CHAPTER 6

Genetics

6.1. Mendelian Genetics

6.1.1. F_n will have 2^n copies of each gene.

6.1.2.

	DW	dW	Dw	dw
DW	$DDWW$	$DdWW$	$DDWw$	$DdWw$
dW	$DdWW$	$ddWW$	$DdWw$	$ddWw$
Dw	$DDWw$	$DdWw$	$DDww$	$Ddww$
dw	$DdWw$	$ddWw$	$Ddww$	$ddww$

Genotype proportions are 1/16 for $DDWW$, $ddWW$, $DDww$, and $ddww$; 1/8 for $DdWW$, $Ddww$, $DDWw$, and $ddWw$; 1/4 for $DdWw$. Phenotype 7proportions are 1/16 for dwarf wrinkled-seed; 3/16 for dwarf round-seed; 3/16 for tall wrinkled-seed; 9/16 for tall round-seed.

6.1.3. a. $\mathcal{P}(\text{tall wrinkled-seed}) = \mathcal{P}(\text{tall})\mathcal{P}(\text{wrinkled-seed})$. But

$$\begin{aligned}\mathcal{P}(\text{tall}) &= 1 - \mathcal{P}(\text{dwarf}) = 1 - \mathcal{P}(dd)\\ &= 1 - \mathcal{P}(d \text{ from first parent})\mathcal{P}(d \text{ from second parent})\\ &= 1 - (1/2)(1) = 1/2,\end{aligned}$$

$$\begin{aligned}\mathcal{P}(\text{wrinkled-seed}) &= \mathcal{P}(ww)\\ &= \mathcal{P}(w \text{ from first parent})\mathcal{P}(w \text{ from second parent})\\ &= (1/2)(1/2) = 1/4.\end{aligned}$$

Therefore $\mathcal{P}(\text{tall wrinkled-seed}) = (1/2)(1/4) = 1/8$.

b. Using the calculations in part (a),

$$\begin{aligned}\mathcal{P}(\text{tall round-seed}) &= \mathcal{P}(\text{tall})\mathcal{P}(\text{round-seed})\\ &= \mathcal{P}(\text{tall})(1 - \mathcal{P}(\text{wrinkled-seed}))\\ &= (1/2)(1 - 1/4) = 3/8.\end{aligned}$$

6.1.4. a. Since the probability of having the allele is 1/31 for the male and also 1/31 for the female, assuming these are independent the probability is $(1/31)^2 \approx .00104$.

b. Since the child must inherit the recessive allele from each parent, the probability is $(1/2)(1/2) = 1/4$.

c. $(1/31)^2(1/4) \approx .0002601$.

6.1.5. a. Four – ABC, aBC, AbC, and abC.

b. 9 genotypes are possible: $AABBCC$, $AaBBCC$, $aaBBCC$, $AABbCC$, $AaBbCC$, $aaBbCC$, $AAbbCC$, $AabbCC$, $aabbCC$. 4 phenotypes are possible: the offspring could have the dominant or recessive phenotype from either of the first two genes, but must have the dominant phenotype from the third.

6.1.6. a. 2^n

b. 3^n genotypes and 2^n phenotypes

c. There are $3^k 2^{l-k}$ possible genotypes (3 possibilities for each of genes 1–k, 2 possibilities for each of genes $(k+1)$–l, and only 1 possibility for the remaining genes). These give 2^l different phenotypes, since genes 1–l might give dominant or recessive traits while the remaining ones must be recessive. (Note we are using that at genes $(k+1)$–l the first individual is homozygous recessive.)

6.1.7. a. $AA \times aa$ dominant:recessive=1:0; $Aa \times aa$ dominant:recessive=1:1; $aa \times aa$ dominant:recessive=0:1.

b. $DdwwYY$

c. Crossing with a homozygous recessive allows all parental alleles to manifest themselves in phenotypes of the progeny, whereas crossing with a homozygous dominant would result only in progeny of the dominant phenotypes. Quantitatively, the ratios in part (a) are all different, so the parental phenotype can be distinguished, while for a cross with a homozygous dominant, all ratios would be dominant:recessive=1:0. The parental phenotype has no effect.

6.1.8. a. From $BBRR \times bbrr$, all offspring have genotype $BbRr$, with black and normal length fur.

b. In F_2, 1/2 of the rabbits will be homozygous for the color gene (BB or bb) and 1/4 will be homozygous for both genes. Of the black rabbits, 1/6 will be homozygous for both genes. (For all the rabbits, BB:Bb:bb=1:2:1, but only BB and Bb are black, so $1/(1+2) = 1/3$ of the black rabbits are BB. Of these 1/2 are homozygous at the second gene with rr or RR.)

c. Black rabbits with normal length fur have genotypes $BBRR$, $BbRR$, $BBRr$, or $BbRr$. In the entire F_2 population these occur in proportions 1/16, 2/16, 2/16, and 4/16, for a total of 9/16. Thus the genotype ratios for black rabbits with normal length fur homozygous for both genes is 1:2:2:4 giving proportions $1/9, 2/9, 2/9, 4/9$.

6.1.9. a. Genotype $WwGg$, with round yellow seed phenotype.

b. If the genes assort independently, F_2 should be: 1/16 with wrinkled green seeds, 3/16 with wrinkled yellow seeds, 3/16 with round green seeds, and 9/16 with round yellow seeds.

c. If Mendel's data did not exactly match these proportions, he should not necessarily doubt the independent assortment hypothesis. After all, these proportions are really probabilities, so only for very large amounts of data should the fit be very close. The more data he collected, the closer he should expect his data to match these proportions if the hypothesis is valid. Deciding how close is close enough for a match, taking into account the amount of data collected, will be discussed in the next section.

6.1.10. The cross is $Y^l y \times Y^l y$. Embryo genotype ratios will be $Y^l Y^l$:$Y^l y$:yy=1:2:1, but only the last two genotypes will be born. Thus the viable progeny will have genotypes $Y^l y$ or yy, with respective phenotypes yellow and agouti, in proportions 2/3 and 1/3.

6.1.11. a. Since one child is homozygous recessive, and neither parent is, both parents must be heterozygous.

b. From a cross of two heterozygotes, the probability that a child is not homozygous recessive is 3/4.

c. Since the sons do not have sickle-cell anemia, the possible genotypes are homozygous dominant or heterozygous. Since all offspring have probabilities

1/4 and 1/2 of these genotypes, for a disease-free son the probabilities are $(1/4)/(1/4+1/2) = 1/3$ and $(1/2)/(1/4+1/2) = 2/3$.

