

INTRODUCTION TO EVOLUTIONARY BIOLOGY

1. List and briefly describe/define the various meanings of the word “evolution.”
2. Give examples (as specific as possible and as many as possible) of the kinds of current issues understanding evolutionary biology can help us with.
3. Briefly describe the two current HIV epidemics in terms of their size, infection rate, and affected populations. In general, where is the epidemic the most severe?
4. Describe the basic structure and function of HIV, with special attention to the role of reverse transcriptase in its life cycle. How does HIV cause disease?
5. Using AZT resistance as your example, explain why HIV is so hard to treat. Be sure to clearly explain the features of HIV that most directly lead to this problem.
6. Define the term virulence and explain the evidence that virulence in HIV is not a function of some biological constraint on the virus. Describe the transmission rate hypothesis for the high virulence of HIV. Be sure your explanation addresses the “virulent” and “benign” strategies and their relative costs and benefits under different regimes of sexual behavior. Outline the two “natural experiments” currently underway to test this hypothesis and state the specific outcomes the hypothesis predicts for each.
7. Describe the patterns of HIV resistance that have been currently identified and their molecular basis. Briefly discuss the evidence that resistance to HIV may be the result of selection for some other trait in the past.
8. Briefly describe how vaccines work and why understanding the evolutionary history of HIV is important in addressing the likelihood of developing a vaccine. What do recent analysis of the phylogeny of HIV tell us about its origin and history, and what does this suggest about the likelihood of developing a functional vaccine?
9. Summarize the major conclusions that have resulted from evolutionary analyses of HIV/AIDS. Do you think that these conclusions would be as strong if the evolutionary perspective were not included?

DARWIN AND THE EVIDENCE FOR EVOLUTION

1. Discuss the nature of scientific explanations. What are their components, and how are they tested? Be sure your explanation includes a discussion of how evidence is gathered and the kinds of reasoning used to analyze the evidence.

2. What is the difference between a hypothesis and a theory? Are scientific explanations every completely “proven”? Does that mean we can never establish scientific facts? Explain.
3. Briefly outline Plato’s Theory of Forms and how it was modified by Aristotle. What was the long-term significance of this idea for understanding evolution?
4. Discuss Aristotle’s Theory of Causes and Scala Naturae and describe their significance for understanding evolution. Briefly explain how Plato’s and Aristotle’s ideas were incorporated in Western Christianity during the Renaissance and discuss the relationship between those ideas and special creation.
5. Briefly outline the important contributions of the Enlightenment to understanding evolution. Why did progress in biology lag behind that in physics and chemistry at this time? What important findings were produced in geology and comparative anatomy/embryology?
6. Describe Lamarck’s model for “descent with modification” and explain why it was not accepted. Why was Lamarck’s work important to Darwin?
7. When was *The Origin* published? Why was natural selection not accepted as
8. What was the Modern Synthesis? What were the two “schools” of thought about the nature of genetic variability? How were they reconciled with each other? How did this reconciliation lead to the acceptance of natural selection?
9. Describe the reasoning Darwin used to present his evidence for descent with modification. Discuss the evidence, with attention to the evidence for (1) a young earth; (2) variation within species and changes in species over time; and (3) the “genealogical relatedness” of extant species to previously-existing species (i.e., descent).
10. Why is descent with modification considered a historical fact by the modern scientific community?

DARWINIAN NATURAL SELECTION

1. Outline the basic model of Darwinian natural selection, being sure to include mechanisms as appropriate.
2. Define the terms “fitness” and “adaptation.” Is fitness absolute? Explain.

3. Using the medium ground finches of the Galápagos as an example (but including others as appropriate), demonstrate that Darwin's postulates can be tested and verified in nature. Explain why these birds make a good model system for the study of natural selection.
4. Did natural selection occur in medium ground finches? Did evolution? Justify your answer.
5. What, precisely, is the effect of selection on individuals? On populations? Does selection cause adaptive variation to arise? Explain.
6. If selection acts on phenotypes, how does evolutionary change over time take place?
7. Explain the statement "Selection is 'backward-looking', not 'forward-looking'".
8. Explain, using the examples discussed in class, how selection can produce new traits (including complex traits) even though it can only act on existing variation.
9. What is the "random" element in natural selection? In what sense is evolution non-random? Is evolution progressive? Justify your answer.
10. Can natural selection produce perfect adaptation? Outline and discuss the constraints on selection.
11. Can a trait arise "for the good of the species"? Explain.

