Answers to Study and Review Questions

Answers are given below for calculations, problems, and short answers; a reference to the relevant section(s) of the chapter is given for longer answers and definitions or explanations of technical terms; or a reference to further reading is given for topics not explicitly discussed in the text.

Chapter 1

1. See Section 1.1.
2. Adaptation.
3. The popular concept had evolution as progressive, with species ascending a one-dimensional line from lower forms to higher. Evolution in Darwin's theory is tree-like and branching, and no species is any "higher" than any other — forms are adapted only to the environments they live in.
4. Darwin's theory of natural selection and Mendel's theory of heredity.

Chapter 2

1. The terms are explained in the chapter.
2. (i) 100% AA; (ii) 1 AA : 1 Aa; (iii) 1 AA : 2 Aa : 1 aa; (iv) 100% AB/AB; and (v) 100% AB/AB.
3. As fractions: (i) 1/4 AB, 1/4 Ab, 1/4 aB, 1/4 ab; and (ii) $(1-r)/2\ AB$, $(1-r)/2\ ab$, $r/2\ Ab$, $r/2\ aB$. As ratios: (i) 1 AB : 1 Ab : 1 aB : 1 ab; and (ii) $(1-r)\ AB$: $(1-r)\ ab$: $r\ Ab$: $r\ aB$.

Chapter 3

1. Approximately the species level; the pigeon example might stretch it to genera, but higher categories do not evolve in human lifetimes.
2. (i) If you look at any one time and place, living things usually fall into distinct, recognizable groups that could be called "kinds." (ii) If you look over a range of space (if the "kinds" in question are species) the kinds break down; if you look through a range of times (if the kinds are species or any higher category) the kinds also break down. The differences between higher categories can also be broken down by studying the full range of diversity on Earth: you might think that plants and animals are less clear categories after studying the range of unicellular organisms.
3. (a), (b), and (d) are homologies; (c) is an analogy.

4. It is an accident in the sense that other codes with the same four letters could work equally well. It is frozen in the sense that changes in it are selected against. See Section 3.8.
5. This is intended more as a discussion topic: for the idea see Section 3.9.
6. Because a form would have existed in time before the series of fossils (of vertebrates from fish to mammals) that can be strongly argued to be its ancestors.

Chapter 4

1.

Age interval (days)	Number (as density/m^2) surviving to day x	Proportion of original cohort surviving to day x	Proportion of original cohort dying during interval
0–250	100	100	0.9989
251–500	0.11	0.11	0.273
501–750	0.08	0.08	0.75
751–1,000	0.06	0.06	–

2. (a) See Section 4.2. (b) In technical terms, drift (on which see Chapter 6). The gene frequencies would change between generations because there is heritability (condition 2) and some individuals produce more offspring than others (condition 3). But if the differences in reproduction are not systematically associated with some character or other, the changes in gene frequency between generations will be random or directionless. (c) No evolution at all. If the character conferring higher than average fitness is not inherited by the individual's offspring, natural selection cannot increase its frequency in the population.
3. The requirements of inheritance and association between high reproductive success and some character have also to be met.
4. The mechanism has to: (i) perceive the change in environment; (ii) work out what the appropriate adaptation is to the new environment; (iii) alter the genes in the germ line in a manner to code for the new adaptation. (i) is possible; (ii) could vary from possible in a case such as simple camouflage to impossible in a case requiring a new complex adaptation, such as the adaptations for living on land of the

first terrestrial tetrapods; and (iii) would contradict what is known about genetics and it is difficult to see how it could be done. The mechanism would have to work backwards from the new phenotype (something like a long neck in a giraffe) to deduce the needed genetic changes, even though the phenotype was produced by multiple, interacting genetic and environmental effects.

5. (a) Directional selection (for smaller brains); (b) stabilizing selection; and (c) no selection.

6. (a) Here are two arguments. (i) If every pair produced two offspring, natural selection would favor new genetic variants that produced three, or more, offspring. After the more fecund form had spread through the population the average would still be two but the greater competition among individuals to survive would lead to variation in the success of the broods of different parents. (ii) Random accidents alone will guarantee that some individuals fail to breed; then for the average to be two, as it must be for any population that is reasonably stable in the long term, all successfully reproducing individuals will produce more than two offspring. (b) Ecologists discuss this in terms of r and K selection, or life history theory: in some environments there is little competition and selection favors producing large numbers of small offspring; whereas in others there is massive competition and selection favors producing fewer offspring and investing a large amount in each. Many other factors can also operate.

Chapter 5

1. Populations 1 and 5 are in Hardy–Weinberg equilibrium; populations 2–4 are not. As to why they are not, in population 4 it looks like AA is lethal, in 2 there may be a heterozygote advantage, and in 3 a heterozygote disadvantage. Population 2 could also be produced by disassortative mating, and 3 by assortative mating. In population 3 there could also be a Wahlund effect. All the deviations are so large that random sampling is unlikely to be the whole explanation.

