Answers to Problems

Chapter 1

1.1 ¼ A_1A_1: ½ A_1A_2: ¼ A_2A_2.

1.2 1/16 $A_1A_1B_1B_1$: 1/8 $A_1A_1B_1B_2$: 1/16 $A_1A_1B_2B_2$: 1/8 $A_1A_2B_1B_1$: ¼ $A_1A_2B_1B_2$: 1/8 $A_1A_2B_2B_2$: 1/16 $A_2A_2B_1B_1$: 1/8 $A_2A_2B_1B_2$: 1/16 $A_2A_2B_2B_2$.

1.3 The two loci are located on different chromosomes.

1.4 Complementary DNA ATG AAA CCC TAA

Coding DNA strand TAC TTT GGG ATT

mRNA AUG AAA CCC UAA

tRNA anticodon UAC UUU GGG AUU

Amino acids met lys pro stop (note that the code is read from mRNA)

1.5 Expected numbers are 65 males and 65 females. χ^2 = 6.92, d.f. = 1, probability = 0.0085. Since the probability < 0.05, this represents a significant deviation from the 1:1 expectation.

1.6 Possible families: 4 females: 3 females and 1 male: 2 females and 2 males: 1 female and 3 males: and 4 males, with probabilities of 1/16: ¼: 3/8: ¼: 1/16, respectively.

1.7 The expected numbers are 90: 30: 30: 10, χ^2 = 7.778, d.f. = 3, probability = 0.051. Thus the observed numbers do not differ from the expectations.

1.8 Mean = 1.556 offspring and Standard deviation = 1.13.

1.9 IUCN category Critically endangered under D: number of mature individuals < 50 adults.

1.10 IUCN category Vulnerable under category A: numbers dropped by 90% in 30 years, or ~ 30% in 10 years.

1.11 IUCN category Extinct.

1.12 IUCN category Endangered; A decline of 5% per years i.e. ~ 50% in 10 years.

Chapter 2

2.1 Inbreeding is the production of offspring from individuals that are related by descent.

2.2 Inbreeding reduces offspring numbers and survival (inbreeding depression) in essentially all well-studied naturally outbreeding species (and in most inbreeding species as well) and consequently increases extinction risk.

2.3 The association in bighorn sheep could be due to demographic stochasticity (fluctuations), environmental stochasticity, catastrophes, inbreeding depression, loss of genetic diversity or to combinations of these. Spread of disease from domestic sheep (environmental stochasticity, or a catastrophe, depending upon severity) and inbreeding depression were favoured by the author.

2.4 Reproductive fitness is the number of offspring produced by an individual that survives to sexual maturity. Components in animals include adult survival, mating ability, male sperm viability, competitiveness and fertilizing ability, zygote survival to sexual maturity and zygote fertility. Components in plants include adult survival, pollen production, ability of pollen to disperse to stamen, pollen ability to fertilize, zygote viability, seed ability to grow into a plant and survive to flowering and its fertility.

Chapter 3

3.1 Genetic diversity is required for species to evolve to cope with environmental change. Further, loss of genetic diversity is associated with inbreeding and this reduces reproduction and survival rates.

3.2 Electrophoresis separates proteins according to their charge. Some DNA base differences results in different amino acids in proteins. Some amino acids are basic, some neutral and some acidic. Thus, some of the amino acid differences result in charge differences that are detectable by electrophoresis.

3.3 Microsatellites are short tandem repeats in DNA that are often highly variable e.g. $[AC]_{10}$ versus $[AC]_{12}$.

3.4 Amplified fragment length polymorphism. Genomic DNA is cut with a restriction enzyme, specific DNA bases (adaptors) added, and the DNA amplified using primers that are

complementary to the adaptor sequences. Polymorphism is detected as presence, or absence of DNA fragments.

3.5 Randomly amplified polymorphic DNA. Short synthetic DNA primer sequences (often 10 bases in length) are used to prime DNA amplification. Polymorphisms are detected as the presence, or absence of fragments.

3.6 A DNA fingerprint is a bar-code like banding pattern that is revealed by cutting DNA with a restriction enzyme and probing with a repeat sequence that occurs in variable numbers at multiple sites throughout the genome. The repeats are typically ~ 100 base pairs in length.

3.7 Microsatellites, RAPD, and AFLP. Further, any locus for which primers can be designed (including mtDNA) can be amplified and typed by sequencing, SSCP, or by cutting with restriction enzymes.

3.8 Evolutionary potential depends primarily on quantitative genetic variation for reproductive fitness characters.

3.9 Levels of genetic diversity for allozymes are significantly lower in vertebrates than in invertebrates or plants.

3.10 Endangered species, on average have lower levels of genetic diversity than taxonomically related non-endangered species.

Chapter 4

4.1 $p_M = 0.913$, $q_N = 0.087$

4.2 The Hardy-Weinberg equilibrium expected frequencies are 0.8336, 0.1589 and 0.0076, and the expected numbers (expected frequencies x total numbers) are 474.3, 90.4 and 4.3. $\chi^2 = 0.137$, d.f. = 1 (3 – 1 for total – 1 for using allele frequency), so probability is 0.71. Thus, the deviation from expectations is not significant.

4.3 $f_{85} = 0.193$, $f_{91} = 0.648$, $f_{93} = 0.023$, $f_{95} = 0.136$, and sum = 1.0.

4.4 Observed heterozygosity = $(\underline{13 + 2 + 12}) = 0.614$.

4.5 The expected frequencies of the 6 genotypes are as follows:

	Genotypes						
	91/91	91/95	91/97	95/95	95/97	97/97	Total
Expected freq.	f_{91}^2	$2f_{91}f_{95}$	$2f_{91}f_{97}$	f_{95}^2	$2f_{95}f_{97}$	f_{97}^2	1
	$.364^2$	2x.364x.352	2x.364x.284	$.352^2$	2x.352x.284	$.284^2$	1
	0.1325	0.2563	0.2068	0.1239	0.1999	0.0807	1.0001
Expected #	5.83	11.28	9.10	5.45	8.80	3.55	44.01
Observed #	7	10	8	5	11	3	44

χ^2 = 1.185, d.f. = 6 – 1 – 2 = 3, probability = 0.76. Thus, the observed numbers do not differ significantly from Hardy-Weinberg expectations.

4.6	FFF	FFS	FSS	SSS	Total
Expected freq.	0.6^3	$3x0.6^2x0.4$	$3x0.6x0.4^2$	0.4^3	1
	0.216	0.432	0.288	0.064	1

4.7 Expected frequency of AA x OO mating = 2 x f(AA) x f(OO) = 2 x 0.09 x 0.36 = 0.0648.

4.8	MM	MN	NN	Total
#	406	744	332	1482
Frequencies	0.274	0.502	0.224	1.0

Mating	Obs	Expected numbers
MM x MM	58	0.274^2 x741 = 55.63
MM x MN	202	2x0.274x0.502x741 = 203.85
MM x NN	88	2x0.274x0.224x741 = 90.96

MN x MN	190	0.502^2x741	= 186.73
MN x NN	162	2x0.502x0.224x741	= 166.65
NN x NN	41	0.224^2x741	= 37.18
Total	741		= 741.00

χ^2 = 0.794, d.f. = 6 – 1 – 2 = 3, probability = 0.85. Thus, the observed numbers do not differ significantly from those expected under random mating.

4.9 $n_e = \frac{1}{(0.73^2 + 0.27^2)} = 1.65.$

4.10 Proportion of nucleotides polymorphic p_n = 30/2379 = 0.0126.

Nucleotide diversity π = sum of 15 proportions of nucleotide differences/15 = 0.0837/15 = 0.0058

Haplotype diversity $h = = 1 - \Sigma f_i^2 = 1 - 6x(1/6)^2 = 0.833$.

