# An Ecology Problem Book

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**INTRODUCTION**

This problem book has many objectives:

- To get you to think about the course each night: do not wait until the last minute to begin working on the problems.
- To get you to deal with data. Statistics courses that you take in the future will be more meaningful once you understand the kinds of data that arise in ecological studies.
- To get you to be more comfortable with theoretical and quantitative methods. Not every ecologist uses those methods, but one should not be put off by them.
- To familiarize you with material as it appears in the professional literature.

Many questions are open-ended. In part this is because there is no "right" answer and in part because you should think widely and broadly about what the problems mean.

In problems involving mathematics (mainly algebra -- although there are cases in which elementary calculus is used) the quality of mathematical exposition (i.e. can the reader follow the steps, do you write full equations, etc.) matters. Graphs <u>must</u> be done either on graph paper or using statistical software. No credit will be given for problems involving graphing that are done on regular notebook paper. Some sections contain advanced material, appropriate for graduate sutdents. Most of the material is appropriate for undergraduate students.

In problems involving verbal answers, the quality of your presentation (i.e. full sentences, sentence structure, choice of words) matters. In either case, when answering questions, be specific: points will be deducted for irrelevancies in your answer.

Advanced problems are intended for students who have taken an advanced undergraduate course with me or for graduate students.

**Acknowledgements:**

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## ECOLOGICAL CHOPS

### From Introductory Biology

1. Order the geological time scale for the following eras and periods. Indicate whether each is an era or a period

Cambrian
Cenozoic
Cretaceous
Devonian
Jurassic
Mesozoic
Missippian
Ordovician
Paleozoic
Pennsylvanian
Permian
Quaternary
Tertiary
Triassic

2. What are the differences between spiders and insects?

3. Tuna are a fish but warm blooded. How can that be?

4. Diapause hormone in the silk moth *Bombyx mori* has the following structure:

Thr-Asp-Met-Lys-Asp-Glu-Ser-Asp-Arg-Gly-Ala-His-Ser-Glu-Arg-Gly-Ala-Leu-Cys-Phe-Gly-Pro-Arg-Leu$NH_2$

i) What is diapause?
ii) What is the DNA code for this hormone?
iii) In which spot of the DNA code would you expect the most variability and why?
iv) Give an example showing how the same hormone could be coded by two different DNA sequences.

5. Imagine a single locus in a diploid organism. If there are only two alleles A and B at this locus, there is only one kind of heterozygote (AB). If there are three alleles, A, B and C, there are three kinds heterozygotes (AB, AC, and BC).

i) How many kinds of heterozygotes are there for 4,5, 6 and 7 alleles?

ii) How many homozygotes are there for n alleles?

iii) Plot the number of heterozygotes vs. the number of alleles and the number of homozygotes vs. the number of alleles. What inferences can you make from this plot?

6. Methanogenic bacteria are characterized by their extraordinary way of collecting energy from the environment. They form methane by reducing carbon dioxide and oxidizing hydrogen.

i) What is the formula for methane?

ii) Write down the balanced metabolic reaction

iii) Estimate the energy gain from this reaction.

7. When wood burns, the carbon and hydrogen in the wood combine with oxygen to produce water and carbon dioxide. What is the balanced chemical reaction?

**From High School Mathematics**

1. The Fibonacci series is often used to describe plant morphology (e.g. R.V. Jean. **Phyllotaxis. A systematic study in plant morphology**, Cambridge University Press, 1994). It is defined as follows

$$x_1 = 1, \quad x_2 = 1, \quad x_{n+1} = x_n + x_{n-1}$$

Write out the first 10 terms in the Fibonacci series.

2. On graph paper, plot the data points (1,4), (5,4), (1,8), (5,8).

i) Suppose that the data were measured without error. Draw the best line that approximates the data. What is the slope of this line.

ii) Now suppose that x-values are measured perfectly, but that you have no confidence in the y-values. Draw the best line that approximates the data. What is the slope of this line.

iii) Now suppose that y-values are measured perfectly, but that you have no confidence in the x-values. Draw the best line that approximates the data. What is the slope of this line.

iv) Repeat parts a-c, except assume that the points are (x,y), (x+u,y), (x,z) and (x+u,z+s) where x, y, u, z, and s are all positive.

3. A parasitic wasp has a 60% chance of producing a daughter (fertilized egg) on the next oviposition and a 40% chance of producing a son (unfertilized egg).

i) Suppose that she lays three eggs in a row. Draw the tree showing the possible outcomes and assign chances to each.

ii) Suppose that she lays four eggs in a row. Do the same.

4. A 8 kg salmon has Gonadal-Somatic-Index (GSI) of 14%, where GSI is 100 times the gonadal mass divided by the gonadal mass plus the somatic mass. What is the gonadal mass?

5. Solve $x^2 + 6x + 5=0$ by completing the square.

**Advanced Material**

1. Normally distributed error is used in linear regression and the diffusion model of animal dispersal is based on the normal density. The normal probability density with mean m and variance at is

$$f(x,t) = \frac{1}{\sqrt{2\pi a t}} \exp\left(-\frac{(x-m)^2}{2at}\right)$$

where $\exp(x)=e^x$.

i) What does this distribution look like in general and what is the interpretation of f(x,t)?

ii) What is $\int_{-\infty}^{\infty} \exp\left(-\frac{(x-m)^2}{2at}\right) dx$?

iii) What happens to f(x,t) as t-->0? How do you interpret this result?

iv) Show that f(x,t) satisfies the following partial differential equation (which is called the diffusion equation)

$$\frac{\partial f}{\partial t} = \frac{a}{2}\frac{\partial^2 f}{\partial x^2}$$

2. In the development of the marginal value theorem, we will use gain functions G(t) that depend on residence time in patches. Two possible gain functions are

$$G(t) = 1 - e^{-kt}$$

$$G(t) = \frac{rt}{rt + t_0}$$

where k, r, and $t_0$ are constants. Find the derivatives of these two functions.

3. The binomial distribution for k successes in N trials is

$$p(k,N)= \binom{N}{k} p^k(1-p)^{N-k}.$$

i) What does the notation $\binom{N}{k}$ mean?

ii) What is p(0,N)?

iii) Derive an equation that relates p(k+1,N) and p(k,N).

iv) Write a computer program to evaluate the terms of the binomial distribution.

4. The Poisson distribution for k encounters when the encounter rate is r is $p(k) = \frac{e^{-r} r^k}{k!}$

i) What is p(0)?

ii) What is $\sum_{k=0}^{\infty} \frac{r^k}{k!}$

iii) Derive an equation relating p(k) and p(k-1).

iv) Write a computer program to evaluate the terms of the Poisson distribution.

## THE SEARCH FOR PATTERN

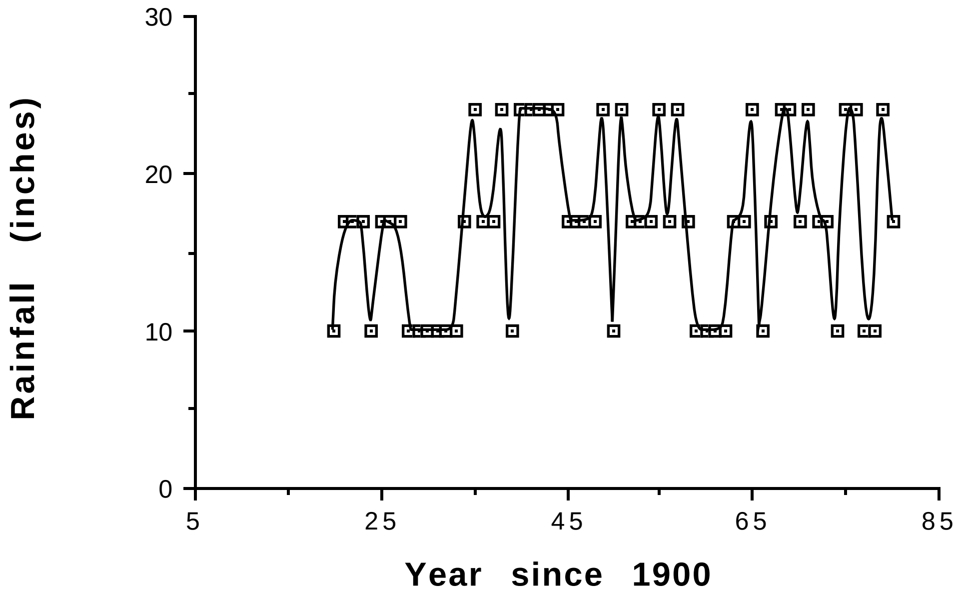
1. By combining data of Tramer and Whittaker, we can relate plant productivity and the number of different species of birds in different habitats

| Habitat Type | Approximate Productivity ($g\ m^{-2}\ yr^{-1}$) | Average Number of bird species |
|---|---|---|
| Marsh | 2000 | 6 |
| Grassland | 500 | 6 |
| Shrubland | 600 | 14 |
| Desert | 70 | 14 |
| Coniferous forest | 800 | 17 |
| Upland deciduous forest | 1000 | 21 |
| Floodplain deciduous forest | 2000 | 24 |

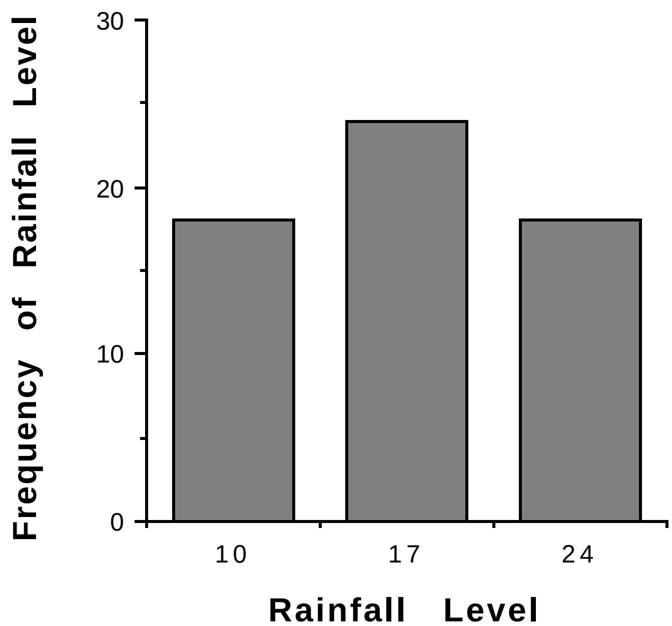
i) Make a plot of number of bird species (ordinate) vs. productivity(abcissa).

ii) What inferences can you draw from the plot?

2. In an appendix to his book **The Fisherman's Problem**, McElvoy gives rainfall data in Sacramento. For presentation, I have put the data into three categories: 10 inches of rain/year, 17 inches/year and 24 inches per year. The time course of the rainfall over about a 50 year period then looks like this:



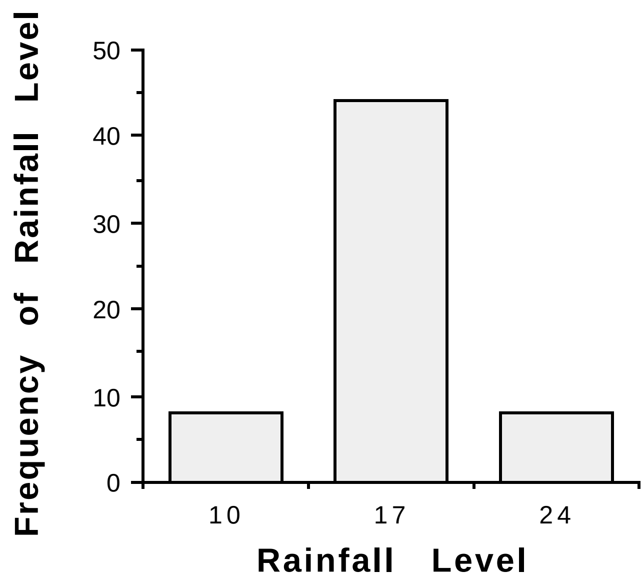

These data can be summarized as frequency distributions:



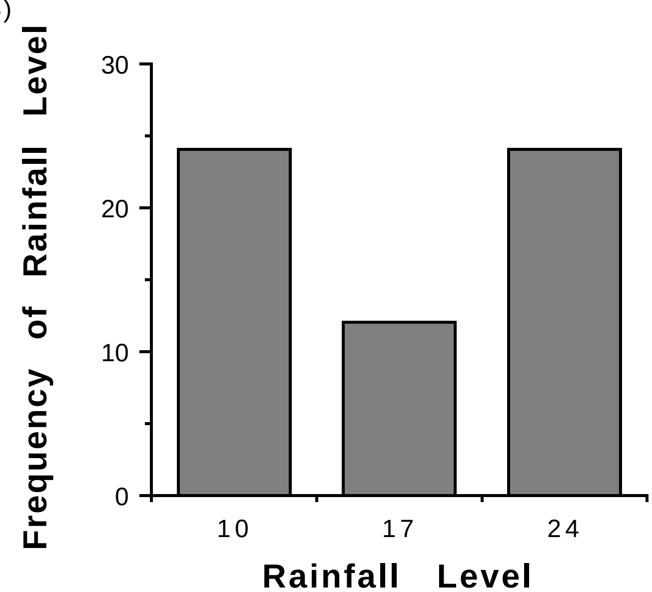

i) What is the "average" rainfall according to this figure? The weather people usually report this as "normal". Is that a good choice of word?

Consider two alternative possible frequency distributions for rainfall:

A)




B)




Both of these have average rainfall 17 inches/year.

ii) What are the differences in the physical environments for panels A and B? How might you characterize them. You may use statistical jargon if you want to, but be certain that you know what you are talking about and that you compute appropriate quantities.

iii) What different kinds of characteristics would you expect for organisms living in the two different kinds of environments?

iv) Return to the original time series of rainfall data (the first figure in this problem). Do the frequency distributions shown after it tell the entire story?