2. (a) $p^2/(1 - sq^2)$; (b) $p/(1 - sq^2)$; and (c) $1 - sq^2$.

3. $(1/3)(3 - s) = 1 - (s/3)$.

4. If you do it in your head, $s \approx 0.1$. To be exact, $s = 0.095181429619$.

5. That the fitness differences are in survivorship (not fertility), and in particular in survivorship during the life stage investigated in the mark–recapture experiment. (By the way, mark–recapture experiments are also used by ecologists to estimate absolute survival rates: they require the additional assumptions that the animals do not become "trap shy" or "trap happy," and that the mark and release treatment does not reduce survival. These assumptions are not needed when estimating relative survival. However,

we do need the second-order assumption that these factors are the same for all genotypes.)

6. AA 1/2; aa 1/2. The gene frequencies are 0.5 and the Hardy–Weinberg ratio 1/4 : 1/2 : 1/4. The observed to expected ratios are 2/3 : 4/3 : 2/3, which when scaled to a maximum of 1 give the fitnesses 1/2 : 1 : 1/2.

7. (a) 0.5; and (b) 0.5625. You need equation 5.13; $t = 1$. For (a) it looks like this: $0.625 = 0.5 + (0.75 - 0.5)(1 - m)$. And for (b) it looks like this: $x = 0.5 + (0.625 - 0.5)(1 - 0.5)$.

8. (a) The aa genotype is likely to be fixed. If aa mate only among themselves and AA and Aa mate only with AA and Aa, whenever there is an $Aa \times Aa$ mating, some aa progeny are produced, who will subsequently only mate with other aa individuals. (b) Now AA mate only with AA, Aa with Aa, and aa with aa. The homozygous matings preserve their genotypes, but when Aa mate together they produce 1/4 aa and 1/4 AA progeny. In an extreme case, the population diverges into two species, one AA the other aa and the heterozygotes are lost. (c) (i) The dominant allele will be fixed; and (ii) the recessive allele will be fixed.

9. $$p' = \frac{p(1 - s)}{1 - p^2 s - 2pqs}$$

The denominator can be variously rearranged.

10. $$p^\star \approx \sqrt{\frac{m}{s}}$$

The derivation starts with the equilibrium condition, $p^2 s = qm$. We then note that $q \approx 1$, and $p^2 s \approx m$; divide both sides by s and take square roots.

Chapter 6

1. Either 100% A or 100% a (there is an equal chance of each).
2. See (a) Section 6.1, and (b) Section 6.3.
3. (1) 0.5; (2) 0.5; (3) 0.375; and (4) 0. See Section 6.5.
4. (a) and (b) 10^{-8}. Population size cancels out in the formula for the rate of neutral evolution.
5. (a) $1/(2N)$; and (b) $(1 - (1/2N))$.
6. Both manipulations requires substituting $1 - H$ for f and then some canceling and multiplying though by -1 to make the sign positive.

Chapter 7

1. See Figure 7.1a and b.
2. The main observations suggesting neutral molecular evolution are not also seen in morphology. This was discussed for the constancy of evolutionary rates in Section 7.3. The other original observations (for absolute rates and heterozygosities,

and for the relation between rate and constraint) either have not been made, or such observations as there are do not suggest that the problems found in selective explanations for molecular evolution also apply to morphology.

3. (i) A high rate of evolution; (ii) high levels of polymorphism; (iii) a constant rate of evolution; and (iv) functionally more constrained changes have lower evolutionary rates.

4. (i) The molecular clock is not constant enough; (ii) generation time effects seem to differ between synonymous and non-synonymous substitutions; (iii) genetic variation is too similar between species with different population sizes, and heterozygosity is too low in species with high N; and (iv) [not discussed in the text, but for completeness] rates of evolution do not have a predicted relation with levels of genetic variation.

5. (a) The key variable in the neutral explanation is the chance that a mutation is neutral: it is arguably higher for regions with less functional constraints (Section 7.6.2). (b) The key variable in the selective explanation is the chance that a mutation has a small rather than large effect, and so may cause a fine-tuning improvement (Section 7.6.2).

6. No; the main evidence is from codon usage biases (Section 7.11.4).

7. (a) This is a fairly standard figure. Non-synonymous substitutions are rarer, probably because more of them are deleterious than synonymous substitutions. It could be that almost all evolution for both kinds of change is by neutral drift. (b) Either selection has positively favored amino acid changes, elevating the rate of non-synonymous evolution, or selection has been relaxed and non-synonymous changes that are normally disadvantageous are here neutral. (c) It looks like selection is driving amino acid changes in the protein coded for by this gene.

Chapter 8

1.