6.1.12. a. The trait is dominant. If it were recessive, all children of the parents would exhibit brachydactyly. The parents must each be heterozygotes, since one child has normal length fingers. The child with normal length fingers is a homozygous recessive. The child with short fingers is either homozygous dominant or heterozygous.

b. The probability that one child has normal fingers is 1/4, and since the two children's phenotypes are independent, the probability that both have normal length fingers is $(1/4)^2 = 1/16$.

6.1.13. a. $(1/4)^3 = 1/64 = .015625$

b. $(1/2)^3 = 1/8 = .125$

c. The proportion homozygous only for the first gene is (1/2)(1/2)(1/2)=1/8. Similarly, 1/8 is homozygous only for the second, and 1/8 is homozygous only for the third. Thus 1/8+1/8+1/8=3/8 is homozygous for exactly one of the genes.

d. The proportion homozygous for at least one gene is

$$1 - (\text{proportion heterozygous for all three}) = 1 - (1/2)^3 = 7/8 = .875.$$

6.1.14. F_1 has genotype Ww only, with pink flower phenotype. F_2 has genotypes WW, Ww, and ww in proportions 1/4, 1/2, and 1/4, with red flower, pink flower, and white flower phenotypes, respectively.

6.1.15. $a_1a_3 \times a_2a_3$ produces genotypes a_1a_2, a_1a_3, a_2a_3, and a_3a_3 in frequencies 1/4, 1/4, 1/4, and 1/4. This gives phenotypes associated to a_1, a_2, and a_3 in frequencies 1/2, 1/4, and 1/4.

6.1.16. a. Type A: I^AI^A, I^AI^O; Type B: I^BI^B, I^BI^O; Type AB: I^AI^B; Type O: I^OI^O

b. $I^AI^A \times I^BI^O$ produces offspring with genotypes I^AI^B and I^AI^O with equal probability. Thus type AB and type A blood occur with relative frequencies 1/2 and 1/2.

c. From $I^AI^O \times I^BI^O$ we expect 1/4 of the progeny to have type O blood (genotype I^OI^O). So out of four children, we would expect one to have type O blood. However, any number might have this blood type. The probability of any one child having it is 1/4, and it is really only in a very large number of trials (much greater than 4) that we can be reasonably confident that close to 1/4 of the trials will produce this outcome. For instance, there is a probability of $(1/4)^4 = 1/256$ that all four children will have type O blood, and of $(3/4)^4 = 81/256$ that none of them will. (See the next section for a more careful definition of the word 'expect'.)

6.1.17. a. $RRpp \times rrpp$ produces only $Rrpp$, for a rose comb phenotype. $rrPP \times rrpp$ produces only $rrPp$, for a pea comb phenotype.

b. $RRpp \times rrPP$ produces an F_1 of $RrPp$ which have walnut comb phenotype. Interbreeding to produce F_2 gives 3/16 rose comb (1/16 $RRpp$ and 2/16 $Rrpp$), 3/16 pea comb (1/16 $rrPP$ and 2/16 $rrPp$), 1/16 single comb (1/16 $rrpp$), and 9/16 walnut comb (1/16 $RRPP$, 2/16 $RrPP$, 2/16 $RRPp$, and 4/16 $RrPp$).

6.2. Probability Distributions in Genetics

6.2.1. $HHHTT$, $HHTHT$, $HTHHT$, $THHHT$, $HHTTH$, $HTHTH$, $THHTH$, $HTTHH$, $THTHH$, $TTHHH$; $\binom{5}{3} = \frac{5\cdot4\cdot3\cdot2\cdot1}{(3\cdot2\cdot1)(2\cdot1)} = \frac{5\cdot4}{2} = 10$.

6.2.2. $\mathcal{P}(\text{exactly 0 tails in 3 flips}) = \binom{3}{0}(1/2)^0(1/2)^3 = 1/8$,
$\mathcal{P}(\text{exactly 2 tails in 3 flips}) = \binom{3}{2}(1/2)^2(1/2)^1 = 3/8$,
$\mathcal{P}(\text{exactly 3 tails in 3 flips}) = \binom{3}{3}(1/2)^3(1/2)^0 = 1/8$;
The sum of the four probabilities is 1, since the outcomes are mutually exclusive and exhaust all possibilities.

6.2.3. Use $\mathcal{P}(i) = \binom{4}{i}(3/4)^i(1/4)^{4-i}$.

6.2.4. The values of $\binom{10}{k}$ for $k = 1, 2, \ldots 10$ are 1, 10, 45, 120, 210, 252, 210, 120, 45, 10, 1.
a. The value is smallest when $k = 0$ or 10. If we choose no objects, or all 10 objects, there is only one way to do so. If we choose any number from 1 to 9, there is more than one way to do so.
b. The value is largest for $k = 5$. It does seem intuitively reasonable that there are more ways to choose exactly half of the objects than there are to choose fewer, or more. With fewer or more, there is less freedom in varying what is chosen.
c. $\binom{n}{k}$ increases with k until k is half of n and then decreases, $\binom{n}{k} = \binom{n}{n-k}$, $\binom{n}{1} = n$; these patterns hold for all n.

6.2.5. a. In choosing only one object, the various ways are: choose the first, choose the second, ..., choose the nth. Thus $\binom{n}{1} = n$. Choosing $n-1$ objects is equivalent to picking the one object *not* chosen, so $\binom{n}{n-1} = \binom{n}{1} = n$.
b. There is only one way to choose no objects, so $\binom{n}{0} = 1$. To choose n objects from n, we must choose them all, so $\binom{n}{n} = 1$.

6.2.6. a. $\binom{6}{4}(\frac{1}{2})^4(\frac{1}{2})^2 = 15\frac{1}{64} = \frac{15}{64} \approx .2344$
b. $\mathcal{P}(\text{exactly } i \text{ boys in 6 children}) = \binom{6}{i}(\frac{1}{2})^6$, so for $i = 0, 1, 2, \ldots 6$, the values are: .0156, .0938, .2344, .3125, .2344, .0938, .0156.
$\mathcal{P}(\text{exactly } i \text{ girls in 6 children})$ has exactly the same values.
c. The expected number of boys is $\sum_{i=0}^{6} i\mathcal{P}(\text{exactly } i \text{ boys in 6 children}) = 0(.0156) + 1(.0938) + 2(.2344) + 3(.3125) + 4(.2344) + 5(.0938) + 6(.0156) = 3$.
Alternately, for a binomial distribution, the expected value is $n \cdot p = 6 \cdot \frac{1}{2} = 3$.
d. $\mathcal{P}(4 \text{ or more girls of 6 children}) = \mathcal{P}(4 \text{ girls}) + \mathcal{P}(5 \text{ girls}) + \mathcal{P}(6 \text{ girls}) = .2344 + .0938 + .0156 = .3438$.

