

- E1. If we hypothesize two genes independently assorting, the predicted ratio is 9:3:3:1. There is a total of 427 offspring. The expected numbers of offspring are

$$\begin{aligned}9/16 \times 427 &= 240 \text{ purple flowers, long pollen} \\3/16 \times 427 &= 80 \text{ purple flowers, round pollen} \\3/16 \times 427 &= 80 \text{ red flowers, long pollen} \\1/16 \times 427 &= 27 \text{ red flowers, round pollen}\end{aligned}$$

Plugging these values into our chi square formula,

$$\begin{aligned}\chi^2 &= \frac{(296 - 240)^2}{240} + \frac{(19 - 80)^2}{80} + \frac{(27 - 80)^2}{80} + \frac{(85 - 27)^2}{27} \\ \chi^2 &= 13.1 + 46.5 + 35.1 + 124.6 \\ \chi^2 &= 219.3\end{aligned}$$

Looking up this value in the chi square table under 3 degrees of freedom, we find that such a large value is expected by chance less than 1% of the time. Therefore, we reject the hypothesis that the genes assort independently.

- E2. They could have used a strain with two abnormal chromosomes. In this case, the recombinant chromosomes would either look normal or have abnormalities at both ends.
- E3. The top of the Conceptual Level column in Figure 5.6 shows the chromosomes of McClintock's cross. This experiment could be modified to a standard testcross in the following way. In the heterozygous parent, the *C* (colored) and *Wx* (starchy) alleles could be on the knobbed, translocation chromosome and the *c* (colorless) and *wx* (waxy) alleles on a normal chromosome. The other parent would have two cytologically normal copies of chromosome 9 and be homozygous for the recessive alleles (i.e., *cc wxwx*). If the cross were done in this way, nonrecombinant offspring would be colored and starchy, or colorless and waxy; recombinant offspring would be colored and waxy, or colorless and starchy. The recombinant offspring should inherit a chromosome with a knob but no translocation, or a translocation but no knob.
- E4. A gene on the Y chromosome in mammals would only be transmitted from father to son. It would be difficult to genetically map Y-linked genes because a normal male has only one copy of the Y chromosome, so you do not get any crossing over between two Y chromosomes. Occasionally, abnormal males (XYY) are born with two Y chromosomes. If such males were heterozygous for alleles of Y-linked genes, one could examine the normal male offspring of XYY fathers and determine if crossing over has occurred.
- E5. The rationale behind a testcross is to determine if recombination has occurred during meiosis in the heterozygous parent. The other parent is usually homozygous recessive, so we cannot tell if crossing over has occurred in the recessive parent. It is easier to interpret the data if a testcross does use a completely homozygous recessive parent. However, in the other parent, it is not necessary for all of the dominant alleles to be on one chromosome and all of the recessive alleles on the other. The parental generation provides us with information concerning the original linkage pattern between the dominant and recessive alleles.
- E6. The answer is explained in solved problem S5. We cannot get more than 50% recombinant offspring because the pattern of multiple crossovers can yield an average maximum value of only 50%. When a testcross does yield a value of 50% recombinant offspring, it can mean two different things. Either the two genes are on different chromosomes or the two genes are on the same chromosome but at least 50 mu apart.
- E7. The reason why the percentage of recombinant offspring is more accurate when the genes are close together is because there are fewer double crossovers. The inability to detect double crossover causes the map distance to be underestimated. If two genes are very close together, there are very few double crossovers so that the underestimation due to double crossovers is minimized.
- E8. If two genes are at least 50 mu apart, you would need to map genes in between them to show that the two genes were actually in the same linkage group. For example, if gene *A* was 55 mu from gene *B*, there might be a third gene (e.g., gene *C*) that was 20 mu from *A* and 35 mu from *B*. These results would indicate that *A* and *B* are 55 mu apart, assuming dihybrid testcrosses between genes *A* and *B* yielded 50% recombinant offspring.
- E9. He determined this by analyzing the data in gene pairs. This analysis revealed that there were fewer recombinants between certain gene pairs (e.g., body color and eye color) than between other gene pairs (e.g., eye color and wing shape). From this comparison, he hypothesized that genes that are close together on the same chromosome will produce fewer recombinants than genes that are farther apart.