4.11 q^2 = 4/100 = 0.04, thus, $q = \sqrt{0.04} = 0.20$.

4.12 $D = ru - st$ = 0.2x0.1 – 0.5x0.2 = - 0.08.

To obtain the gametic frequencies at equilibrium, we must first obtain the allele frequencies at the 2 loci. These are f_{A1} = 0.5 + 0.2 = 0.7, f_{A2} = 0.3, f_{B1} = 0.4, and f_{B2} = 0.6.

	A_1B_1	A_1B_2	A_2B_1	A_2B_2	Total
Equilibrium freq.	$f_{A1}f_{B1}$	$f_{A1}f_{B2}$	$f_{A2}f_{B1}$	$f_{A2}f_{B2}$	1
	0.7x0.4	0.7x0.6	0.3x0.4	0.3x0.6	1
	0.28	0.42	0.12	0.18	1

$D_{20} = D_0 (1 - c)^t$ = 0.2 x $(1 - 0.05)^{20}$ = 0.0717.

Chapter 5

5.1 Parent mean = 19.971, Offspring mean = 19.229, Parent variance = 0.750, Offspring variance = 1.288, covariance = 0.608.

5.2 Regression equation is Offspring shell length = 3.03 + 0.811 Parent shell length. Thus, the heritability of shell length is 0.811.

5.3 Offspring mean = 6.0, Parent mean = 6.0, Covariance = 5.6/6 = 0.933, Parental variance = 28/6 = 4.667, and regression = 0.933/4.667 = 0.20. Thus the heritability is 0.20

5.4 $h^2 = 2 \times 0.27 = 0.54$.

5.5

A_1A_1	A_1A_2	A_2A_2
a	a	$-a$

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5.6 First we must compute the mean $X = p^2xa + 2pqx0 - q^2xa = p^2a - q^2a = a(p^2 - q^2)$

$= a(p - q)(p + q) = a(p - q)$, as $p + q = 1$.

The genotypic variance is computed as

$$V_A = \frac{\sum f_i (X_i - \bar{X})^2}{\sum f_i} = \frac{p^2[a - a(p-q)]^2 + 2pqx[0 - a(p-q)]^2 + q^2[(-a - a(p-q)]^2}{p^2 + 2pq + q^2}$$

$$= \frac{a^2[p^2(1 - p + q)^2 + 2pq(p-q)^2 + q^2(-1 - p + q)^2}{1} = \frac{a^2[p^2(2q)^2 + 2pq(p-q)^2 + q^2(-2p)^2}{1}$$

$$= a^2(4p^2q^2 + 2p^3q - 4p^2q^2 + 2pq^3 + 4p^2q^2) = 2pqa^2(p^2 + 2pq + q^2) = 2pqa^2$$

5.7 V_A will increase by 10% as it is directly related to $2pq$, while the heritability will increases by less than 10% as V_A is both the numerator and present in the denominator. V_D will increase by 21%, as it depends upon $(2pq)^2$.

5.8 V_A will drop by 50%, h^2 will drop by < 50% and V_D will drop by 75%.

5.9 $S = 8 - 10 = -2$.

5.10 $S = 410 - 450 = -40$g. $R = S\,h^2 = -40 \times 0.35 = -14$g.

5.11 $S = 9.96 - 9.42 = 0.54$mm. $R = 0.54 \times 0.73 = 0.39$mm.

Chapter 6

6.1 Natural selection – differential reproduction and survival of diverse genotypes.

6.2 Divide all survival values by 90 to obtain the following relative fitnesses:

A_1A_1	A_1A_2	A_2A_2
1	$1 - hs$	$1 - s$
1	0.978	0.444

Thus, $s = 1 - 0.444 = 0.556$ and $hs = 1 - 0.978 = 0.022$.

6.3 $q_1 = 0.127$, $q_2 = 0.112$ and $q_3 = 0.101$.

6.4 $t = \frac{1}{q_t} - \frac{1}{q_0} = \frac{1}{0.001} - \frac{1}{0.17} = 994$ generations.

6.5

	Genotypes			
	AA	Aa	aa	Total
Genotype frequencies at fertilization	0.09	0.42	0.49	1.0

Relative fitnesses	1	1	0.9	
After selection	0.09	0.42	0.441	0.951
Adjust so total is 1	0.095	0.442	.464	1.001

New frequency of A = $p_1 = \frac{[(2 \times 0.095) + 0.442]}{2} = 0.316$

Change in frequency $\Delta p = p_1 - p_0 = 0.316 - 0.300 = 0.016$

6.6

	Genotypes			
	AA	Aa	aa	Total
Genotype frequencies at fertilization	p^2	$2pq$	q^2	1.0
Relative fitnesses	1	$1 - s/2$	$1 - s$	
After selection	p^2	$2pq(1 - s/2)$	$q^2(1 - s)$	$1 - spq - sq^2 = 1 - sq$
Adjust so total is 1	$\frac{p^2}{1 - sq}$	$\frac{2pq(1 - s/2)}{1 - sq}$	$\frac{q^2(1 - s)}{1 - sq}$	

New frequency of A = $p_1 = \frac{p^2 + pq(1 - s/2)}{1 - sq} = \frac{p^2 + pq - \frac{1}{2}spq}{1 - sq} = \frac{p - \frac{1}{2}spq}{1 - sq}$

Change in frequency $\Delta p = p_1 - p_0 = \frac{p - \frac{1}{2}spq}{1 - sq} - p = \frac{p - \frac{1}{2}spq - p(1 - sq)}{1 - sq}$

$= \frac{p - p - \frac{1}{2}spq + spq}{1 - sq} = \frac{\frac{1}{2}spq}{1 - sq}$

6.7 Use equations from Table 6.2 with $p = 0.1$, $q = 0.9$, $s = 0.1$ and $h = 0.02 / 0.1 = 0.2$

(a) $\Delta q = \frac{-\frac{1}{2} spq}{(1 - sq)} = \frac{-0.5 \times 0.1 \times 0.1 \times 0.9}{(1 - 0.1 \times 0.9)} = -0.0049$

(b) $\Delta q = \frac{-spq^2}{(1 - sq^2)} = \frac{-0.1 \times 0.1 \times 0.9^2}{(1 - 0.1 \times 0.9^2)} = -0.0088$

(c) $\Delta q = \frac{-sp^2q}{[1 - s(1 - p^2)]} = \frac{-0.1 \times 0.1^2 \times 0.9}{[1 - .1\,(1 - .1^2)]} = -0.0010$

(in this case p and q must be reversed in the equation in Table 6.2, case c.

(d) $\Delta q = \frac{-spq\,[q + h\,(p - q)]}{(1 - 2hspq - sq^2)} = \frac{-0.1 \times 0.1 \times 0.9\,[0.9 + 0.2\,(0.1 - 0.9)]}{(1 - 2 \times 0.2 \times 0.1 \times 0.1 \times 0.9 - 0.1 \times 0.9^2)} = -0.0073$

Chapter 7

7.1 The allele will increase in frequency by $up = 0.9 \times 10^{-4} = 0.00009$.

7.2 The equilibrium frequency is given by $\hat{q} = \frac{u}{(u + v)} = \frac{10^{-5}}{(10^{-5} + 10^{-6})} = 0.909$.

7.3 $t = \frac{\ln p_0 - \ln p_t}{u} = \frac{\ln 1 - \ln 0.6}{4 \times 10^{-6}} = 127{,}706$ generations.