Population	Frequency of			Value of D
	A_1B_1	A_1	B_1	
1	7/16	1/2	1/2	+3/16
2	1/4	1/2	1/2	0
3	1/9	1/3	1/3	0
4	11/162	1/3	1/3	−7/162

Note that the haplotype frequency is found by the sum of homozygotes plus 1/2 the heterozygotes (as for a gene frequency, Section 5.1). If you have figures in the A_1B_1 frequency column for population 1 such as 11/16 or 14/16 you may have not divided the frequency of A_1B_1/A_1B_2 by 2.

2. Populations 1 and 4 may show fitness epistasis, in which, in population 1, A_1 has higher fitness in combination with B_1 than with B_2, and vice versa in poulation 2. Fitnesses are independent (maybe multiplicative or additive) in populations 2 and 3.

3. Populations 1 and 2 should equilibrate at haplotype frequencies of 1/4, 1/4, 1/4, and 1/4 for the four haplotypes; populations 3 and 4 should equilibrate at 1/9, 2/9, 2/9, and 4/9. Populations 2 and 3 are already at equilibrium and should not change through time; populations 1 and 4 will evolve toward the equilibrium frequencies at a rate determined by the recombination rate between the two loci.

4. Observed heterozygosities are arguably a little on the low side for the neutral theory (Section 7.6); the effect of a section at one locus is on average to reduce heterozygosities at linked loci, producing a net reduction in average heterozygosity through the genome.

5. See Figure 8.8b. The equilibrium is at the top of the hill.

Chapter 9

1. See Section 9.2, particularly Figures 9.3 and 9.4. In statistical theory, the argument is formalized as the central limit theorem.

2. +1. The answer is incomplete without the sign.

3. (a) $V_P = 300/8 = 37.5$; $V_A = 48/8 = 6$; and $h^2 = 6/37.5 = 6.16$. (b) +3: you add the additive effects inherited from each parent.

4. 106.

5. This is not explicitly discussed in the chapter, but see Section 13.x (p. 000). You might predict it will evolve toward a canalizing type relation, as in Figure 9.11b, because then an individual is most likely to have the optimal phenotype.

6. It will go through an intermediate phase with many recombinant genotypes produced by crossing-over between the three initial chromosomes; it should end up with only the chromosomal type that yields the optimal character by means of a homozygote: all +++−−−−.

Chapter 10

1. They cannot explain adaptation. There is no reason except chance why a new genetic variant should be in the direction of improved adaptation, and random chance change will not produce adaptation. If (as in the "Lamarckian" theory) the new genetic variants are in the direction of adaptation, it implies there is some adaptive mechanism behind the production of new variants. Natural selection is the only known theory that could explain such a mechanism.

2. See Figures 10.2 and 10.3.

3. Superficially, yes, but the adaptive information — all the metabolic processes of the cyanobacteria that evolved

photosynthesis—probably evolved in small steps and therefore nothing deep in Fisher's or Darwin's arguments is violated.

4. (a) Many small steps; and (b) some larger initial steps, followed by more small steps — the full distribution may be a negative exponential (Orr 1998).

5. No, it just turned out that way. Sometimes, by chance, an organ that works well in one function turns out to work well in another function after relatively little adjustment.

6. (a) (i) Natural selection, in the form of negative selection. The absent regions represent maladaptive forms which, when they arise as mutations, are selected out. (ii) Developmental constraint. Something about the way the organisms develop embryonically makes it impossible, or at least difficult, for these forms to arise. (b) Four kinds of evidence were mentioned in Section 10.7.3. The kind that most was said about was the use of artificial selection: if the character can be altered, its form is unlikely to be due to constraint.

Chapter 11

1. Many answers are possible, but the main examples in this chapter were: (a) adaptations for finding food; (b) eating as much food as possible to maximize reproductive rate; or cannibalism; or destructive fighting; or producing a 50 : 50 sex ratio in a polygynous species; (c) restraining reproduction to preserve the local food supply; and (d) segregation distortion in which the total fertility of the organism is reduced.

2. You might explain it in terms of two factors, the relative rates of extinction of altruistic and selfish groups and the rate of migration. Or you might reduce them to the one variable m, which is the average number of successful emigrants produced by a selfish group during the time the group exists (before it goes extinct). The fate of the model is then determined by whether m is greater or smaller than 1 (Section 11.2.5).

3. b can be estimated as the number of extra offspring produced by the nests with helpers: $2.2 - 1.24 \approx 1$. But that is produced by 1.7 helpers, giving $b \approx 1/1.7 \approx 0.6$. c can be estimated either as zero (if the helper has no other option) or as the number of offspring produced by an unhelped pair (if it could breed alone), in which case $c = 1.24$. With $r = 1/2$ it should help if it cannot breed alone but should breed if it can. This way of estimating b and c does have problems, however.

4. Kin selection applies to a family group, or more generally a group of kin (indeed it is not theoretically necessary that the kin live in groups, though they do have to be able to influence one another's fitness); group selection, at least in the pure sense, applies to groups of unrelated individuals. Kin selection is a plausible process, because the conditions

for an individual to produce more copies of a gene may be improved more by helping relatives than by breeding more itself. Group selection requires more awkward conditions (see question 2!).