3. R.T. Paine (1980) studied the geographic variation in the diet competition of the predatory sea star. A simplified version of the data is shown below:

| Prey taxa | Proportion of Prey in diet at Punta Baja Mexico | Monterey Bay California | Friday Harbor Washington | Torch Bay Alaska |
|---|---|---|---|---|
| Mytilus mussels | .30 | .17 | .12 | .80 |
| Barnacles | .55 | .60 | .51 | .18 |
| Gastropods | .10 | .13 | .29 | .02 |
| Chitons | .03 | .04 | .07 | 0 |

What patterns can you discover in these data? What ideas do the patterns suggest?

4. Twenty years ago, a small fish was introduced to three different ponds in a reserve near in Sacramento. No fishing is allowed in any of the ponds. The populations (number of individuals) have been monitored since then:

| Years | Population in Pond #1 | #2 | #3 |
|---|---|---|---|
| 1 | 50 | 50 | 50 |
| 2 | 60 | 112 | 125 |
| 3 | 69 | 78 | 31 |
| 4 | 77 | 120 | 95 |
| 5 | 84 | 60 | 109 |
| 6 | 89 | 120 | 79 |
| 7 | 92 | 60 | 128 |
| 8 | 94 | 120 | 20 |
| 9 | 96 | 60 | 68 |
| 10 | 97 | 120 | 133 |

| | | | |
|---|---|---|---|
| 11 | 98 | 60 | 1 |
| 12 | 98 | 120 | 3 |
| 13 | 98 | 60 | 11 |
| 14 | 98 | 120 | 40 |
| 15 | 98 | 60 | 112 |
| 16 | 98 | 120 | 71 |
| 17 | 98 | 60 | 132 |
| 18 | 98 | 120 | 5 |
| 19 | 98 | 60 | 19 |
| 20 | 98 | 120 | 65 |

i) Make three separate plots of population size (ordinate) as a function of time (abcissa).

ii) What can you infer about the three different populations?

iii) For Population #3, now make new plot of the population in year t+1 (ordinate) versus the population in year t (abcissa). Does this tell you anything more than the previous graph?

5. In his article "The nature of colonization in birds" published in **Evolution and the Diversity of Life. Selected Essays**, Ernst Mayr gives data on the introduction of bird species on some islands and in Australia:

| Location | Native Species | | Introduced Species | |
|---|---|---|---|---|
| | Living | Extinct | Successful | Unsuccessful |
| New Zealand | 79 | 38 | 34 | 60 |
| Hawaii | 28 | 10 | 44 | 47 |
| Lord Howe | 10 | 7 | 6 | 2 |
| Bermuda | 6 | 0 | 7 | 1 |
| Sydney County, Australia | 204 | 0 | 15 | 35 |

Make plots of i) the chance of successful invasion vs. living species and ii) the chance of successful invasion vs. the total number of species (living + extinct). Interpret your results.

6. Whalen and LaBar (Canadian Journal of Fisheries and Aquatic Sciences 51:2164-2169) studied the survival of Atlantic salmon fry as a function of density (number/100m$^2$) Some of their results are shown below:

| Density at Age-0 | | Density at Age-1 | |
|---|---|---|---|
| 1989 | 1990 | 1989 | 1990 |
| 8 | 12 | 1.9 | 3.2 |
| 17 | 25 | 4.2 | 3.0 |
| 13 | 50 | 2.4 | 4.9 |
| 11 | 50 | 3.3 | 2.9 |
| 15 | 25 | 3.5 | 3.2 |
| 30 | 12 | 3.9 | 4.3 |
| 16 | 50 | 1.8 | 4.3 |
| 11 | 12 | 3.0 | 3.9 |
| 9 | 25 | 1.5 | 3.0 |

What pattern do you discern relating density at age 0 and density at age 1? How might this be explained?

7. When I taught ecology at UC Davis in Spring 1996, Alana Goodman, Tina Gutierrez and Camilla Kallin conducted an experiment in which they measured the number of species as a function of area at a site on the UCD campus. (This experiment is described later in the **Problem Book**.) The unit of area is one sheet of 8.5" x 11" notebook paper and their data are as follows:

| Area (notebook sheets) | Number of species |
|---|---|
| 1 | 7 |
| 2 | 7 |
| 3 | 9 |
| 4 | 10 |
| 5 | 12 |
| 6 | 13 |

i) Make a plot log the number species vs. the area and estimate the slope of the best-fit line (you can fit this line by eye). Use it to predict the number of species in an area of 10 notebook sheets.

ii) Repeat the plot using log(number of species) vs. log(area). Interpret the slope. Make the same prediction about the area of 10 notebook sheets and compare this with your previous result.

8. In 1997, Roger Hewitt, Valerie Loeb and Völker Siegel published information relating a recruitment index of southern ocean krill (*Euphausia superba*) to an environmental index (ice cover). Here are the data

| Year | Index | |
|---|---|---|
| | Environment | Recruitment |
| 1979 | 5.29 | 0.07 |
| 1980 | 6.43 | 0.55 |
| 1981 | 4.9 | 0.75 |
| 1982 | 5.12 | 0.66 |
| 1983 | 3.9 | 0.11 |
| 1984 | 4.48 | 0.21 |
| 1985 | 4.15 | 0.17 |
| 1986 | 6.77 | 0.63 |
| 1987 | 5.79 | 0.3 |
| 1988 | 3.76 | 0.28 |
| 1989 | 2.56 | 0.05 |
| 1990 | 4.35 | 0.1 |
| 1991 | 5.33 | 0.58 |
| 1992 | 4.27 | 0.01 |
| 1993 | 3.91 | 0.02 |
| 1994 | 4.86 | 0.14 |
| 1995 | 5.08 | 0.62 |

The environmental index is measured over the winter. The recruitment index is measuring during the spring and reproduction takes place during the fall.

That is, you can imagine a time-line like this (S=spring, F = fall, W = winter, E = environmental measurement, R = reproduction, I = recruitment index):

| | | | | | |
|---|---|---|---|---|---|
| W | S | F | W | S | F |
| E | I | R | E | I | R |

There are two hypotheses (at least) regarding these data:

$H_1$: The environment affects the population through the fecundity and reproduction of adults.

$H_2$: The environment affects overwinter survival of the newest age class.

i) Formulate these two hypotheses as correlations between an environmental variable and the recruitment index.

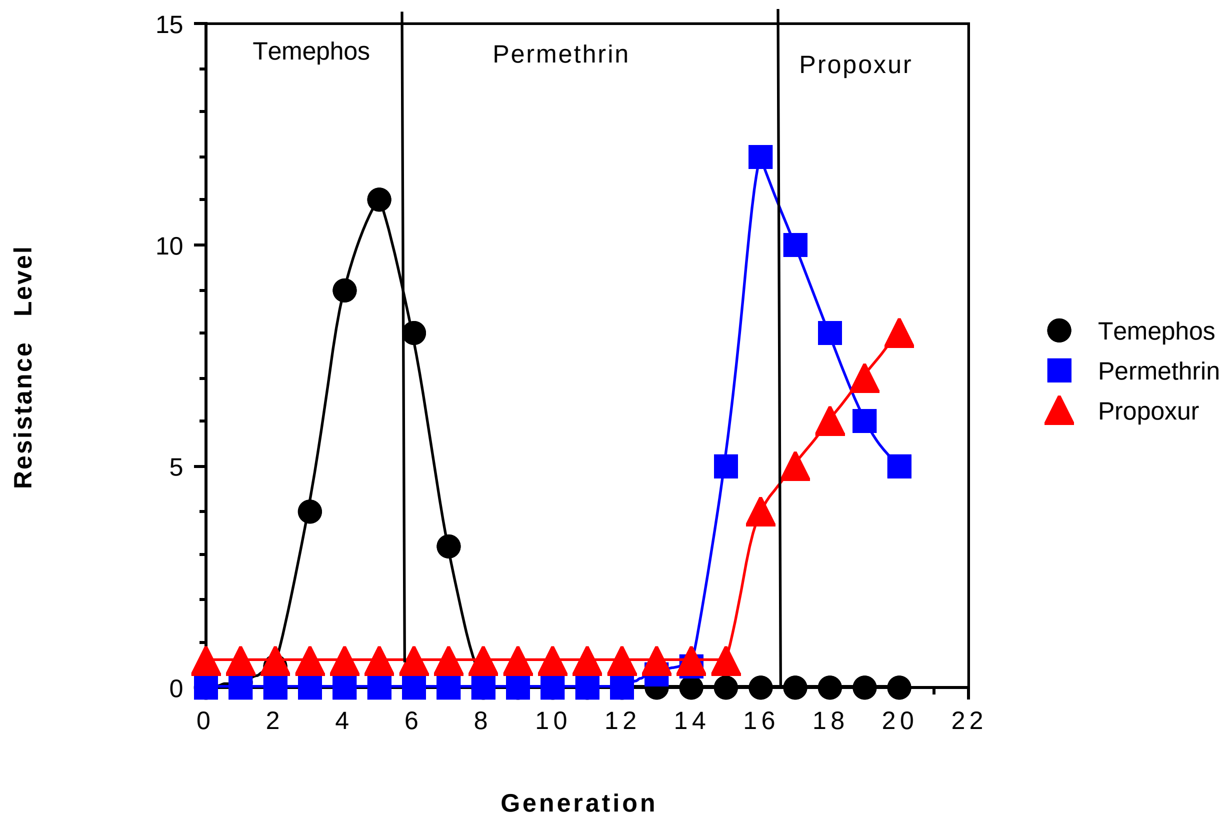
ii) Investigate each of these hypotheses statistically. Can you make definite statistical conclusions about either of them?

iii) What biological and conservation conclusions can you draw from this?

## DARWINIAN PARADIGM

1. Professor G. Georghiou at UC Riverside studied the development of resistance in mosquitoes during selection by three different insecticides (temephos, permethrin or propoxur). The results are shown below:

**Resistance Leve vs Generation during Three Selection Regimes**




That is, in the first period of selection, temephos alone is used to select, but resistance to all three is measured. In the second period of selection, permethrin is used alone, and in the third period of selection propoxur is used alone. Provide a selectionist explanation of what is happening here. Be certain to highlight what you consider to be the most interesting aspects of the data.

2. Consider the following situation concerning insecticide resistance. Assume that individuals are haploids and that resistance is conferred by the R gene, with the alternative being the r gene. Assume that when individuals are sprayed the survivorship of R types is 90% and

of r type is 20%, that each surviving individual makes 10 offspring and that the initial number of R types is 2 and of r types is 50. Plot the number of R types, r types and the fraction of the population that is R for 100 generations, using time steps of 5 generations.

3. Johnson and Abrahams (Canadian Journal of Fisheries and Aquatic Sciences 48:243-247, 1991) studied the foraging behavior of wild and hatchery-wild hybrid juvenile steelhead trout *Onchorhynchus mykiss*. They paired fish according to weight and length and then observed whether the fish foraged in a risky area or a safer area. Some of their results are shown below:

| Replicate | Length (mm) | % of Foraging Time in Risky Area<br>Hybrid Fish | <br>Wild Fish |
|---|---|---|---|
| 1 | 4.3 | 10.9 | 3.6 |
| 2 | 4.5 | 22.6 | 12.2 |
| 3 | 4.5 | 2.5 | 2.5 |
| 4 | 4.9 | 1.5 | 1.0 |
| 5 | 6.6 | 7.2 | 1.8 |
| 6 | 5.9 | 1.2 | 0 |
| 7 | 6.8 | 16.8 | 29.8 |
| 8 | 6.2 | 10.4 | 4.5 |
| 9 | 8.0 | 6.5 | 2.4 |
| 10 | 7.4 | 8.1 | 2.6 |

i) Interpret these results, comparing foraging behavior of hybrid and wild fish in a Darwinian perspective.

ii) Can you make any inferences about the relationship between length and foraging behavior?

4. Are the following accurate assessments of evolution by natural selection:

i) Great tits (*Parus major)* occupy hedgerows and forests in Europe. Males maintain territories around their nest sites. These territories prevent overcrowding in the nesting habitat, so that resources are not depleted beyond what the population needs to survive and reproduce at optimal levels.

ii) California fuchsia (*Eplobum canum*) is pollinated primarily by hummingbirds such as Anna's hummingbird *Calypte anna*. Hummingbirds frequently move from plant to plant to increase the cross-pollinaton of fuschsia, which increases the seed set of the individual fuchsia plants.

