KEY

BEFORE YOU START: WRITE YOUR NAME ON EACH PAGE!!!!

Read the questions carefully before answering to ensure that you fully understand what we are looking for. Answer the questions in sufficient detail to let us know that you fully understand the critical issues, but do not use the shotgun approach of throwing everything under the sun into your answer in the hope that something will hit the target. Good luck and wow us with your ecological knowledge!

PART A. Shorter answers, graphs or calculations. Your answers can be in point form.

1. Biogeography is the study of the geographic distributions of organisms. You win a fantastic trip to the southern continents and on your trip you notice a plant with a similar and distinctive morphology occurring in Australia, South Africa and South America. Without a field guide, you know nothing about the taxonomic status of the plant on the various continents (same species? closely related species? unrelated taxa?). Name three explanations that could account for the curious geographic distribution of these plants (a one or two word explanation is sufficient for each). **Briefly**, what critical information is needed to support each specific hypothesis? (6 points).

(1) Convergence (2) continental drift and (3) dispersal.
Need information on phylogenetic relationships and dispersal abilities:
Convergence: species are unrelated, dispersal not involved and not an issue
Continental drift: species are related, they are poor dispersers.
Dispersal: species are related and have dispersed (either on own or by humans).

2. Exponential population growth can be described by a simple model where time is a continuous variable: $N_t = N_o e^{rt}$. This equation can be easily altered to calculate the time that it takes for the population to double in size. Show, by manipulating this equation and substituting d (doubling time) for t, how one converts the above equation to obtain a measure of d. Show all of the steps, and don't just give the final answer. Recall that natural logarithm (ln) of $e^x = x$ (4 points).

Let d = doubling time
In the doubling time, d, the population will double, therefore $N_d = 2N_o$
With this:

$$N_t = N_o e^{rt}.$$
$$2N_o = N_o e^{rd}.$$
$$2 = e^{rd}.$$

taking natural logarithm of both sides

$$\ln 2 = rd$$
$$(\ln 2)/r = d$$

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3. You are one of the biologists in charge of conserving the relatively small population of grizzly bears in Yellowstone Park. On your annual bear counts, you notice that the population fluctuates, as reflected in your estimates of λ which tells you about population change across years. In good years $\lambda = 2.0$, in bad years $\lambda = 0.4$, and good and bad years occur with equal frequency. Your colleague insists that the bear population is in fine shape because the arithmetic mean of λ is 1.2 and plugging this value into the deterministic population shows that the population will grow over the long-term. Being a well-trained ecologist, you correct them and insist that a stochastic population model is needed here.

a). What is the fundamental difference between a stochastic population model and deterministic population model? (3 points).

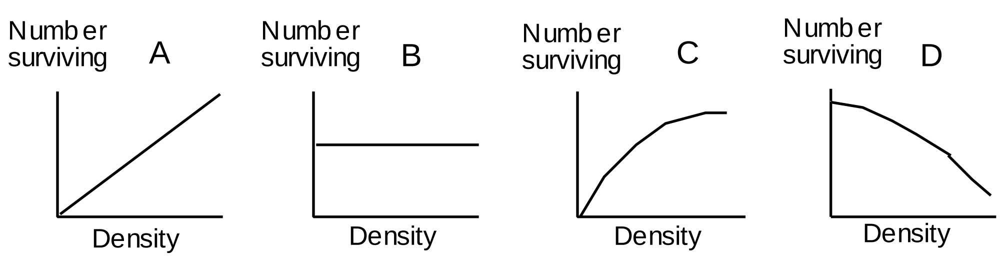
Stochastic models have random events (chance) built into them.

b). Even without running any model you can do a quick calculation with the above λ values to obtain the appropriate estimate of an 'average' λ value that accurately predicts long-term prospects for the bear population. Show this calculation. Is the population growing, stable or declining over the long-term? Why? (4 points).

geometric mean of λ, not arithmetic mean, tells us what population will do.
geometric mean of λ = square root (2.0 x 0.4) = square root (0.8)
square root of a number less than one is also less than one.
geometric mean of λ < 1, therefore population declining

4. Ecologists recognize a variety of types of density-dependence. Four of the following five types are represented below. Match the graphs to their correct name type, and indicate which type in the list is not illustrated by a graph. Carefully check the y axis and consider rates versus numbers (5 points).

a. __________ Allee effect
b. __________ Undercompensating density-dependence
c. __________ Overcompensating density-dependence
d. __________ Exactly compensating density-dependence
e. __________ Density independence