5. The average individual is likely to be worse off, as Figure B11.1 illustrates. Competition between individuals reduces the efficiency of the group. Whole bodies would have the same problem if there were no mechanisms to suppress competition between genes, or cells, within a body.

6. (a) The whole genome; and (b) the chromosome.

Chapter 12

1. (a) 33%; and (b) 67%.

2. (a) Crudely, it has to be high; more exactly, a total deleterious mutation rate of more than one per organism per generation is needed. On its realism, see the end of Section 12.2.2: the evidence is inconclusive and neither rules it out or in. (b) Relation 1 in Figure 12.6. The y-axis is logarithmic. Relation 2 corresponds to independent fitness effects, in which sex (before the 50% cost) is indifferent. Relation 3 is the diminishing returns type of epistasis, in which sex is positively daft, even before the 50% cost. Again, you can argue reality either way: see the end of Section 12.2.2.

3. The material in the text (Section 12.2.3) would suggest looking at the relation between the frequency of sex and parasitism in taxa that can reproduce both ways; or looking into the genetics of host–parasite relations and measuring the frequency of resistance genes in hosts or penetration genes in parasites. Other answers would be possible too, going beyond the textual materials.

4. See Section 12.4.4: if the character were cheap to produce, males of all genetic qualities would evolve to produce it.

5. See Section 12.4.3: a female who did not choose extreme males would on average mate with a less extreme male than would other females in the population; she would produce less extreme than average sons; and they would grow up into a population in which most females prefer extreme males. Her sons would have low reproductive success and their mother's lack of preference would be selected against.

6. See Section 12.5.1: if more daughters than sons were produced by most members of the population, the fitness of a male would be higher than that of a female. Individuals who produced more sons than daughters would be favored by selection. A sex ratio of one is a stable point at which there is no advantage to producing more offspring of either sex.

7. (a) Positive, and (b) negative frequency-dependent selection.

8. (a) Yes, and (b) no. When different levels of selection conflict, adaptation cannot be perfect at all levels. You can find another example of a constraint on perfection in Holland & Rice's (1999) imposed monogamy experiment.

Chapter 13

1. Look at Section 13.2.
2. (i) 1, (ii) 2, and (iii) 1.
3. See Section 13.3, particularly Table 13.1.
4. G_{ST} is 0 for species 1, 0.5 for species 2, and 0 for species 3. Biological factors influencing G_{ST} include: the recency of origin of the species, the speed of evolution, how uniform the environment is through space, and the amount of gene flow between populations.
5. It can be argued both ways; see the second part of Section 13.7.2. If asexual species are discrete in the same way that sexual species seem to be, that suggests the force maintaining species as discrete clusters is ecological rather than interbreeding.
6. (i) Typological; (ii) population (or so I would argue); (iii) population; (iv) two schools of thought implicitly argue it each way (do you think we have a set number of real, distinct emotions?); (v) typological; and (vi) most would argue typological, I suspect, but Hull (1988) makes the opposite case, that scientific theories are like biological species.
7. See the work of Grant and Grant described in Section 13.7.3. Chapter 14 contains more material on the genetic theory of postzygotic isolation.
8. (i) (a), (b), and (c) (probably) yes; (ii) (a) yes, (b) and (c) no; and (iii) (a), (b), and (c) can be yes.

Chapter 14

1. Pleiotropy and hitch-hiking (Section 14.3.2), perhaps partly due to sexual selection (Section 14.11). Figure 14.3 shows an example from Darwin's finches.
2. (a) Postzygotic isolation can be expressed by the fitness reduction of hybrid offspring compared with offspring of crosses within a population (or within a near species). (b) The index we saw (Figure 14.2) was (number of matings to same type − number of matings to other type)/(total number of matings), which gives: (i) $I = 1$; (ii) $I = 0.5$; and (iii) $I = 0$.
3. It shows that the neighboring populations are more closely related: the northeast populations are more closely related to the southeast populations than to any other populations (such as southwest or northwest). It could have been that the populations evolved from formerly fragmented ranges, and expanded to the current distribution, but the phylogeny suggests a gradual evolution of the current songs in the current places. Also, the phylogeny shows that the gap in the range on the east side is probably only because there is a desert; there is an underlying continuity. The birds still evolved in a ring, with the northeast birds derived from the southeast birds.