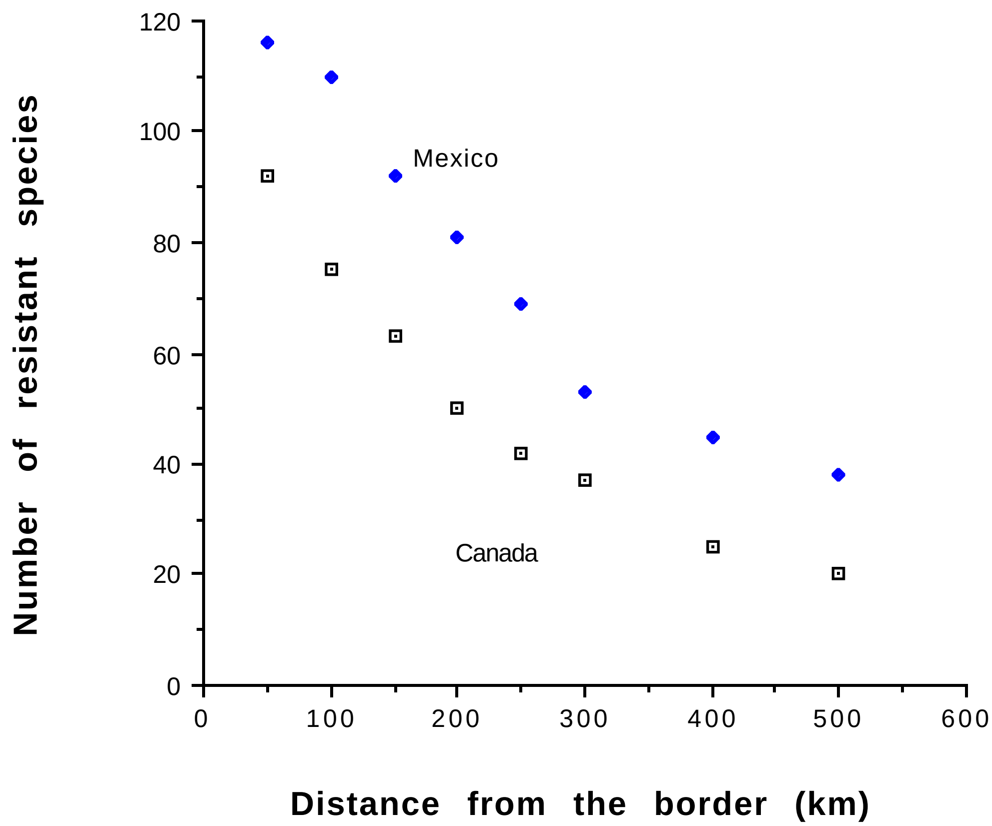
iii) When a population has a 1:1 sex ratio (equal numbers of males and females), animals are better off if they are monogamous because all individuals breed and raise offspring. This situation will naturally increase the productivity of the population.

Be certain to justify your answer.

5. What is the most successful organism and why?

6. Amoxicilin is a penicilin derivative antibiotic that is a prescription drug in the United States but is available over the counter in Canada and Mexico.

The number of species of bacteria resistant to pencilin-class antibiotics as a function of distance from the Mexico-US or Canada-US border is shown below:




i) Develop a Darwinian explanation for the general pattern that each series of data shows.

ii) Develop two hypotheses about the difference between the Mexico and Canada data series. Propose experiments or measurements to test these ideas.

## PHYSIOLOGICAL AND BEHAVIORAL ECOLOGY

1. In his famous 1966 paper on allometry and size, Stephen Jay Gould reported the results of Stahl on mammalian allometric relationships. I have simplified these to

$$\text{lifetime} = 8.8\text{x}10^{3}\ M^{.29}$$
$$\text{breath time} = 4.4 \times 10^{-5}\ M^{.28}$$
$$\text{cardiac-beat-time} = 1.1\text{x}10^{-5} M^{.28}$$

where M is body mass.

i) Why report breath time and cardiac-beat-time instead of breath rate and heart rate?

ii) How are these allometric relationships to be interpreted?

iii) Note that lifetime/breathtime = 2 $\text{x}10^{8} M^{.01}$ and breathtime/cardiac-beat-time = 4. How are these ratios to be interpreted?

2. S. Harrison, who is a faculty member at UCD in the Division of Environmental studies, studies the tussock moth *Orgyia vetusta* which feeds on bush lupine at the Bodega Marine Reserve. In her work, she discovered that the moth larvae will leave a bush before they completely defoliate it. Is this unexpected; why or why not? Suppose you did a manipulative experiment and went to Bodega and removed half of the bush lupine. What is your prediction about the residence of the larvae on the remaining bushes?

3. In the February 1992 issue of the **American Naturalist,** K. Justice and F. Smith published results of a study relating energetic requirements of maintenance, gut capacity and body weight. They found that the maintenance energy for a mammal of mass W is

$$ME = 140\ W^{.75}\ \text{kcal/day}$$

and that the gut capacity (holding volume) for a mammal of mass W is

$$GC = .065\ W^{1.05}\ \text{kg.}$$

i) How does the ratio maintenance energy/gut capacity scale with body size?

ii) What is the interpretation of the ratio ME/GC?

iii) What do your results suggest about the diet of mammals of various sizes?

4. Irons et al. studied the foraging of glaucous winged gulls on intertidal organisms at Chicago Harbor, Attu Island, Alaska. They estimated the following

| Prey type | Search time (s) | Handling time (s) | Energy per prey item (kJ) |
|---|---|---|---|
| Chitons | 37.9 | 3.1 | 24.5 |
| Urchins | 35.8 | 8.3 | 7.5 |
| Limpets | 9.9 | 1.5 | 2.9 |
| Mussels | 18.9 | 2.9 | 1.4 |
| Barnacles | 14.1 | 2.1 | .16 |

i) Extend the two-prey type diet choice theory to handle up to five types.

ii) Use your extension to predict the diet of the gulls if they are maximizing energy intake.

5. This question deals with allometry of metabolic rate.

i) What are the fundamental units of calorie and joule?

ii) What is the etymology of allometric?

iii) Assume the Kleiber formula $MR = 73.3M^{.74}$, where the units of M are kg and the units of MR are kcal/day. Compute the metabolic rate of animals weighing 300 kg, 3 kg and .03 kg.

iv) Which of these animals uses more energy (does this question make sense)?

6. Forseth, Ugedal and Jonsson (Journal of Animal Ecology 63:116-126, 1994) studied the energy budget, niche shift and growth in the Arctic charr *Salvelinus alpinus*. They found that as a function of weight W (in grams) the energy intake $E_i(W)$ was

$$E_i(W) = -2.33 + 12.27\,W - .16W^2 \quad \text{kJ/day}$$

and that the energetic cost $E_c(W)$ was

$$E_c(W) = -5.31 + 3.35W - .012W^2 \quad \text{kJ/day}$$

i) What is the optimal size for a fish?

ii) What is the maximum size of a fish?

iii) Suppose that a fish does not reproduce in its first year of life but in subsequent years it can allocate half of its surplus energy to reproduction. What would be the energetic value of reproduction for the first 30 days of its second year, assuming that it weighs 45 gm at that time?

7. Use simple geometric scaling relations to explain why the a priori prediction for metabolic rate as a function of mass is $MR = A\ M^{2/3}$. To do this, assume that heat is generated according to mass but that the organism cools according to surface area and that for any organism to live, heat production and cooling must be in balance.

8. P. Lee, P. Majluf and I.J. Gordon (Journal of Zoology, London 225:99-114; 1991) provide data on maternal weight, neonatal weight, weaning age and weaning weight in a number of mammals; some of these data are:

| Species | Maternal Weight (kg) | Neonate Weight (kg) | Wean Weight (kg) | Age of Weaning (months) |
|---|---|---|---|---|
| *Aepyceros melampus* | 45.3 | 5.49 | 15.87 | 4.5 |
| *Alcelaphus buselaphus* | 135 | 13.25 | 52.19 | 5.5 |
| *Alces alces* | 369.1 | 14.00 | 94.04 | 4.0 |
| *Antilocapra americana* | 40.8 | 2.44 | 11.43 | 3.0 |
| *Capra ibex* | 59.8 | 2.78 | 17.09 | 4.5 |
| *Ceratotherium simum* | 1500 | 55 | 299 | 12 |
| *Choeropsis liberiensis* | 237.5 | 5.5 | 50.5 | 3 |
| *Connochaetes taurinus* | 184.9 | 17.75 | 55.6 | 7.5 |
| *Cervus elaphus* | 117.0 | 6.2 | 37.3 | 6.5 |
| *Dama dama* | 38.3 | 4.7 | 18.2 | 4.9 |
| *Damaliscus dorcas* | 63.9 | 6.9 | 23.2 | 4.0 |

i) What are the common names of these species?

ii) Construct the following allometric relationships using weight and log(weights):

Neonate Weight vs. Maternal Weight
Wean Weight vs. Neonate Weight
Wean Age vs. Neonate Weight

iii)) Interpret the general patterns from the allometric relationships.

iv) Pick your two favorite species from the list, and compare and contrast the allometric information with other life history information that you can find.

9. If a forager simply took items according to the rate that it encountered them, then the fraction of type 1 items in its diet would be

$$\text{Fraction of type 1 items} = \frac{\lambda_1}{\lambda_1+\lambda_2} .$$

Plot the fraction of type 1 items as a function of $\lambda_1$ for $\lambda_2$= 1, 2 or 3. Compare the diet choice for an individual maximizing energy intake with that of an individual randomly selecting food if $\lambda_2$=3 sec$^{-1}$ and the switching value is $\lambda_{1s}$=4.5 sec$^{-1}$.

10. i) Show that

$$\frac{E_1\lambda_1}{1+\lambda_1 h_1} > \frac{E_1\lambda_1 + E_2\lambda_2}{1+\lambda_1 h_1 + \lambda_2 h_2}$$

is the same as $\lambda_1 > \frac{E_2}{E_1 h_2 - E_2 h_1}$ . What does this mean if $E_2$ increases, $h_1$ increases, or $h_2$ increases?

ii) A forager encounters prey item type 1 one item every10 seconds, type 2 one item every 8 seconds, both items are worth 10 cal, but type 1 takes 5 seconds to handle, type 2 requires 10 seconds to handle. If the forager is maximizing energy, do you predict that it will specialize or generalize?

11. For a predator in a patchy environment, the rate of energy flow is R(t) = G(t)/(t+τ) where G(t) is the gain from a patch residence time of t and t is the travel time between patches. Suppose that the travel time is very large compared to patch residence time. What is an approximate formula for the rate of energy flow and what does this mean for predictions about how much of the patch is removed?

12. Suppose that the feeding rates of individuals in groups of different sizes on a feeding territory are the following:

| Number of Individuals in a Group | Individual Feeding Rate (kcal/day) |
|---|---|
| 1 | 50 |
| 2 | 75 |
| 3 | 110 |
| 4 | 80 |
| 5 | 40 |
| 6 | 10 |

Assume that individuals arrive one at a time onto the territory and either forage by themselves or join an existing group, according to the behavior that is best for them in terms of individual feeding rate and that once an individual is in a feeding group it stays there.

i) Predict structure of the feeding groups after the arrival of a) the third individual, b) the fifth individual, c) the tenth individual.

ii) Suppose that individuals could quit groups. How would your predictions change?

13. Wise (**Spiders in Ecological Webs**, Cambridge University Press, 1993) studied the effect of supplemental food and prey density on the growth of immature filmy dome spiders. A simplified version of the results is (with Wt = weight in grams) and initial weight corresponding to August 5, final weight to September 9.

| Food Supply | Spider Density | $\frac{\text{Wt. on September 9}}{\text{Wt. on August 5}}$ |
|---|---|---|
| Natural | Low | 1.94 |
| Supplemented | Low | 2.24 |
| Natural | High | 2.03 |
| Supplemented | High | 2.67 |

i) What inferences can you make about the role of food and spider density on the rate of growth?

ii) If the final sizes of spiders in the natural prey situation was 15 mg, what were the initial sizes?

iii) If the final sizes of spiders in the supplemented prey situations were 24 mg, what were the initial sizes?

iv) What are the corresponding rates of growth?

14. Spiller (Oecologia 64:322-331, 1984) studied the relationships between prey consumption and reproduction in two species of spiders in natural settings. A simplified version of his data is

| Spider and Year | Prey Consumption (mg/spider/day) | Reproduction eggs/sac/female |
|---|---|---|
| *Metepeira* | | |
| 1982 | .39 | 50 |
| 1983 | .58 | 66 |
| *Cyclosa* | | |
| 1982 | .12 | 19 |
| 1983 | .18 | 20 |

i) Assuming that the two species are functionally similar, use the data to propose a relationship between prey consumption rate and reproduction.

ii) Comment on this relationship for the limiting cases in which prey become exceedingly abundant or exceedingly rare.

15. Two spatially separated habitats are characterized by the following feeding rate data.

| Number of Individuals in Habitat | Feeding Rate (kcal/hour) Habitat 1 | Habitat 2 |
|---|---|---|
| 1 | 6 | 5.5 |
| 2 | 8 | 7.5 |
| 3 | 6 | 7 |
| 4 | 4 | 5 |
| 5 | 2 | 3 |
| 6 | 1 | 2 |

i) Sketch plots of feeding rate vs group size for each habitat

ii) Predict the distribution of animals if animals can choose to be in either habitat and they adjust to maximize individual feeding rate and there are a total of 1,3,6 or 9 animals present in the two habitats.

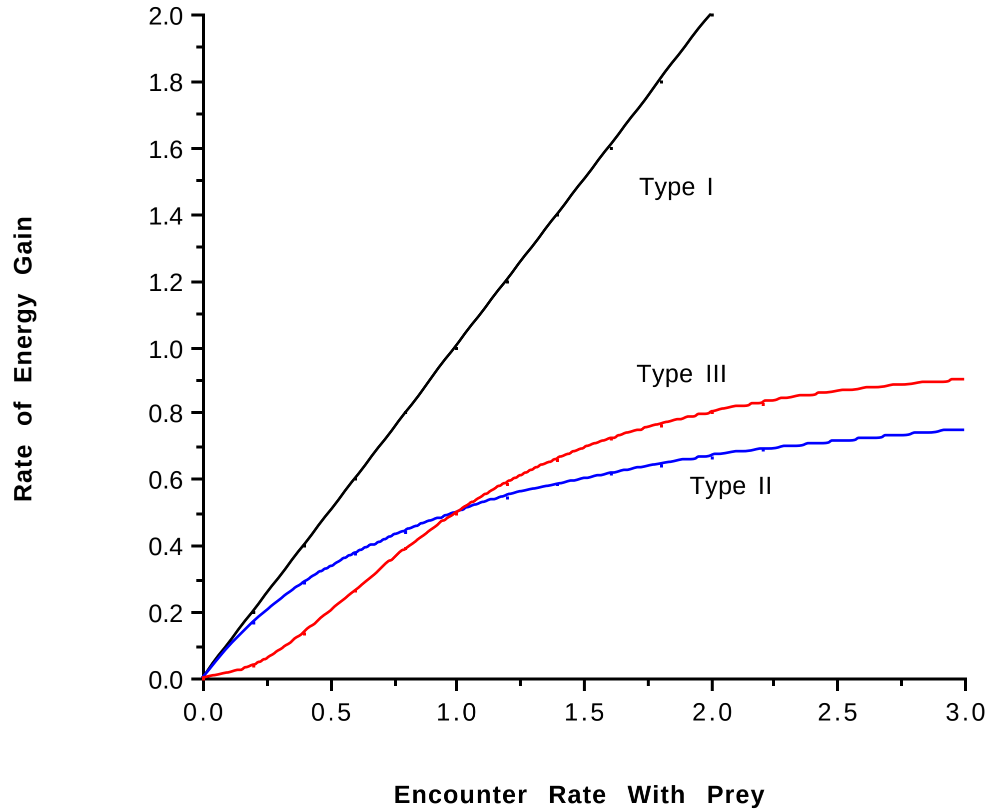
16. When there is only one type of prey, the foraging model for prey encounters during diet choice is called the Holling Type II functional response

$$R(\lambda) = \frac{l}{(1+h\lambda)}$$

where R is the rate at which prey are consumed.

i) What are the biological interpretations of $\lambda$ and h, including units?

ii) The type I and type III functional responses are shown below. What are the biological interpretations that you give to these other functional responses?