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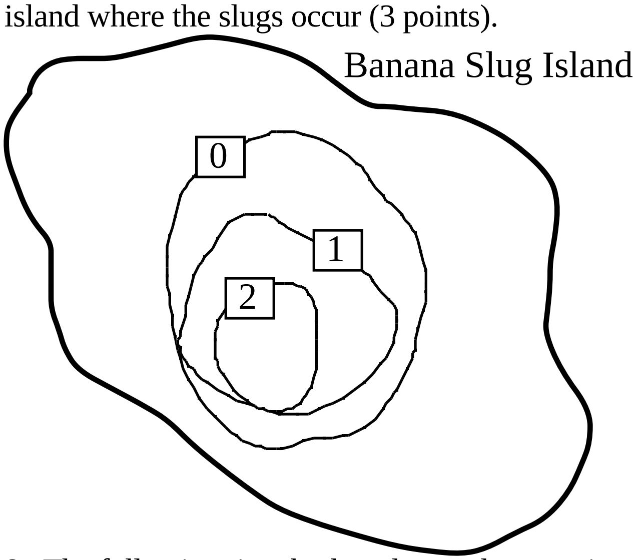
5. Patterns of sexual size dimorphism are interesting because they not only illustrate that body size is an adaptation, but that the sexes differ in the selection pressures (natural/sexual) that select for body size. Provide (i) one example of dimorphism where males are bigger than females and (ii) one example where females are bigger than males. In each case, name a selection pressure that typically differs between sexes and could account for the increased size of the bigger sex (4 points).

Elephant seals or other pinnipeds. Males bigger than females due to sexual selection.
Raptors, angler fish, crabs. Females bigger due to fecundity selection.

6. Outline the process of natural selection. Which part is ecological, and why? (5 points).

1. Phenotypic variation in a trait
2. Genetic basis ofvariation (heredity)
3. Better survival or reproduction associated with some of the variants (varition in trait associated with variation in fitness)
4. Change in phenotype/genotype over time (not sure I covered this sufficiently so we can be lenient with part 4.
Part three, phenotypic selection, is the ecological part of the process. Organisms that have traits that enable them to better 'solve' ecological problems (i.e. better survival or reproduction) will pass on more genes; thus natural selection selects for the phenotypes (traits) that are best at solving the ecological problems.

7. Below is a map of Banana Slug Island. Banana Slugs are common on parts of the island. However, the rate of population change of local populations (λ) varies with location. This variation can be plotted as a contour map of λ values, where each line denotes the outer limit to the specific λ indicated. Outside of the line (i.e. toward the water), λ is smaller, inside the line λ is $\geq$ than the value on the line. The slugs, being rather sluggish, show no dispersal; therefore only births and deaths on an extremely local level affect λ and we can thus use the contour maps of λ to predict where stable populations will occur. Shade in the part of the island where the slugs occur (3 points).



8. The following time budget data and energetic costs or benefits of activities is gathered for two types of strategies in a population of Anna's hummingbirds: (1) ***Territorial individuals*** and (2) ***Non-territorial individuals.***

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ACTIVITY	Costs of activity (Kcal/hour)	Time spent by territorial individuals in each activity	Time spent by non-territorial individuals in each activity
Foraging	2 Kcal/h	4 hours	8 hours
Sitting	1 Kcal/h	5 hours	2 hours
Fighting	3 Kcal/h	1 hours	0 hours

BENEFITS: The rate of food intake while foraging is:

6 Kcal/ hour for a **territorial** individual
4 Kcal/hour for a **non-territorial** individual

a) Based on the time budget data and the costs or benefits of each activity per hour of activity, determine whether the territorial or non-territorial strategy yields the highest **NET energy intake** (costs minus benefits) for a ten hour day. Show all of your calculations (4 points).

COSTS	**foraging costs**	**sitting costs**	**fighting costs**	**total costs**
Terr	**4h x 2**	**5h x 1**	**1h x 3**	**8 + 5 + 3 = 13 Kcal**
Non terr	**8h x 2**	**2h x 1**	**0h x 3**	**16 + 2 + 0 = 18 Kcal**

BENEFITS	**foraging intake**
Terr	**4h x 6 = 24 Kcal**
Non-terr	**8h x 4 = 32 Kcal**

Net energy gain per 10 hour day: **Territorial 24 - 13 = 11 Kcal**
Non terr 32 - 18 = 14 Kcal

Therefore non-territorial individuals get more net energy per day.

b) Optimal foraging models are useful tools for determining what fitness currencies are important to organisms. Based on your results above, name one currency that territorial birds could be optimizing relative to non-territorial individuals, and one currency that they are not, and show why with the results (4 points)?

