Chapter 2: Solutions to Problems 1-15

1.
$$\hat{q} = \frac{\frac{1}{2}N_{12} + N_{22}}{N}$$
$$\hat{q}_G = \frac{\frac{1}{2}(42) + 64}{117} = 0.726$$
$$\hat{p}_C = 1 - \hat{q}_G$$
$$\hat{p}_C = 1 - 0.726 = 0.274$$
$$N_{11} = N_{CC} = Np^2 = 117(0.274^2) = 8.8$$
$$N_{12} = N_{CG} = N(2pq) = 117(2)(0.274)(0.726) = 46.5$$
$$N_{22} = N_{GG} = Nq^2 = 117(0.726^2) = 61.7$$

2.
$$\hat{p}_i = \frac{N_{ii} + \frac{1}{2}\sum_{j=1}^{n} N_{ij}}{N}$$
$$\hat{p}_1 = \frac{8 + \frac{1}{2}(38) + \frac{1}{2}(121)}{847} = 0.103$$
$$\hat{p}_2 = \frac{27 + \frac{1}{2}(38) + \frac{1}{2}(252)}{847} = 0.203$$
$$\hat{p}_3 = \frac{401 + \frac{1}{2}(121) + \frac{1}{2}(252)}{847} = 0.694$$
$$X^2 = \sum_{i=1}^{k} \frac{(O-E)^2}{E}$$
$$X^2 = \frac{(8-8.99)^2}{8.99} + \frac{(38-35.42)^2}{35.42} + \frac{(121-121.09)^2}{121.09} + \frac{(27-34.90)^2}{34.90} + \frac{(252-238.65)^2}{238.65} + \frac{(401-407.95)^2}{407.95}$$
$$X^2 = 2.95$$
$$df = 6 - 2 - 1 = 3$$

Genotypic frequencies do not deviate significantly from Hardy-Weinberg proportions.
with 3 df the critical value is 7.81 ($\alpha = 0.05$)

3.

$$P = p_f p_m$$
$$H = p_f q_m + p_m q_f$$
$$Q = q_f q_m$$
$$P = (0.6)(0.2) = 0.12$$
$$H = (0.6)(0.8) + (0.2)(0.4) = 0.56$$
$$Q = (0.4)(0.8) = 0.32$$
$$p' = \frac{1}{2}(p_f + p_m)$$
$$p' = \frac{1}{2}(0.4 + 0.8) = 0.6$$
$$P = (0.4)(0.4) = 0.16$$
$$H = (0.6)(0.4) + (0.6)(0.4) = 0.48$$
$$Q = (0.6)(0.6) = 0.36$$

If $H = p_m q_f + p_f q_m$ (expression 2.6*a*) and $2pq = 2\left[\left(\frac{1}{2}(p_f + p_m)\right)\left(\frac{1}{2}(q_f + q_m)\right)\right]$, then:

$$\begin{aligned}
H - 2\overline{pq} &= (p_m q_f + p_f q_m) - 2\left[\left(\tfrac{1}{2}(p_f + p_m)\right)\left(\tfrac{1}{2}(q_f + q_m)\right)\right] \\
&= (p_m q_f + p_f q_m) - \tfrac{1}{2}(p_f + p_m)(q_f + q_m) \\
&= (p_m q_f + p_f q_m) - \tfrac{1}{2}(p_f q_f) - \tfrac{1}{2}(p_f q_m) - \tfrac{1}{2}(p_m q_f) - \tfrac{1}{2}(p_m q_m) \\
&= \tfrac{1}{2}(p_f q_m) + \tfrac{1}{2}(p_m q_f) - \tfrac{1}{2}(p_f q_f) - \tfrac{1}{2}(p_m q_m)
\end{aligned}$$

if $q_m = 1 - p_m$ and $q_f = 1 - p_f$, then:

$$\begin{aligned}
&= \tfrac{1}{2}\left(p_f(1 - p_m) + p_m(1 - p_f) - p_f(1 - p_f) - p_m(1 - p_m)\right) \\
&= \tfrac{1}{2}\left(p_f - p_f p_m + p_m - p_m p_f - p_f + p_f^2 - p_m - p_m^2\right) \\
&= \tfrac{1}{2}\left(p_f^2 - 2p_f p_m - p_m^2\right) \\
&= \tfrac{1}{2}(p_f - p_m)^2
\end{aligned}$$