7.4 $\hat{q} = \sqrt{\frac{u}{s}} = \sqrt{\frac{2 \times 10^{-5}}{1}} = 4.5 \times 10^{-3}$

This is far lower than the observed frequency of 17%.

7.5 The mutation rate is estimated by rearranging equation 7.4 and substituting, as follows:

$u = sq^2 = 1 \times 0.17^2 = 0.0289$

This is unrealistic as it is about 1,000 times higher than typical mutation rates. Consequently, the chondrodystrophy allele is unlikely to be in mutation-selection equilibrium. Its high frequency is probably due to chance changes associated with the population bottleneck experience by the California condor (see Chapter 8).

7.6 $\Delta q = \Delta q_{mutation} + \Delta q_{selection} = up - \frac{½spq}{(1 - sq)} \sim up - ½spq$

(the denominator of the selection term ~ 1 for a rare allele)

At equilibrium $\Delta q = up - ½spq = 0$

$\therefore ½spq = up$

$\hat{}$

so $q = \frac{2u}{s}$

7.7 The frequency of affected individuals (Dd + DD) is 10/94,000, so

$2pq + q^2 = 10/94{,}000 = 1 - p^2$

thus $p = 0.999947$, so $q = 5.3 \times 10^{-5}$.

The relative fitness is 20%, so $1 - s = 0.2$, and $s = 0.8$.

The mutation-selection equilibrium for an autosomal dominant is:

$\hat{}$

$q = \frac{u}{s}$

Thus the mutation rate u is

$u = sq = 0.8 \times 5.3 \times 10^{-5} = 4.24 \times 10^{-5}$

7.7 For loci with $s = 0.1$ and $u = 10^{-5}$, the equilibrium frequencies with different modes of inheritance are as follows:

Recessive autosomal $\hat{q} = 10^{-2}$

Autosomal additive $\hat{q} = 2 \times 10^{-4}$

Autosomal dominant $\hat{q} = 10^{-4}$

Sex-linked recessive $\hat{q} = 3 \times 10^{-4}$

Haploid $\hat{q} = 10^{-4}$

Thus, the equilibrium frequencies are usually greater for diploids than haploids (most mutations are recessive, or partial recessives), and greater for recessive than for dominants.

7.9 By rearranging equation 7.5, we obtain:

$$m = \frac{q_1 - q_0}{q_m - q_0}$$

The data supplied is $q_0 = 0.000$ (Africans), $q_m = 0.422$ (US Causcaians) and $q_1 = 0.045$ (US African Americans).Thus,

$$m = \frac{0.045 - 0}{0.422 - 0} = 0.11$$

Chapter 8

8.1 This is the probability of 3 A_2A_2 offspring = $(¼)^3$ = 1/64.

8.2 The expected offspring are ¼ A_1A_1: ¼ A_1A_2: ¼ A_1A_3: ¼ A_2A_3. Thus the probability that 4 individuals do not contain A_1 is the probability of 4 A_2A_3 offspring = $(¼)^4$ = 1/256. The probability that A_2 is absent from the 4 offspring = $(½)^4$ = 1/16, and the probability that A_3 is absent in the 4 offspring is also 1/16.

8.3 The probability that an individual does not contain A_2 is 0.9^2. (a) Thus, the probability that 12 individuals do not contain A_2 = 0.9^{24} = 0.080. (b) The probability that 100 individuals do not contain A_2 is 0.9^{200} = 7 x 10^{-10}. The chance of losing an allele is greater in a small than in a large population.

8.4 The probability that an offspring does not have the A_1 allele is ½, and the probability that *n* offspring do not have it is $(½)^n$. To be 95% certain that the allele is retained, we set this equal to 0.05 and solve for n i.e. $(½)^n$ = 0.05, so *n* = log (0.05)/log (0.5) = 4.3 i.e. about 5 individuals.

8.5 Proportion of heterozygosity retained is 1 – 1 / (2*N*), so (a) ½, (b) 0.9, (c) 0.964, (d) 0.993, (e) 0.9999983.

8.6 The probability that an allele with a frequency of *q* is lost following a single generation bottleneck is $(1 – q)^{2N}$. Thus, (a) 0.9^2 = 0.81, (b) 0.656, (c) 2.66 x 10^{-5}, (d) 0.077.

Chapter 9

9.1 $H_e = \frac{4N_eu}{(4N_eu + 1)} = \frac{4 \times 20 \times 10^{-7}}{(4 \times 20 \times 10^{-7} + 1)} = 0.000008$

$n_e = 4N_eu + 1 = 1.000008$

9.2 p_A = 0.802 and q_S = 0.198, respectively. The observed and Hardy-Weinberg expected numbers are as follows:

	AA	AS	SS	Totals

Observed	400	249	5	654
Expected	420.7	207.7	25.6	654

The deviation from Hardy-Weinberg expectations in adults is significant ($\chi^2 = 25.8$, d.f. = 1, $P < 0.0001$). Thus, there is an excess of heterozygotes and a deficiency of homozygotes. The frequencies of the A and S alleles in infants are 0.814 and 0.186, respectively. The equivalent test for deviation from Hardy-Weinberg expectation in infants is non-significant ($\chi^2 = 0.14$, d.f. = 1, $P = 0.71$).

9.3 $s_1 = 0.01$ and $s_2 = 0.03$. Thus, the equilibrium frequency of A_2, q is

$$\hat{q} = \frac{s_1}{(s_1 + s_2)} = \frac{0.01}{(0.01 + 0.03)} = 0.25$$

9.4

	RR	RS	SS
Survival	0.3	0.8	0.56
Relative fitness	0.375	1.0	0.70
	$1 - s_1$	1	$1 - s_2$

Thus, $s_1 = 0.625$ and $s_2 = 0.30$, and the equilibrium frequency for the R allele (p) is

$$\hat{p} = \frac{s_2}{(s_1 + s_2)} = \frac{0.3}{(0.625 + 0.3)} = 0.324.$$

9.5 The selection coefficients s_1 and s_2 are 0.3 and 0.1. Thus, the equilibrium frequency q for the A_2 allele in all populations is

$$\hat{q} = \frac{s_1}{(s_1 + s_2)} = \frac{0.3}{(0.3 + 0.1)} = 0.75$$

9.6

	A_1A_1	A_1A_1	A_1A_1	Total

Zygotic freq.	p^2	$2pq$	q^2	1
Relative fitnesses	$1 - s_1$	1	$1 - s_2$	
After selection	$p^2(1 - s_1)$	$2pq$	$q^2(1 - s_2)$	$1 - s_1p^2 - s_2q^2$
Adjusted	$\frac{p^2(1 - s_1)}{1 - s_1p^2 - s_2q^2}$	$\frac{2pq}{1 - s_1p^2 - s_2q^2}$	$\frac{q^2(1 - s_2)}{1 - s_1p^2 - s_2q^2}$	1

New frequency of A_1 $p_1 = \frac{p^2(1 - s_1) + pq}{1 - s_1p^2 - s_2q^2} = \frac{p - s_1p^2}{1 - s_1p^2 - s_2q^2}$

$$\Delta p = \frac{p - s_1p^2}{1 - s_1p^2 - s_2q^2} - p = \frac{p - s_1p^2 - p(1 - s_1p^2 - s_2q^2)}{1 - s_1p^2 - s_2q^2} = \frac{p - s_1p^2 - p + s_1p^3 + s_2pq^2}{1 - s_1p^2 - s_2q^2}$$

$$= \frac{pq(s_2q - s_1p)}{1 - s_1p^2 - s_2q^2}$$

At equilibrium, $\Delta p = 0$.