4. The intermediate stages (heterozygotes) would be selected against.
5. (a) "When in the F_1 offspring of the two different animal races one sex is absent, rare, or sterile, that sex is the heterozygous one" (Section 14.4.6). (b) Males. (c) By postulating that some of the genes in the Dobzhansky–Muller theory are on the X chromosome, and recessive (Box 14.1).
6. Valley crossing means that evolution passes through a phase in which fitness goes down. (a) No, (b) no, and (c) yes.
7. Reproductive character displacement, or character displacement for prezygotic isolation. There are two main explanations. (i) Reinforcement. Females in allopatry have not been selected to discriminate against heterospecific males, because in evolutionary history the ancestors of the modern females have never met those males; females in sympatry are descended from females that have been exposed to both kinds of male. Females who mated with heterospecific males produced hybrid offspring of low fitness, so selection favored discrimination. (ii) Without reinforcement. There are various versions of the alternative explanation; the one most explained in the text (Section 16.8) is as follows. Different individuals of the two species in the past may have shown various degrees of isolation from the other species. In areas where they now coexist in sympatry, if reproductive isolation was low, the two species would fuse and probably now look more like one of the species (and so be classified as a member of it); if reproductive isolation was high, the two would coexist and remain distinct. Thus only where isolation was high do we now see the two species in sympatry. In areas where the species are now allopatric, whatever the reproductive isolation, they continue to exist. Thus the average isolation will be lower than for sympatry.
8. Theoretical reasons: the conditions required for reinforcement maybe too short lived. Empirical reasons: the evidence from artificial selection is poor, and the evidence from reproductive character displacment is open to alternative interpretations.
9. (a) "Secondary": divergent evolution in separate populations occurred in the past, followed by range expansion, and the two populations come into contact at what is now a hybrid zone. (b) "Primary": a stepped cline evolved within the population, which became large enough for the forms on either side of the step to be recognized as distinct taxonomic forms.
10. See Figure 14.14. On sympatric speciation, the closest relatives of a species should live in the same area; on allopatric speciation, the closest relatives should be in a different area.

Chapter 15

1.
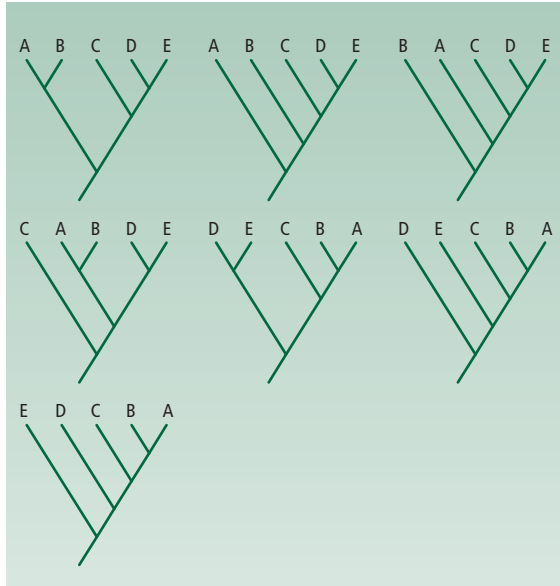
2.
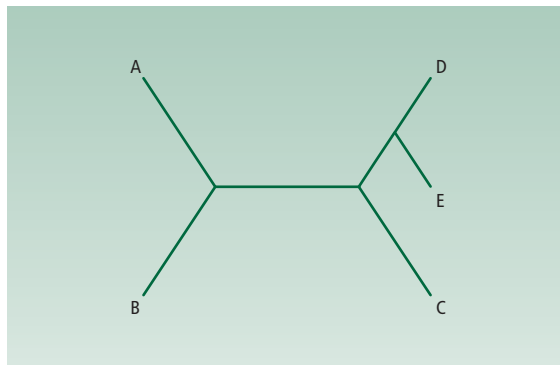
3. Evolutionary rates are approximately equal in all lineages.
4. See Section 15.4.
5. *A* is ancestral and *A'* derived in all three, but the inference is most certain in (a) and least certain in (c). (If *A* is ancestral in the group of species 1 + 2, then the minimum number of events in (a), (b), and (c), respectively, are 2, 3, and 3; whereas if *A'* were ancestral, the minimums would be 3, 4, and 4.)
6. See Section 15.8.

7. When more than one evolutionary change underlies an observed difference (or identity) between two sequences.
8. (a) $(1 - 3p)^3 p^2$; (b) 16.
9. $2 \times 3 \times 1$.

Chapter 16

1. See Table 16.1.

   Evolutionary: paraphyletic, monophyletic.
   Cladistic: monophyletic.
   Phenetic: polyphyletic, paraphyletic, monophyletic.

2. (i) Cow (lungfish, salmon); (ii) cow (lungfish, salmon); (iii) (cow, lungfish), salmon. See the end of Section 16.3.
3. (i) The Euclidean distances are obtained by Pythagoras's theorem, and I picked the numbers to give a 3, 4, 5 triangle: the three species can be drawn on a graph with one character per axis. (ii) The mean character distance is the average of the distances for the two characters. See Section 16.5.

|	Species 1	Species 2	Species 3
Species 1		3	4
Species 2	1.5		5
Species 3	2	3.5	

The two distance measures imply contradictory groupings of the three species. This is a case where the classification chosen by the numeric phenetic method would be ambiguous, and therefore arguably subjective.