NOT net energy rate: 11 < 14
Three possiblities:

- **Minimize metabolic costs (energy burned) 13 < 18**
- **Maximize time sit 5> 2**
- **Minimize time fight 0 < 1.**

9. If a physiological ecologist wanted to study the physiology of an organism that is temperature generalist (i.e. able to tolerate a broad range of temperatures), as opposed to a specialist, which biome should they head to, the tundra or tropical rainforest? Why? Justify your answer in terms of climatic variation. What simple astronomical fact about planet earth explains this variation? (4 points)

Arctic, because the range of climatic conditions is much more extreme due to much more pronounced seasons. Organisms have to deal with a much broader range of temperatures in the arctic. Tilt in the earth's rotational axis, relative to orbit around the sun, explains this variation in seasonality.

10. Why are experiments necessary? Illustrate by discussing a pattern (one discussed in class or make one up) that could lead to an incorrect conclusion about causal mechanism of

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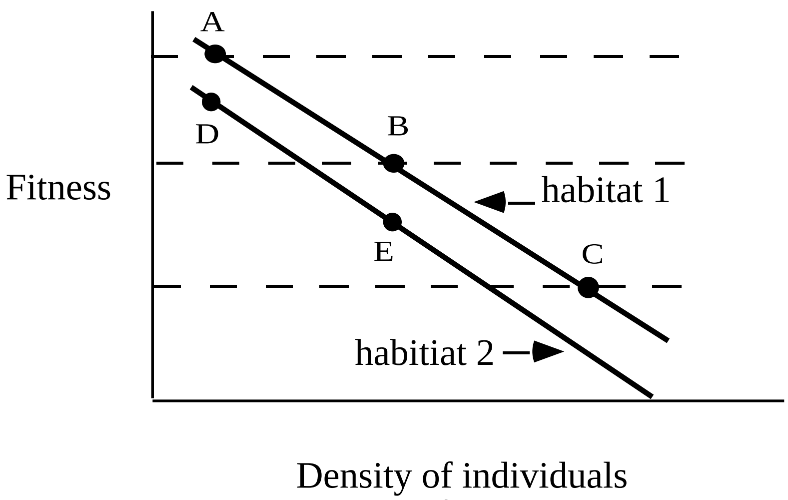
the observed pattern without an experimental investigation (point out how the pattern could mislead). Show how an experiment could clarify your conclusions (6 points).

Experiments are necessary to disentangle or uncouple spurios correlations or weak patterns.
Example: ducklings in bigger broods have better survival. Suggests safety in numbers.
But bigger broods might be on better territories or better females; better survival could reflect quality differences among females, not brood size effects. If randomize brood zise and quality via brood size experiments, can test brood size effects directly. There are tons of examples students could use: all the distributional patterns. Presence/absence could be due to any of 4 factors (dispersal, habitat choice, interactions, abiotic); we need experiments to uncouple. Any reasonable and logical pattern or confound the students suggest is fine.

11. The Ideal Free Distribution theory of habitat selection predicts how animals should settle in habitats of different qualities, given that they are free to settle where they choose and that they choose habitats to maximize their Darwinian fitness. This concept is illustrated by the graph below for two different habitats, a good habitat settled by individuals A,B and C (upper line) and a bad habitat settled by individuals D and E (lower line). The dashed lines serve only as reference lines to facilitate fitness comparisons among individuals.



a) What sequential order should the five individuals settle in the habitats according to the model. List the letters in the predicted order of settlement (i.e. 1st, 2nd, 3rd...) (4 points).
A D B E C
b) Ideal free settlement can lead to paradoxical patterns. When our five individuals have settled, what would we conclude about the quality of the two habitats if we were simply to compare the average fitness of the individuals in the two habitats? (2 points).

At equilibrium, fitness in better habitat 1 is actually lower than in territory 2 because of increased density. We would conclude that hab 2 was better.

(c) What experiment could you perform to accurately assess habitat quality? (2 points).
Control density; at lowest density (1 individual) the true differences are apparent.

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PART B. Answer 2 of the following 3 essay questions. 20 points each.

*** ONLY ANSWER 3 QUESTIONS!!!*****

1. Optimality is a useful way of studying adaptation, and it has been widely used to study foraging behavior. Some critics have viciously attacked the approach by suggesting that it is stupid to expect animals to be perfectly optimal at what they do. Counter this attack with a discussion of optimal foraging, outlining the general approach and goals. Provide support for your discussion with examples, and these examples can either be case histories that we discussed in class or, if you prefer, potential experiments that you propose on your own.