6.2.7. a. $\mathcal{P}(\text{exactly 30 agouti in 40 offspring}) = \binom{40}{30}(\frac{3}{4})^{30}(\frac{1}{4})^{10} \approx .1444$;
$\mathcal{P}(\text{exactly 300 agouti in 400 offspring}) = \binom{400}{300}(\frac{3}{4})^{300}(\frac{1}{4})^{100} \approx .0460$
b. Even though these results indicate the probability of having exactly 3/4 of the offspring with agouti fur decreases as the number of offspring increases, these results are consistent with expecting 3/4 of a large number of offspring to have agouti fur. We don't expect *exactly* 3/4 to have agouti fur, but rather that for a very large number of offspring, the proportion with agouti fur is likely to be close to 3/4, and is *on average* 3/4.

6.2.8. $1 \cdot \frac{1}{6} + 2 \cdot \frac{1}{6} + 3 \cdot \frac{1}{6} + 4 \cdot \frac{1}{6} + 5 \cdot \frac{1}{6} + 6 \cdot \frac{1}{6} = 3.5$

6.2.9. a. The outcomes $k = 2, 3, \ldots 7$ can each occur in $k-1$ ways, namely $1+(k-1)$, $2+(k-2)$, ... $(k-1)+1$. The outcomes $k = 7, 8, \ldots, 12$ can each occur in $13-k$ ways, namely $6+(k-6)$, $5+(k-5)$, ..., $(k-6)+6$. Each of the individual outcomes listed occurs with probability $(1/6)^2 = 1/36$. Therefore the probabilities of the sum being 2, 3, ..., 12 are: 1/36, 2/36, 3/36, 4/36, 5/36, 6/36, 5/36, 4/36, 3/36, 2/36, 1/36. The expected value of the sum is

$2(1/36)+3(2/36)+4(3/36)+5(4/36)+6(5/36)+7(6/36)+8(5/36)+9(4/36)+10(3/36)+11(2/36)+12(1/36)=7$.

b. By problem 6.2.8, the expected value for one die toss is 3.5. Letting X_1 and X_2 denote the random variables for the two dice, $E(X_1)=E(X_2)=3.5$ so $E(X_1+X_2)=E(X_1)+E(X_2)=7$.

6.2.10. a. $p=1/6$, $q=5/6$, $k=3$, $n=10$; $\binom{10}{3}(\frac{1}{6})^3(\frac{5}{6})^7\approx .1550$

b. $p=5/6$, $q=1/6$, $k=7$, $n=10$; $\binom{10}{7}(\frac{5}{6})^7(\frac{1}{6})^3\approx .1550$

6.2.11. a. Choosing k objects out of n is exactly equivalent to designating the $n-k$ objects that are *not* chosen. Since 'choose' and 'designate' mean essentially the same thing here, this means $\binom{n}{k}=\binom{n}{n-k}$.

b. $\binom{n}{n-k}=\frac{n!}{(n-(n-k))!(n-k)!}=\frac{n!}{k!(n-k)!}=\frac{n!}{(n-k)!k!}=\binom{n}{k}$.

6.2.12. a. $1/2$

b. $(1/2)(1/2)=1/4$

c. $\binom{2}{1}(1/2)(1/2)=1/2$

d. $\binom{2}{1}(1/2)(1/2)+\binom{2}{2}(1/2)^2(1/2)^0=3/4$, or, computing the probability that it is not the case that no children are albinos, $1-\binom{2}{0}(1/2)^0(1/2)^2=3/4$.

e. Using the formula for the expected value of a binomial random variable, $2(1/2)=1$, or, using the definition of expected value, $0\cdot\binom{2}{0}(1/2)^0(1/2)^2+1\cdot\binom{2}{1}(1/2)^1(1/2)^1+2\cdot\binom{2}{2}(1/2)^0(1/2)^2=1$.

6.2.13. a. The probability of any particular offspring being fat with agouti fur is $(3/4)(1/4)=3/16$, assuming these genes assort independently. The number of progeny in 25 with this phenotype is a binomial random variable. Thus the expected value of it is $(25)(3/16)=75/16=4.6875$

b. $\binom{25}{4}(3/16)^4(13/16)^{21}\approx .1997$

c. $\sum_{i=0}^{4}\binom{25}{i}(3/16)^i(13/16)^{25-i}\approx .4837$

d. $1-\sum_{i=0}^{3}\binom{25}{i}(3/16)^i(13/16)^{25-i}\approx .7160$

6.2.14. a. $\mathcal{P}(\text{age at death}=0)=1/2$;
$\mathcal{P}(\text{age at death}=1)=(1/2)(3/4)=3/8$;
$\mathcal{P}(\text{age at death}=2)=(1/2)(1/4)(3/4)=3/32$;
$\mathcal{P}(\text{age at death}=3)=(1/2)(1/4)(1/4)(1)=1/32$.
These probabilities add to 1 since the events are disjoint and exhaust all possibilities.

b. $0(1/2)+1(3/8)+2(3/32)+3(1/32)=.65625$

6.2.15. a. Recall from problem 6.1.10, that the probability an offspring is yellow is $2/3$. Then the probability 5 of 12 have normal coloring is $\binom{12}{5}(1/3)^5(2/3)^7\approx .1908$.

b. $\sum_{i=10}^{12}\binom{12}{i}(2/3)^i(1/3)^{12-i}\approx .1811$

c. $\sum_{i=0}^{3}\binom{12}{i}(2/3)^i(1/3)^{12-i}\approx .0039$

6.2.16. a. Since the probability that any given child in the family will develop Huntington disease is $1/2$, the probability that none of 4 do is $\binom{4}{0}(1/2)^0(1/2)^4=1/16$.

b. The probability that at least one of the 4 develops the disease is $1-\mathcal{P}(\text{none of 4})=1-1/16=15/16$.

c. The probability that 3 or more develop the disease is $\binom{4}{3}(1/2)^3(1/2)^1+\binom{4}{4}(1/2)^4(1/2)^0=5/16$.