E10. Sturtevant used the data involving the following pairs: *y* and *w*, *w* and *v*, *v* and *r*, and *v* and *m*.

E11. Map distance:

$$\begin{aligned} &= \frac{64 + 58}{333 + 64 + 58 + 380} \times 100 \\ &= 15.1 \text{ mu} \end{aligned}$$

E12. A. Since they are 12 mu apart, we expect 12% (or 120) recombinant offspring. This would be approximately 60 *Aabb* and 60 *aaBb* plus 440 *AaBb* and 440 *aabb*.

B. We would expect 60 *AaBb*, 60 *aabb*, 440 *Aabb*, and 440 *aaBb*.

- E13. We consider the genes in pairs: there should be 10% offspring due to crossing over between genes *A* and *B* and 5% due to crossing over between *A* and *C*.
- A. This is due to a crossover between *B* and *A*. The parentals are *Aa bb Cc* and *aa Bb cc*. The 10% recombinants are *Aa Bb Cc* and *aa bb cc*. If we assume there is an equal number of both types of recombinants, there are 5% *Aa Bb Cc*.
- B. This is due to a crossover between *A* and *C*. The parentals are *Aa bb Cc* and *aa Bb cc*. The 5% recombinants are *aa Bb Cc* and *Aa bb cc*. If we assume there are an equal number of both types of recombinants, there are 2.5% *aa Bb Cc*.
- C. This is also due to a crossover between *A* and *C*. The parentals are *Aa bb Cc* and *aa Bb cc*. The 5% recombinants are *aa Bb Cc* and *Aa bb cc*. If we assume there are an equal number of both types of recombinants, there are 2.5% *Aa bb cc*.
- E14. Due to the large distance between the two genes, they will assort independently even though they are actually on the same chromosome. According to independent assortment, we expect 50% parental and 50% recombinant offspring. Therefore, this cross will produce 150 offspring in each of the four phenotypic categories.
- E15. A. One basic strategy to solve this problem is to divide the data up into gene pairs and determine the map distance between two genes.

184 tall, smooth  
 13 tall, peach  
 184 dwarf, peach  
 12 dwarf, smooth

$$\text{Map distance} = \frac{13 + 12}{184 + 13 + 184 + 12} = 6.4 \text{ mu}$$

153 tall, normal  
 44 tall, oblate  
 155 dwarf, oblate  
 41 dwarf, normal

$$\text{Map distance} = \frac{44 + 41}{153 + 44 + 155 + 41} = 21.6 \text{ mu}$$

163 smooth, normal  
 33 smooth, oblate  
 31 peach, normal  
 166 peach, oblate

$$\text{Map distance} = \frac{33 + 31}{163 + 33 + 31 + 166} = 16.3 \text{ mu}$$

Use the two shortest distances to compute the map:

Tall, dwarf 6.4 Smooth, peach 16.3 Normal, oblate

- E16. A. If we hypothesize two genes independently assorting, then the predicted ratio is 1:1:1:1. There are a total of 390 offspring. The expected number of offspring in each category is about 98. Plugging the figures into our chi square formula,

$$\begin{aligned} \chi^2 &= \frac{(117 - 98)^2}{98} + \frac{(115 - 98)^2}{98} + \frac{(78 - 98)^2}{98} + \frac{(80 - 98)^2}{98} \\ \chi^2 &= 3.68 + 2.95 + 4.08 + 3.31 \\ \chi^2 &= 14.02 \end{aligned}$$

Looking up this value in the chi square table under 3 degrees of freedom, we reject our hypothesis, since the chi square value is above 7.815.

B. Map distance:

$$\begin{aligned}\text{Map distance} &= \frac{78 + 80}{117 + 115 + 78 + 80} \\ &= 40.5 \text{ mu}\end{aligned}$$

Because the value is relatively close to 50 mu, it is probably a significant underestimate of the true distance between these two genes.

