the parental types (+ +/ and *se e/*) in equal frequency. Consequently, one half of all the F2 progeny produced in a cross of F1 females with F1 males will be wild-type because they get the + +/ gamete from the male. The other one half of the F2 progeny is the product of the *se e/* male gamete and is effectively the result of a testcross gamete. Hence, an estimation of the recombination frequency can be made by deducting one half of the total F2 progeny number from the wild-type category and then treating the rest of the data as testcross data. If the data from Pamela Marshall's article are treated in this way, the following is obtained:

	F2 DATA			
	wild-type	*cinnabar*	*brown*	white
F1 (+ +//*cn bw*) X F1 (+ +//*cn bw*) →	3553	595	629	703
	wild-type	*cinnabar*	*brown*	white
F1 female (+ +//*cn bw*) X white male (*cn bw//cn bw*) →	141	91	98	121
F1 male (+ +//*cn bw*) X white female (*cn bw//cn bw*) →	144	0	0	119

Frequency of recombination as determined by a testcross of F1 female =

$$\frac{91+98}{141+91+98+121} = \frac{189}{451} = .4191 = 41.91\%$$

Frequency of recombination as determined from dihybrid data =

$$\frac{595+629}{(3553-2740)+595+629+703} = \frac{1224}{2740} = .4467 = 44.67\%$$

	Raw Data	One-half of Total	Data After Treatment
Wild-type eyes, wild-type body	569	- 420	= 149
Wild-type eyes, *ebony* body	80		80
Sepia eyes, wild-type body	63		63
Sepia eyes, *ebony* body	127		127
total number	839/2 = 419.5 or approximately 420		419

Frequency of recombination $= \frac{80+63}{419} = \frac{143}{419} = .3413$ or 34.13 %

Thirty-four plus percent recombination or 34 map units is a much better estimate of the true recombination frequency between *sepia* and *ebony* but is still less than the official map distance probably because of the underestimation of the recombination frequency due to the inability to detect double crossovers, as well as other factors. We have no explanation why the testcross of Pamela Marshall's F1s gave such a low recombination frequency.

We routinely do open-ended experiments like this as part of the introductory genetics course at Ball State University and have types of open-ended experiments suggested in our book. For example, one recent semester involved an experiment with epistatic interaction of eye colors using the linked autosomal eye color genes, *cinnabar* and *brown*. A homozygous recessive double mutant *cinnabar-brown* fly (*cn bw//cn bw*) with the phenotype white eye was crossed to wild-type (+ +//+ +) to produce F1 flies that were wild-type in phenotype but heterozygous (+ +//*cn bw*). These F1 flies were either mated together to produce dihybrid F2 data or were testcrossed to produce dihybrid testcross data. Reciprocal F1 testcrosses were made. The following are the crosses and resulting F2 data:

The F1 male testcross shows that no recombinants are produced by the male F1.

Occasionally, a new isolate of a *Drosophila* species from nature will show some recombination in males for certain chromosomes, but as far as we know *Drosophila melanogaster* males used in most standard laboratories show a lack of recombination for genes on any of their chromosomes.

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Thomas R. Mertens
Distinguished Professor Emeritus
Past President of NABT

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Response

It was not my intent to insinuate that Drs. Mertens and Hammersmith do not comprehensively cover this topic in their lab manual, as they do. I hope that others will use their excellent lab manual for their genetics course, if appropriate.

I appreciate Drs. Hammersmith and Mertens' letter and their insightful discussion of the theory behind mapping F2 data. Clearly, deducing crossing over values from F2 data can be a very useful learning experience for undergraduates, as their letter states. I hope their letter, their lab manual, and my article will give instructors insight into using the data from non-test crosses for analysis.

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