This occurs when $s_1p = s_2q$

Thus, the equilibrium frequency for A_2 is

$$\hat{q} = \frac{s_1}{(s_1 + s_2)}.$$

9.7 The relative fitnesses of the 3 pollen alleles are determined as follows:

		Offspring		
Female parent	Pollen	S_1S_2	S_1S_3	S_2S_3
1/3 S_1S_2	S_3	-	1/6	1/6
1/3 S_1S_3	S_2	1/6	-	1/6

1/3 S_2S_3	S_1	1/6	1/6	-

This assumes that there is sufficient pollen to fertilise all plants. After reproduction, the 3 pollen alleles have made the same contributions to the progeny, $S_1 = S_2 = S_3 = 1/3$, so their fitnesses are:

Fitness S_1 = freq. now / freq. before = $\frac{(1/3)}{(1/6)} = 2$

Fitness $S_2 = \frac{(1/3)}{(1/3)} = 1$

Fitness $S_3 = \frac{(1/3)}{(1/2)} = 2/3$

Consequently, their relative fitnesses (obtained by dividing by the highest fitness of 2) are $S_1 = 1$, $S_2 = 1/2$ and $S_3 = 1/3$. Thus, the rarest allele has the highest relative fitness and the most common the lowest fitness.

9.8 The relative fitnesses of the pollen alleles are determined as shown below:

Female	Pollen	Offspring					
Parent		S_1S_2	S_1S_3	S_2S_3	S_1S_4	S_2S_4	S_3S_4
1/3 S_1S_2	.97 S_3	-	.1617	.1617			
	.03 S_4				.005	.005	
1/3 S_1S_3	.97 S_2	.1617	-	.1617			
	.03 S_4				.005		.005
1/3 S_2S_3	.97 S_1	.1617	.1617	-			
	.03 S_4					.005	.005
Totals		.3234	.3234	.3234	0.01	0.01	0.01

The contributions of the 4 pollen alleles to the progeny are 0.3234 A_1, 0.3234 A_2, 0.3234 A_3, and 0.03 A_4. If we compare these contributions to their frequencies in the pollen to obtain their fitnesses, we obtain

$$\text{Fitness } S_1 = \frac{0.3234}{0.33} = 0.98$$

$$\text{Fitness } S_2 = \frac{0.3234}{0.33} = 0.98$$

$$\text{Fitness } S_3 = \frac{0.3234}{0.33} = 0.98$$

$$\text{Fitness } S_4 = \frac{0.03}{0.01} = 3$$

Thus the relative fitnesses of the 4 pollen alleles, S_1, S_2, S_3 and S_4 are 0.33, 0.33, 0.33 and 1, respectively i.e. the new S_4 allele has a much higher fitness than the existing alleles and will increase in frequency.

9.9 Selective neutrality occurs approximately when $s < 1/2N$, so an allele with a selection coefficient of 0.02 is effectively neutral when $N < \frac{1}{(2 \times 0.02)}$ i.e. when $N < 25$.

Chapter 10

10.1 A genome is the entire DNA (or all the chromosomes) in species.

10.2 A genome enabled species is one that has not been sequenced, but is taxonomically closely related to a sequenced species.

10.3 A microarray is a slide with spots of many short DNA sequences, suitable for either genotyping many loci, or measuring gene expression at many loci.

10.4 Micro RNAs are short noncoding RNAs, found in many plants and animals, that often inhibit gene expression post-transcriptionally.

10.5 The transcriptome is the array of transcripts from the genome.

10.6 (a) Heterozygote advantage can lead to greater than expected retention of genetic diversity at nearby loci (as for the MHC). (b) Directional selection driving an initially rare allele to fixation will often result in a selective sweep, reducing genetic diversity in surrounding DNA. (c) Background selection against new deleterious mutations slightly reduces genetic variation in surrounding DNA, compared to neutral expectations.

10.7 The ratio of nonsynonymous to synonymous polymorphic sites is 76/49 = 1.55, is indicative of strong balancing selection (this ratio is typically << 1 for neutral loci). The complete lack of fixed differences between the two species indicates close linkage to sites subject to balancing selection.

Chapter 11

11.1 (a) $\frac{H_t}{H_0} = \left(1 - \frac{1}{2N_e}\right)^t = \left(1 - \frac{1}{2x60}\right)^{100/20} = 0.959.$

(b) $\frac{H_t}{H_0} = \left(1 - \frac{1}{20}\right)^5 = (19)^5 = 0.774.$

11.2 (a) $\frac{H_t}{H_0} = 0.5 \sim e^{-t / 2Ne}$, then take natural logarithms of both sides, yielding

$$\ln (0.5) = \frac{-t}{2N_e}$$

Thus,

$$t = -2 \ln (0.5) N_e = 1.4 N_e$$

(b) Set $e^{-t / 2Ne} = 0.05$, and then take ln of both sides, and rearrange yielding

t = - 2 ln (0.05) N_e = 6 N_e

11.3 $\frac{H_t}{H_0} = \prod_{i=1}^{n}(1 - \frac{1}{2N}) = (1 - \frac{1}{2\text{x}100})(1 - \frac{1}{2\text{x}10})(1 - \frac{1}{2\text{x}100})(1 - \frac{1}{2\text{x}200})$

= 0.938

The second case is identical to the first, as the same terms enter the equation, but in a different order.

11.4 $N_e = \frac{t}{\Sigma[1/N_i]} = \frac{4}{\Sigma(1/10 + 1/100 + 1/1000 + 1/250)} = 34.8$

11.5 $N_e = (4N - 2) / (V_k + 2)$. The mean family size = (0 + 1 + 2 + 5)/4 = 2 i.e a stable population. The variance in family size V_k is given as follows:

$$V_k = \frac{1}{N}\Sigma(k - \bar{k})^2 = \frac{[(0-2)^2 + (1-2)^2 + (2-2)^2 + (5-2)^2]}{4} = \frac{14}{4} = 3.5$$

(There is a complete census of the population, so that n replaces n - 1 in the equation for the variance).

Since there are 4 families, N = 8. Thus,

$$N_e = \frac{(4 \text{ x } 8 - 2)}{(3.5 + 2)} = 5.45.$$

This is only 68% of the population size of 8 potentially reproductive individuals.

11.6 $N_e = \frac{4N_{ef}N_{em}}{(N_{ef} + N_{em})} = \frac{4 \times 605 \times 6}{(605 + 6)} = 23.8$

If the population had a "normal" sex-ratio, N_e = 605.7, ~ 25 times higher.

11.7 The population size is not stable ($k \neq 1$), so we have to use equation 11.5.

For females:

$$N_{ef} = \frac{(Nk - 1)}{[k - 1 + (V_k / k)]} = \frac{(80 \times 2.09 - 1)}{[2.09 - 1 + (16.61 / 2.09)]} = 18.4$$

Thus, for males

$$N_{em} = \frac{(Nk - 1)}{[k - 1 + (V_k / k)]} = \frac{(60 \times 2.46 - 1)}{[2.46 - 1 + (22.5 / 2.46)]} = \frac{146.6}{10.606} = 13.8$$

Finally, we combine these two estimates

$$N_e = \frac{4\ N_{ef}N_{em}}{(N_{ef} + N_{em})} = \frac{4 \times 18.4 \times 13.8}{(18.4 + 13.8)} = 31.5$$

Thus the effective population size is ~ 23% of the actual population size.