6.2.17. For each trait, the probability an individual exhibits the dominant phenotype is $3/4$, so the probability of an individual exhibiting the dominant phenotype for all three traits is $(3/4)^3=27/64$. The probability that 20 of 30 progeny will

exhibit all three dominant phenotypes is therefore $\binom{30}{20}(27/64)^{20}(37/64)^{10} \approx .0040$.

The probability an individual exhibits the dominant phenotype for at least one trait is $1 - \mathcal{P}(\text{recessive phenotype for all 3 traits}) = 1 - (1/4)^3 = 63/64$. The probability that at least 2 of 30 progeny exhibit the dominant phenotype for at least one trait is $1-\binom{30}{0}(63/64)^0(1/64)^{30}-\binom{30}{1}(63/64)^1(1/64)^{29} \approx 1-(1.2339\times 10^{-51}) \approx 1$.

6.2.18. a. There are n choices for the first ball. The remaining $n-1$ balls give $n-1$ choices for the second ball. Then there are $n-2$ choices for the third ball, etc., so there are $n-l+1$ choices for the lth ball.

b. To see how many ways k balls could be chosen (in order), we simply multiply the number of possible choices at each successive picking of a ball. This gives $n(n-1)(n-2)\cdots(n-k+1)$.

c. Picking k of k balls (in order), by the reasoning in (a) and (b), can be done in $k(k-1)(k-2)\cdots(2)1 = k!$ ways.

d. If the various choices of ordered balls counted in (b) are grouped according to the *unordered* set of balls chosen, then each group will have in it the count in (c). Thus the number of unordered sets of balls that could be chosen is $n(n-1)(n-2)\cdots(n-k+1)/(k!)$.

e. $\frac{n(n-1)(n-2)\cdots(n-k+1)}{k!} = \frac{n(n-1)(n-2)\cdots(n-k+1)(n-k)(n-k-1)\cdots(2)1}{(k!)(n-k)(n-k-1)\cdots(2)1} = \frac{n!}{k!(n-k)!}$.

6.2.19. a. $(x+y)^2 = x^2+2xy+y^2 = \binom{2}{0}x^2+\binom{2}{1}xy+\binom{2}{2}y^2$

$(x+y)^3 = x^3+3x^2y+3xy^2+y^3 = \binom{3}{0}x^3+\binom{3}{1}x^2y+\binom{3}{2}xy^2+\binom{3}{3}y^3$

$(x+y)^4 = x^4+4x^3y+6x^2y^2+4xy^3+y^4 = \binom{4}{0}x^4+\binom{4}{1}x^3y+\binom{4}{2}x^2y^2+\binom{4}{3}xy^3+\binom{4}{4}y^4$

b. $(x+y)^n = (x+y)(x+y)\cdots(x+y)$. To multiply this out, we must multiply each term in the individual factors by the terms in other factors in all possible ways. Since there are n factors, a term x^ky^{n-k} will be produced for every way we can choose k of the n factors to contribute an x, with the remaining $n-k$ factors contributing a y. But $\binom{n}{k}$ by definition gives the number of ways these choices can be made, so the product will contain exactly $\binom{n}{k}$ copies of x^ky^{n-k}. Collecting these produces the given formula.

c. $\sum_{i=0}^n \binom{n}{i} = 2^n$ for all n, since $\sum_{i=0}^n \binom{n}{i} = \sum_{i=0}^n \binom{n}{i}1^i1^{n-i} = (1+1)^n = 2^n$

6.2.20. a. $E = \sum_{i=0}^n i\frac{n!}{i!(n-i)!}p^iq^{n-i}$

b. Use straightforward algebra.

c. Note the $i=0$ term in E is 0, so

$$\begin{aligned}
E &= \sum_{i=1}^{n} i\frac{n!}{(n-i)!i!}p^iq^{n-i} = pn\sum_{i=1}^{n}\frac{(n-1)!}{(n-i)!(i-1)!}p^{i-1}q^{(n-1)-(i-1)} \\
&= pn\sum_{j=0}^{n-1}\frac{(n-1)!}{(n-1-j)!j!}p^jq^{(n-1)-j} \qquad \text{(replacing } i \text{ with } j+1) \\
&= pn\sum_{j=0}^{n-1}\binom{n-1}{j}p^jq^{(n-1)-j} \\
&= pn(p+q)^{n-1} = pn(1)^{n-1} = pn
\end{aligned}$$

6.2.21. a.

$$\begin{aligned} E(X_1 + X_2) &= \sum_k k\mathcal{P}(X_1 + X_2 = k) \\ &= \sum_k \sum_{i,j \text{ with } i+j=k} (i+j)\mathcal{P}(X_1 = i)\mathcal{P}(X_2 = j) \\ &= \sum_{i,j} (i+j)\mathcal{P}(X_1 = i)\mathcal{P}(X_2 = j) \end{aligned}$$

Note the last step simply reorders the sum.
b.

$$\begin{aligned} &\sum_i \sum_j (i+j)\mathcal{P}(X_1 = i)\mathcal{P}(X_2 = j) \\ &\quad = \sum_i \sum_j i\mathcal{P}(X_1 = i)\mathcal{P}(X_2 = j) + \sum_j \sum_i j\mathcal{P}(X_1 = i)\mathcal{P}(X_2 = j) \\ &\quad = \sum_i i\mathcal{P}(X_1 = i) \sum_j \mathcal{P}(X_2 = j) + \sum_j j\mathcal{P}(X_2 = j) \sum_i \mathcal{P}(X_1 = i) \end{aligned}$$

c. The two summations mentioned each give 1, so the result in part (b) is $E(X_1) + E(X_2)$.