MUTATION AND GENETIC VARIATION

1. Describe the basic structure of DNA and briefly summarize the processes of replication, DNA repair, transcription, and translation.
2. Explain why the genetic code is called a triplet code. What is a codon? In what way is the code redundant?
3. Define the terms gene, locus, and allele.
4. Is all of the DNA in eukaryotic genomes used to build proteins? Explain. Briefly describe the structure of eukaryotic genes, being sure to define the terms intron and exon. What is mRNA processing?
5. What are point mutations? What causes them, and what are the different kinds? Which are more common, transitions or transversions, and why? Discuss the effects

of point mutations on fitness, using sickle-cell anemia to illustrate.

6. What is a loss-of-function mutation, and how (in general) are they used to calculate mutation rates? Does using this type of mutation accurately estimate mutation rates? Why or why not?
7. How common is mutation? Do mutation rates vary? If so, how, and why?
8. How does gene duplication occur? Why is this phenomenon important evolutionarily? What evidence do we have that gene duplication has occurred? Illustrate using the globin gene family.
9. Describe the likely origin of the *jingwei* mutation in *Drosophila*, including the evidence that duplication via reverse transcription is likely to have occurred and that the locus is functional in the species in which it occurs.
10. How do chromosomal inversions occur, and what is their significance? Be sure to include a brief discussion of linkage.
11. In what kind(s) of organisms is polyploidy common? How does it occur, and what is/are its evolutionary consequence(s)?
12. Outline the mechanisms discussed in class for determining genotypes. Given the appropriate data, be able to calculate allele frequency, mean heterozygosity, and percent polymorphism. How much variation, in general, seems to exist in natural populations?
13. Explain why the classic view was that genetic variation would be limited in natural populations? Briefly describe the two hypotheses for why natural populations are more variable than had been expected.

MENDELIAN GENETICS IN POPULATIONS 1: SELECTION AND MUTATION

1. Explain what is meant by the statement that the Hardy-Weinberg equilibrium equations are a null model.
2. What, specifically, do the Hardy-Weinberg equations describe (be sure to explain any conditions that are assumed by the model)?
3. Clearly explain what each of the following represents in the Hardy-Weinberg equations: p , q , P , Q , R . Write out and verbally describe the mathematical relationships among those variables and the conditions under which those

relationships hold.

4. Given genotype frequencies, be able to calculate allele frequencies. Given allele frequencies and assuming the conditions of Hardy-Weinberg are met, be able to calculate genotype frequencies.
5. When the conditions of the Hardy-Weinberg equations are met, what happens to allele frequencies in populations over time? What happens to genotype frequencies?
6. How can you test whether or not a population is in Hardy-Weinberg equilibrium? Given data in the form of genotype frequencies, be able to perform this test.
7. Under what condition(s) does selection lead to evolutionary change?
8. Describe Cavener and Clegg's work on selection in *Drosophila*. What did they test, how did they test it, and what were their results?
9. Will the current AIDS epidemic lead to an increase in the frequency of the CCR5- Δ 32 allele within the near future (the next 100 years)? Why or why not (be sure to explain the evidence for your conclusion)?
10. Describe Dawson's findings from his study of selection in *Tribolium* beetles. What was the "surprising" result of this study? Describe the mechanism responsible for this result and its general implication for selection acting on deleterious recessive traits.
11. Briefly discuss the differences between selection acting on recessive alleles and selection acting on dominant alleles.
12. Define heterozygote superiority and explain its effects on allele frequencies over time. Use sickle-cell anemia as an example in your explanation. Define balanced polymorphism and explain its relationship to heterozygote superiority.
13. Define heterozygote inferiority and explain its effects on allele frequencies over time. In what way are its effects similar to those of heterosis and in what way are they different?
14. What is frequency-dependent selection? Discuss Hori's studies on scale-eating fish and clearly explain how he supported the hypothesis that the balanced polymorphism in these fish was the result of negative frequency-dependent selection. What are the general effects of this form of selection?
15. Describe the reasoning used by U.S. geneticists to support compulsory sterilization to

reduce the incidence of “feble-mindedness” in the U.S. Explain, using Hardy-Weinberg principles, why this was a poor plan even from a “purely” evolutionary standpoint (i.e., without regard to basic principles of human rights).