If $Q = q_f q_m$ (expression 2.6*a*) and $\overline{q} = \frac{1}{2}(q_f + q_m)$, then:

$$\begin{aligned}
Q - \overline{q}^2 &= q_f q_m - \left[\tfrac{1}{2}(q_f + q_m)\right]^2 \\
&= q_f q_m - \left[\tfrac{1}{2}(q_f + q_m)\right]\left[\tfrac{1}{2}(q_f + q_m)\right] \\
&= q_f q_m - \left[\tfrac{1}{2}q_f + \tfrac{1}{2}q_m\right]\left[\tfrac{1}{2}q_f + \tfrac{1}{2}q_m\right] \\
&= q_f q_m - \tfrac{1}{4}\left[q_f^2 + 2q_f q_m + q_m^2\right] \\
&= q_f q_m - \tfrac{1}{4}q_f^2 - \tfrac{1}{2}q_f q_m - \tfrac{1}{4}q_m^2 \\
&= \tfrac{4}{4}q_f q_m - \tfrac{2}{4}q_f q_m - \tfrac{1}{4}q_f^2 - \tfrac{1}{4}q_m^2 \\
&= \tfrac{2}{4}q_f q_m - \tfrac{1}{4}q_f^2 - \tfrac{1}{4}q_m^2 \\
&= -\tfrac{1}{4}(q_f^2 - 2q_f q_m + q_m^2) \\
&= -\tfrac{1}{4}(q_f - q_m)^2
\end{aligned}$$

if $q_m = 1 - p_m$ and $q_f = 1 - p_f$, then:

$$\begin{aligned}
&= -\tfrac{1}{4}(p_m - p_f)^2 \\
&= -\tfrac{1}{4}(p_f - p_m)^2
\end{aligned}$$

4. $q'_f = \frac{1}{2}(q_f + q_m)$

$q'_m = q_f$

$q_{f(gen1)} = \frac{1}{2}(0.3 + 0.0) = 0.15$

$q_{m(gen1)} = 0.3$

$q_{f(gen2)} = \frac{1}{2}(0.15 + 0.3) = 0.225$

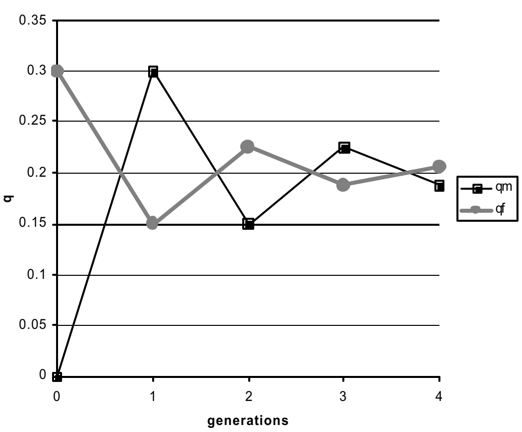
$q_{m(gen2)} = 0.15$

$q_{f(gen3)} = \frac{1}{2}(0.225 + 0.15) = 0.1875$

$q_{m(gen3)} = 0.225$

$q_{f(gen4)} = \frac{1}{2}(0.1875 + 0.225) = 0.206$

$q_{m(gen3)} = 0.1875$



$$d_t = \left(-\frac{1}{2}\right)^t d_0 \qquad \text{or} \qquad t = \frac{\log\left(\frac{d_t}{d_o}\right)}{-\log 2}$$

$\overline{q} = \frac{2}{3}q_f + \frac{1}{3}q_m$

$\overline{q} = \frac{2}{3}(0.3) + \frac{1}{3}(0.0) = 0.2$

$d_0 = 0.3 - 0.2 = 0.1$

$$t = \frac{\log\left(\frac{0.001}{0.1}\right)}{-\log 2} = 6.64 \text{ or 7 generations}$$

5. $$\hat{p} = \frac{N_{11} + \frac{1}{2}N_{12}}{N}$$

$$\hat{q} = \frac{\frac{1}{2}N_{12} + N_{22}}{N}$$

$$\hat{p} = \frac{25 + \frac{1}{2}(14)}{60} = 0.533$$

$$\hat{q} = \frac{\frac{1}{2}(14) + 21}{60} = 0.467$$

$$X^2 = \sum_{i=1}^{k} \frac{(O-E)^2}{E} \text{ where } E_{11} = \hat{p}^2 N \text{ , } E_{12} = 2\hat{p}\hat{q}N \text{ , } E_{22} = \hat{q}^2 N$$

$$X^2 = \frac{\left(N_{11} - \hat{p}^2 N\right)^2}{\hat{p}^2 N} + \frac{\left(N_{12} - 2\hat{p}\hat{q}N\right)^2}{2\hat{p}\hat{q}N} + \frac{\left(N_{22} - \hat{q}^2 N\right)^2}{\hat{q}^2 N}$$