17. The feeding rate of individuals in groups of different sizes is

| Group Size | Individual Feeding Rate |
|---|---|
| 1 | 10.3 kcal/hour |
| 2 | 13.6 |
| 3 | 15 |
| 4 | 17.2 |
| 5 | 14 |
| 6 | 12 |
| 7 | 11.2 |
| 8 | 9.1 |

i) What is your prediction for the optimal group size?

ii) What is your prediction for the equilibrium group size?

iii) What predictions would you make concerning field data if there were 5, 10, or 40 individuals present in the feeding ground.

18. In the development of the marginal value theorem, we assumed that all patches were the same and that the travel time between patches was constant. Imagine a different situation, in which patches are still the same but in which there is a 60% chance that the travel time is 10 minutes and a 40% chance in which the travel time is 20 minutes.

i) Many researchers expected that animals should stay in patches longer after a long travel time. Explain why would they might expect this to be true.

ii) Describe how you would find the optimal residence time if there are different travel times, but do not do the computation.

19. A study of the germination and growth of fir seeds in open and screened plots lead to the following data:

| Number of Plants | Open | Screened |
|---|---|---|
| Initial | 100 | 100 |
| At the end of the pre-germination period | 47 | 63 |
| At the end of the germination period | 21 | 35 |
| One year after germination | 8 | 17 |

Losses in the pre-germination period are due to fungi, insects, rodents, birds, and other sources; in the germination period to fungal attack and seed dormancy; in the post-germination period to fungi and other causes.

i) Estimate survivorship for each of these periods.

ii) If you could affect only one of the three intervals through some action, which one would it be and why?

20. At the meeting of the Working Group on Ecosystem Monitoring and Management (sponsored by the Commission for the Conservation of Antarctic Living Resources) in Bergen, Norway 1996, S.M Kasatkima presented results in which the size distribution of 60 krill *Euphausia superba* captured by fishery trawl nets and research survey nets were compared. The average size of krill in the fishery nets was 46.3 mm with standard deviation 3.6 mm; in the research survey nets the average size was 42.6 mm with standard deivation 3.8 mm.

i) Are these sizes statistically different?

ii) What are the implications of these data for the estimation of krill biomass using surveys or fishing data?

iii) Macaroni penguins (*Eudyptes chrysolophus*) were found to have no small (28-38 mm) krill in their stomachs and an overrepresentation of large (58-62 mm) krill. What does this suggest?

## Advanced Material

1. This problem arose in my discussions with David Boose (who completed a Ph.D. in ecology at UC Davis in 1995) on his work concerning hummingbirds. Imagine a forager that enters patchs that contain cells of food. When it enters a patch, it randomly encouters cells and empties cells as they are encountered. It does not remember cells that it has encountered. .

Suppose that a patch contains N cells, all of which are full when the forager arrives. Let p(k,v) be the probability that after v visits to cells, k of them have been emptied.

i) What is p(k,v) if k> v and why?

ii) Why is p(1,1)=1?

iii) Explain why

$$p(k,v) = p(k,v-1)\left(\frac{k}{N}\right) + p(k-1,v-1)\left(\frac{N-[k-1]}{N}\right)$$

iv) Suppose that the gain after v visits is denoted by G(v). Explain why

$$G(v) = \sum_{k=1}^{v} k\, p(k,v)$$

v) Assume now, as in the maringal value theorem, that the travel time between clumps is $\tau$ and that the rate of gain after v visits is $R(v) = \frac{G(v)}{v+\tau}$ . Write a program to compute p(k,v), the gain, the rate of gain, and thus determine the optimal number of visits as a function of N and $\tau$.

2.Suppose that the gain from residence time t in a patch of food is

$G(t) = \frac{At}{At + t_0}$ in which A and $t_0$ are constants. If travel time between patches of food is t, the rate of gain of resource is R(t) = $\frac{At}{[At+t_0][t+t]}$ .

i) Use calculus to show that the optimal residence time is $t^*= \sqrt{\frac{t_0 t}{A}}$ . What is the interpretation of A?

ii) Suppose that $t_0=2$ Write a program that computes t* for t=1,3,7 as A varies from 10 to 30.

iii) Plot the results, with A as the independent variable and t* as the dependent variable. Interpret the relationship between patch quality (how is that defined?) and optimal residence time.

iv) Use your program from Problem 5 to do a similar computation. Why are the results so different? What implications would this have for field observations?

3. Krebs et al. (Animal Behavior 25:30-38, 1977) studied prey selection in the great tit (*Parus major*). Five different birds were used and were fed meal worms with either 4 segments or 8 segments, so that $E_1 = 2E_2$. The handling times ware these:

| Bird | $h_1$ (8 segments) | $h_2$ (4 segments) |
|---|---|---|
| 1 | 10.5 sec | 10.5 sec |
| 2 | 5 | 9 (not a misprint, at least from their paper) |
| 3 | 8.5 | 12.5 (ditto) |
| 4 | 14.5 | 8.0 |
| 5 | 6.0 | 5.0 |

i) Show that it is appropriate to refer to 8 segmented worms as the more profitable prey.

They used five encounter rate treatments (A-E)

| Treatment | $\lambda_1$ | $\lambda_2$ |
|---|---|---|
| A | .025 $sec^{-1}$ | .025 $sec^{-1}$ |
| B | .05 | .05 |
| C | .15 | .05 |
| D | .15 | .15 |
| E | .15 | .30 |

ii) Compute the switching value of $\lambda_1$ for each bird.
They allowed each bird to eat 50 prey (I have somewhat massaged their data) and discovered the following:

| Treat-ment | Number of More Profitable Prey Eaten by Bird # 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| A | 26 | 27 | 26 | 28 | 25 |
| B | 25 | 26 | 22 | 29 | 28 |
| C | 43 | 47 | 41 | 41 | 39 |
| D | 49 | 43 | 40 | 24 | 39 |
| E | 32 | 46 | 39 | 20 | 35 |

iii) On the same graph, but using different symbols, plot the fraction of more profitable prey in the diet as a function of encounter rate. For each bird, show the switching value.

iv) Now assume a different foraging model. Suppose that a bird always accepts the more profitable prey when it is encountered, but accepts the less profitable prey only with probability p. Assume that the experiment proceeds until 50 prey items are taken. Suppose that S is the search time. Explain why

$$\lambda_1 S + p\lambda_2 S = 50$$

v) Write a program that computes the sum of squared deviations between the observed and predicted (using the preceding equation) number of prey items taken in each of the five treatments. This program should plot the sum of squared deviations as a function of p, for p going in steps of .05 or .1 from 0 to 1. Interpret the results.

4. Suppose that a forager is an energy maximizer and has two prey types in its environment. Although it knows the energy content and handling times of the two prey types, it must estimate encounter rates. This is done using what psychologists would call a linear operator, so that the estimate for the encounter rate with the more preferred prey type at the start of interval t+1 is

$$\lambda_1(t+1) = \frac{[m\lambda_1(t) + (1-m)\lambda_{10}]t + Enc(t)}{t+1}$$

where $0 < m < 1$ and $l_{10} > 0$ are constants and Enc(t) = 0 if no prey type or prey type 2 was encountered in interval t and Enc(t) = 1 if a prey type 1 was encountered in interval t.

i) What are the interpretations of m, $\lambda_{10}$ and s?

ii) Write a program that demonstrates how an energy mazimizing forager that has to learn the encounter rate may show partial preferences.

iii) What is another source of partial preferences?

5. Imagine a parasitoid whose prey come in two phenotypes. Oviposition in a host of type 1 provides an offspring with probability $p_1$ and oviposition in a host of type 2 provides an offspring with probability $p_2 < p_1$. Suppose that the probability of encountering a host of type i in a single period is $l_i$, that the probability of mortality while searching is m, that the probability of mortality while ovipositing is $m_{ov}$, and that the season lasts T periods. Let F(t) denote the maximum expected fitness accumulated from period t to period T. Finally, assume that the parasitoid always oviposits in the higher quality host, but facultatively responds to the lower quality host.

i) Explain why F(T)=0.

ii) For t < T, explain why

$$F(t) = (1-\lambda_1-\lambda_2)(1-m)F(t+1) + \lambda_1 \{ p_1 + (1-m)(1-m_{ov})F(t+1) \}$$
$$+ \lambda_2 \max \{ p_2 + (1-m)(1-m_{ov}) F(t+1) \; ; \; (1-m) F(t+1) \}$$

iii) When will the parasitoid accept the lower quality host?

iv) Write a program that evaluates F(t) and the appropriate behaviors for T = 50, m=.03, $p_1$=1 and conduct a sensitivity analysis of behavioral predictions related to the other parameters.

v) Use the output of this program to make behavioral predictions.

6. Write a program to plot the Hamiltonian sex ratio

$$r^* = \frac{N-1}{2N}$$

What does this tell you about the opportunities for observing extraordinary sex ratios in the field?

7. This problem was suggested by Ms. C. Kostrub, when she took EVE 221 (Behavioral Ecology) in Spring 1995. Imagine the two prey diet choice problem, but now assume that there is a handling time cost of switching. That is, the two prey items are ranked according to $\frac{E_1}{h_1} > \frac{E_2}{h_2}$ but if the predator generalizes, it must relearn how to handle the prey, so that the handling time when switching prey is the average

$$h_{1,2} = \frac{\lambda_1}{\lambda_1 + \lambda_2} h_1 + \frac{\lambda_2}{\lambda_1 + \lambda_2} h_2.$$

That is, if the sequence of prey items is 1,1,1,2,2,1,2 then the handling times are $h_1$, $h_1$, $h_1$, $h_{12}$, $h_2$, $h_{12}$, $h_{12}$. Derive the resulting switching rule and compare it with the previous case.

9. In this exercise, you will develop a theory of territory size for fish that takes into account the increased costs of defending a territory and the gain of food as territory size increases. After you have done this, couple it to an allometric relationship for metabolic rate and movement to predict territory size as a function of body size.

Suppose that the total time activity time T is split between time $T_f$ feeding and time $T_c$ chasing intruders away. Consequently $T = T_f + T_t$. Suppose that territory is circular with diameter R. Assume that the density of intruders is $d_i$ intruders/unit length/day

i) Explain why the number of intruders per day will be $2\pi R d_i$. Assume that the territory holder sits at the center of the territory and that when an intruder arrives, the holder rushes to the boundary, chases the intruder off and returns to the center of the territory.

ii)With these assumptions, explain why

$$T_c = \frac{4pRd_i}{v} \qquad (1)$$

where v is the territory holder's speed. Given (1), the time available for feeding is

$$T_f = T - \frac{4\pi R d_i}{v} \qquad (2)$$

Assume that the rate at which food drifts into the territory is $d_fR$ kcal/unit time, so that the energy obtained from feeding is

$$E_f = d_fRT_f \qquad (3)$$

iii) What is the interpretation and are the units of $d_f$?
Assume that the cost of chasing intruders is a kcal/unit time, so that the net energy gain is

$$E_{net} = d_fRT_f - aT_c \qquad (4)$$

iv) Derive an equation for optimal territory size, assuming that the holder chooses territory size to maximize net energy gain.

v) What are the effects of intruder pressure ($d_i$), food density ($d_f$) and metabolic cost of chasing (a) on territory size.

vi) In his book **The Ecological Implications of Body Size** R.H. Peters reports that for salmon that v scales with body size S according to

$$v = AS^{.2} \qquad (5)$$

where S is weight (over the range .002 - 2 kg). Use this to determine a prediction for the relationship between body size and territory size. You may have to derive this relationship numerically.

10. This problem involves analysis of optimal age and size at maturity. Assume that until it reaches maturity, a fish grows according to the von Bertalanfy form

$$L(t) = L_{inf}(1- e^{-K(t-t_0)}) \qquad (1)$$

where t is time measured in years and $L_{inf}$ is the asymptotic length. The parameter $t_0$ is included to take account for the differences in the early life history (egg and larvae) growth patterns and later ones, to which the growth curve is usually fit. After maturity, at time $t_m$, length is fixed at $L_m = L(t_m)$.