16. Why is mutation considered to provide the raw material for evolutionary change? By itself, does mutation cause substantial evolutionary change?
17. Describe the mutation-selection balance model for the maintenance of deleterious alleles in populations. How can a mutation-selection balance hypothesis be tested? Use spinal muscular atrophy and cystic fibrosis to illustrate. What mechanism is most likely (given current evidence) to explain the relative abundance of deleterious CFTR alleles? Explain the evidence for this view.

MENDELIAN GENETICS IN POPULATIONS II: MIGRATION, DRIFT, NON-RANDOM MATING

1. Define migration in the context of evolutionary biology. Describe the one-island model of migration and explain its key predicted outcome.
2. Explain the role of selection and migration in the maintenance of polymorphism in banding patterns in island forms of the Lake Erie water snake. Be sure to discuss what pattern would be expected if either process were operating without the other.
3. Describe Giles and Goudet’s study of red bladder campion and the effects of migration on genetic diversity in these plants. Be sure to explain the natural history of their study site and the way(s) in which this created a good model system for the study of migration. What predictions did they make and how did they test them? What were their key findings?
4. Define the term “genetic drift” and give a verbal explanation of this process. Defend the statement that drift results in evolutionary change, but not in adaptive change. What is the general relationship between the effect of drift and population size?
5. Explain the founder effect using relevant examples.
6. If drift is allowed to continue over many generations, what changes are predicted in allele frequency and heterozygosity? Illustrate these patterns using Buri’s experimental study of fruit flies, Templeton et al.’s studies of Ozark collared lizards, and Young et al.’s plant studies.
7. List and briefly describe some of the different forms of non-random mating. Is non-random mating the rule or the exception for most organisms?

8. What is inbreeding and what is its effect on allele and genotype frequencies. Does inbreeding cause evolutionary change? Why or why not?
9. Define the term “inbreeding depression” and illustrate using human infant mortality and reduction in hatching success in great tits. What broad patterns have been revealed about inbreeding depression through experimental studies on angiosperms?
10. Describe the conservation history of the greater prairie chicken in Illinois and explain Westemeir et al.’s hypothesis for its decline even after reserves had been established and existing populations protected. Discuss how they tested their hypothesis and explain the results of those tests. Is the scenario presented by this species likely to be unusual for endangered species generally, or are the causes of its decline likely to apply to a number of species? Explain.

EVOLUTION AT MULTIPLE LOCI: LINKAGE, SEX, AND QUANTITATIVE GENETICS

1. Define “heritability”, clearly explaining what this quantity does and does not measure. Describe the relationship among heritability, phenotypic variation, genetic variation, and environmental variation.
2. How is narrow-sense heritability measured? Under what condition(s) is this method valid? Use Dmuth and Dhondt’s study of heritability in beak size in song sparrows to illustrate. Can heritability be measured for traits that are universal within populations? If not, does that mean that such traits are without a genetic component? Explain.
3. Explain the conceptual relationship between measuring differences in fitness and measuring the strength of selection. Describe how to calculate the selection differential and the selection gradient. Is one of these two measures preferred over the other? Why or why not? Justify your answer using the Grants’ study of beak size in Galápagos finches as an example (and be sure to address the important findings of that work).
4. Describe the conceptual basis of the response to selection (R). In biological (rather than mathematical) terms, explain its relationship to heritability and selection differential.
5. Describe Galen’s experimental studies of selection on flower size in alpine skypilots. Be sure to clearly identify the hypotheses she tested and the ways in which her experiments allowed her to use the techniques of quantitative genetics. What were her findings and conclusions?