$$X^2 = \frac{\left(25 - (0.533)^2(60)\right)^2}{(0.533)^2(60)} + \frac{\left(14 - 2(0.533)(0.467)(60)\right)^2}{2(0.533)(0.467)(60)} + \frac{\left(21 - (0.467)^2(60)\right)^2}{(0.467)^2(60)}$$

$$X^2 = \frac{63.276}{17.045} + \frac{251.853}{29.861} + \frac{62.642}{13.085} = 3.712 + 8.431 + 4.787 = 16.93$$

$$X^2 = \sum_{i=1}^{k} \frac{(O-E)^2}{E} \text{ where } E_{N_{11}} = \frac{N\hat{p}_i(2N\hat{p}_i - 1)}{2N-1}, E_{N_{12}} = \frac{4N^2\hat{p}_i\hat{p}_j}{2N-1}, E_{N_{22}} = \frac{N\hat{q}_i(2N\hat{q}_i - 1)}{2N-1}$$

$$E_{N_{11}} = \frac{(60)(0.533)(2(60)(0.533) - 1)}{2(60) - 1} = 16.920$$

$$E_{N_{12}} = \frac{4((60)^2)(0.533)(0.467)}{2(60) - 1} = 30.120$$

$$E_{N_{22}} = \frac{(60)(0.467)(2(60)(0.467) - 1)}{2(60) - 1} = 12.960$$

$$X^2 = \frac{(25 - 16.92)^2}{16.92} + \frac{(14 - 30.12)^2}{30.12} + \frac{(21 - 12.96)^2}{12.96} = 3.859 + 8.627 + 4.988 = 17.47$$

6. $$p_n = \frac{H_E - H_O}{1 + H_E}$$

$$\hat{H}_O = \frac{\sum N_{ij}}{N}$$

$$\hat{H}_O = \frac{18}{49} = 0.367$$

$$H_E = 1 - \sum_{i=1}^{n} p_i^2$$

$$H_E = 1 - ((0.531)^2 + (0.469)^2) = 0.498$$

$$p_n = \frac{0.498 - 0.367}{1 + 0.498} = 0.087$$

7. $$\hat{q} = \left(\frac{N_{22}}{N}\right)^{\frac{1}{2}}$$

$$\hat{q} = \left(\frac{1}{2500}\right)^{\frac{1}{2}} = 0.02$$

$$\hat{p} = 1 - \hat{q} = 0.98$$

$$N_{12} = 2\hat{p}\hat{q} = 2(0.98)(0.02) = 0.0392$$

$$P = (2pq)^2 = (0.392)^2 = 0.0015$$

8. $$A_1 = \frac{1}{41} = 0.024$$

$$A_2 = \frac{4}{41} = 0.098$$

$$A_3 = \frac{3}{41} = 0.073$$

$$A_4 = \frac{21}{41} = 0.512$$

$$A_5 = \frac{4}{41} = 0.098$$

$$A_6 = \frac{1}{41} = 0.024$$

$$A_7 = \frac{7}{41} = 0.171$$

$$\hat{H} = \frac{N}{N-1}\left((1 - \sum_{i=1}^{n} \hat{p}_i^2)\right)$$

$$\hat{H} = \frac{41}{41-1}\left(1 - (0.024^2 + 0.098^2 + 0.073^2 + 0.512^2 + 0.098^2 + 0.024^2 + 0.171^2\right)$$

$$\hat{H} = 1.025(1 - 0.317) = 0.700$$

9. $melanic/carbonaria = \frac{N_{11} + N_{12} + N_{13}}{N}$

$$insularia = \frac{N_{22} + N_{23}}{N}$$

$$typicals = \frac{N_{33}}{N}$$

$$\hat{p}_i = 1 - \left(\frac{N_{22} + N_{23} + N_{33}}{N}\right)^{\frac{1}{2}}$$

$$\hat{p}_2 = \left(\frac{N_{22} + N_{23} + N_{33}}{N}\right)^{\frac{1}{2}} - \left(\frac{N_{33}}{N}\right)^{\frac{1}{2}}$$

$$\hat{p}_3 = \left(\frac{N_{33}}{N}\right)^{\frac{1}{2}}$$

$$\hat{p}_i = 1 - \left(\frac{5+448}{760}\right)^{\frac{1}{2}} = 0.228$$

$$\hat{p}_2 = \left(\frac{5+448}{760}\right)^{\frac{1}{2}} - \left(\frac{448}{760}\right)^{\frac{1}{2}} = 0.004$$