6.2.22. a. Progeny of the specified cross should display the dominant phenotype with probability 3/4. The number of progeny in 1000 that display the dominant phenotype is a random variable with binomial distribution, so its expected value is (1000)(3/4)=750. We thus expect 750 dominant and 250 recessive phenotypes.
If 700 dominant and 300 recessive phenotypes are observed, then

$$\chi^2 = \frac{(700 - 750)^2}{750} + \frac{(300 - 250)^2}{250} = 13.333.$$

With $\alpha = .05$ and 1 degree of freedom, the critical value is $\chi^2_{crit} = 3.841$. Since this is less than our computed value, we find the data is not in accord with the Mendelian model at the .05 significance level.
b. If instead 725 dominant phenotypes are observed in 1000 progeny, $\chi^2 = 3.333$. This is less than the critical value in part (a), so the data is in accord with the Mendelian model at the .05 significance level.
c. If N dominant phenotypes are observed in 1000 progeny, then

$$\chi^2 = \frac{(N - 750)^2}{750} + \frac{(1000 - N - 250)^2}{250} = \frac{4(N - 750)^2}{750}.$$

Thus the data is in accord with the Mendelian model at the .05 significance level when

$$\begin{aligned} \frac{4(N - 750)^2}{750} &< 3.841 \\ (N - 750)^2 &< 720.1875 \\ |N - 750| &< 26.8363 \\ 723.1637 < N &< 776.8363 \end{aligned}$$

Since N must be an integer, this means $724 \leq N \leq 776$.

6.2.23. In the table, moving across a row means α decreases (with the degrees of freedom not changing). Since a smaller α means a χ^2 value computed from data is *less likely* to exceed the critical value, the critical value must get larger. Moving down a column means the degrees of freedom increases (with α held fixed). Since a larger degrees of freedom means more terms are added to compute χ^2, we expect χ^2 values to typically be larger. Thus for a fixed significance level, the critical value must be larger in order that computed χ^2 values exceed it the same percentage of times.

6.2.24. With 556 individuals included in the table, and independent assortment of the genes implying expected proportions of 9/16, 3/16, 3/16, and 1/16 of the phenotypes in the order listed, the expected frequencies are 312.75, 104.25, 104.25, and 34.75. This gives $\chi^2 = .47$. This is well below the critical value if α is taken to be .01, .05, or even .10. Thus the data is judged to be in accord with independent assortment at any of these significance levels.

6.2.25. a. For a significance level of .01, the critical value would appear further to the right than the value shown in Figure 6.2. It should be located so that the area under the curve to the right of it is one fifth of the shaded area.
b. The shape of the curve shows that typically the values of χ^2 from data described by a model will be small, but not too small. Most values will lie in the region on the horizontal axis that is below the 'hump'. Very large values of χ^2 are rare when the model describes the production of the data well, and the use of a cut-off critical value in the goodness-of-fit test simply formalizes how rare. Note also that extremely small values of χ^2 are also rare.

6.3. Linkage

6.3.1. a. Since Albert was not a hemophiliac, he must have had genotype X^+Y. Since so many of Victoria's children carried the hemophilia allele, it is unlikely they all were the result of new mutations, so Victoria had genotype X^+X^h.
b. 1/2; 0 ; 1/2
c. $\binom{9}{3}(1/2)^3(1/2)^6 \approx .1641$

6.3.2. F_1 is composed of X^+X^w and X^+Y genotypes, so the probability of each of the genotypes X^+X^+, X^+Y, X^+X^w and X^wY for an individual in F_2 is 1/4. Thus we expect the phenotypes listed in the order in Table 6.9 to occur in proportions 1/2, 0, 1/4, and 1/4. With 4252 progeny, we'd expect 2126, 0, 1063, and 1063 of the phenotypes. While the model is in rough agreement with the data, it's not that close. Perhaps the white-eyed males have reduced viability, lowering the count for that group below the theoretical prediction. On the other hand, even if the model is correct, this experiment's results may simply be due to random fluctuations.

6.3.3. a. X^wX^w and X^+Y
b. F_1 is composed of X^+X^w, which are red-eyed females, and X^wY, which are white-eyed males, in proportions 1/2 and 1/2.
c. F_2 is composed of X^+X^w (red-eyed females), X^wX^w (white-eyed females) X^+Y (red-eyed males) and X^wY (white-eyed males) in equal proportions.

6.3.4. The expected proportion of each of the four phenotypes is 1/4, so with 435 progeny, we'd expect 108.75 of each. Thus $\chi^2 = 17.4598$. With $\alpha = .05$, and three degrees of freedom, $\chi^2_{critical} = 7.81473$. Thus we do not find the data in accord with the model at the .05 significance level.

Notice, however, that this discrepancy could be explained if the white-eyed allele also results in reduced viability, since the white-eyed progeny of both sexes appeared in smaller numbers than expected. It is important to look deeper than the bald result of the χ^2 test in order to form new hypotheses.

6.3.5. a. Since the parents are X^+X^d and X^+Y, the probability a son has the disease is $1/2$.

b. The probability a daughter is heterozygous is $1/2$.

c. Note that daughters can not be homozygous for the disease-causing allele, so the probability two daughters are carriers is $(1/2)^2 = 1/4$.

6.3.6. a. The first cross is $X^+X^+ \times X^cY$. A daughter of this cross must be X^+X^c. Her offspring are from $X^+X^c \times X^+Y$, and so her sons are X^+Y and X^cY with equal probability. Thus the probability that a son is color blind is $1/2$.

b. Her daughters are X^+X^+ and X^+X^c with equal probability, and so (assuming the color-blindness allele is recessive) the probability of a daughter being color blind is 0.

c. $\binom{3}{2}(1/2)^2(1/2)^1 = 3/8$.

6.3.7. a. For expression in all male offspring, the mother must be X^aX^a. For expression in no female offspring, the father must be X^+Y and the a allele must be recessive.

b. For expression in 50% of male offspring, the mother must be X^+X^a. For expression in 50% of female offspring, the father must be X^aY if the a allele is recessive, or X^+Y if it is dominant.

c. For expression in no male offspring, the mother must be X^+X^+. For expression in all female offspring, the father must be X^aY and the a allele must be dominant.

d. For expression in 50% of male offspring, the mother must be X^+X^a. For expression in no female offspring, the father must be X^+Y and the a allele must be recessive.

e. Expression in 25% of the progeny can only occur through i) expression in no males and 50% of females, ii) expression in 25% of males and 25%of females, or iii) expression in 50% of males and no females. Case (i) cannot occur, since expression in no males requires the mother is X^+X^+, and then expression in a single female requires the father be X^aY and the allele dominant, which would then result in expression in all females. Case (ii) cannot occur either, since the model can only produce expression in all, half, or none of a sex. Case (iii), which is analyzed in part (d) must occur.

6.3.8. The standard model of one sex-linked gene cannot explain such data. One possibility is a cross $X^+X^a \times X^aY$ with the mutant phenotype displayed only by those individuals with 2 mutant alleles, so X^aY, X^+Y and X^+X^a all display wildtype phenotype while X^aX^a displays mutant phenotype. Other possibilities include not having a single type of cross due to a parental population of several genotypes, or involvement of multiple genes. Other valid answers no doubt exist.