NOTE: students do not have to have all of the examples I outline below, but a complete answer should contain the generalities I outlined in the first paragraph. Be harsh on students who state that the approach is about finding out if animals are optimal or that they are optimal.

The goal of optimality is *not to test* whether animals are *optimal*. Goal is to figure out if and how natural selection has shaped evolution of traits or in the case of foraging, the decisions animals make, *within the set of possibilities* shaped by *constraints* or *trade-offs*. The approach is based on the assumption that natural selection will optimize traits that maximize fitness, given the range of traits that are biologically feasible given trade-offs and constraints. *We therefore start by choosing a fitness currency that we believe is being optimized, determine the set of possible traits or decisions that are possible given constraints/trade-offs, and then predict what decision or trait we should see under a specific situation.* If the model fails to predict the behavior of an organism, we can build a new model that either incorporates a new fitness currency or considers new constraints. *Thus, the approach not only allows us to identify fitness currencies that are important to the organisms as well as to identify constraints and trade-offs.*

The graphical marginal value theory, tested by the field study of starlings, illustrates many of these ideas. It is assumed that the birds are maximizing the rate of food (energy) delivery to their chicks (more food, more babies, higher fitness) and the question is how long to stay in a patch. Travel time and foraging rate in patch are constraints we set. Students may show the marginal value theorem in graphical form; they should point out the above aspects (currency, rate, and how to optimize) with reference to the model. Key points: foraging rate in patch shows diminishing returns, time is travel time plus foraging time, solve by straight line (slope is energy/ time, i.e. rate), we maximize rate (slope) by tangent to foraging curve (i.e. within constraints set by model). Field study of starlings produced diminishing curve by dispensing rate of worms at increasingly slower rate to feeding tray. Move tray different distances, predict actual number of worms they should take if they are maximizing energy rate. Excellent fit between observed at predicted; conclude have identified a fitness currency that selection shapes decisions to optimize (2) starlings can keep track of time and rate of energy they get in a patch. WE DO NOT CONCLUDE that starlings are optimal.

Risk-sensitive foraging is one example that shows how currencies can differ; variance in energy return is a different currency than just mean rate. (Points deducted if refer to risk in terms of predation). Can test by offering low variation and high variation rewards and test preference. Sometimes shrews (bees, small birds) avoid risky reward, sometimes prefer. Has to do with energy balance and need for the big payoff. Illustrates decisions for different currencies under different contexts.

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Study of territoriality in sunbirds nicely shows optimality approach. Question was why defend same number of flowers on a territory while territory size varied so much. Can test by constructing mathematical energetics models, looking at how different currencies and behaviors change with changes in flower number, and then compare theoretical predictions with observed behavior of sunbirds. Excellent fit with one currency, minimize metabolic costs (or gross energy spent), pretty good fit with maximize time sitting, very poor fit with maximizing net energy or ratio energy costs: benefits. We have learned what currencies seem to be important to territorial sunbirds, and can guess why (longterm survival important, no kids to feed so Max Energy Rate less important).

Finally, some students may refer to the energetics study of why be territorial. This is cost/benefit approach and we seek to show that energetic benefits exceed costs (i.e. territories can be economically defended (Ben > Costs). One problem with this is we do not know how benefit specifically. Study above on optimal territory size answered that questions.

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2. Habitat selection is one explanation for why individuals of a species are found in some areas (i.e. some habitats) but not others (i.e. other habitats). Outline an experimental design and experimental result that could confirm that habitat selection does affect the distribution of a species. The question "why do animals show habitat preference" can be examined on both a proximate (learned or innate?) and an ultimate (evolutionary fitness) level. Outline an experiment that one could perform to address the proximate question, and another that one could perform to examine the ultimate question. In each case, point out how you would interpret the results of the experiment.

EXPERIMENT: Transplant experiment: transplant animal to habitat it is absent from. If it leaves, on its own without the influence of other species (predators, competitors) this suggests that habitat preference might explain the distributional pattern by habitat.

BUT: we need to be sure animal leaves the habitat and returns to habitat it prefers. If we track the animal and it returns back to the appropriate habitat, this is strong evidence.

Two forms of weaker evidence:
(1) The animal does not persist in the habitat, but we do not know where it goes. We need to know why it does not persist. Did it die (predation), was it chased out by competition, or did it choose to leave without interacting with other species?
(2) If it chose to leave, we need to be sure that it returned to its 'right' habitat (i.e. where it typically occurs) and wasn't just moving to another area in the 'wrong' habitat. Perhaps transplants cause animals to move away from where they were dropped off. Some sort of control for movement after transplant might sort this out; ie. transplant animals within the right habitat and see if animals move after transplant within right habitat.
AGAIN: best information is to observe animals, ensure that are not chased out by competitors, also track animals and ensure that they return to right habitat.