If mortality M is assumed to be constant across body sizes, survival to time t is $e^{-Mt}$. Assuming that weight is proportional to length cubed and that reproductive success is proportional to weight, the definition of fitness as expected reproductive success is

$$F(t) = e^{-Mt}[L_{inf}(1- e^{-K(t-t_0)})]^3 \qquad (2)$$

i ) Show that the optimal age at maturity

$$t^* = \frac{1}{K} \log(\frac{Mc + 3Kc}{M}) \qquad (3)$$

where $c = \exp(Kt_0)$. Why does asymptotic size does not appear in this relationship?

ii) Define the size at maturity as $L(t^*)$ and show that the relative size at maturity is

$$\frac{L_m}{L_{inf}} = 1 - \frac{M}{M+3K} = \frac{3K}{3K+M} \qquad (4)$$

Plot the relative size at maturity as a function of K/M. What is the interpretation of this plot?

iii) Suppose that instead of the von Bertalanfy relationship, you had used the Richards formula

$$L(t)^s = L_{inf}^s - [\, L_{inf}^s - L_0^s]e^{-Kt} \qquad (5)$$

with s=1. Show that the optimal age at maturity is now

$$t^* = \frac{1}{K} \log\left( \left(\frac{M+3K}{M}\right)\left(\frac{L_{inf}-L_0}{L_{inf}}\right)\right) = \frac{1}{K} \log\left( \left(\frac{M+3K}{M}\right)\left(1 - \frac{L_0}{L_{inf}}\right)\right) \qquad (6)$$

This depends upon both asymptotic size and initial size. What is going on?

11. a) Suppose that an animal which settles in habitat with quality q receives scaled reproductive succes

$$RS(q) = \frac{2q}{q+q_0} \qquad (1)$$

where $q_0$ is a fixed parameter (that you get to pick when you do computations), characteristic of the life history of the animal. Now suppose that habitat quality is a random variable, which for simplicity we assume to take discrete values according to the following probability distribution

$$\Pr\{\text{ quality } = q\} = p(q) = c_{norm}\exp\left(\frac{-(q-\bar{q})^2}{2\sigma^2}\right) \qquad q=1,2,3,....q_{max} \qquad (2)$$

where $\bar{q}$, $q_{max}$ and $\sigma$ are parameters that you get to pick when you do computations; $c_{norm}$ is a normalization constant and $q_{max}$ is the maximum habitat quality.

i) How is the normalization constant computed? What are the interpretations of $\bar{q}$ and $\sigma$?

ii) Write a computer program to find the expected reproductive success

$$E\{RS\} = \sum_{q=1}^{q_{max}} p(q)\ RS(q) \qquad (3)$$

and use your program to make a plot of E{RS} as a function of s.

Now imagine a herbivore that attacks a plant with an inducible defense. When attacked, the plant produces a toxin and the herbivore experiences a metabolic cost when dealing with this toxin. Suppose that the cost C(t) of having to detoxify a level t is

$$C(t) = \exp(bt)-1 \qquad (4)$$

where b is a constant. Assume that plants vary in the level of toxic response. In particular, assume that the toxic response of a plant has the probability distribution

$$\Pr\{\text{ toxic response } = t\} = p(t) = c_{norm}\exp\left(\frac{-(t-\bar{t})^2}{2\sigma^2}\right) \quad t=1,2,3,....t_{max} \qquad (5)$$

where the parameters and functions have similar interpretations to those from (2); you also get to pick these.

iii) Write a computer program to determine the expected cost that the herbivore will experience

$$E\{C\} = \sum_{t=1}^{t_{max}} p(t)\ C(t) \qquad (6)$$

iv) What do your results suggest about the relationships between habitat choice and variability and plant choice and variability.

v) Sketch the cost and benefit curves and use them to elucidate your results.

vi) Now look at Figure 3E (pg. 1945) in the paper by B.A. Stockhoff, 1993, "Diet heterogeneity: implications for growth of a generalist herbivore, the gypsy moth". **Ecology** 74:1939-1949. What predictions do you make about the preference for diet nitrogen variability of gypsy moth?

12. According to the marginal value theorem, as travel time increases the residence time increases (or, more formally, does not decrease) for almost any reasonable gain function. In this problem, you will investigate if a similar prediction can be made when travel time is fixed and gain functions vary. The two gain functions are

$$G_1(t) = \frac{At}{At+t_0} \qquad (1)$$

and

$$G_2(t) = B\left(1-\exp\left(\frac{-t}{t_0}\right)\right) \qquad (2)$$

where A, B and $t_0$ are parameters.

i) What are the interpretations of A, B and $t_0$?

ii) If the travel time between patches is t, derive formulas for the optimal residence times as a function of A and $t_0$.

iii) Explore how the optimal residence times change as A varies and $t_0$ is fixed or $t_0$ varies and A is fixed. Explain your results.

iv) What intuition do you draw about the relationship between the gain function and optimal residence time?

13. In the seminar that he gave at UC Davis in 1995, Peter Turchin described a population that had density dependent growth characterized by a logistic equation, which was also subject to predation by generalist and specialist predators. His model was this

$$\frac{dN}{dt} = rN(1-\frac{N}{K}) - \frac{aSN}{N + n_1} - \frac{bGN^2}{N^2 + n_2{}^2}$$

where S and G are the number of specialist and generalist predators respectively and a, b, $n_1$ and $n_2$ are constants.

i) Explain why $\frac{aSN}{N + n_1}$ might be used to characterize the rate of predation from specialist predators. What are the interpretations of a and $N_1$, including units?

ii) Explain why $\frac{bGN^2}{N^2 + n_2{}^2}$ might be used to characterize the rate of predation from generalist predators. What are the interpretations of b and $N_2$, including units?

iii) Does the explanation in part ii) coincide with what you would conclude from our work on the two prey diet choice problem?

## LIFE HISTORY

1. Draw survivorship curves $l_x$ for organisms that live no more than 20 years for the following cases

    i) most of the mortality occurs at ages >15

    ii) a constant number of individuals die each year

    iii) a constant fraction of individuals die each year

    iv) most of the mortality occurs before age 1

Carefully label the axes and each curve.

2. Harcourt and Leroux (1967) provide data on the mortality of the diamondback moth (*Plutella maculipennis*) on cabbage in Ontario, Canada. A simplified version of the data is shown below

| Life history stage | Number of Individuals | Source of Mortality |
|---|---|---|
| Oviposited | 1600 | - |
| End of egg stage | 1580 | Infertility |
| Larval stage | | |
| Young | 356 | Rainfall |
| Old | 258 | Rainfall |
| Oldest | 199 | Parasitism |
| Pupae | 107 | Parasitism |

Estimate the rate of mortality (fraction of animals killed) as a result of rainfall and parasitism.

3. Aksnes and Giske (Marine Ecology Progress Series 64:209-215; 1990) proposed that we use the following for basic reproductive rate

$$R_0 = be^{-MT_g}$$

where $T_g$ is generation time (days), M is rate of mortality (days$^{-1}$) and b is the fecundity of an individual who makes it to maturity.

i) How would this be connected to a life table? That is, what are the analogies of $l_x$ and $m_x$?

ii) For the copepod *Paraclanus parvus*, they give the following data

| Depth (m) | M | $T_g$ | b (eggs) |
|---|---|---|---|
| 0-1 | .22 | 11 | 91 |
| 1-5 | .19 | 12 | 70 |
| 5-10 | .15 | 17 | 13 |
| 10-20 | .10 | 26 | 7 |
| 20-50 | .03 | 32 | 0 |

The copepod eats phytoplankton and is preyed upon by other plankton and fish.

iii) What explanations might you propose for the patterns of M, $T_g$ and b with depth?

iv) Compute $R_0$ using the data given above and make a prediction about the vertical distribution of this copepod population.

4. The grass *Poa Annua* has the following life table

| Age(quarters) | Number alive | Fecundity |
|---|---|---|
| 0 | 843 | 0 |
| 1 | 722 | 300 |
| 2 | 527 | 620 |
| 3 | 316 | 430 |
| 4 | 144 | 210 |
| 5 | 54 | 60 |
| 6 | 15 | 30 |
| 7 | 3 | 10 |
| 8 | 0 | |

i) Compute $l_x$ and $m_x$.

ii) Draw survivorship trajectories for an individual that lives longer than average and for an individual that lives shorter than average.

iii) Compute $R_0$. What does this say about seed to adult survival if the population is not increasing in size? That is, what can you infer about the entire adult ---> seed ----> adult life cycle?

iv) In general, can $m_x>1$ if $R_0=1$?

5. Lowe (1969) provides data on the life table of red deer on the Island of Rhum, Scotland. A modified version of those data are shown below, in which I give the number of surviving adult females.

| Age (yrs) | Number Alive | Fecundity |
|---|---|---|
| 1 | 129 | 0 |
| 2 | 114 | 0 |
| 3 | 113 | .311 |
| 4 | 81 | .278 |
| 5 | 78 | .302 |
| 6 | 59 | .400 |
| 8 | 55 | .358 |
| 9 | 25 | .447 |
| 10 | 9 | .289 |
| 11 | 8 | .283 |
| 12 | 7 | .285 |
| 13 | 2 | .283 |
| 16 | 2 | .285 |
| 17 | 0 | |

i) What does it mean that fecundity < 1?

ii) In the table, data are missing for year 7 and years 14 and 15. The reason is this: in year 7, the population size increased from 59 (in year 6) to 65. In year 14 the population fell to 1, but in year 15 it jumped to 4. What can these jumps upward possibly mean?

iii) Compute $R_0$ and $T_c$ for this population.

6. Wise (**Spiders in Ecological Webs**, Cambridge University Press, 1993) measured the effects of supplemental food and density on the survival of filmy dome spiders. A simplified version of the results are shown below

| Food Supply | Spider Density | Proportion Surviving to Reproductive State |
|---|---|---|
| Natural | Low | .54 |
| Supplemented | Low | .56 |
| Natural | High | .36 |
| Supplemented | High | .48 |

Wise also measured the effects of density and food on the fecundity (egg production) of maturing females. A simplified version of those data are

| Food Supply | Spider Density | Fecundity |
| --- | --- | --- |
| Natural | Low | 89 |
| Supplemented | Low | 95 |
| Natural | High | 71 |
| Supplemented | High | 83 |

i) Interpret the effects of food supplementation and spider density on juvenile survivorship and on fecundity.

ii) Suppose that we consider simply two "age classes" of juvenile (non-reproductive) and adult (reproductive). What is the formula for basic reproductive rate?

iii) Assume that the natural situation for the spiders is high density, unsupplemented food, and that adults have a 56% chance of laying an egg sac. What would the effect of supplemented food be on the basic reproductive rate? Suppose that the natural situation is low density and unsupplemented food. How would the results change?

7. In this question, you will discover the quantity called "Residual Reproductive Value", usually denoted by RRV.

i) Explain why the expected reproduction from age a onwards is given by $R_a = \sum_{x=a} l_x m_x$.

ii) Rewrite $R_a$ as

$$R_a = l_a m_a + \sum_{x=a+1} l_x m_x = l_a \{ m_a + \sum_{x=a+1} \frac{l_x}{l_a} m_x \}$$

iii) Interpret $\frac{l_x}{l_a}$ in terms of population numbers.

iv) The quantity

$$V_a = \sum_{x=a+1} \frac{l_x}{l_a} m_x$$

is called residual reproductive value. Explain why it would be called this.

v) Compute the RRV for Poa Annua at ages 1,3,5,7 using the data from question 4 in this section.

8. A field study of a beetle allows one to measure the day of death and the egg load on that day by dissection of the beetle, which each day buries all of its eggs in spots that are difficult to locate and open without destroying the eggs. Results for 30 beetles are shown below:

| Individual Number | Day of Death | Egg Load on Day of Death |
|---|---|---|
| 1 | 3 | 11 |
| 2 | 16 | 16 |
| 3 | 5 | 15 |
| 4 | 10 | 18 |
| 5 | 29 | 7 |
| 6 | 4 | 13 |
| 7 | 21 | 12 |
| 8 | 15 | 16 |
| 9 | 9 | 18 |
| 10 | 14 | 17 |
| 11 | 23 | 11 |
| 12 | 32 | 6 |
| 13 | 12 | 18 |
| 14 | 5 | 15 |
| 15 | 21 | 12 |
| 16 | 25 | 10 |
| 17 | 12 | 18 |
| 18 | 15 | 16 |
| 19 | 13 | 17 |
| 20 | 9 | 18 |
| 21 | 7 | 17 |
| 22 | 6 | 16 |
| 23 | 23 | 11 |
| 24 | 2 | 8 |
| 25 | 3 | 11 |
| 26 | 25 | 10 |
| 27 | 7 | 17 |
| 28 | 3 | 11 |
| 29 | 30 | 7 |
| 30 | 13 | 17 |

i) Draw the survivorship curve for individuals 1, 5, 17 and 30.
ii) Estimate the survivorship curve $l_x$.
iii) Estimate fecundity $m_x$.
iv) Compute the basic reproductive rate $R_0$
v) Compute the cohort generation time $T_c$.

9. In his book **Vertebrate Zoology**, Hairston gives the following data for *Sceloporus oliveaceous*

| Age x (years) | $l_x$ | $m_x$ |
|---|---|---|
| 0 | 1 | 0 |
| 0.167 | .215 | 0 |
| 1.167 | .0415 | 6.36 |
| 2.167 | .0133 | 36.60 |
| 3.167 | .0028 | 49.00 |
| 4.167 | .0005 | 49 |

i) What kind of animal is *Sceloporus oliveaceous*?

ii) Is this population self-sustaining?

iii) How would you find the distribution of individuals in the different age classes?