6.3.9. a. Letting b denote the gene for black body color, and X^v that for vermillion eye color, the cross is $BbX^+X^v \times bbX^vY$. Analyzing the genes separately, $1/2$ the progeny will have black bodies and $1/2$ gray bodies, while both males and females will be $1/2$ vermillion-eyed and $1/2$ red-eyed. Thus each of the 8 phenotypes will occur in proportion $1/8$.

b. From $BbX^vX^v \times BBX^+Y$, all progeny will have gray bodies, 1/2 will be red-eyed females and 1/2 vermillion-eyed males.

6.3.10. The expected number of each phenotype is 312.25, so $\chi^2 = 425.3603$, which is considerably larger than the critical value. Thus the data is not consistent, at the .05 significance level, with the assumption of independent assortment of genes.

6.3.11. a. The probability is 6/7, since regardless of what chromosome the first gene lies on, the probability the second is not on that chromosome is 6/7.

b. The probability that two genes chosen at random assort independently would be greater than 6/7, since all genes on different chromosomes assort independently, and those far apart on the same chromosome do as well.

6.3.12. a.

Phenotype	Number
tall, normal sheaf	303
tall, white sheaf	163
dwarf, normal sheaf	169
dwarf, white sheaf	290
Total	925

b. $(163 + 169)/925 = .3589$, so the genetic distance is estimated as 35.89 cM.

c. This does not agree with the genetic distance of 37 cM in the text, since by collapsing the table, we lost information on the double crossovers. As a result, we undercounted recombinants, and got a distance that is smaller than the true one.

6.3.13. Assuming independent assortment, this cross would produce the 4 phenotypes in roughly equal proportions. Since the observed proportions are far from equal, there is evidence for linkage. The recombination frequency is $(39 + 35)/(198 + 228 + 39 + 35) = 74/500 = .1480$.

6.3.14. a. sn^+m^+ and $sn\,m$ each in proportion .425, sn^+m and $sn\,m^+$ each in proportion .075.

b. Wildtype bristles and wings in proportion

$$3(.425^2) + 4(.425)(.075) + 2(.075^2) = .680625;$$

Wildtype bristles and miniature wings in proportion

$$2(.425)(.075) + .075^2 = .069375;$$

Singed bristles and wildtype wings in proportion

$$2(.425)(.075) + .075^2 = .069375;$$

Singed bristles and miniature wings in proportion $.425^2 = .180625$

6.3.15. The genes on different autosomes assort independently, and thus can be analyzed separately. An $a^+b^+/a\,b$ produces gametes a^+b^+, a^+b, $a\,b^+$, and $a\,b$ in proportions .45, .05, .05, and .45. Crossing with a homozygous recessive thus yields the 4 phenotypes associated to these alleles in the same proportions. Similarly, the cross will yield phenotypes associated to c^+d^+, c^+d, $c\,d^+$, and $c\,d$ in proportions .43, .07, .43, and .07. Thus the 16 phenotypes and their proportions will be: $a^+b^+c^+d^+$, (.45)(.43)=.1935; $a^+b^+c^+d$, (.45)(.07)=.0315; $a^+b^+c\,d^+$, .0315; $a^+b^+c\,d$, .1935; $a^+b\,c^+d^+$, (.05)(.43)=.0215; $a^+b\,c^+d$, (.05)(.07)=.0035; $a^+b\,c\,d^+$, .0035; $a^+b\,c\,d$, .0215; $a\,b^+c^+d^+$, .0215; $a\,b^+c^+d$, .0035; $a\,b^+c\,d^+$, .0035; $a\,b^+c\,d$, .0215; $a\,b\,c^+d^+$, .1935; $a\,b\,c^+d$, .0315; $a\,b\,c\,d^+$, .0315; $a\,b\,c\,d$, .1935.

6.3.16. A trans configuration can be used in genetic mapping, though then the recombinant phenotypes are those that are wildtype for both traits or mutant for both traits. Even if it was not known that the heterozygous parent had a cis or trans configuration, the sizes of the phenotypic classes resulting from the cross with a homozygous recessive would indicate which one.

6.3.17. The physical distance separating genes a and b is likely to be larger than that separating c and d, since for the probability of a crossover occuring between them to be the same, near the centromere the physical distance would usually need to be larger.

6.3.18. With a tetrad drawn as in Figure 6.3 of the text, label the strands 1,2,3, and 4 from top to bottom. Then have strands 1 and 3 crossover between the 2 genes, and strands 2 and 4 crossover as well.

No two-gene configuration can produce 3 recombinant and one parental type since two strands must crossover to produce two of the recombinants, and a third strand must crossover with another strand to produce the third. This last strand cannot be one of the first two (why not?) so it must be the fourth. However, this would produce 4 recombinants.

Note that there are three-gene configurations producing three recombinants and one parental type.

6.3.19. The rare phenotypes are those associated to $(a^+b^+c^+)$ and $(a\,b\,c)$ so these must come from double crossovers. Since the parental types were (a^+b^+c) and $(a\,b\,c^+)$, we deduce the gene order $a\,c\,b$.

6.3.20. a. Any of $cl^+dp^+rd^+/cl\,dp\,rd$, $cl^+dp^+rd/cl\,dp\,rd^+$, $cl^+dp\,rd^+/cl\,dp^+rd$, or $cl^+dp\,rd\,/cl\,dp^+rd^+$ could be crossed with a homozygous recessive.

b. Since $cl^+dp\,rd$ is the result of a double crossover, the gene order must be $dp\,cl\,rd$.

6.3.21. The phenotypes normal-eyes, hairy-legs, prickly-antennae and enlarged-eyes, hairless-legs, smooth-antennae both occur with frequency $(1/2)(.88)(.85)=.374$; the phenotypes enlarged-eyes, hairy-legs, prickly-antennae and normal-eyes, hairless-legs, smooth-antennae both occur with frequency $(1/2)(.12)(.85)=.051$; the phenotypes normal-eyes, hairy-legs, smooth-antennae and enlarged-eyes, hairless-legs, prickly-antennae both occur with frequency $(1/2)(.88)(.15)=.066$; the phenotypes normal-eyes, hairless-legs, prickly-antennae and enlarged-eyes, hairy-legs, smooth-antennae both occur with frequency $(1/2)(.12)(.15)=.009$.