4. (a) 2.31; (b) 2.5; (c) species 1 and 2 equally; (d) with a nearest nearest neighbor cluster statistic the grouping is (1,2)(3(4,5)); with a nearest average neighbor cluster statistic it is ((1,2)3)(4,5); and (e) see Section 16.5 for the moral.
5. A critic would reply that the same problem would resurface in another form. Maybe the average and nearest neighbor statistics in the case of Figure 14.5 could be made to agree by adding five further characters. However, those two are just two of many cluster statistics, and the result would almost certainly still be ambiguous with respect to some other cluster statistic. The ambiguity could only be removed if there were one non-ambiguous phenetic hierarchy in nature, and there is no reason to suppose such a hierarchy exists.
6. (a) The difference reflects evolutionary theory's scientific peculiarity as a historic theory. The hierarchy in a phylogenetic classification is historic, and is used for the reasons discussed in the chapter. The periodic table is non-historic and

non-hierarchical. Its structure represents two of the fundamental properties that determine the nature of an element, and the position of an element in the table can be used to predict what the element will be like. The position of an organism in a phylogenetic classification cannot be used to predict much about what the organism will be like. Much more could be said about the nature of different theories in science, and the way different theories imply different kinds of classifications. (b) See Section 16.8!

Chapter 17

1. See Section 17.1 and Figure 17.2.
2. Going down the column: 1/2, 1/2, 1/2, and 1.
3. My first three counts gave 26, 27, and 26 dispersal events from older to younger islands, and 13, 12, and 12 dispersals from younger to older islands, respectively! The correct answer is something close to these numbers, but you have the idea if your figures are in this region. Compare Figure 17.6. There is no reason why there should be so many more dispersal events from older to younger islands if speciation was created by splitting a larger range, whereas it makes sense if it was the result of dispersal because the older island would have been occupied first.
4.
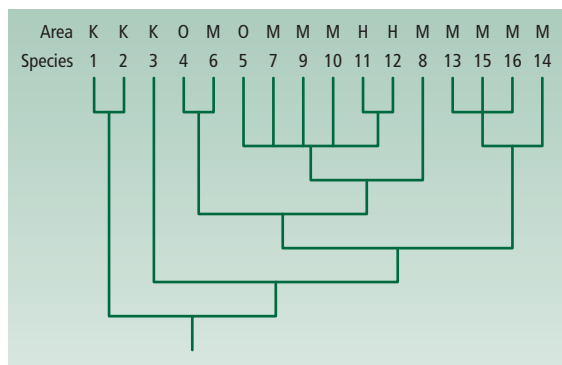
Some minor variants would also be possible, depending on how ancestral species like species 8 and 14 are represented.

5. (a)–(b), (a)–(c), and (e)–(f) are congruent. (a)–(d), (a)–(f), (c)–(d), (c)–(f), (e)–(b), and (e)–(d) are incongruent.
6. There are two main hypotheses. (i) The competitive superiority of North American mammals, perhaps due to a history of more intense competition, and reflected in their relative encephalization. (ii) Environmental change, such that the North American mammals were competitively superior in South American environments after the Interchange.

Chapter 18

1. See Section 18.1 and Figure 18.1.
2. Using the rounded figure of 1.2×10^{-4} for the decay constant:

	$^{14}C : {}^{14}N$	Age
(a)	1 : 1	5,776
(b)	2 : 1	3,379
(c)	1 : 2	9,155

3. RNA can be single-stranded, allowing both metabolism and replication in one molecule. RNA can also have many shapes, enabling many reactions, including catalysis.
4. There are several possibilities. (i) The molecular evidence is wrong, for instance because of an error in calibration or non-constant rates of evolution. (ii) The fossil date is wrong, for instance because the record is incomplete or a fossil has been misdated. (iii) The estimates concern different events — the molecular clock gives a time of common ancestor, and the fossil evidence gives a time of proliferation.
5. See Section 18.5.
6. The mammals evolved in many stages, and the changes were in adaptive characters.
7. (i) Brain size, (ii) bipedality, and (iii) jaw reduction and associated changes in teeth. You might also mention changes in cultural, social, and linguistic behavior, and even changes in the thumb and big toe in the hand and foot.

Chapter 19

1. (a) By the molecular clock. (b) Several answers are possible, but the chapter noticed, for instance, the 2R hypothesis about the origin of vertebrates, and the possible association of gene duplications with the origin of dicotyledons.
2. (i) Gene transfer between bacteria and humans, or (ii) gene loss in a lineage leading to worms and fruitflies. They can be tested once we have an expanded knowledge of the phylogenetic distribution of the genes (see Figure 19.3).
3. Genes on the X and Y chromosomes do not recombine, and will have been diverging since recombination stopped. The four regions of gene similarity suggest that recombination was shut down in four stages, perhaps by inversions. Autosomal genes recombine and this prevents them from diverging.