11.8 $\frac{H_t}{H_0} = 0.43 = e^{-t/2Ne} = e^{-17/2Ne}$

Take ln of both sides, and rearranging yields

$$N_e = \frac{-17}{} = 10$$

2 ln (0.43)

11.9 We multiply mutation rate per year by generation length (24 years) to obtain the neutral mutation rate per generation $u = 24 \times 1.5 \times 10^{-8} = 3.6 \times 10^{-7}$. By substituting into equation 11.9

$$N_{ef} = \Theta = \frac{0.0216}{2u} = \frac{0.0216}{2 \times 3.6 \times 10^{-7}} = 30{,}000$$

11.10 Time for all alleles in a population to coalescence is approximately

$$4N_e [1 - (1/k)] = 4N_e [1 - (1/4)] = 3N_e \text{ generations}$$

i.e. 150 generations for $N_e = 50$, and 30 generations for $N_e = 10$.

Chapter 12

12.1 $F = ¼$.

12.2 $F = 1 - (1 - \frac{1}{2N_e})^t = 1 - (1 - \frac{1}{10})^{10} = 0.65$.

12.3 $F = 1 - \prod_{i=1}^{t}(1 - \frac{1}{2N_e}) = 1 - (1 - \frac{1}{4})(1 - \frac{1}{200})(1 - \frac{1}{4})(1 - \frac{1}{200}) = 0.44$.

12.4 Using $p = 0.83$, $q = 0.17$ and $F = 0.5$, the expected genotype frequencies with selfing are:

f (++) $= p^2 + Fpq = 0.83^2 + 0.5 \times 0.83 \times 0.17 = 0.76$

f (+dw) $= 2pq(1 - F) = 2 \times 0.83 \times 0.17 \ (1 - 0.5) = 0.14$

f (dwdw) $= q^2 + Fpq = 0.17^2 + 0.5 \times 0.83 \times 0.17 = 0.10$

These sum to 1.0, as they should.

12.5. $q = 0.01$, so $p = 0.99$.

(a) Full-sib mating ($F = 0.25$), Ratio $= 1 + \frac{Fp}{} = 1 + \frac{0.25 \times 0.99}{} = 25.75$.

q 0.01

(b) For single first cousin mating (F = 1/16), Ratio = $1 + \frac{0.99}{16 \times 0.01} = 7.19$.

12.6 $F_t = ¼ (1 + 2 F_{t-1} + F_{t-2})$. Thus, the inbreeding coefficients for the first 5 generations of full-sib mating are 0.25, 0.375, 0.50, 0.594, and 0.672, respectively.

12.7 $2pq(1 – F) = 2 \times 0.4 \times 0.6 (1 – 0.47) = 0.254$.

12.8 $F_e = 1 – H_I / H_M = 1 – (0.36/0.792) = 0.545$.

12.9 $F_X = \Sigma(½)^n(1 + F_{ca})$. The paths are

Path	n	F_{ca}	Contribution to F_X
IE**A**GJ	5	0	$(½)^5$
IE**B**GJ	5	0	$(½)^5$
IF**C**HJ	5	0	$(½)^5$
IF**D**HJ	5	0	$(½)^5$

Thus, F_X = 1/8

12.10 $F_X = \Sigma(½)^n(1 + F_{ca})$. Parents L and M have G, C, A and B as common ancestors. The paths and their contributions to F are as follows:

Path	n	F_{ca}	Contribution to F_X
LIFC**A**DGJM	9	0	$(½)^9$
LIGD**B**EHKM	9	0	$(½)^9$
LIGD**B**EJM	8	0	$(½)^8$
LIF**C**GJM	7	0	$(½)^7$
LI**G**JM	5	1/8	$(½)^5(1 + 1/8)$

$F_X = 26/512 = 0.0508$

12.11 Individuals A, B, D, E, G and I are common ancestors causing relationships between parents I and L. The 11 paths of relationship, the number of paths joining parents through

common ancestors (n), the inbreeding coefficients of common ancestors, and the contribution of each of the paths to the inbreeding coefficient F_X (rounded to four decimal places), are shown in the table. A, B and E are all assumed to be unrelated.

Individual I is the results of an inbred mating; there are 3 common ancestors of it parents F and G, A, B and D. The 3 paths to consider are

FC**A**DG, contributing $(½)^5$ to the inbreeding coefficient of I (F_I)

FC**B**DG, contributing $(½)^5$ to F_I, and

F**D**G, contributing $(½)^3$ to F_I

Thus, $F_I = (½)^5 + (½)^5 + (½)^3 = 3/16$

Paths of relationship (common ancestors are underlined)	*n*	F_{ca}	Contribution to F_X
IFC**A**DHJKL	9	0	$(½)^9$
IFC**A**DGJKL	9	0	$(½)^9$
IFC**B**DHJKL	9	0	$(½)^9$
IFC**B**DGJKL	9	0	$(½)^9$
IF**D**HJKL	7	0	$(½)^7$
IF**D**GJKL	7	0	$(½)^7$
IG**D**HJKL	7	0	$(½)^7$
IG**E**HJKL	7	0	$(½)^7$
I**G**JKL	5	0	$(½)^5$

IKL	3	3/16	$(½)^3$ (1 + 3/16)
IL	2	3/16	$(½)^2$ (1 + 3/16)
		F_x = 264/512 = 0.515625	

12.12 Pr (homozygosity for a rare recessive lethal at one locus) = $q^2 + Fpq \sim Fq$

= 0.5 x 5 x 10^{-4} = 2.5 x 10^{-4}.

Pr (not homozygous lethal at one locus) = 1 – Fq = 1 – 2.5 x 10^{-4}

Pr (not homozygous lethal at 2,000 loci) = $(1 - Fq)^{2,000}$ = $(1 - 2.5 \times 10^{-4})^{2,000}$ = 0.61.

Thus, Pr (individual is homozygous lethal for at least one locus) = 1 – 0.61 = 0.39.

By contrast, with random mating Pr (individual homozygous for lethal for at least 1 locus) = $1 - (1 - q^2)^{2000}$ = 5 x 10^{-4}

Chapter 13

13.1 $\Sigma 2pqdF$ i.e. number of loci polymorphic for deleterious alleles (Σ), heterozygosity for deleterious alleles ($2pq$), dominance of alleles (d), and inbreeding coefficient (F).

13.2 None, there are no heterozygotes and no hidden deleterious alleles.

13.3 Inbreeding depression = $2pqdF$. p = 0.9, q = 0.1, and F = 0.5. To compute inbreeding depression (ID) we require d.

(a) $d = 89 - (\underline{90 + 70}) = 9$.

2

Thus, ID = 2 x 0.9 x 0.1 x 9 x 0.5 = 0.81.

(b) $d = 90 - (\underline{80 + 70}) = 15$

2

Thus, ID = 2 x 0.9 x 0.1 x 15 x 0.5 = 1.35

(c) $d = 80 - \frac{(90 + 70)}{2} = 0$.

Thus $ID = 0$.

13.4 $\delta = 1 - \frac{\text{inbred fitness}}{\text{outbred fitness}} = 1 - \frac{0.45}{0.75} = 0.4$

(i.e. a 40% reduction in survival due to inbreeding).

13.5 The regression equation relating juvenile survival and F is $\ln S = -0.221 - 2.52 F$.

Thus (a) $LE_{haploid} = B = 2.52$. (b) $LE_{diploid} = 2B = 2 \times 2.52 = 5.04$.

13.6 Using equation 13.5 and Example 13.3, we can express the ratio of progeny production of

$\frac{\text{full-sibs}}{\text{unrelated}} = \frac{e^{-a-BF}}{e^{-a}} = e^{-BF} = 1 - 0.79 = 0.21$.