$$\hat{p}_3 = \left(\frac{448}{760}\right)^{\frac{1}{2}} = 0.768$$

10. $F = 1 - \frac{H}{2pq}$ or $H = -2pq(F-1)$

$$H = -2(0.3(0.7))(-0.05-1) = 0.441$$

$X = F^2 N$ or $N = \frac{X^2}{F^2}$

Using α=0.05, $X^2 = 3.84$ $N = \frac{3.84}{(-0.05)^2} = 1536$

11. $\bar{p} = \frac{N_i}{N} \sum p_i$

$V(\hat{p}) = \sum \frac{N_j}{N} \left(\hat{p}_j - \bar{p}\right)^2$ or $V(\hat{p}) = \left[\sum \frac{N_j}{N} \hat{p}_j^2\right] - \bar{p}^2$

$$X^2 = \frac{2NV(\hat{p})}{\bar{p}\bar{q}}$$

$$\bar{p}_{site1} = \frac{25}{75}(0.22) + \frac{50}{75}(0.37) = 0.32$$

$$V(\hat{p})_{site1} = \frac{25}{75}(0.22-0.32)^2 + \frac{50}{75}(0.37-0.32)^2 = 0.005$$

$$X^2_{site1} = \frac{2(75)(0.005)}{(0.32)(0.68)} = 3.45$$

$$\overline{p}_{site2} = \frac{25}{75}(0.04) + \frac{50}{75}(0.03) = 0.033$$

$$V(\hat{p})_{site2} = \frac{25}{75}(0.04-0.033)^2 + \frac{50}{75}(0.03-0.033)^2 = 0.000022$$

$$X^2_{site2} = \frac{2(75)(0.000022)}{(0.033)(0.967)} = 0.103$$

$$X^2_{(sites1\&2)} = X^2_{(sites1)} + X^2_{(site2)} = 3.45 + 0.103 = 3.55$$

$$J_{xy} = \sum_{i=1}^{n} p_{i.x}\, p_{i.y} \qquad J_x = \sum_{i=1}^{n} p^2_{i.x} \qquad J_y = \sum_{i=1}^{n} p^2_{i.y}$$

$$I = \frac{J_{xy}}{\left(J_x J_y\right)^{\frac{1}{2}}} \qquad D = -\ln(I)$$

$$J_{xy_{site1}} = (0.22)(0.37) + (0.78)(0.63) = 0.5728$$

$$J_{x_{site1}} = p^2_{i.x} = (0.22)^2 + (0.78)^2 = 0.6568$$

$$J_{y_{site1}} = p^2_{i.y} = (0.37)^2 + (0.63)^2 = 0.5338$$

$$I_{site1} = \frac{0.5728}{\left((0.6568)(0.5338)\right)^{\frac{1}{2}}} = 0.9674 \qquad D_{site1} = -\ln(0.9674) = 0.033$$

$$J_{xy_{site2}} = (0.04)(0.03) + (0.96)(0.97) = 0.9324$$

$$J_{x_{site2}} = p^2_{i.x} = (0.04)^2 + (0.96)^2 = 0.9232$$

$$J_{y_{site2}} = p^2_{i.y} = (0.03)^2 + (0.97)^2 = 0.9418$$

$$I_{site2} = \frac{0.9324}{\left((0.9232)(0.9418)\right)^{\frac{1}{2}}} = 0.9999 \qquad D_{site2} = -\ln(0.9999) = 0.000$$

$$J_{xy_{site1\ \&\ 2}} = (0.22)(0.37) + (0.78)(0.63) + (0.04)(0.03) + (0.96)(0.97) = 1.5052$$

$$J_{x_{site1\&2}} = p^2_{i.x} = (0.22)^2 + (0.78)^2 + (0.04)^2 + (0.96)^2 = 1.58$$

$$J_{y_{site1\&2}} = p^2_{i.y} = (0.37)^2 + (0.63)^2 + (0.03)^2 + (0.97)^2 = 1.4756$$

$$I_{site1\&2} = \frac{1.5052}{\left((1.58)(1.4756)\right)^{\frac{1}{2}}} = 0.9858 \qquad D_{site1\&2} = -\ln(0.9858) = 0.014$$

12. $p_s = \frac{\#segregating\_sites}{length\_sequenced} = \frac{8}{15} = 0.5333$

$$p = \frac{\sum_{i=1}^{n-1} \sum_{j=1+i}^{n} k_{ij}}{\frac{n(n-1)}{2}}$$ (from class notes)