PROXIMATE: Is the preferred habitat learned or innate?
Strong Test For Innate: **Raise naive offspring in captivity with no exposure to either of the habitats. When they are mature, offer them a habitat choice experiment with two habitat types, and see if they show an innate preference for the appropriate habitat. If we see them spending a disproportionate amount of time in the correct habitat, innate recognition is supported. Random habitat choice implicates learning, but is weak evidence because it is not direct evidence.**
Strong Test For Learned: **Raise naive offspring in each of the habitats, if as adults they prefer the habitat they have early experience with, habitat preference is learned.**

In reality, it could be both. (1) Learning modifies innate: e.g. strong test for innate shows innate in absence of exposure, but strong test for learned shows learning component.
(2) Interaction between innate and learning components, so that animals show a stronger learning response to the right type of habitat.

ULTIMATE: Transplant individuals to each of the two habitats and observe their fitness. If habitat preference has evolved due to fitness differences, then individuals in the preferred habitat should have higher fitness (better survival, more babies).

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3. The metabolic rates of organisms scales with body mass in a way that has profound consequences for the pace that large and small animals live their lives. This scaling also has a huge impact on the ecological lifestyle that is feasible. Show why this is so by contrasting the allometry of **whole organism metabolic rate** and **mass specific metabolic rate**. Be specific about allometric slopes (b). Then, given that energy reserves (fat stored) scale to body size with an allometric slope of 1 (i.e. scales M^1), show how endurance time (time an organism can live of stored reserves) scales with body mass and why. Show how these relationships account for the drastic differences in the lifestyles of whales versus shrews.

(A complete answer should provide some background on allometry and slopes, as is done in the first paragraph. Students may have this information sprinkled throughout, where appropriate)

What allometry is: study of relationship between body size (mass, M) and various biological variables (physiological, life history). Uses the comparative approach, comparing across individuals within a species or among species. In arithmetic scale, these relationships follow a power curve ($Y = aM^b$). When converted to a log-log scale, these power curves become linear (log y = log a + b log M). The slope of the line, b, is all important and reveals the proportional change in Y relative to body mass M. If b = 1, the changes are proportional, if b > 1, then Y increases faster than mass, if b < 1, then Y increases more slowly than mass. As long as b > 0, Y increases as M increases. Only when b < 0 does Y actually decrease with increases in M.

Metabolic rate is the rate at which the body burns energy, and is measured by volume of O_2 burned per unit time. Allometry of metabolic rate per whole organism ($\dot{V}O_2$ per organism) scales with $M^{.75}$ This means that metabolic rate increases more slowly than mass. Larger animals burn more *total* energy per unit time, but *relatively* less. This is most easily shown by converting whole organism metabolic rate to *mass specific* metabolic rate. To do this, we divide $M^{.75}$ by M^1 (since mass = M^1), which shows that mass specific metabolic rate scales with body size $M^{-.25}$. These patterns are particularly clear when we examine these relationships on arithmetic plots. Whole organism metabolic rate shows a diminishing curve relationship, mass specific metabolic rate decreases with increases in M, and the decrease is extremely steep near the limit to small size (shrews). Thus, the cost of maintaining a gram of shrew tissue is extremely high compared to a gram of elephant or whale tissue: *size brings efficiency*! Elephants and whales still need more *total* energy. However, the relation between efficiency and size has big implications for the length of time animals can live of fat stores.

Endurance time on stored reserves is simply the amount of stores divided by the rate of consumption of the stores (i.e. metabolic rate). We are interested in the endurance time of the *whole organism*. Therefore endurance time scales M^1 /$M^{.75}$ i.e. scales $M^{1 - .75}$... scales $M^{.25}$. This means that endurance time increases with increased body size. Shrews would burn stores at an incredible rate and have very low endurance time: they have to eat constantly and need things like torpor to survive the night or cold spells (i.e. they drop temperature and metabolic rate to save energy). In contrast, whales have enormous endurance times, as reflected in the annual cycle of southern fin whales. These whales forage for 4 months on superabundant krill during the Antarctic summer. Krill is very seasonal, given that we are in a polar biome, so the food is only available for the 4 months). The whales put on blubber (fat stores), migrate to warmer areas to the north, and last the next 8 months primarily on stored reserves. Energetic calculations , based on

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allometric predictions, confirm that they can last for 8 months on the amount of blubber they store.