Upon substituting $F = 0.25$ we have $e^{-0.25B} = 0.21$

By taking natural logarithms (ln) and rearranging we obtain

$B = \frac{-\ln(0.21)}{0.25} = 6.24$

Thus, this population is exhibiting 6.24 haploid lethal equivalents for total fitness and 2 x 6.24 = 12.48 diploid lethal equivalents.

Chapter 14

14.1 The impacts of fragmentation depend upon the details of gene flow among population fragments. If gene flow among the fragments is less than about one effective migrant per generation, then population fragments will become inbred and lose genetic diversity at an accelerated rate (compared to a single large population) and are likely to suffer elevated extinction rates.

14.2 $\sigma_q^2 = 0.015$

14.3 $\sigma_q^2 = pq\,[1 - (1 - \frac{1}{2N_e})^t]$

(a) $\sigma_q^2 = 0.3 \times 0.7\,[1 - (1 - \frac{1}{2 \times 50})^{20}] = 0.038$

(b) $\sigma_q^2 = 0.3 \times 0.7\,[1 - (1 - \frac{1}{2 \times 50})^{100}] = 0.133$

14.4 $F_{ST} = \frac{1}{4N_e m + 1}$ (equation 14.7), so

$N_e m = \frac{(1 / F_{ST}) - 1}{4} = \frac{(1/0.2) - 1}{4} = 1$

14.5 (a) $H_I = \frac{(0.5 + 0.2)}{2} = 0.35$

$H_S = \frac{2p_1q_1 + 2p_2q_2}{2} = \frac{2 \times 0.5 \times 0.5 + 2 \times 0.5 \times 0.5}{2} = 0.5$

$H_T = 2pq$ (using combined allele frequencies) $= 2 \times 0.5 \times 0.5 = 0.5$

(b) $H_I = \frac{0.5 + 0.32}{2} = 0.41$

$H_S = \frac{2p_1q_1 + 2p_2q_2}{2} = \frac{2 \times 0.5 \times 0.5 + 2 \times 0.8 \times 0.2}{2} = 0.41$

2 2

$H_T = 2pq$ (using combined allele frequencies) = 2 x 0.35 x 0.65 = 0.455

(c) $H_I = \frac{0.5 + 0.13}{2} = 0.315$

$H_S = \frac{2p_1q_1 + 2p_2q_2}{2} = \frac{2 \times 0.5 \times 0.5 + 2 \times 0.2 \times 0.8}{2} = 0.41$

$H_T = 2pq$ (using combined allele frequencies) = 2 x 0.35 x 0.65 = 0.455

14.6 $F_{IS} = 1 - \frac{H_I}{H_S} = 1 - \frac{0.052}{0.074} = 0.30$

$F_{ST} = 1 - \frac{H_S}{H_T} = 1 - \frac{0.074}{0.098} = 0.24$

$F_{IT} = 1 - \frac{H_I}{H_T} = 1 - \frac{0.052}{0.098} = 0.47$

There is inbreeding within populations ($F_{IS} > 0$; probably as a result of selfing) and substantial differentiation among populations ($F_{ST} > 0$).

14.7 $H_I = \frac{(0.038 + 0.028 + 0.021)}{3} = 0.029$

$H_S = \frac{(0.061 + 0.045 + 0.033)}{3} = 0.046$

$F_{IS} = 1 - \frac{H_I}{H_S} = 1 - \frac{0.029}{0.046} = 0.37$

$F_{ST} = 1 - \frac{H_S}{H_T} = 1 - \frac{0.046}{0.053} = 0.13$

$F_{IT} = 1 - \frac{H_I}{H_T} = 1 - \frac{0.029}{0.053} = 0.45$

14.8 For the population of size 50, $F_{50} = 1 - (1 - \frac{1}{2N_e})^t = 1 - (\frac{99}{100})^{30} = 0.26$

For populations of size 25, $F_{25} = 1 - (\frac{49}{50})^{30} = 0.45$

Chapter 15

15.1 $N_e = \frac{V_A}{2\,V_m} = \frac{V_A}{2 \times 3 \times 10^{-3}\, V_E} = \frac{167\, h^2}{1 - h^2} = 29.$

15.2 Under these conditions, $V_m = 3 \times 10^{-4}\, V_E$, so $N_e = 294$.

15.3 Using equation 11.1: $\frac{H_t}{H_0} = (1 - \frac{1}{2N_e})^t \sim e^{-t / 2Ne}$

and substituting $\frac{H_t}{H_0} = 0.95$ and $t = \frac{100}{L}$ generations

$$0.95 \sim e^{-100/2LNe}$$

taking ln gives

$$\ln 0.95 = \frac{-100}{2LN_e}$$

$$\text{Thus } N_e = \frac{-100}{2\,L\,\ln(0.95)} = \frac{975}{L}$$

15.4 $N_e = \frac{475}{L} = \frac{475}{(1/3)} = 1425$

15.5 $N_e = \frac{475}{L} = \frac{475}{20} = 23.75$

15.6 (a) From 15.3, $N_e = \frac{975}{L}$ is required to retain 95% of genetic diversity for 100 years, thus,

for elephants

$$N_e = \frac{975}{26} = 37.5$$

and for deer mice $N_e = \frac{975}{(1/3)} = 2925$.

(b) To retain 90% of genetic diversity for 50 years, $\underline{H_t} = 0.90$ and $t = \underline{50}$

H_0 L

$0.90 \sim e^{-50 / 2LNe}$

taking ln and rearranging yields

$N_e = \frac{-50}{2L \ln 0.90} = \frac{237}{L}$

Thus, for elephants $N_e = \frac{237}{26} = 9.1$, and for deer mice $N_e = 237 \times 3 = 711$.

15.7 The recovery goal of 2 x 150 wild populations and 1 x 150 captive populations will not cause immediate additional genetic problems of rapid inbreeding depression. If the recover goal results in an N_e of about 300 x 0.1 + 150 x 0.3 ~ 75, then the rate of inbreeding per generation is only 0.0067. As the condor has a long generation interval, the increase in inbreeding per year will be slow. Given the prior history of small population size in the condor, it is already likely to have low evolutionary potential and modest inbreeding and thus, to be fragile to environmental change. N_e of 75 will not prevent further slow deterioration in genetic diversity and a slow increase in inbreeding.

Chapter 16

16.1 Taxonomic uncertainties may result in undiagnosed species being left to go extinct, species being hybridised to other species with deleterious consequences, resources being wasted on misdiagnosed populations belonging to common species, or hybrid populations that are not distinct species being conserved. Further, crosses of differentiated populations within species may result in outbreeding depression.

16.2 Two populations are sympatric if they share the same geographic location.

16.3 (a) Separate species as the distinct chromosome numbers indicate that they are not exchanging genes.

(b) They are not random mating, so they may be separate species. Information on additional loci would be desirable.

(c) As there are no alleles in common they are not exchanging genes, so they are likely to be separate species.

(d) Both populations share allele 1, so there may be gene flow. They probably belong to the same species, but more information is required to be certain as there is some degree of genetic differentiation.

16.4 Two populations are allopatric if they are found in the different geographic location.

16.5 (a) Separate species as they have distinctly different chromosome numbers.

(b) There are insufficient grounds to classify Sumatran tigers as a separate species, based on the biological species concept. The substantial isolation and the minor difference in mtDNA may be sufficient to classify them as a separate sub-species.

(c) Separate species, as they show extremely large genetic differences between the forms, well beyond the differences found for other 'good' species.