	1	2	3	4	5
1					
2	4				
3	4	0			
4	0	4	4		
5	4	8	8	4	

$$\frac{\frac{40}{15}}{\frac{5(4)}{2}} = \frac{2.667}{10} = 0.2667$$

13. Using data from problem 12, following is the output from MEGA:

```
Title: : Problem12.fasta
Description
No. of Taxa : 5
Gaps/Missing data : Complete Deletion
Codon Positions : Noncoding
Distance method : Nucleotide: Number of differences  [Pairwise distances]
No. of Sites : 15
d : Estimate

[1] #1
[2] #2
[3] #3
[4] #4
[5] #5

[      1     2     3     4     5 ]
[1]
[2]  4.000
[3]  4.000 0.000
[4]  0.000 4.000 4.000
[5]  4.000 8.000 8.000 4.000
Nucleotide/amino acid diversity (pi) = 0.266667
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14. $\Pr(i) = \frac{N!}{i!\,j!} x^i (1-x)^j$

To solve, sum the Pr(84), Pr(85), Pr(86)..Pr(122)

$\Pr(84) = \frac{122!}{84!38!}(0.603)^{84}(0.397)^{38} = 0.011$ and $\Pr(85) = \frac{122!}{85!37!}(0.603)^{85}(0.397)^{37} = 0.008$

Iterations can be done in a math program (e.g. Excel) yielding Pr(84…122) = 0.032

i	N!/(i!*j!)	p^i	q^j	Pr(i)
84	5.6968E+31	3.5209E-19	5.676E-16	0.01138487
85	2.5468E+31	2.1231E-19	1.4297E-15	0.00773071
86	1.0957E+31	1.2802E-19	3.6013E-15	0.00505184
87	4.534E+30	7.7198E-20	9.0713E-15	0.00317512
88	1.8033E+30	4.655E-20	2.285E-14	0.0019181
89	6.8891E+29	2.807E-20	5.7555E-14	0.00111298
90	2.526E+29	1.6926E-20	1.4498E-13	0.00061985
91	8.8826E+28	1.0206E-20	3.6518E-13	0.00033107
92	2.993E+28	6.1545E-21	9.1985E-13	0.00016944
93	9.655E+27	3.7112E-21	2.317E-12	8.3021E-05
94	2.9787E+27	2.2378E-21	5.8363E-12	3.8903E-05
95	8.7792E+26	1.3494E-21	1.4701E-11	1.7416E-05
96	2.4692E+26	8.137E-22	3.703E-11	7.4399E-06
97	6.6184E+25	4.9066E-22	9.3274E-11	3.029E-06
98	1.6884E+25	2.9587E-22	2.3495E-10	1.1736E-06
99	4.093E+24	1.7841E-22	5.9181E-10	4.3215E-07
100	9.4139E+23	1.0758E-22	1.4907E-09	1.5097E-07
101	2.0505E+23	6.4871E-23	3.7549E-09	4.9948E-08
102	4.2217E+22	3.9117E-23	9.4582E-09	1.5619E-08
103	8.1975E+21	2.3588E-23	2.3824E-08	4.6066E-09
104	1.4976E+21	1.4223E-23	6.0011E-08	1.2783E-09
105	2.5674E+20	8.5767E-24	1.5116E-07	3.3284E-10
106	4.1175E+19	5.1717E-24	3.8076E-07	8.108E-11
107	6.1569E+18	3.1185E-24	9.5909E-07	1.8415E-11
108	8.5513E+17	1.8805E-24	2.4158E-06	3.8848E-12
109	1.0983E+17	1.1339E-24	6.0852E-06	7.5787E-13
110	1.298E+16	6.8376E-25	1.5328E-05	1.3604E-13
111	1.4033E+15	4.1231E-25	3.861E-05	2.2339E-14
112	1.3782E+14	2.4862E-25	9.7253E-05	3.3324E-15
113	1.2197E+13	1.4992E-25	0.00024497	4.4793E-16
114	9.6289E+11	9.0401E-26	0.00061706	5.3712E-17
115	6.6984E+10	5.4512E-26	0.0015543	5.6754E-18
116	4042116078	3.2871E-26	0.0039151	5.2019E-19
117	207288004	1.9821E-26	0.00986172	4.0518E-20
118	8783390	1.1952E-26	0.0248406	2.6078E-21
119	295240	7.2071E-27	0.06257077	1.3314E-22
120	7381	4.3459E-27	0.157609	5.0556E-24
121	122	2.6206E-27	0.397	1.2692E-25
122	1	1.5802E-27	1	1.5802E-27
				0.03164562

15. $p = \frac{\sum_{i=1}^{n-1} \sum_{j=1+i}^{n} k_{ij}}{\frac{n(n-1)}{2}}$ (from class notes)

$$\frac{\frac{1+4+2+5+6+10}{900}}{\frac{4(3)}{2}} = \frac{0.0311}{6} = 0.0052$$