6. Discuss the key flaws in Murray and Herrnstein's claim (in *The Bell Jar*) that differences in IQ between African Americans and European Americans is due to genetic differences between the two groups. Be sure to address the utility (or lack thereof) of using heritability to understand differences among populations. Ideally, what kind(s) of experiments could we do to test Murray and Herrnstein's claim directly? What kinds of outcomes might such experiments produce, based on work with other organisms?
7. Define the term "mode of selection." For each major mode of selection, describe the "direction" of selection, the relationship between fitness and values of the trait in question, and how the mean value and variance of the trait will change over time. Be sure you can identify each of these patterns graphically, and give at least one good example of each.
8. What is the "evolutionary puzzle" presented by the assumption that directional and stabilizing selection are the most common modes of selection? How is that puzzle resolved?

EVOLUTIONARY ANALYSIS OF FORM AND FUNCTION

1. What three key pieces of information do we need to know to reconstruct the evolutionary history of a trait? Compare and contrast the "historical" and "current function" definitions of adaptation. Which one is right? Explain.
2. What is "naive adaptationism"? How can it best be avoided?
3. Why are experiments particularly powerful tools in science? What are their disadvantages, if any? Use the example of Greene et al.'s study of wing markings and wing waving in tephritid flies to illustrate the major aspects of good experimental design. Be sure your explanation includes a clear statement of the hypotheses and predictions that were tested and the conclusions the investigators drew from their experimental work.
4. What is the fundamental difference between experimental and observational studies? Use Simmons and Scheepers' observational study of neck length in giraffes to illustrate how observation can be used to derive and test hypotheses about adaptation.
5. Using the observational evidence from the text, evaluate the hypothesis that garter snakes make adaptive choices when looking for nighttime retreats. Be sure to frame your discussion in terms of the general hypothesis, its logical alternatives, the specific predictions derived from the hypothesis, and the observations used to test those

predictions. Hint: Think of the data on the thermal properties of different refugia (burrows, thin rocks, etc.) as part of the background data/information used to make specific predictions.

6. What, in general terms, is “the comparative method”? Why is knowing the evolutionary relationships among species used in comparative studies necessary? Describe, verbally and graphically, Felsenstein’s method of phylogenetically independent contrasts. Why is this technique (or others like it) necessary in comparative studies? Illustrate your answer using Hosken’s study of testes size in flying foxes.
7. What is phenotypic plasticity? Using the data on variation in phototactic behavior in *Daphnia magna*, illustrate how to test the hypothesis that phenotypic plasticity is adaptive and has evolved. Be sure your explanation includes a discussion genetic variation in phenotypic plasticity and its role in hypothesis testing.
8. Using the data on flower size and pollination in *Begonia involucrata* and flower color change in *Fuchsia excorticata* as examples, explain the role of trade-offs and constraints in evolution. What general implications do these studies have for the study of adaptation?

SEXUAL SELECTION

1. Describe the “puzzle of sexual dimorphism” and explain how, in general terms, Darwin solved it. Defend the statement that sexual selection is simply a special case of natural selection rather than a separate process.
2. Explain how asymmetries in reproductive investment set the stage for sexual selection. In general, which sex makes the greatest reproductive investment? In general, what two forms does sexual selection take (and why)? What are the general exceptions to these “rules”?
3. Under what conditions might we expect male-male competition to be an important form of sexual selection? Describe Wikelski et al.’s studies of Galapagos marine iguanas and explain how they arrived at and tested the hypothesis that sexual size dimorphism is sexually selected via direct male combat.
4. What forms can male-male competition take besides combat? Give examples (including studies and evidence, as appropriate) of each. Describe the general “sneaky male” strategy and explain when it might be expected to be used.
5. Describe the “direct benefits”, “good genes”, and “sensory bias” mechanisms for female choice. In what important way(s) do the direct benefit and good genes hypotheses differ from sensory bias? Discuss the studies that have evaluated these

hypotheses and explain their findings. Are these mechanisms mutually exclusive?

6. In what kinds of plants might we expect to find sexual selection? In general, which sex makes the least investment in reproduction? Explain the asymmetry that results from this, and discuss how this asymmetry is predicted to affect flower structure.