6.3.22. a. Since the male parent in this cross is recessive for all genes, the offspring, whether male or female, will display phenotypes associated with the maternal gamete. Thus the proportion of each phenotype should be the same in the male and female offspring.

b. The data does give evidence of linkage since the sizes of the phenotype classes are far from equal.

c. The rare phenotypes arise from maternal gametes ct^+s^+v and $ct\,s\,v^+$, so these result from double crossovers. Given the genotype of the mother, the gene order must be $ct\,v\,s$.

The genetic distance from ct to v is estimated as $(8+125+105+5)/1919 = 243/1919 \approx .1266 = 12.66cM$. The genetic distance between v and s is estimated as $(8+71+106+5)/1919 = 190/1919 \approx .0990 = 9.9cM$

6.3.23. a. $(.082)(.125)(2000) = 20.5$

b. $c = 3/20.5 = .1463$

c. No interference would mean $c = 1$, so $I = 0$. At the other extreme, if interference is so great that no double crossovers occur, then $c = 0$ so $I = 1$. In general I increases if interference produces fewer crossovers.
c. $I = .8537$

6.4. Gene Frequency in Populations

6.4.1. a. Let p be the frequency of ct in the population. Then $p^2 = 9/450$, so $p \approx .1414$.
b. The percentage of the population heterozygous for the gene is $2p(1-p) \approx .2428$.

6.4.2. a. The color-blindness allele occurs with frequency $p = .08$, so $q = .92$.
b. About $.08^2 = .0064$ of the female population is color blind, while about $2(.08)(.92) = .1472$ of the females have normal vision but carry the color-blindness allele.

6.4.3. a. $2p(1-p) = .4$ implies $p^2 - p + .2 = 0$, so $p = (1 \pm \sqrt{1-.8})/2 = (1 \pm \sqrt{.2})/2 \approx .2764$ or $.7236$, with q being the other value.
For $2p(1-p) = H$, the values of p and q are $(1 \pm \sqrt{1-2H})/2$.
b. $H = 2p(1-p)$ is maximized when $p = 1/2$, $q = 1/2$. This can be seen either by graphing the parabola, or by using calculus.

6.4.4. a. $(p+q)^2 = p^2 + 2pq + q^2$. Assuming p is the frequency of alleles a and q the frequency of allele A, the terms in this expansion give the frequencies of aa, Aa, and AA genotypes produced in a population with random mating.
b. $(p+q+r)^2 = p^2 + q^2 + r^2 + 2pq + 2pr + 2qr$. Assuming p, q, r are frequencies of the alleles a_1, a_2, a_3 of a triallelic gene in a randomly mating population, these terms are the frequencies of the genotypes of the next generation a_1a_1, a_2a_2, a_3a_3, a_1a_2, a_1a_3 and a_2a_3.
c. Yes, the Hardy-Weinberg equilibrium concept still makes sense. For instance, in the next generation of gametes, the frequency of allele a_1 is $p^2 + (1/2)2pq + (1/2)2pr = p(p+q+r) = p \cdot 1 = p$. The frequencies of the other alleles are similarly shown to be constant.

6.4.5. a. Let p, q, and r denote the frequencies of the alleles I^A, I^B, and I^O. Assuming random mating in the population,

$$p^2 + 2pr = .32,\ q^2 + 2qr = .15,\ 2pq = .04,\ r^2 = .49.$$

Solving these gives $r = .7$, $p = .2$, and $q = .1$. Note that even though there are 4 equations in only 3 unknowns here, these values makes all equations hold.
b. The equations to be solved are

$$p^2 + 2pr = .40,\ q^2 + 2qr = .11,\ 2pq = .05,\ r^2 = .44.$$

From the last we find $r = .6633$. Then the first gives $p = .2532$, and the second gives $q = .0783$. With these values $2pq = .0396$, so the third equation is *not* satisfied. (Also, $p + q + r \neq 1$.) Thus the system has no exact solution.
It could be that the population is not in a Hardy-Weinberg equilibrium, or that the data is flawed. Given the relative ease of collecting bloodtype data, and the doubtfulness of the random mating assumption applying to the U.S. population, the first is more likely.

6.4.6. Assume allele a_1 is dominant over a_2 and a_3, and a_2 dominant over a_3. Let p_1, p_2, and p_3 denote their frequencies in the population. Then knowing the frequency of the phenotype associated to a_3 would let us solve for p_3. Knowing

the frequency of the phenotype associated to a_2 along with p_3 would let us solve for p_2. Since $p_1 + p_2 + p_3 = 1$, we could then determine p_1. Thus knowing two phenotype frequencies is sufficient. Since there are two independent variables (p_2 and p_3, say), knowing a single phenotype frequency is not enough.
In general, for a gene with n alleles, at least $n-1$ phenotype frequencies must be known.

6.4.7. a. $p = (2Np_1 + 2Np_2)/(4N) = (p_1 + p_2)/2$
b.After the flood, a^+a^+ has frequency $(p_1^2 + p_2^2)/2$, a^+a has frequency $p_1(1 - p_1) + p_2(1 - p_2)$, and aa has frequency $((1 - p_1)^2 + (1 - p_2)^2)/2$.
A Hardy-Weinberg equilibrium would predict the three frequencies were $(p_1 + p_2)^2/4$, $(p_1 + p_2)(2 - p_1 - p_2)/2$, and $(2 - p_1 - p_2)^2/4$.
These disagree (for most values of p_1, p_2) since the population has not yet undergone random mating. There is no reason to expect a Hardy-Weinberg equilibrium.

6.4.8. The model becomes

$$p_{t+1} = \frac{p_t^2 + p_t q_t}{p_t^2 + 2p_t q_t + q_t^2} = \frac{p_t(p_t + q_t)}{(p_t + q_t)^2} = p_t.$$

This means the frequencies are unchanging, and in Hardy-Weinberg equilibrium. Note that here there is no selection operating, but mating is still random.