16.6 (a) $I_{xy} = \dfrac{\Sigma p_{ix} \, . \, p_{iy}}{(\Sigma p_{ix}^2 \, . \, \Sigma p_{iy}^2)^{1/2}} = \dfrac{(0.1^2 + 0.2^2 + 0.7^2)}{(0.1^2 + 0.2^2 + 0.7^2)^{1/2}} = 1$

$D = - \ln I_{xy} = - \ln (1) = 0$

(b) $I_{xy} = 0, \; D = \infty$

(c) $I_{xy} = \dfrac{(0.5 \times 0 + 0.5 \times 0.7 + 0.3 \times 0)}{[(0.5^2 + 0.5^2 + 0)(0 + 0.7^2 + 0.3^2)]^{1/2}} = \dfrac{0.35}{0.5385} = 0.65$

$D = -\ln(0.65) = 0.43$

16.7 $I_{VG} = \frac{(0.023 \times 0.981 + 0.977 \times 0.019 + 0.0 \times 0)}{[(0.023^2 + 0.977^2) \times (0.981^2 + 0.019^2)]^{1/2}} = \frac{0.041126}{(0.955058 \times 0.962722)^{1/2}}$.

$= 0.043$

$D = -\ln(0.043) = 3.15$

16.8 A and B are classified as

0 0 and so should be managed as a single unit.

0 0

Conversely, (A, B) versus C is classified as ** since they differ at microsatellite loci

**

(reject genetic exchangeability for both recent and historical times frames) and for heritable characters likely to be of ecological significance (reject ecological exchangeability for both recent and historical times frames). Consequently, C should be managed as a separate unit from A-B.

16.9 Outbreeding depression is a reduction in reproductive fitness that is sometimes observed in crosses between populations. It is of conservation concern, as it may increase the risk of population extinction. The risk of its occurrence is primarily determined by the magnitude of differential adaptation and the extent of this depends upon the forces of differential selection, extent of genetic diversity, effective population size, number of generations and reduction in gene flow.

Chapter 17

17.1 Introduce mainland individuals into the Barrow Island euro population. Females would probably have to be used as male aggression may make male introductions difficult.

17.2 Use the small population as it has a different genotype and so should alleviate inbreeding depression.

17.3 The best procedure would be to genotype all populations before deciding. If the population of concern and the large populations have the same genotypes, use the small population as it has more heterozygosity.

17.4 Introduce genetic material (e.g. pollen) from other populations. Since plants often show adaptive genetic differentiation, this should be done using nearby populations, but ones with distinct SI locus alleles. Check the chromosomes to ensure all populations have the same ploidy before allowing any pollen flow.

17.5 Move individuals among the population fragments, such that $N_e m$ is greater than 1 i.e move about 1-5 individuals among populations each generation on average.

17.6 Snail, as it is likely to have the lowest rate of gene flow.

17.7 The average size of mature trees is likely to decline, as the harvest results in selection for smaller sized trees.

17.8 As this species is an asexual clone, management should aim to minimise threats from demographic and environmental stochasticity and catastrophes by increasing the population size and having replicate populations in different locations.

17.9 Individuals used for translocations should be adapted to the intended site, and have high genetic diversity and low inbreeding. If the translocation is for genetic rescue, the translocated individuals when combined with residents should result in high genetic diversity and low inbreeding.

Chapter 18

18.1 Potential methods of controlling cane toads are (a) biological control using a disease from its native range, (b) poisoning, (c) immunocontraception, or (d) genetic control. Given its huge population size and wide distribution, (a) has the greatest potential.

18.2 As native mammals in parts of Australia have previously evolved resistance to 1080 (the poisonous compound is found in some native peas), foxes are likely to evolve resistance. The waiting time until resistance evolves depends on genetic diversity in Australian foxes for 1080 resistance, on the selection applied via fox baiting with 1080, on N_e of the Australian fox population, on immigration of foxes from non-baited to baited areas and on number of generations.

18.3 Particular transgenes may have either beneficial or deleterious effects, or little impacts on biodiversity. Use of disease resistance transgenes might allow recovery of species impacted by introduced disease, as is being tried in the American chestnut. Escape of transgenes containing resistance to environmental extremes from crop plants to invasive weeds may extend the range and adverse impacts of invasive species on biodiversity. Transgenes in crop plants grown in regions without other related species to which gene flow can occur may involve little risk. The risk of gene flow is less in selfing species than in outcrossing ones, other things being equal.

18.4

	NN	NC	CC	Total
Zygotic frequencies	p^2	$2pq$	q^2	1
Relative fitnesses	1	0	0.1	
After selection	p^2	0	$0.1\,q^2$	$p^2 + 0.1\,q^2$
Adjusting for total	$\frac{p^2}{p^2 + 0.1\,q^2}$	0	$\frac{0.1\,q^2}{p^2 + 0.1\,q^2}$	1

New frequency of N $p_1 = \frac{p^2}{p^2 + 0.1\,q^2}$

Change in frequency of N $\Delta p = p_1 - p = \frac{p^2}{p^2 + 0.1\,q^2} - p = \frac{p^2 - p(p^2 + 0.1\,q^2)}{p^2 + 0.1\,q^2}$

$$= \frac{pq\,(p - 0.1\,q)}{p^2 + 0.1\,q^2}$$

At equilibrium, $\Delta p = 0$, so $p = 0.1\,q$

Yielding

$$q = \frac{1}{1.1} = 0.909$$

Thus, the compound strain needs to be released in greater than a 10-fold excess to replace the normal strain.

18.5 $p = q = 0.5$ (workings similar to 18.4 above).

Chapter 19

19.1 Captive populations deteriorate genetically due to inbreeding depression, loss of genetic diversity, mutational accumulation and genetic adaptations to captivity that are deleterious in the wild.

19.2 $k_{GH} = \frac{1}{16}$.

19.3 The most familiar way to complete this problem is to determine the inbreeding coefficient for a progeny X of Thelma and Rita if they could have one.

Path	Contribution to F_X
Thelma-**A**-H-Rita	1/16
Thelma-F-**A**-H-Rita	1/32
Thelma-F-**B**-H-Rita	1/32

$k_{Th\text{-}R} = F_X = 1/16 + 1/32 + 1/32 = 1/8$

19.4 $k_{Th\text{-}Th} = ½ (1 + F_{Th}) = ½ (1 + ¼) = 5/8$

19.5 mean $k_{Ri} = \dfrac{\Sigma(k_{Rita\text{-}Thelma} + k_{Rita\text{-}Louise} + k_{Rita\text{-}Rita} + k_{Rita\text{-}Robert})}{4}$

$= \dfrac{1/8 + 1/8 + 1/2 + 0}{4} = 0.1875$

19.6 A 4-population group can be labelled as populations 1("genotype" AB), 2 (CD), 3 (EF), and 4 (GH). In the 1st generation, males move from 1 group to the right, 1 to 2, 2 to 3, 3 to 4 and 4 to 1. Progeny in group 1 will have "genotype" ABGH, 2 ABCD, 3 CDEF, 4 EFGH. In the 2nd generation males are moved 2 groups to the right, 1 to 3, 2 to 4, 3 to 1 and 4 to 2. Progeny in all four groups will all have "genotype" ABCDEFGH, so avoidance of inbreeding is no longer possible in future generations.

19.7 Cloning is widely used in plant conservation i.e. cutting can be taken so that individual plants can be conserved, either by planting in the wild, or by taking them into botanical gardens. Tissue culture is another form of cloning that can be done with many plants. These forms of cloning can be used to rapidly increase population sizes without major costs to the individual. In mammals, only a few species that are closely related to domestic animals can be cloned using nuclear transplantation. Animal cloning also requires a recipient mother from the same or a closely related species. The use of closely related species may lead to later behavioural problems, inappropriate learned skills etc.