10. In this problem, you will investigate the effects of inbreeding on the reproductive performance of rainbow trout. The data reported here come from a paper by G-S Su et al. (Aquaculture 142:139-148, 1996). If population size is Ne, the rate of inbreeding is $\Delta F=1/2Ne$ and the coefficient of inbreeding in generation t is

$$F(t) = 1 - (1-\Delta F)^t \qquad (1)$$

i) One of the populations studied by Su et al. had Ne=16. Use this information and Eqn 1 to make a plot of the coefficient of inbreeding as a function of time. Su et al. report that the trout had a mean spawning data of 730 days and a mean egg load of 2032 eggs.

ii) Assuming that we can describe the trout as semelparous, that daily mortality of adult fish is m and of egg toadult survival is s, explain why

$$R_0 = 2032\sigma \ \exp(-730m) \qquad (2)$$

iii) Compute $R_0$ if m= .0005 and $\sigma$ =.0008. Interpret this result in terms of population decline or growth. Su et al. found that inbreeding increased the age at spawning of fish and decreased the number of eggs that they had. In particular, each percent increase in inbreeding coefficient increased spawning date by 0.49 days and decreased egg number by 12.3 eggs.

iv) Suppose that S(t) denotes the spawning age of individuals in generation t and E(t) denotes the number of eggs of individuals in generation t. Explain why

$$S(t) = 730 + .49(100\ F(t))$$

$$E(t) = 2032 - 12.3 \, (100 \; F(t) \qquad (3)$$

v) Now $R_0$ will also be a function of generations, which we can denote by $R_0(t)$. Explain why it is given by

$$R_0(t) = \sigma E(t) \; \exp(-mS(t)) \qquad (4)$$

and make a plot of $R_0(t)$ vs t for t running up to 20 years.

vi) What do you conclude about the growth/decline of the population over this interval.

vii) How big would the effective population have to be to prevent declining populations over this 20 year time horizon?

11. Peter Waser and Scott Creel published the following information on the life history of mongoose in the Serengeti:

| Age (a) | l(a) | m(a) |
|---|---|---|
| 0 | 1 | 0 |
| 1 | .41 | 0 |
| 2 | .328 | .21 |
| 3 | .252 | .39 |
| 4 | .182 | .95 |
| 5 | .142 | 1.32 |
| 6 | .085 | 1.48 |
| 7 | .057 | 2.45 |
| 8 | .031 | 3.78 |
| 9 | .021 | 2.56 |
| 10 | .014 | 4.07 |
| 11 | .005 | 3.76 |
| 12 | .005 | 3 |
| 13 | .002 | 2 |
| 14 | .002 | 0 |

i) Compute $R_0$ from these data.

ii) What happens to $R_0$ if survivorship decreases by just 5% for ages 5 and onwards?

iii) What happens to $R_0$ if individuals delay reproduction so that there is no reproduction at age 2, 3 and 4?

iv) Interpret your results.

## Advanced Material

1. Write a computer program to determine the growth rate of the population from the equation

$$\sum_{a=a_{min}}^{a_{max}} l_a m_a e^{-r} = 1$$

In which $a_{min}$, $a_{max}$, $\{l_a, m_a\}$ are input parameters. Use it to investigate tradeoffs in $l_a$ and $m_a$ in a population that is growing at 1% per year.

2. This problem involves the analysis of a matrix model for a population in which there are two age classes. Young individuals survive to adulthood with probability $s_0$, adults survive from one year to the next with probability $s_1$, and the adult fecundity is b.

i) What are the units of $s_0$, $s_1$ and b? Be thoughtful and specific.

ii) Let $N_0(t)$ and $N_1(t)$ denote the population sizes of young and adults in year t. What are the equations relating the population sizes in year t+1 to those in year t?

iii) Write a computer program for which these parameters and the initial population sizes are input parameters and which then computes the population size at subsequent years. Use this program to compute the population growth rate.

iv) Now compute the population growth rate analytically from the eigenvalue calculation.

v) Use the result in part iv) to explain why $bs_0/s_1^2$ is an invariant of the life history, in the sense that when $s_1$ is fixed, the same growth rate is obtained whenever the proposed invariant is constant.

3. Some years ago, Andy Dobson and Anna Marie Lyles proposed a simple stage structured model for primate life histories. The population is coarsely divided into three stage classes: Infants (I), Juveniles (J), and Adults (A) and time is measured by the inter-birth-interval (ibi). Assume the following: a) the survival of a juvenile or adult through one ibi is s; b) the survival of an infant to the juvenile stage is si; c) adult fecundity is F per ibi. Assume that the age at first reproduction is two inter-birth-intervals.

i) Convert these statements to a matrix model.

ii) Show that the growth rate of the population satisfies

$$\lambda^2 = -\frac{Fs^2i}{s-l}$$

and write a program to compute the growth rate when F, s and i are input parameters.

iii) How is your matrix model modified if a) the age at first reproduction is three inter-birth-intervals, so that there are two juvenile age classes, b) adult fecundity depends upon total population size?

iv) Froechlich et. al. (Journal of Primatology 2:207-306, 1981) give the following information on howler monkeys (*Alouatta palliata*)

Age at first reproduction = 4 years
Birth rate = .48/yr
Survival to
Age 1 = 0.6
Age 4 =0 .37

Explain how these data would be used to estimate the parameters in the stage structured model.

5. i) What is the difference between a Lefkovitch and a Leslie matrix?

ii) The following might apply to an insect population

| | egg | larva | adult |
|---|---|---|---|
| egg | 0 | 0 | F |
| larva | $s_{el}$ | $s_{ll}$ | 0 |
| adult | 0 | $s_{la}$ | $s_{aa}$ |

Tell me everything that you know about F, $s_{el}$ and $s_{ll}$.

iii) Explain how you would empirically determine F and $s_{la}$.

iv) Describe an analytical and a computation method for finding the stable age distribution, but do not do so.

4) The Pacific sardine life cycle can be described as follows:

| Stage name | Duration (days) | Daily Instantaneous Mortality Rate | Eggs per fish per day |
|---|---|---|---|
| Egg | 3 | .3 | 0 |
| Yolk-sac larva | 4 | .3 | 0 |
| Early larva | 11 | .14 | 0 |
| Late | | | |

| | | | |
|---|---|---|---|
| larva | 42 | .0556 | 0 |
| Early juvenile | 25 | .0365 | 0 |
| Juvenile I | 100 | .0239 | 0 |
| Juvenile II | 142 | .0140 | 0 |
| Juvenile III | 170 | .0025 | 0 |
| Juvenile Iv | 170 | .0021 | 0 |
| Pre-recruit | 175 | .0021 | 0 |
| Early Adult | 381 | .00178 | 170 |
| Adult | 663 | .00178 | 462 |
| Late Adult | 2773 | .00178 | 1259 |

i) Give the formula, but do not evaluate, the probability that a early larva survives to the next stage.

ii) Explain how you would construct a Lefkovitch matrix for the sardine in which all stages were used. Then explain what you would do if the stages were Egg, Larva, Juvenile, and Adult.

iii) In his classic analysis of the collapse of the sardine fishery, M.B. Schaefer using a logistic model

$$\frac{dP}{dt} = rP(1-\frac{P}{K})$$

with harvesting. What are the general interpretations of r and K in this equation? How would you use the detailed stage data to estimate these parameters?

## SINGLE SPECIES POPULATION GROWTH

1. Often, we can only approximately determine population size; in that case we require an estimate of abundance. In this question, you will derive a estimator for population abundance based on capture and recapture.

It proceeds to estimate the number of individuals N in a population by capturing some of them, marking the captured individuals, and recapturing a mixture of marked and unmarked individuals. We set

N = the number of individuals in a population
M= the number of individuals marked the first time
C = the total number of individuals captured the second time
R = the number of individuals in the second sample that are marked

i) Explain the logic that one uses to set

$$\frac{N}{M} = \frac{C}{R}$$

from which the estimator is $N_{est} = \frac{MC}{R}$ . (This is actually a biased estimator, overestimating population size, but we will work with it. See Krebs, C. 1989. **Ecological Methodology**. Harper and Row, for further details.)

ii) Discuss the biological assumptions that underlie the logic in part i).

The 95% confidence interval for population size is approximately found as follows. Set (for more details see Seber, G.A.F. 1982. **The Estimation of Animal Abundance**. MacMillan, New York):

$$V = \frac{(M+1)(C+1)(M-R)(C-R)}{(R+1)^3}$$

This yields an approximate 95% confidence interval of

$$N_{est} \pm 1.96 \sqrt{V}$$

and a measure of the relative width of the confidence interval is $1.96 \sqrt{V} / N_{est}$.

iii) Explore these various equations by using the following hypothetical data

| M | C | R |
|---|---|---|
| 90 | 40 | 6 |
| 180 | 80 | 12 |
| 360 | 160 | 24 |
| 1800 | 800 | 120 |

iv) My colleague Mark Abrahams described the following situation in Lindeman Pond in Winnipeg Mannitoba. The lake has an unknown number of yellow perch, but was recently stocked with 300 perch from a local hatchery. The hatchery fish have a banding pattern sufficiently different from the local perch that it can be considered a mark. During resampling, 550 fish were captured, of which 93 were hatchery fish. Estimate the population size of the yellow perch population (and the approximate 95% confidence interval) in this lake.

2. In this exercise, you will explore the implications of the "energy equivalence hypothesis of Sean Nee et al (Nature 351:312-313, 1991). If metabolic rate for an individual scales as

$$[illegible] R = AW^B$$

where W is wei[illegible] and A and B are constants, then the total energetic needs [illegible]ulation of N individuals with identical weight is $NAW^B$. If the[illegible]ergy flow to this population is E and flow in is balance with po[illegible]tion use [illegible] energy, then

$$[illegible] \qquad (1)$$

i) Explain why this must be true.

ii) What does this equation predict for the relationship between logarithm of population size and logarithm of weight?

iii) For salmon, B=.92 (N.R. Glass, Journal of the Fisheries Research Board of Canada 26:2643-2650, 1969) and Egglishaw and Shackley (Journal of Fish Biology 11:647-672) determined the following data on Atlantic salmon, *Salmo salar* L., on the Shelligan Burn -- a small stream in Scotland where I do some of my research. I give the information for so-called 0+, 1+ and 2+ salmon -- those which are newly emerged or have spent one year or two years in the river:

| Year | Length (mm) | | | Density of Fish (number/$m^2$) | | |
|---|---|---|---|---|---|---|
| | 0+ | 1+ | 2+ | 0+ | 1+ | 2+ |
| 1966 | 46 | 93 | 127 | 3.1 | .11 | .06 |
| 1967 | 47 | 93 | 124 | 2.23 | .18 | .01 |
| 1968 | 48 | 100 | 124 | 1.95 | .14 | .03 |
| 1969 | 50 | 100 | 136 | 2.92 | .19 | .03 |
| 1970 | 54 | 101 | 129 | .98 | .2 | .01 |
| 1971 | 54 | 99 | 128 | 2.48 | .18 | .02 |
| 1972 | 52 | 99 | 128 | 1.54 | .41 | .01 |
| 1973 | 62 | 101 | 129 | 1.32 | .30 | .01 |
| 1974 | 58 | 105 | - | 1.36 | .25 | .00 |
| 1975 | 55 | 98 | 129 | 3.09 | .25 | .01 |

Use these data to test the relationship that you derived in step ii).

iv) Equation (1) is based on the assumption that all fish are the same size. This is not so, as evidenced by the salmon data. But it is clear that all 0+ fish are more similar to each other and all 1+ fish to each other than to other age classes. Forgetting about 2+ fish, how does equation (1) generalize when there are two weights $W_1$ and $W_2$? What does this generalization tell you about the mixture of individuals in the population?

3. In June 1994, I participated in the "Potential Biological Removal" workshop held at the Southwest Fisheries Science Center, in response to the re authorization of the Marine Mammal Protection Act. The amendments to the act determine that PBRs would be found from the formula

$$PBR = N_{min} \frac{1}{2} R_{max} F_r$$

where $N_{min}$ is a minimum estimate of population size, $R_{max}$ is the maximum value of per capita reproduction and $F_r$ is a safety feature defined as $F_r$ = .9 for populations at or above 60% of carrying capacity, $F_r$= .5 for populations that were depleted or of unknown status and $F_r$ =.1 for threatened or endangered populations. Scientists studied population dynamics using the "A logistic model":

$$N_{t+1} = N_t + rN_t\{1-(N_t/K)^A\} - PBR_t$$

where $N_t$ is the size of the population in year t and $PBR_t$ is the PBR in year t. Generally, the value of A=2.4 is used.

i) What is the carrying capacity in this model?

ii) What is the maximum per capita reproduction in this model?

iii) For harbor seals, K=25,000 and r=.12. Provide a graph of per capita reproduction vs. population size.

iv) Provide a graph of total population reproduction vs. population size.

4. A population is called a "sink population" if its instantaneous rate of growth $r < 0$ or an individual's lifetime reproduction $R<1$. Such populations can be sustained by immigration. Suppose that the immigration rate per year is constant at I and let N(t) denote the population size in year t. The dynamics are then

$$N(t+1) = I + RN(t)$$

i) Explain the origin of this equation.

ii) Show that the steady state population level is

$$N^* = \frac{I}{1-R}$$

iii) Suppose that a mutant with growth rate R' evolves in the sink population itself (e.g. that the sink population is an island). If M(t) is the size of the mutant population at time t then

$$M(t+1) = R'M(t)$$

since there is no immigration of mutants. Thus the ratio of mutants to normal individuals is

$$\frac{M(t+1)}{N(t+1)} = \frac{R'M(t)}{I + RN(t)}$$

Assume that the normal population is at its steady value $N^*$ and then show that the condition for the mutant to increase, in the sense that

$$\frac{M(t+1)}{N^*} > \frac{M(t)}{N^*}$$

is $R' > 1$.

iv) Interpret this result in terms of the likelihood that we can count on a mutation to save a sink population.

5. Palmblad (1968) studied the density dependence of reproduction and growth of the plantain *Plantago major*. A simplified version of the data is shown below

| Quantity | Sowing Density (seeds per pot) | | | | |
|---|---|---|---|---|---|
| | 1 | 5 | 50 | 100 | 200 |
| % Germination | 100 | 100 | 93 | 91 | 90 |
| % Mortality | 0 | 7 | 6 | 10 | 24 |
| % Reproducing | 100 | 93 | 72 | 52 | 34 |
| Total dry weight per pot (gm) | 8.1 | 11.1 | 13.1 | 13.7 | 12.6 |
| Seeds per reproductive plant | 11980 | 2733 | 228 | 126 | 65 |
| Seeds per pot | 11980 | 12760 | 8208 | 6552 | 4420 |

i) What is plantain?

ii) Make plots of each of the quantities versus sowing density and interpret your results. In the plots use number, rather than percentage, of reproducing plants.

iii) Use your results to construct a single species growth model.