MECHANISMS OF SPECIATION

1. Defend the view that species are real entities. Compare and contrast the morphological (typological and phenetic) and biological species concepts. What are the strengths and weaknesses of each? For what group(s) of organisms does each work well and for what groups does each work poorly. Why? Be sure to define all relevant terms. Is the red wolf a valid biological species? Why does the answer matter? Defend your answer.
2. Compare and contrast anagenesis (phyletic change) with cladogenesis. Which represents “true” speciation (i.e., produces an increase in the number of species)?
3. Outline the three basic steps of cladogenesis. Compare and contrast allopatric speciation with sympatric speciation in terms of the geographic distribution of diverging species proposed by each. What kinds of barriers to gene flow do allopatric speciation models propose? Define and give examples of both dispersal and vicariant events and explain how each can be tested using the examples in the text to illustrate. What kinds of barriers to gene flow do sympatric speciation models propose? Outline the basic process by which each can produce a barrier to gene flow, using relevant examples to illustrate your answer.
4. Explain the role played by genetic drift and natural selection in causing the genetic divergence of isolated populations. Discuss Mayr’s model of allopatric speciation by peripheral isolation. Does the current evidence support as important a role for genetic drift as he proposed? Explain. Using the example of *Rhagoletis pomella* to illustrate, describe how selection can promote genetic divergence of isolated populations. Be sure to include the experimental tests of the relevant hypotheses in your answer.
5. Describe Dobzhansky’s reinforcement hypothesis for the evolution of reproductive isolating mechanisms. What is the current evidence for the importance (or non-importance) of reinforcement? Outline the major reproductive isolating mechanisms as classified by Dobzhansky, being sure to define and give an example of each.
6. Discuss the range of outcomes that can occur when reproductive isolation is incomplete. Relate these outcomes to the concern some scientists have expressed over the potential for the evolution of “superweeds”. Are their concerns justified? Explain using Arriola and Ellstrand’s experiments on sorghum and johnsongrass to

support your answer.

RECONSTRUCTING EVOLUTIONARY TREES

1. In the most general terms, how is phylogeny reconstructed? What general kinds of evidence, what basic premise, and what basic reasoning are used?
2. Describe cladistic analysis by identifying the different “types of similarity” that can exist among characters and explaining which “types of similarity” are useful for inferring phylogeny. Discuss outgroup comparison and explain the problem presented by character reversal. How, in general, is this problem addressed? Illustrate your answer with the example we used in class, but be able to apply your understanding to other examples (hint: use the bird phylogeny in Box 13.1 as practice).
3. Given a cladogram, be able to identify/define tips, nodes, and sister groups. You should also be able to describe in words the pattern of relationship shown by the cladogram.
4. Examine fig. 2.5 (p. 30) and read the accompanying text. If elasmobranchs (sharks, skates, and rays) were used as the outgroup for an analysis of the evolution of lungs and swim bladders, how would the conclusions differ from Liem’s? Discuss the relevance of this difference for phylogenetic inference in general.
5. Discuss the kinds of data that can be used in phylogenetic analyses, including any advantages or disadvantages associated with each. How, in general, does the amount of variability in a character affect its usefulness for phylogenetic analysis?
6. Given the huge number of trees that can be drawn for even a relatively small group of organisms, how do investigators select the “best” tree? What criteria do they use and how, in general, are the criteria applied? Use examples as appropriate to illustrate your answer.
7. When a phylogenetic analysis is done and a cladogram (or other tree diagram) generated, is that the “final word”? Why or why not?
8. Define the terms systematics, taxonomy, and classification. Why is a uniform system of biological nomenclature important? What are the essential features of the biological classification system used today?
9. Compare and contrast cladistic (phylogenetic) and evolutionary (traditional) systematics in terms of the kind(s) of information they “store” in their classifications, the kinds of groups they consider legitimate to name formally, and the advantages and disadvantages of each. Which system is more commonly used today? Explain.

10. Use the case studies of coevolution between ants and fungi and HIV in dental patients to illustrate the different uses of phylogenetic analysis. For each, be sure to clearly identify the key hypotheses and predictions, and how evolutionary trees were used to test those predictions.