Chapter 20

1. (a) Pedomorphosis; and (b) neoteny and progenesis (see Table 20.1).

2. The eyes of insects and vertebrates are at some level homologous, but not necessarily as eyes. The gene, for instance, could simply be a regional selector for a certain part of the head, that happens to have eyes in these two taxa. Alternatively, the common ancestor may have had eyes of some sort, developmentally controlled by the gene, but the structures we now observe as eyes in insects and vertebrates still built up independently in evolution.

3. (a) Evolvability is the chance that a species will undergo evolutionary change. The "evolutionary change" in the definition could refer to: (i) any genetic change, (ii) change in the form of speciation, or (iii) macroevolutionary, innovative change. (b) See Section 20.8: genetic switches enable genes to be recruited to act in new circumstances. Genes can acquire new functions without compromising their old function.

Chapter 21

1.

x_1	t_1	x_2	t_2	Rate
2	11	4	1	0.0693
2	11	20	1	0.2303
20	11	40	1	0.0693
20	6	40	1	0.1386

If you have answers like 0.2, 1.8, 2, and 4 you forgot to take logs. If you have minus numbers you have x_1 and x_2, or t_1 and t_2, the wrong way round.

2. (a) An inverse relation (see Figure 21.3). (b) One possibility is that long periods with rapid change and short periods with slow change have been excluded from the study, perhaps because the former would transform the character beyond commensurability and the latter seemed unworthy of notice.

3. See Section 21.5.

4. There are three possible answers. (i) Allopatric speciation, in which case punctuated equilibrium is orthodox. (ii) Speciation by valley crossing, in which case the theory is backing an unorthodox — some would say discredited — theory of speciation. (iii) Saltational macromutations, in which case the theory is unorthodox to the point of probably being erroneous.

5. The text contains two types of evidence: (i) rates of change in arbitrarily coded characters (see Figure 21.9), and (ii) taxonomic rates, in which the longevity of living fossil genera is longer than average (see Table 21.2).

Chapter 22

1. (a) Cospeciation and host shifts are more likely when hosts are phylogenetically closer. (b) Host shifts that are independent of phylogeny, for instance between hosts that are chemically similar but phylogenetically distant.

2. Biologists have seen whether the diversity of each taxon increases simultaneously in the fossil record. They have also made phylogenetically controlled comparisons between plants that do and do not interact with insects to see if the former have higher diversity. (And phylogenetically controlled comparisons between insects that do and do not interact with flowering plants to see if the former have higher diversity.)

3. Cophylogeny, and some evidence about the timing of the branches, for instance from molecular clocks.

4. In order of increasing virulence: (iv) < (i) < (ii) < (iii). (ii) and (iii) might be about the same, but this was not specifically discussed in the text. See Ewald (1993).

5. (a) See Section 22.6.1. Antagonistic biological interactions, such as between predator and prey, have evolved to become more dangerous over time: predators have become more dangerously armed, prey more powerfully defended. (b) The level of defensive adaptation in prey can be measured in such features as the thickness of molluskan shells and the habitats they occupy. Predatory adaptations have primarily been studied by the numbers of specialist as opposed to generalist predators: the presence of specialists suggests a more dangerous condition. It is important to test escalation by the proportion of species types through time, because there is more of everything in more recent fossil records. See Figures 22.12–22.14.

6. Antagonistic coevolution in general, and antagonistic coevolution with a dynamic equilibrium in particular. Van Valen suggested that total ecological resources may be constant through time, and the selective pressure on a species is proportional to the loss of resources it suffers due to lagging behind competing species.

Chapter 23

1. Because there was a lack of knowledge of the global distribution of species and (for large-bodied animals, whose geographic distributions were best known) the difficulty of assigning disarticulated fossil bone fragments to species (Section 23.1).

2. (a) In a real extinction all the members of a lineage die without leaving descendants; in a pseudoextinction the lineage continues to reproduce but its taxonomic name changes in mid-lineage, or the lineage persists but is temporarily unrepresented in the fossil record (Lazarus taxa). See Box 23.1. (b) Pseudoextinction of type (a) in Figure B23.1 snarls up

tests of both. If the extinctions of species with differing developmental modes in Figure 23.9, or in the test of synchroneity in Figure 23.3, were pseudoextinctions, the explanation for the trend, or synchronous pattern, would be something to do not with nature but with the habits of taxonomists. Lazarus-type pseudoextinction would also suggest the results are artifacts. Pseudoextinction of type (b) in Figure B23.1 may be less damaging. (Also, the test of the Red Queen hypothesis by survivorship curves in Chapter 22 may be little damaged by either of the taxonomic causes of pseudoextinction. The hypothesis might be recast in terms of rate of change rather than chance of extinction.)