6. Alfred Lotka (of Lotka-Volterra fame) used data on the human population of the US from 1790 to 1910 to estimate the parameters of the logistic equation and concluded that "if the population of the United States continues to follow this growth curve in future years, it will reach a maximum of some 197 million souls by the year 2060". In fact, this level (197 million) was crossed by about 1970.

Recently Henry Tuckwell and James Koziol (Nature 359:200) fit population data of the world from 1950 to 1985 to the logistic. Their model accurately estimated the population in 1992 (about 5.5 billion) and they estimated that the carrying capacity of the world is 23.8 billion and that this will be achieved by 2250.

i) Why do you think Lotka was so off in his prediction?

ii) What do you think of the work of Tuckwell and Koziol in light of the information about Lotka

7. We have studied populations that are said to grow in continuous time, according to

$$\frac{dN}{dt} = rN \qquad N(0)=N_0.$$

For populations that grow in a discrete manner (for example, seasonally), the analog is usually written as

$$N(t+1) = \lambda N(t) \qquad N(0) = N_0$$

where l is called the coefficient of geometric increase.

i) What is the expression for N(t) in terms of $N_0$?

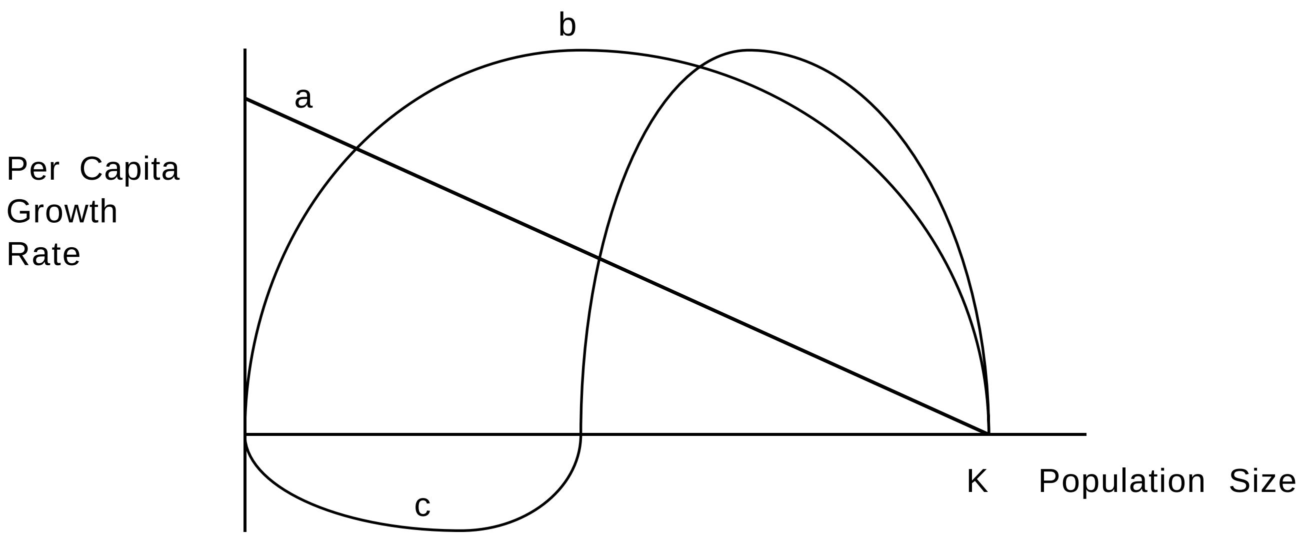
ii) What happens to N(t) if l >1, l=1 or l <1?

8. The general population growth rate can be formulated as

$$\frac{dN}{dt} = B - D + (I-E)$$

where B is a birth rate, D is a death rate, I is immigration and E is emigration. We have focused the role of predators primarily upon the death rate D. Explain how predators might affect <u>one</u> of the other terms B, I or E and propose an experiment to test your idea.

9. Three possible forms of the dependence of per capita growth rate are shown below. Curve a leads to the logistic equation




i) What biological interpretations do you ascribe to curves b and c?

ii) What predictions about population growth rate can you make? In particular, compare the population growth rates associated with curves b and c with the logistic.

10. The logistic description of population growth $\frac{1}{N}\frac{dN}{dt} = r(1-\frac{N}{K})$ is said to have "strict" negative density dependence: for all values of population size an increase in population size causes a decrease in per capita growth rate.

i) Explain this idea using a graph in which per capita growth rate is plotted against population size.

ii) Imagine an organism that had "peaked" density dependence, so that per capita growth rate initially climbs with population size, but then declines (and reaches zero at carrying capacity). On the same graph as the one above, illustrate this kind of density dependence. What predictions would you make about population dynamics? What biological mechanisms might lead to this kind of density dependence?

iii) Density dependence is often said to be an "enemy" of conservation. What do you think is meant by this and why?

11. This question deals with the logistic model

$$\frac{dN}{dt} = .1N(1-\frac{N}{200})$$

where time is measured in weeks and biomass is measured in kilograms.

i) What is the maximum per capita growth rate, including units?

ii) What is the carrying capacity, including units?

iii) Plot per capita growth rate vs. population size, showing carrying capacity.

iv) Plot the growth rate of the population as a function of population size.

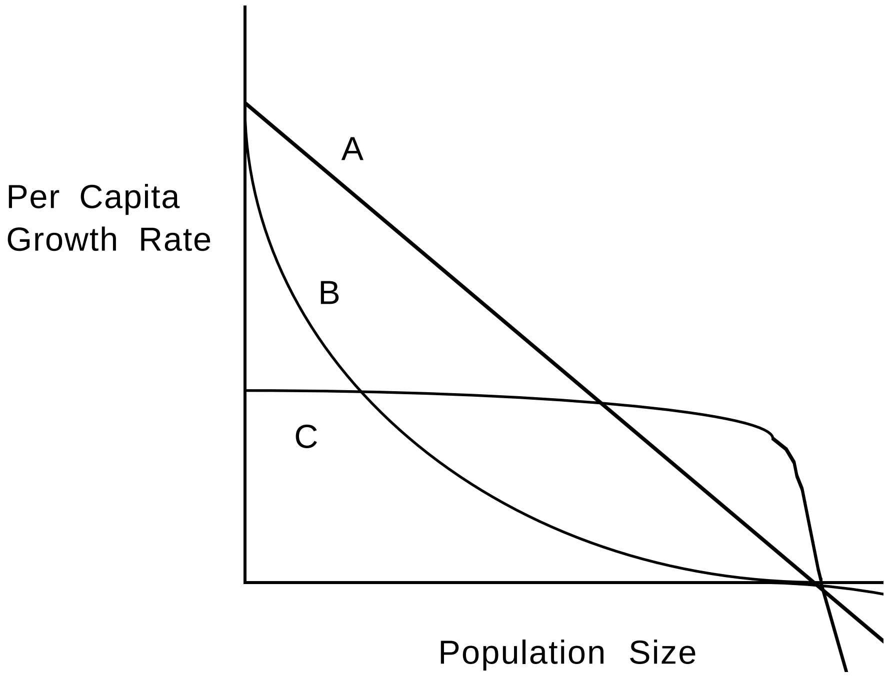
v) Suppose habitat is destroyed so that carrying capacity declines at a rate of 10% per week. Approximately compute the trajectory of the population for 10 weeks. To do this, rewrite the logistic equation by treating dt=1 as

$$N(t+1) = N(t) - .1N(1-\frac{N}{K(t)})$$

$$K(t+1) = .9\, K(t)$$

with N(0)=K(0)=200. In addition, explain where these equations come from.

12. What characteristics would you expect of organisms if they had one of these three different relationships between per capita growth rate and population size?




13. An alternative to the logistic equation for populations that grow seasonally is

$$N_{t+1} = \frac{rN_t}{1 + aN_t}$$

Here $N_t$ is the size of the population in year t.

i) What is the maximum per capita growth rate?

ii) What are the units of r and a?

iii) What is the steady state level (analog of carrying capacity) for this population?

14. An alternative to the logistic equation has been proposed for the flour beetle *Tribolium*. In this description

$$\text{Birth rate} = b(N) = b_0 N \exp(-b_1 N)$$

$$\text{Death rate} = d(N) = d_0 N.$$

where N is population size at time t. The growth rate of the population is assumed to be

$$\frac{dN}{dt} = b(N) - d(N)$$

i) Peters, Mangel and Costantino (Bulletin of Mathematical Biology 51:625-638, 1989) give the following parameter values

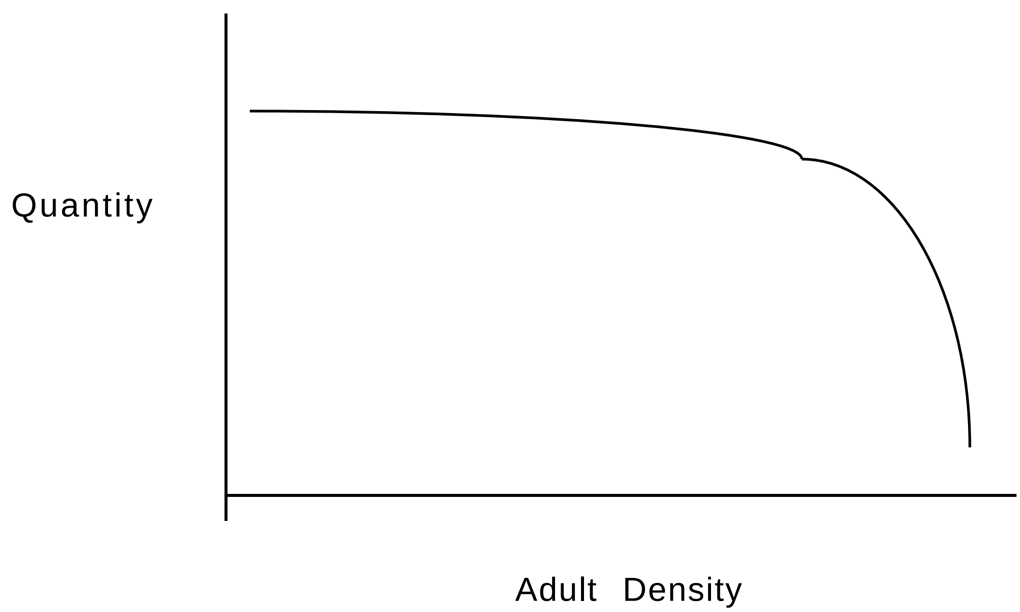
$b_0 = 0.237$, $d_0 = 0.088$ and $b_1 = 0.0165$

If time is measured in weeks and population size in numbers of individuals, what are the units of these parameters?

ii) In general, what is the steady state level of population size in terms of the three parameters $b_0$, $d_0$ and $b_1$? What is the steady state population size for the parameters given in 1) above?

iii) Rewrite the logistic equation as $\frac{dN}{dt} = rN - \frac{rN^2}{K}$ and interpret the two terms on the right hand side. What is the fundamental difference in the world view provided by the flour beetle model and that of the logistic equation?

15. In his work on many large mammal populations, Charles Fowler has shown that per capita reproduction has the following shape.




i) Contrast this with the density dependence of the per capita reproduction of the logistic equation.

ii) How would the population dynamics compare with the logistic equation?

16. When he first moved from theoretical physics to ecology, R.M. May believed that an appropriate discrete time version of the logistic equation

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) \qquad (1)$$

would be

$$N(t+1) = N(t) + rN(1-\frac{N}{K}) \qquad (2)$$

i) Explain why this is a natural interpretation.

ii) Equation (2) is now called the logistic map. Assume that N(0)=60, K=100 and plot N(t) for t=1 to 50 for r=0.4, r=2.5 and r=2.7 The case of r=2.5 is called a "period 2" map and the case of r=2.7 is called "deterministic chaos". What justifies these words?

iii) Make plots of N(t+1) vs. N(t) for the case in which r=2.7. What does this tell you that the time series did not?

17. In this problem, you will use the method of partial fractions from introductory calculus to solve the logistic equation

$$\frac{dN}{dt} = rN(1-\frac{N}{K}) \qquad \text{with } N(0)=N_0$$

But first: If the unit of t is years, the unit of N is kg, what are the units of r and K?

i) Separate variables according to

$$\frac{dN}{rN(1-\frac{N}{K})} = r\,dt$$

ii) Write $\frac{1}{rN(1-\frac{N}{K})} = \frac{A}{N} + \frac{B}{1-\frac{N}{K}}$ and show that A=1, B=$\frac{1}{K}$.

iii) Show that this means

$$\log(N) - \log(1-\frac{N}{K}) = rt + \text{constant}$$

iv) which means

$$\log\left(\frac{N}{1-\frac{N}{K}}\right) = rt + \text{constant}$$

v) which means that

$$\frac{N}{1-\frac{N}{K}} = ce^{rt} \text{ where c is a constant.}$$

vi) so that

$$N(t) = \frac{ce^{rt}}{1+\frac{ce^{rt}}{K}} \quad .$$

vii) And since when t=0, $N=N_0$, that

$$c=\frac{N_0K}{K-N_0}$$

viii) from which

$$N(t) = \frac{N_0Ke^{rt}}{K + N_0(e^{rt}-1)} \, .$$

Show using this last equation that $N(0)=N_0$. and that N(t) --> K as t increases, regardless of $N_0$.