THE ORIGINS OF LIFE AND PRECAMBRIAN EVOLUTION

1. What is a ribozyme, and why, in general, was the discovery of this type of RNA so important to hypotheses about the origin of life? Explain the statement that RNA can simultaneously possess both a genotype and a phenotype, and why DNA and proteins cannot.
2. Describe the basic RNA World hypothesis and discuss the evidence that RNA is ancient, as predicted by this hypothesis.
3. Describe Beaudry and Joyce's experimental evidence that RNA can evolve. Defend the statement that a self-replicating population of RNA would have the essence of life even in the absence of cellular organization.
4. Why is the RNA-dependent RNA autoreplicase the Holy Grail for origins-of-life research? Describe Bartel et al. selective breeding experiments, and discuss their implications for the development of catalytic RNAs capable of self-replication.
5. What four major questions must be answered when attempting to reconstruct the advent of information-containing, self-replicating organic molecules? Discuss evidence from the Murchison meteorite and studies of the composition of the early atmosphere on Earth that simple organic molecules might have arrived on Earth from extraterrestrial sources. What are some of the critical arguments against this hypothesis?
6. Describe the Oparin-Haldane model for prebiotic evolution. Discuss the relevance of Stanley Miller's experiments on the prebiotic synthesis of amino acids and Juan Oro's experiments on the prebiotic synthesis and nitrogenous bases to this model. What difficulties remain with the hypothesis that the Earth possessed all the necessary ingredients and the appropriate conditions for the origins of life, and what precursors to the RNA World have been proposed?
7. Explain the hydrolysis problem with models of prebiotic biological polymerization. What solution have Ferris et al. proposed, and what evidence supports their hypothesis?
8. What advantages would cellular membranes have offered to early forms of life? What

evidence does the fossil record provide about the origin of cellular life? Discuss the primary challenge in using nucleotide sequence data to address this question, being sure to include a description of the characteristics necessary for a given gene to be useful for this type of analysis. In what ways does the small-subunit RNA meet the relevant criteria?

9. Describe the universal phylogeny developed by Woese and colleagues from rRNA sequences. How does the pattern represented by this phylogeny differ from that implied by the traditional five kingdom classification scheme? Discuss how the universal phylogeny (if correct) can be used to infer characteristics of the last common ancestor of modern life forms.
10. How do the Eucarya differ from Bacteria and Archaea? Discuss the endosymbiotic hypothesis for the origin of mitochondria and chloroplasts, including the evidence supporting it.

THE CAMBRIAN AND BEYOND

1. What is a fossil? Compare and contrast the four major types of fossils, with special attention to how the fossil is formed and the part(s) of the organism each preserves for study. In general, which are the most common, and why?
2. Describe the three types of bias in the fossil record and discuss the implications of these biases for our ability to gain useful information from the fossil record.
3. What, in brief, was the Cambrian explosion? What were some of the major morphological innovations that arose during the Cambrian explosion?
4. Describe the Ediacaran and Burgess Shale faunas and discuss their significance for our understanding of the events before and during the Cambrian. Describe the disparity between the fossil and the molecular data for the timing of deep branches in the phylogeny of animal phyla (including the kinds of evidence used to support each view).
5. Describe the ecological differences apparent between the Ediacaran and Burgess Shale faunas. Discuss the possible roles of increasing oxygen levels and predation pressure in the evolution of larger, more complex bodies, mineralized shells, novel locomotor systems, and diversification of feeding ecology during the Cambrian explosion.
6. Define and give two examples of adaptive radiation. Describe the key factors that seem to be involved in most adaptation radiations and give several examples of each.

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7. What, in general terms, is the impact hypothesis for the end-Cretaceous (K-T) extinction? Did this extinction event affect all groups of organisms equally? Explain.

 8. Memorize the Eons, Eras, and the Epochs of the Cenozoic. What are some of the major biological events that took place during the Paleozoic, Mesozoic and Cenozoic Eras?