- E17. In the backcross, the two parental types would be the homozygotes that cannot make either enzyme and the heterozygotes that can make both enzymes. The recombinants would make one enzyme but not both. Because the two genes are 12 mu apart, 12% would be recombinants and 88% would be parental types. Because there are two parental types produced in equal numbers, we would expect 44% of the mice to be unable to make either enzyme.
- E18. The percentage of recombinants for the green, yellow and wide, narrow is 7%, or 0.07; there will be 3.5% of the green, narrow and 3.5% of the yellow, wide. The remaining 93% parentals will be 46.5% green, wide and 46.5% yellow, narrow. The third gene assort independently. There will be 50% long and 50% short with respect to each of the other two genes. To calculate the number of offspring out of a total of 800, we multiply 800 by the percentages in each category.

$$\begin{aligned}(0.465 \text{ green, wide})(0.5 \text{ long})(800) &= 186 \text{ green, wide, long} \\ (0.465 \text{ yellow, narrow})(0.5 \text{ long})(800) &= 186 \text{ yellow, narrow, long} \\ (0.465 \text{ green, wide})(0.5 \text{ short})(800) &= 186 \text{ green, wide, short} \\ (0.465 \text{ yellow, narrow})(0.5 \text{ short})(800) &= 186 \text{ yellow, narrow, short} \\ (0.035 \text{ green, narrow})(0.5 \text{ long})(800) &= 14 \text{ green, narrow, long} \\ (0.035 \text{ yellow, wide})(0.5 \text{ long})(800) &= 14 \text{ yellow, wide, long} \\ (0.035 \text{ green, narrow})(0.5 \text{ short})(800) &= 14 \text{ green, narrow, short} \\ (0.035 \text{ yellow, wide})(0.5 \text{ short})(800) &= 14 \text{ yellow, wide, short}\end{aligned}$$

- E19. A. If we represent *B* (bushy tail) and *b* (normal tail) for one gene, and *Y* (yellow) and *y* (white) for the second gene:

Parent generation: *BBYY* × *bbyy*

F<sub>1</sub> generation: All *BbYy* (NOTE: if the two genes are linked, *B* would be linked to *Y* and *b* would be linked to *y*.)

Testcross: F<sub>1</sub> *BbYy* × *bbyy*

Nonrecombinant offspring from testcross: *BbYy* and *bbyy*

*BbYy* males—bushy tails, yellow

*bbyy* males—normal tails, white

*BbYy* females—normal tails, yellow

*bbyy* females—normal tails, white

Recombinant offspring from testcross: *Bbyy* and *bbYy*

*Bbyy* males—bushy tails, white

*bbYy* males—normal tails, yellow

*Bbyy* females—normal tails, white

*bbYy* females—normal tails, yellow

We cannot use the data regarding female offspring, because we cannot tell if females are recombinant or nonrecombinant, because all females have normal tails. However, we can tell if male offspring are recombinant.

If we use the data on males to conduct a chi-square analysis, we expect a 1:1:1:1 ratio among the male offspring. Since there are 197 male offspring total, we expect 1/4, or 49 (rounded to the nearest whole number), of the four possible phenotypes. To compute the chi square:

$$\begin{aligned}\chi^2 &= \frac{(28 - 49)^2}{49} + \frac{(72 - 49)^2}{49} + \frac{(68 - 49)^2}{49} + \frac{(29 - 49)^2}{49} \\ \chi^2 &= 9.0 + 10.8 + 7.4 + 8.2 \\ \chi^2 &= 35.4\end{aligned}$$

If we look up the value of 35.4 in our chi square table, with 3 degrees of freedom, the value lies far beyond the 0.01 probability level. Therefore, it is very unlikely to get such a large deviation if our hypothesis of independent assortment is correct. Therefore, we reject our hypothesis and conclude that the genes are linked.

B. To compute map distance:

$$\frac{28 + 29}{28 + 72 + 68 + 29} \times 100 = 28.9 \text{ mu}$$

E20. Let's use the following symbols: *G* for green pods, *g* for yellow pods, *S* for green seedlings, *s* for bluish green seedlings, *C* for normal plants, *c* for creepers.

The parental cross is *GG SS CC* crossed to *gg ss cc*.

The  $F_1$  plants would all be *Gg Ss Cc*. If the genes are linked, the alleles *G*, *S*, and *C* would be linked on one chromosome and the alleles *g*, *s*, and *c* would be linked on the homologous chromosome.