Amphibians have been cloned, but we are not aware of birds being cloning. Currently, animal cloning makes little contribution to conservation as so few species can be cloned. In the future, it may be used to increase the numbers of individuals of highly threatened species. However, it is likely to remain a costly venture that can be afforded in only a limited range of high profile species.

19.8 The options to manage recessive hairlessness in red ruffed lemurs are:

(a) ignore it, (b) remove affected individual from the gene pool, (c) remove potential carriers and affected individual from the gene pool, or (d) remove affected individual from the gene pool and re-pair carriers that produce hairless offspring. Given the allele frequency, about 1% of the progeny (q^2) will be hairless, so ignoring the condition, or removing affected individual are both feasible options. If carriers were to be removed from the pedigree this would lead to removal of ~ 18% ($2pq$) of the individuals – this is too great a loss for an endangered species with only 125 individuals in captivity. Removal of all potential carriers would involve even greater losses of individuals. The final option minimises the number of hairless offspring produced and removes only a few individuals from the breeding pool. If a molecular test for carriers was devised, removal of the deleterious allele should be a realistic option once the population size was expanded.

Chapter 20

20.1 Genetic adaptation to captive conditions results in improved reproductive fitness in captivity, but these adaptations typically reduce fitness when captive populations are reintroduced into the wild.

20.2 Genetic adaptation to captivity depends upon (a) the heritability of reproductive fitness in captivity (genetic diversity), (b) selection in captivity (dependent upon the mortality rate and the difference in environment between captive and wild environments), (c) N_e, (d) the extent of gene flow from wild populations, and (e) the number of generations in captivity.

20.3 The genetic issues in reintroduction programs are: (a) inbreeding and loss of genetic diversity that occurred during the decline of the wild population, (b) genetic deterioration in captivity due to inbreeding, loss of genetic diversity and genetic adaptations to captivity that reduce reproductive fitness in the wild environment, (c) choice of reintroduction sites and the likely adaptation of the captive population to the sites, (d) choice of individuals to reintroduce, including impact of reintroductions on the captive population, and impact of reintroductions on genetic diversity in the reintroduced population, and (e) inbreeding, genetic diversity and reproductive fitness of the reintroduced population.

20.4 Removal of an individual with high mean kinship (and low H_e) will reduce mean kinship in the captive population and thus will increase heterozygosity (from equation 19.4).

Chapter 21

21.1 (a) ¾, (b) $N_e = \frac{4 \times 1 \times 4}{(4+1)} = 3.2$, thus $\frac{H_1}{H_0} = (1 - \frac{1}{2 \times 3.2}) = 0.84$, (c) 7/8, (d) 19/20.

21.2 (a) 0, (b) ½, (c) 4/5

21.3 mtDNA $\frac{H_{75}}{H_0} = \frac{0.067}{0.80} = 0.084 = (1 - \frac{1}{N_{ef}})^{75} \sim e^{-t / Nef} = e^{-75 / Nef}$

Taking ln and rearranging yields

$$N_{ef} = \frac{-75}{\ln(0.084)} = 30$$

21.4 (a) Asexual/clonal.

(b) Compatible with selfing: Only alleles present in the mother are found in the offspring and the ratio of genotypes fits selfing. However, data from further loci would be necessary to exclude outbreeding.

(c) Outcrossing; alleles not found in the mother are present in the offspring. Only one male (A_2A_3) is necessary to account for the offspring.

(d) Outbreeding; at least 2 males are necessary to account for the offspring (e.g. A_2A_3 and A_4A_5).

(e) Haplo-diploid, or sex-linked locus; females diploid and males haploid. If all loci show this pattern, it is haplo-diploid, while if only a few loci of several showed this, it would indicate sex-linked inheritance.

21.5 The Wollemi pine may be asexually reproducing, or it could be a highly homozygous population that is selfing, or even outcrossing. The issue remains unresolved.

21.6 Only gosling 5 belongs to the nest attendants. Gosling 1 is excluded by locus J, gosling 2 by M, gosling 3 by E, I & M, and gosling 4 by A, E, G and M. For gosling 2 putative father is excluded, while for goslings 3 and 4 father and mother excluded.

Chapter 22

22.1 For the first time step from 1960 to 1961, r = ln (350/70) = 1.609. For the full data set 1960-1986, mean r = - 0.052 and variance (r) = 0.841

22.2 The major recommendations for the northern hairy-nosed wombat would be to preserve the habitat (cattle have been removed) and attempt to increase the population size. To avoid catastrophes, establishment of another population is strongly recommended (e.g. Deniliquin where a population previously existed). Captive breeding is not recommended as this species has not been bred in captivity. Research into captive breeding of the related southern hairy-nosed wombat is recommended

22.3 The only immediate option is captive breeding, with populations maintained at several sites to avoid catastrophes. To reintroduce Partula into the wild would require extermination of

the introduced carnivorous snail (improbable), or reintroduction to an island lacking the predatory snail. Reserve populations in captivity would still be required to avoid losing wild populations due the spread of the carnivorous snail.

22.4 With small overall populations and continued threats in the wild, reserve captive populations are required (there are some captive animals). Management of the wild populations requires habitat preservation, control of poaching and genetic management to restore gene flow. Artificial insemination may be feasible to improve gene flow in this species. It may be possible to move females of this species, but it is likely to be difficult and costly.

Revision

R.1 Endangered as $N < 250$.

R.2	AA	AB	BB	AC	BC	CC	Total
Expected frequencies	0.04	0.12	0.09	0.20	0.30	0.25	1

R.3 $D = -0.10$, so the population is not in linkage disequilibrium.

R.4 $h^2 = \underline{Cov_{OP}} = \underline{5.183} = 0.63$

V_P 8.18

^

R.5 $q = \underline{u} = \underline{4 \times 10^{-6}} = 1.3 \times 10^{-5}$

s 0.3

R.6 $t = (\underline{\ln p_0 - \ln p_t}) = (\underline{\ln 1 - \ln 0.8}) = 2231$ generations.

u 10^{-4}

R.7	AA	Aa	aa
Relative fitnesses	0.9529	1	0.9647

$1 - s_1$ 1 $1 - s_2$

$\hat{p} = \frac{s_2}{(s_1 + s_2)} = \frac{0.0353}{(0.0471 + 0.0353)} = 0.43$

R.8 $\frac{H_t}{H_0} = (1 - \frac{1}{(2 \times 30)})^{10} = 0.845$

R.9 $N_e = 58.8$

R.10 $F = \frac{1}{16}$.

R.11 F_{ST} is a measure of the inbreeding due to differentiation in allele frequencies among populations. F_{ST} is inversely related to gene flow among populations, being 0 for undifferentiated populations, and 1 for completely differentiated populations

R.12 $I_N = \frac{0.6}{(0.46 \times 1)^{1/2}} = 0.885$ and $D = 0.12$

R.13 The populations are showing some reproductive isolation. They probably belong to one species, but they may be sub-species. It would be necessary to have additional information, such as on further informative loci to make a definitive assessment.

R.14 The first step would be to identify the clonal genotypes (these will often be in different populations) and then conserve the clones in the wild (and typically in captivity as well). In the wild the efforts should be to preserve habitat and to increase their population sizes.

R.15 Minimising mean kinship maximises the retention of heterozygosity within a population. It does not necessarily minimise inbreeding and so address reproductive fitness, but is also close to optimum for minimising inbreeding. More genetic diversity can be retained if the population is fragmented, provided there are no extinctions of population fragments, but the optimum procedure would still be to minimise kinship within each population fragment.

R.16 $N_e = \frac{475}{L} = \frac{475}{7} = 68$