3. (a) The iridium anomaly (Figure 23.4), perhaps combined with the dated Chicxulub crater. (b) The extinctions should be sudden and synchronous in all taxa, rather than gradual, and they should not in general be preceded by reductions in population size. For the difficulties of testing these predictions, look at Section 23.3.2.

4. At the end of the Cretaceous and Permian (for the top two extinctions); plus either the end Ordovician or the end Triassic (for the top three); plus the Devonian (for the top five).

5. See Figure B23.2. The observed extinction rate in the earlier interval will be (a) high, and (b) low.

6. At mass extinctions there is no relation. In background extinctions the taxa with planktonic development have an extinction rate that is half that of taxa with direct development. The background extinction difference can be explained either by bias in the fossil record (if planktonically developing species are more likely to be preserved) or by their being more likely to survive local difficulties by their dispersing larval stage.

7. Two possibilities we looked at are differences in speciation or extinction rates caused by differences in adaptations of different species, or by differential persistency of niches (see Section 23.6.2).

8. The heritability criterion is as relevant as ever here. In classic group selection problems, the character (such as altruism) is disadvantageous to individuals but advantageous to groups. Selfish individuals can invade groups. Once the group is infected by selfishness, it loses altruism. The character (altruism) is not inherited by groups for long. In classic cases of species selection, there is no question of a species being invaded by some alternative adaptation. Selection favors different adaptations in different species — direct development in some, planktonic development in others, for example. Those attributes are passed down from ancestral species to descendant species. Species selection is possible because there is no conflict between individual and species selection; heritability therefore is possible. Species selection is not a theory of the evolution of adaptation — only of the consequences of adaptations.

9. See Figure 23.11. A double wedge pattern suggests a competitive replacement. If one taxon goes extinct before the other radiates, it suggests non-competitive replacement.

10. Partly by different data compilations (with different taxonomic make ups) but mainly by different statistical corrections for biases in: (i) the amount of rock preserved from different times, and (ii) the amount of rock studied.

References

Abouheif, E., Akam, M., Dickinson, W.J. *et al.* (1997). Homology and developmental genes. *Trends in Genetics* **13**, 432–435.

Abrams, P.A. (2001). The evolution of predator–prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* **31**, 79–105.

Adams, D.C. & Rohlf, F.J. (2000). Ecological character displacement in *Plethodon*: biomechanical differences found from a geometric morphological study. *Proceedings of the National Academy of Sciences USA* **97**, 4106–4111.

Adams, M.B. (ed.) (1994). *The Evolution of Theodosius Dobzhansky*. Princeton University Press, Princeton, NJ.

Adrain, J.M. & Westrop, S.R. (2000). An empirical assessment of taxic paleobiology. *Science* **289**, 100–112.

Ahlberg, P. (ed.) (2001). *Major Events in Early Vertebrate Evolution*. Taylor & Francis, London.

Allen, C., Bekoff, M. & Lauder, G. (eds) (1998). *Nature's Purposes*. MIT Press, Cambridge, MA.

Allison, A.C. (1954). Protection afforded by sickle-cell trait against subtertian malarial infection. *British Medical Journal* **1**, 290–294. (Reprinted in Ridley 1997.)

Alroy, J. (1998). Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science* **280**, 731–734.

Alroy, J. (1999). The fossil record of North American mammals: evidence for a Paleocene evolutionary radiation. *Systematic Biology* **48**, 107–118.

Alroy, J., Marshall, C.R., Bambach, R.K. *et al.* (2002). Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences USA* **98**, 6261–6266.

Alvarez, L.W., Alvarez, W., Asaro, F. & Michel, H.V. (1980). Extraterrestrial cause for the Cretaceous–Tertiary extinction. *Science* **208**, 1095–1108.

Alvarez, W., Asaro, F. & Montanari, A. (1990). Iridium profile for 10 million years across the Cretaceous–Tertiary boundary at Gubbio (Italy). *Science* **250**, 1700–1702.

Alvarez, W., Kauffman, E.G., Surlyk, F., Alvarez, L.W., Asaro, F. & Michel, H.V. (1984). Impact theory of mass extinctions and the invertebrate fossil record. *Science* **223**, 1135–1141.

Anbar, A.D. & Knoll, A.H. (2002). Proterozoic ocean chemistry and evolution: a bioinorganic bridge. *Science* **297**, 1137–1142.

Andersson, D.I., Slechta, E.S. & Roth, J.R. (1998). Evidence that gene amplification underlies adaptive mutability of the bacterial *lac* operon. *Science* **282**, 1133–1135.

Andersson, M. (1994). *Sexual Selection*. Princeton University Press, Princeton, NJ.

Antolin, M.F. & Herbers, J.M. (2001). Evolution's struggle for existence in America's public schools. *Evolution* **55**, 2379–2388.

Antonovics, J. & van Tienderen, P.H. (1991). Ontoecogenophyloconstraints? The chaos of constraint terminology. *Trends in Ecology and Evolution* **6**, 166–168.