The testcross is  $F_1$  plants, which are *Gg Ss Cc*, crossed to *ggsscc*.

To measure the distances between the genes, we can separate the data into gene pairs.

Pod color, seedling color

2,210 green pods, green seedlings—nonrecombinant

296 green pods, bluish green seedlings—recombinant

2,198 yellow pods, bluish green seedlings—nonrecombinant

293 yellow pods, green seedlings—recombinant

$$\text{Map distance} = \frac{296 + 293}{2,210 + 296 + 2,198 + 293} \times 100 = 11.8 \text{ mu}$$

Pod color, plant stature

2,340 green pods, normal—nonrecombinant

166 green pods, creeper—recombinant

2,323 yellow pods, creeper—nonrecombinant

168 yellow pods, normal—recombinant

$$\text{Map distance} = \frac{166 + 168}{2,340 + 166 + 2,323 + 168} \times 100 = 6.7 \text{ mu}$$

Seedling color, plant stature

2,070 green seedlings, normal—nonrecombinant

433 green seedlings, creeper—recombinant

2,056 bluish green seedlings, creeper—nonrecombinant

438 bluish green seedlings, normal—recombinant

$$\text{Map distance} = \frac{433 + 438}{2,070 + 433 + 2,056 + 438} \times 100 = 17.4 \text{ mu}$$

The order of the genes is seedling color, pod color, plant stature or you could say the opposite order. Pod color is in the middle. If we use the two shortest distances to construct our map:

$$\begin{array}{ccccc} S & & 11.8 & & G \\ 6.7 & C & & & \end{array}$$

E21. Let's use the following symbols: *S* for normal nose, *s* for snubnose, *p* for normal tail, *P* for pintail, *J* for normal gait, *j* for jerker.

The parental cross is *ss PP jj* crossed to *SS pp JJ*.

The  $F_1$  offspring would all be *Ss Pp Jj*. If the genes are linked, the alleles *s*, *P*, and *j* would be linked on one chromosome and the alleles *S*, *p*, and *J* would be linked on the homologous chromosome.

The testcross is  $F_1$  mice, which are *Ss Pp Jj*, crossed to *ss pp jj* mice.

To measure the distances between the genes, we can separate the data into gene pairs.

Nose shape, tail length

- 631 snubnose, pintail—nonrecombinant
- 111 snubnose, normal tail—recombinant
- 625 normal nose, normal tail—nonrecombinant
- 115 normal nose, pintail—recombinant

$$\text{Map distance} = \frac{111+115}{631+111+625+115} \times 100 = 15.2 \text{ mu}$$

Nose shape, walking gait

- 662 snubnose, jerker—nonrecombinant
- 80 snubnose, normal—recombinant
- 652 normal nose, normal—nonrecombinant
- 88 normal nose, jerker—recombinant

$$\text{Map distance} = \frac{80+88}{662+80+652+88} \times 100 = 11.3 \text{ mu}$$

Tail length, walking gait

- 571 pintail, jerker—nonrecombinant
- 175 pintail, normal—recombinant
- 557 normal tail, normal gait—nonrecombinant
- 179 normal tail, jerker—recombinant

$$\text{Map distance} = \frac{175+179}{571+175+557+179} \times 100 = 23.9 \text{ mu}$$

The order of the genes is tail length, nose shape, walking gait or you could say the opposite order. Nose shape is in the middle.

If we use the two shortest distances to construct our map:

$$P \quad 15.2 \quad S \quad 11.3 \quad J$$

- E22. According to a hypothesis of independent assortment, we would expect an equal proportion of all four phenotypes. (You should construct a Punnett square if this is not apparent.) There are a total number of 1,074 offspring. Therefore, the expected number of each of the four categories is  $1/4 \times 1,074$ , which equals 268 (rounded to the nearest whole number). We use the value of 268 as our expected value in the chi square calculation.

$$\begin{aligned}\chi^2 &= \frac{(368-268)^2}{268} + \frac{(160-268)^2}{268} + \frac{(194-268)^2}{268} + \frac{(352-268)^2}{268} \\ \chi^2 &= 37.3 + 43.5 + 20.4 + 26.3 \\ \chi^2 &= 127.5\end{aligned}$$

If we look up the value of 127.5 in our chi square table, with 3 degrees of freedom, the value lies far beyond the 0.01 probability level. Therefore, it is very unlikely to get such a large deviation if our hypothesis of independent assortment is correct. Therefore, we reject our hypothesis and conclude that the genes are linked. In the parental (true-breeding) generation, black is linked to chinchilla and brown is linked to Himalayan. Therefore, the recombinant offspring are black Himalayan and brown chinchilla.