HUMAN EVOLUTION

1. What is the first fossil evidence of primates in the fossil record? At what geologic time period did these animals live? Outline prosimian evolutionary trends during the Eocene. What is the fossil evidence for these trends?
2. Outline significant primate evolutionary trends during the Oligocene. What is the fossil evidence for this? What is the significance of the Y-5 pattern found in these fossils?
3. Outline the taxonomic and evolutionary relationships among humans, the great apes, and the other Old World primates. What line(s) of evidence support these relationships? Discuss the evidence for and against chimpanzees as the sister group to humans rather than to gorillas.
4. Compare and contrast the general features of the gracile australopithecines, the robust australopithecines, and early members of the genus *Homo*. What evidence suggests that bipedality arose early in our evolutionary history? Approximately when did brain size begin to increase?
5. Discuss the two phylogenies presented in Figure 16.11, with special attention to the pattern of ancestry each proposes and the specific predictions each suggests about future fossil finds. What major questions still remain about the ancestry of *Homo*, and what general conclusions can be drawn from the existing data?
6. List and briefly describe the major controversies about the taxonomy of various species of *Homo*. On what basic hypothesis do most paleoanthropologists agree? When and where do *H. ergaster/erectus* first appear in the fossil record; when and where does anatomically modern *H. sapiens* appear?
7. Describe the phylogenetic predictions of the African replacement and multiregional models of the evolution of modern *H. sapiens*. Describe the archaeological, paleontological and molecular evidence that has been used to test these models. Does this evidence provide strong support for one model over the other? Explain. On balance, which hypothesis do these studies support, and why?
8. When do the earliest complex stone tools appear in the fossil record? Discuss the paleontological and morphological evidence for and against an early *Homo* as the first maker of complex tools.
9. Discuss the evidence that the capacity for language and a fundamental grammar are innate and universal in modern humans, and that the language organ (i.e., the complex neural circuitry responsible for human language) is a derived modification of neural

circuits common to all primates. Outline the arguments and the evidence for both early and late origins of language in Homo. Does the existing evidence strongly support either hypothesis?

KIN SELECTION AND SOCIAL BEHAVIOR (Fall 2001)

1. List and briefly describe the four possible outcomes of interactions among individual organisms. Which of these are not likely to be encountered in nature, and why?
2. Explain why altruism is a central paradox of Darwinism. Discuss Hamilton's concept of inclusive fitness and discuss how this concept resolves the apparent paradox of altruism. Your answer should include Hamilton's rule, including a description of the terms of that equation. Compare and contrast direct and indirect fitness and clearly relate these to the process of kin selection.
3. What evidence suggests that alarm calling in Belding's ground squirrels has a fitness cost? Discuss Sherman's evidence that this behavior has evolved via kin selection (frame your discussion in terms of specific predictions and tests). If self-sacrificing behavior is directed at close relatives and results in indirect fitness gains, is it truly altruistic? Explain why or why not.
4. Under what conditions is helping at the nest usually found in birds? Why? Discuss Emlen and Wrege's evidence that helping at the nest results in inclusive fitness gains for helpers. Can you think of other benefits these birds might gain from helping?
5. Define eusociality and explain why this represents the epitome of altruism. Explain the haplodiploidy hypothesis for eusociality in hymenopteran insects and discuss the evidence for and against this hypothesis. Be sure your discussion includes specific predictions and tests. How does sociality in paper wasps differ from that in eusocial hymenopterans? Discuss the costs and benefits of each of the strategies employed by this group.
6. Describe the social system in naked mole rats and discuss the evidence that a combination of inbreeding and ecological factors explain the evolution of eusociality in this species.
7. Why is parent-offspring conflict expected to be particularly sharp in birds and mammals? Explain the principle of weaning conflict by discussing the costs and benefits of weaning from the perspective of a mother, one of several full siblings, and one of a litter of half-siblings. Discuss the evidence that harassment in white-fronted bee eaters are attempts by fathers to break up the nesting attempts of their sons in

order to recruit those sons to help at their own nests.

8. What is siblicide? Discuss Loughheed and Anderson's evidence that masked booby parents are more tolerant of siblicidal offspring than are blue-footed booby parents. What hypotheses might explain this difference? How would you test them?
9. Define reciprocal altruism. What kind of cooperation can this process explain, and what conditions are necessary for it to operate? Given those conditions, in what kinds of organisms might we expect to find it? Discuss Wilkinson's evidence that reciprocal altruism explains altruistic feeding behavior in vampire bats. Is reciprocal altruism really altruistic, as altruism is defined in this chapter? Why or why not?
10. Describe the basic social system in African lions. How do females defend their territories against females from neighboring prides? What kind of behavior is predicted to occur based on reciprocal altruism theory? What kind of behavior is actually observed? Why does this discrepancy exist? How could you test your answer?