6.4.9. a. The model shows a gradual increase in frequency of A, toward fixation at $p = 1$. Thus a is eliminated ultimately. It appears that $p = 1$ is a stable equilibrium, and $p = 0$ an unstable one.
b. The model shows a gradual decrease in frequency of A, toward elimination at $p = 0$. Thus A is eliminated ultimately. It appears that $p = 0$ is a stable equilibrium, and $p = 1$ an unstable one.
c. If $p_0 > .5$, the frequency of A increases, toward $p = 1$; if $p_0 < .5$, the frequency of A decreases, toward $p = 0$. Thus the model shows a gradual increase in the frequency of whichever allele is initially more common. Eventually that allele is fixed in the population, while the other dies out. There are stable equilibria at $p = 0$ and 1, and an unstable one at $p = .5$.
d. If $p_0 > .5$, the frequency of A decreases, toward $p = .5$; if $p_0 < .5$, the frequency of A increases, toward $p = .5$. Thus the model shows movement toward an equal proportion of both alleles. While $p = .5$ is a stable equilibria, there are unstable ones at $p = 0$ and 1.

6.4.10. With $w_{AA} = 0$, $w_{Aa} = w_{aa} = 1$, simulations show that the frequency of the allele declines to 0, and that eventually the allele is eliminated from the population. (See problem 6.4.11.)

6.4.11. a. The parameters indicate homozygous dominants do not reproduce, while heterozygotes have no selective disadvantage relative the homozygous recessives. (See problem 6.4.10.)
b. $p_{t+1} = \dfrac{p_t q_t}{2p_t q_t + q_t^2} = \dfrac{p_t}{2p_t + q_t} = \dfrac{p_t}{p_t + 1}$, if $q_t \neq 0$ (or $p_t \neq 1$).
c. $p_1 = \dfrac{p_0}{p_0 + 1}$, so $p_2 = \dfrac{\frac{p_0}{p_0+1}}{\frac{p_0}{p_0+1} + 1} = \dfrac{p_0}{p_0 + (p_0 + 1)} = \dfrac{p_0}{2p_0 + 1}$. In general, if $p_t = \dfrac{p_0}{tp_0 + 1}$, then $p_{t+1} = \dfrac{\frac{p_0}{tp_0+1}}{\frac{p_0}{tp_0+1} + 1} = \dfrac{p_0}{p_0 + (tp_0 + 1)} = \dfrac{p_0}{(t+1)p_0 + 1}$.
Note that this shows that as $t \to \infty$, $p_t \to 0$ so such an allele will die out under random mating.

6.4.12. a. The homozygous recessives have no progeny, while heterozygotes are at no relative advantage to homozygous dominants.
b. $p_{t+1} = 1/(2 - p_t)$
c. $p_t = (t-(t-1)p_0)/((t+1)-tp_0)$, thus as $t \to \infty$, $p_t \to 1$ and the dominant allele becomes fixed.

6.4.13. a. If p is an equilibrium, then

$$p = ((w_{AA}p^2 + w_{Aa}p(1-p))/(w_{AA}p^2 + 2w_{Aa}p(1-p) + w_{aa}(1-p)^2),$$

so

$$w_{AA}p^3 + 2w_{Aa}p^2(1-p) + w_{aa}p(1-p)^2 - w_{AA}p^2 - w_{Aa}p(1-p) = 0.$$

b. $p = 0$ and 1 are two of the three equilibria.
c. The cubic polynomial in (a) factors as

$$p(p-1)((w_{AA} - 2w_{Aa} + w_{aa})p + (w_{Aa} - w_{aa})) = 0.$$

d. The third equilibrium satisfies $(w_{AA} - 2w_{Aa} + w_{aa})p + (w_{Aa} - w_{aa}) = 0$, so straightforward algebra shows it's given by the formula stated.

6.4.14. a. If either $w_{aa} - w_{Aa}$ or $w_{AA} - w_{Aa}$ is 0, then we get one of the two first two equilibria, 0 or 1. Otherwise, since the third equilibrium can be written $p = 1/\left(1 + \dfrac{w_{AA} - w_{Aa}}{w_{aa} - w_{Aa}}\right)$, for it to lie between 0 and 1 we must have $\dfrac{w_{AA} - w_{Aa}}{w_{aa} - w_{Aa}} > 0$. This means the numerator and denominator have the same sign, which is equivalent to the given condition.
b. Again thinking in terms of the signs of the factors in (a), these are seen to be equivalent.

6.4.15. a. Homozygote advantage results in a trend toward fixation of whichever allele is most common initially in the population, and elimination of the other.
b. Heterozygote advantage results in a trend toward non-zero proportions of both alleles in the population. If $w_{AA} = w_{aa}$, then equal proportions of each will occur in the long run, but more generally the allele with the greater homozygous relative fitness is the more common.

6.4.16. The formula for mean fitness shows it is a weighted average of the relative fitness parameters, weighted by the frequencies of the corresponding genotypes in the population. The result that $\overline{w}_{t+1} \geq \overline{w}_t$ says that the mean fitness of a population can only increase. This is a quantitative statement of "survival of the fittest."

6.4.17. For low population sizes, the graphs are quite jagged, and often result in the fixation of one allele and elimination of the other. There is some tendency for the initially more common allele to be fixed, but many exceptions occur. For midsize populations, the size of the fluctuations (as a percentage of population) is much smaller, and fixation/elimination occurs more rarely. For large populations, the fluctuations are quite small (though still present) and one rarely observes fixation/elimination unless initially one allele was quite rare. Despite the fluctuations, the overall trend for large populations is that the frequencies remain roughly constant. This supports the idea that genetic drift is only a significant factor for small populations (or rare alleles).

6.4.18. Introducing selection into the genetic drift model results in biasing the drift along the trends that would occur in a selection model without drift. For example, with dominant advantage, seldom does drift result in elimination of the

dominant allele, although it does occasionally. An interesting case is homozygous advantage, where the tendency of drift to lead to fixation/elimination is tempered, so that both alleles persist for much longer.

6.4.19. By the definition of expected value, $E = 0(.0625) + 1(.25) + 2(.375) + 3(.25) + 4(.0625) = 2$, or, since the random variable has a binomial distribution, $E = 4(1/2) = 2$. This expected value is exactly the Hardy-Weinberg equilibrium. Even in the presence of genetic drift, the idea of a Hardy-Weinberg equilibrium is still valid for expected values of frequencies of alleles.

6.4.20. a. H should tend toward 0, regardless of which allele is fixed, since $H = 2pq$ and either p or q approaches 0.

b. H declines to 0 exponentially. The larger the population size N, the slower the decline. Varying the initial value of H_0 does mean it may take more or less time for H to reach any specified value, but does not affect the rate of exponential decay.

c. $H_t = (1 - \frac{1}{2N})^t H_0$