To compute map distance:

$$\frac{160+194}{368+160+194+352} \times 100 = 33.0 \text{ mu}$$

E23. To answer this question, we can consider genes in pairs. Let's consider the two gene pairs that are closest together. The distance between the wing length and eye color genes is 12.5 mu. From this cross, we expect 87.5% to have long wings and red eyes or short wings and purple eyes, and 12.5% to have long wings and purple eyes or short wings and red eyes. Therefore, we expect 43.75% to have long wings and red eyes, 43.75% to have short wings and purple eyes, 6.25% to have long wings and purple eyes, and 6.25% to have short wings and red eyes. If we have 1,000 flies, we expect 438 to have long wings and red eyes, 438 to have short wings and purple eyes, 62 to have long wings and purple eyes, and 62 to have short wings and red eyes (rounding to the nearest whole number).

The distance between the eye color and body color genes is 6 mu. From this cross, we expect 94% to have a parental combination (red eyes and gray body or purple eyes and black body) and 6% to have a nonparental combination (red eyes and black body or purple eyes and gray body). Therefore, of our 438 flies with long wings and red eyes, we expect 94% of them (or about 412) to have long wings, red eyes, and gray body, and 6% of them (or about 26) to have long wings, red eyes, and black bodies. Of our 438 flies with short wings and purple eyes, we expect about 412 to have short wings, purple eyes, and black bodies, and 26 to have short wings, purple eyes, and gray bodies.

Of our 62 flies with long wings and purple eyes, we expect 94% of them (or about 58) to have long wings, purple eyes, and black bodies, and 6% of them (or about 4) to have long wings, purple eyes, and gray bodies. Of our 62 flies with short wings and red eyes, we expect 94% (or about 58) to have short wings, red eyes, and gray bodies, and 6% (or about 4) to have short wings, red eyes, and black bodies.

In summary:

Long wings, red eyes, gray body	412
Long wings, purple eyes, gray body	4
Long wings, red eyes, black body	26
Long wings, purple eyes, black body	58
Short wings, red eyes, gray body	58
Short wings, purple eyes, gray body	26
Short wings, red eyes, black body	4
Short wings, purple eyes, black body	412

The flies with long wings, purple eyes, and gray bodies, or short wings, red eyes, and black bodies, are produced by a double crossover event.

E24. A.

Parent		Parent
<u><i>b</i> 7 <i>A</i> 4 <i>C</i></u>	×	<u><i>B</i> 7 <i>a</i> 4 <i>c</i></u>
<u><i>b</i> 7 <i>A</i> 4 <i>C</i></u>		<u><i>B</i> 7 <i>a</i> 4 <i>c</i></u>
		<u><i>b</i> 7 <i>A</i> 4 <i>C</i></u> Offspring
		<u><i>B</i> 7 <i>a</i> 4 <i>c</i></u>

B. A heterozygous  $F_2$  offspring would have to inherit a chromosome carrying all of the dominant alleles. In the  $F_1$  parent (of the  $F_2$  offspring), a crossover in the 7 mu region between genes *b* and *A* (and between *B* and *a*) would yield a chromosome that was *BAC* and *bac*. If an  $F_2$  offspring inherited the *BAC* chromosome from its  $F_1$  parent and the *bac* chromosome from the homozygous parent, it would be heterozygous for all three genes.

C. If you look at the answer to part B, a crossover between genes *b* and *A* (and between *B* and *a*) would yield *BAC* and *bac* chromosomes. If an offspring inherited the *bac* chromosome from its  $F_1$  parent and the *bac* chromosome from its homozygous parent, it would be homozygous for all three genes. The chances of a crossover in this region are 7%. However, half of this 7% crossover event yields chromosomes that are *BAC* and the other half yields chromosomes that are *bac*. Therefore, the chances are 3.5% of getting homozygous  $F_2$  offspring.

E25. Yes. Begin with females that have one X chromosome that is  $X^{Nl}$  and the other X chromosome that is  $X^{nL}$ . These females have to be mated to  $X^{NL}Y$  males because a living male cannot carry the  $n$  or  $l$  allele. In the absence of crossing over, a mating between  $X^{Nl}X^{nL}$  females to  $X^{NL}Y$  males should not produce any surviving male offspring. However, during oogenesis in these heterozygous female mice there could be a crossover in the region between the two genes and this will produce an  $X^{NL}$  chromosome and an  $X^{nl}$  chromosome. Therefore, male offspring inheriting these recombinant chromosomes will be either  $X^{NL}Y$  or  $X^{nl}Y$  (whereas nonrecombinant males will be  $X^{nL}Y$  or  $X^{Nl}Y$ ). Only the male mice that inherit  $X^{NL}Y$  will live. The living males represent only half of the recombinant offspring. (The other half are  $X^{nl}Y$ , which are born dead.)  
To compute map distance:

$$\text{Map distance} = \frac{2 (\text{Number of male living offspring})}{\text{Number of males born dead} + \text{Number of males born alive}}$$

E26. A. The first thing to do is to determine which asci are parental ditypes (PD), nonparental ditypes (NPD), and tetratypes (T). A parental ditype will contain a 2:2 combination of spores with the same genotypes as the original haploid parents. The combination of the 502 asci are the parental ditypes. The nonparental ditypes are those containing a 2:2 combination of genotypes that are unlike the parentals. The combination of four asci fits this description. Finally, the tetratypes contain a 1:1:1:1 arrangement of genotypes, half of which have a parental genotype and half of which do not. There are 312 tetratypes in this case. Computing the map distance:

$$\begin{aligned} \text{Map Distance} &= \frac{\text{NPD} + (1/2)(\text{T})}{\text{Total number of asci}} \times 100 \\ &= \frac{4 + (1/2)(312)}{818} \\ &= 19.6 \text{ mu} \end{aligned}$$

If we use the more accurate equation:

$$\begin{aligned} \text{Map distance} &= \frac{\text{T} + 6\text{NPD}}{\text{Total number of asci}} \times 0.5 \times 100 \\ &= \frac{312 + (6)(4)}{818} \\ &= 20.5 \text{ mu} \end{aligned}$$

B. The frequency of single crossovers is 0.205 if we use the more accurate equation.

C. Nonparental ditypes are produced from a double crossover. To compute the expected number, we multiply  $0.205 \times 0.205 = 0.042$ , or 4.2%. Since we had a total of 818 asci, we would expect 34.3 asci to be the product of a double crossover. However, as described in Figure 5.17, only 1/4 of them would be a nonparental ditype. Therefore, we multiply 34.3 by 1/4, obtaining a value of 8.6 nonparental ditypes due to a double crossover. Since we observed only four, this calculation tells us that positive interference is occurring.

E27.

$$\begin{aligned} \text{Map distance} &= \frac{(1, 2)(\text{SDS})}{\text{Total}} \times 100 \\ &= \frac{(1, 2)(22 + 21 + 21 + 23)}{22 + 21 + 21 + 451 + 23 + 455} \times 100 \\ &= 4.4 \text{ mu} \end{aligned}$$

E28. A. Types	B. Number
<i>pro-1 pro-1 pro-1 pro-1 pro+ pro+ pro+ pro+</i>	402
<i>pro+ pro+ pro+ pro+ pro-1 pro-1 pro-1 pro-1</i>	402
<i>pro+ pro+ pro-1 pro-1 pro+ pro+ pro-1 pro-1</i>	49
<i>pro-1 pro-1 pro+ pro+ pro-1 pro-1 pro+ pro+</i>	49
<i>pro+ pro+ pro-1 pro-1 pro-1 pro-1 pro+ pro+</i>	49
<i>pro-1 pro-1 pro+ pro+ pro+ pro+ pro-1 pro-1</i>	49