18. Many insect pest populations have one generation per year, a 50-50 sex ratio and grow exponentially so that if F(t) is the number of females in generation t, the dynamics are

$$F(t+1) = rF(t)$$

i) What kind of growth will the population exhibit if it follows this equation? In the 1950s, E.F. Knipling proposed the Sterile Insect Method (SIM) of pest control in which one releases many sterile males (e.g. sterilized by radiation while in the pupal stage), thus "diluting" the population of reproductively active males. The proposed equation is

$$F(t+1) = r\ F(t)\left(\frac{F(t)}{F(t)+ S(t)}\right)$$

where S(t) is the number of sterile males released in generation t. This is based on the idea that the sex ratio is 50-50 in the fertile population.

ii) Explain the form of this equation.

iii) If S(t) = constant, describe the population dynamics of F(t).

iv) Why might this method of reducing the pest population not work?

19. If a population is rare, we can ignore density dependent effects in describing its dynamics. In such a case, if N(t) denotes the size of the population at time t

$$N(t+1) = \lambda N(t) \qquad (1)$$

where l is the growth rate.

i) Explain why Eqn 1 is the same as

$$\log(N(t+1)) = \log(\lambda) + \log(N(t)) \qquad (2)$$

What prediction do you make if a plot of log(N(t+1)) vs. log(N(t)) is made?

ii) Explain why Eqn 1 is also the same as

$$N(t) = \lambda^t N(0) \qquad (3)$$

What prediction do you make if a plot of log(N(t)) vs time is made?

iii) In a closed area, 50 individuals are released in year 0 and monitored for 15 years by two different methods of indirect observation. The data are these:

| Year | Log of Population Size | |
|---|---|---|
| | Method 1 | Method 2 |
| 1 | 3.99009 | 2.67639 |
| 2 | 4.15902 | 3.47691 |
| 3 | 4.45262 | 4.97188 |
| 4 | 4.07099 | 2.78401 |
| 5 | 3.95114 | 4.30731 |
| 6 | 4.34032 | 4.13149 |
| 7 | 3.65094 | 3.88289 |
| 8 | 4.14319 | 4.41265 |
| 9 | 3.77869 | 5.15262 |
| 10 | 4.19152 | 5.04436 |
| 11 | 4.19249 | 4.66442 |
| 12 | 4.12185 | 5.45714 |
| 13 | 4.75753 | 5.28213 |
| 14 | 3.93198 | 5.22483 |
| 15 | 4.57428 | 5.74244 |

Obtain an estimate for the growth rate $\lambda$ for each time series of data. What conclusions can you draw about the growth of the population.

iv) Suppose we also knew that the population grew at 5% per year because of a complete census. What conclusions would you draw about the methods of indirect observation?

## Advanced Material

1. D. Ludwig et. al. (Journal of Animal Ecology 57:315-332) developed a model for the outbreak of spruce budworm. If B(t) denotes the density of budworms at time t, their model for budworm dynamics is

$$\frac{dB}{dt} = rB(1-\frac{B}{K}) - b\frac{B^2}{a^2+B^2}$$

i) Interpret each of the terms on the right hand side of this equation. In particular, what are the biological meaning of a and b?

ii) Analyze the associated population dynamics and explain why this is a model for an "outbreak" system.

2. . Some years ago, Craig Peters, Bob Costantino and I developed models for the population dynamics of the flour beetle *Tribolium*. Our model focussed only the adult stage (there are also eggs, larvae and pupae). If A(t) is the adult population at time t, then we assume

$$\Pr\{\text{ transition in one day } | A(t)= a\} = 1- e^{-\delta a} \quad (1)$$

and that given a transition occurs that

$$\Pr\{A(t+1) = a + 1 \mid A(t) =a \} = \frac{B(a+d)e^{-Ca}}{B(a+d)e^{-Ca} + Da}$$

$$\Pr\{A(t+1)= a-1 \mid A(t) =a \} = \frac{Da}{B(a+d)e^{-Ca} + Da} \quad (2)$$

i) What are the interpretations of B, C, D, and $\delta$?

ii) Define the steady state population size $a_s$ as the one for which the chance of a transition upwards is the same as the chance of a transitions downwards. Write a program to find this level if B=.237, D=.088, C = .0165, and $\delta$=1.

iii) Derive equations for the stationary probability density v(a) and for the mean time T(a) to hit $a=a_s$ before a=1, starting at A(1)=a.

iv) Attempt to solve these equations.

3. In the theory of colonization and extinction, the steady state frequency of population size n, $\bar{p}(n)$ satisfies the condition that

$$\bar{p}(n) = \frac{\bar{p}(0)\lambda(0)\lambda(1)\cdots\lambda(n-1)}{\mu(1)\mu(2)\cdots\mu(n)}$$

i) Explain the meaning of $\lambda(n)$ and $\mu(n)$. Be precise in your description.

ii) Explain why this result makes sense only if $\lambda(0) > 0$. What notion underlies this.

iii) How does one find $\bar{p}(0)$ from this expression?

4. Imagine fifty petri dishes, each filled with identical medium and containing paramecium that grow according to the logistic equation with a carrying capacity of 100 individuals.

i) Assuming that a dish starts with 25 individuals, sketch the population trajectory in that dish.

ii) Now assume that the initial number of individuals in a dish is approximately normally distributed with mean 25 and variance 10. Sketch the initial frequency distribution of size.

iii) Sketch the frequency distribution of size when the populations have got very close to carrying capacity.

iv) What partial differential equation will the size distribution satisfy?

v) What do your results in parts ii and iii tell you about the solution of this partial differential equation as $t \to \infty$?

5. In this problem, you will explore the connections between discrete and continuous time descriptions of population growth. Imagine a population with a 50:50 sex ratio in which individuals reproduce during a relatively short breeding system and that surviving young can be reproductive at the start of the next breeding cycle. Suppose that

N(y) = number of females at the start of the breeding period in year y

b = expected per capita reproduction (surviving offspring) (1)

i) What does it mean if $b = 1$, if $b < 1$ or if $b > 1$?

ii) Assume that there is no source of mortality. Explain why the population dynamics would then be

$$N(y+1) = (1+b)N(y) \quad (2)$$

from which

$$\frac{N(y+1)}{N(y)} = 1+b \quad (3)$$

iii) We also can charcterize population growth, in the density independent case and in the absence of mortality by

$$\frac{dN}{dt} = \lambda N \quad (4)$$

where $\lambda$ is the instantaneous birth rate and t measures time within the year. Show the follwing: that the solution of this equation is

$$N(t) = N(0)e^{\lambda t}. \quad (5)$$

so that

$$N(y+1) = N(y)e^{\lambda} \quad (6)$$

from which we conclude that

$$e^{\lambda} = 1+b \quad (7)$$

or

$$\lambda = \log(1+b) \quad (8)$$

iii) Now let us include additional sources of mortality. If the continuous time death rate is $\mu$, then the population growh rate is charactierized by

$$\frac{dN}{dt} = (\lambda-\mu)N = rN \quad (9)$$

Typically, we will know b (expected reproductive success) and r (the growth rate of the population). Show that Eqn 9 leads to

$$\frac{N(y+1)}{N(y)} = e^{\lambda-\mu} = e^{r}.$$

so that $\lambda-\mu = r$ or

$$\mu = \log(1+b) - r \qquad (10)$$

This provides a way of inferring instantaneous death rate from two more easily measured quantities.

iv) Make a plot of $\mu$ vs. $r$, with $r$ ranging from 0 to 0.12, for b=0.1, b=1 and b = 5. Interpret your results.

**PREDATORS AND PREY**

1. Peter Larkin (Journal of the Fisheries Research Board of Canada 23:349-356, 1966), in an attempt to understand the invasion of the Great Lakes by sea lampreys, developed a model for the interaction of a fishery for lake trout on the dynamics of lake trout and sea lampreys, which are predators of trout. A. Jensen (Canadian Journal of Fisheries and Aquatic Sciences 51:942-945, 1994) recently reanalyzed the model, which is the following.

Let X(t) and Y(t) denote the abundance of lake trout and sea lamprey respectively and assume that the growth rates are given by

$$\frac{dX}{dt} = rX(1-\frac{X}{K}) - \frac{raXY}{K} \quad (1)$$

$$\frac{dY}{dt} = sY(1-\frac{Y}{M}) + \frac{sbXY}{M} \quad (2)$$

where r, K, a, s, M and b are parameters (numbers with units).

i) What is the biological interpretation of equations (1) and (2)?

ii) Draw the isoclines for the population dynamics and analyze the general patterns that emerge.

iii) Jensen proposes that biomass be measured in numbers, t in years and gives the following numerical values for the parameters:

$K=16 \times 10^6$
$M=2 \times 10^6$
$a= 5.75$
$b=0.2$ to $20$
$r=.5$
$s=.75$

What are the units for each of these parameters?

iv) Explain how you would include a fishery for lake trout, which captures trout in proportion to their abundance, in this model.

2. For a Lotka-Volterra model of predator-prey oscillations,

$$\frac{dV}{dt} = aV(1-\frac{V}{K}) - cPV$$

$$\frac{dP}{dt} = -bP + mPV$$

explain why both predator and prey populations can increase. What is the biological interpretation of this situation? Use a sketch to show where this occurs in the predator-prey phase plane.

3. A study of the predation of midges (chironomids) by fish in small buckets lead to the following data

| Treatment | Average Number of Midges Per Bucket |
|---|---|
| Control (no predators) | 45 |
| Lestids | 10 |
| Sticklebacks | 11 |
| Roach | 10 |

i) What are commonalties in the physiology and life history of lestids, sticklebacks and roach? What are differences?

ii) What do you conclude about the predator vs. control treatments and the predator vs. predator treatments.

iii) If both lestids and sticklebacks were in the bucket, what average number of midges would you predict and why?

4. A number of authors have argued that the Lotka Volterra predator prey equations

$$\frac{dV}{dt} = rV(1-\frac{V}{K}) - bVP$$

$$\frac{dP}{dt} = cVP - mP$$

are inappropriate because they do not include handling time when predators remove prey.

i) Researchers have suggested that the term VP be replaced by $\frac{\lambda VP}{1 + h\lambda V}$. How is this related to the result from diet choice based on searching and handling? How would you interpret $\lambda$ and h?

ii) Modify the Lotka Volterra equations in this manner and describe the population dynamics, using isoclines and the phase plane.

5. Reconsider the Lotka Volterra predator-prey equations

$$dV/dt = rV(1-\frac{V}{K}) - bVP$$

$$dP/dt = cVP - mP.$$

i) What are the units of b and c?

ii) How is b related to the foraging of the predator?

iii) Note that if we take the ratio of the predator growth term to the prey death term, we obtain c/b. How is this to be interpreted?

6. This question deals with the Lotka Volterra predator prey equations

$$\frac{dV}{dt} = 6V(1-\frac{V}{100}) - .5PV$$

$$\frac{dP}{dt} = .1PV - .07P$$

where time is measured in days and biomass in grams.

i) What is the maximum per capita birth rate of the prey, including units?

ii) What is the per capita death rate of the predator, including units?

iii) What is the total rate at which prey are removed by predators?

iv) What is the total rate at which predators appear?

v) Approximately how many prey does it take to "make" a predator.

vi) Plot the isoclines for predator and prey.

vii) Approximately sketch the cycle of predator and prey.

7. This question deals with the Lotka-Volterra predator-prey equations

$$dV/dt = rV(1-\frac{V}{K}) - bVP$$

$$dP/dt = cVP - mP.$$

i) What is the etymology of isocline? Some people argue that instead of isocline we should use the word "null-cline". What is your opinion?

ii) Analyze the following modifications of the Lotka-Volterra predator prey equations and interpret your results

a) Replace mP by $mP^2$

b) Replace bVP by $\frac{bVP}{1+aV}$ . In this case, in your interpretation, be certain to connect the replacement to diet selection by a forager.

8. For the Lotka-Volterra predator prey equations:

$$\frac{dV}{dt} = rV(1-\frac{V}{K}) - bVP$$

$$\frac{dP}{dt} = cVP - mP$$

i) Is it possible for predators and prey both to decrease? Explain your reasoning using the predator-prey phase plane that shows the cycle and provide biological interpretation.

ii) Also use the predator-prey diagram to explain the relationship between the peak in predator population and the peak in prey population.

9. Consider the predator-prey equations

$$dV/dt = rV(1-\frac{V}{K}) - bVP$$

$$dP/dt = cVP - mP$$

where V and P are measured in kg and t is measured in weeks.

i)What are the precise units of r and K?

ii) What are the precise units of b?

iii) What is the maximum per-capita growth rate of prey in the absence of predators?

iv) Draw the cycle a) when the predator growth rate is much slower than the prey growth rate b) when the predator and prey have comparable growth rates, c) when the predator growth rate is much faster than the prey growth rate.

10. David Tilman, at the University of Minnesota, has proposed "resource-based" population ecology. (e.g., American Naturalist 116:362-393 (1980), or D. Tilman, **Resource Competition and Community Structure** Princeton University Press, Princeton, NJ) For a single species, he envisions that the biomass N of the species depends upon a resource R and that the two are linked by the growth equations

$$\frac{dN}{dt} = [\frac{vR}{R+K} - m]N$$

$$\frac{dR}{dt} = r_0 R - vNR$$

i) Interpret each of the terms on the right hand sides of these equations.

ii) Determine the steady levels of biomass and resource and interpret the results.

11. Given Tilman's model for resource based growth

$$\frac{dN}{dt} = [\frac{vR}{R+K} - m]N$$

$$\frac{dR}{dt} = r_0R - vNR$$

i) How would you extend this model to treat the competition between two species that use the same resource?

ii) What prediction does the extension make about the outcome of the competition?

12. Consider the Lotka-Volterra predator-prey equations

$$\frac{dV}{dt} = rV(1-\frac{V}{K}) - dVP$$

$$\frac{dP}{dt} = cdVP - mP$$

i) If P and V were measured in the same units, in general would you expect c to be >1 or <1 and why?

ii) Compute the isoclines and determine the phase plane dynamics for this system.

iii) Sean Nee published a note in **Nature** in 1993 in which he introduced the concept of a "victim threshold density " (VTD) for the prey carrying capacity given by $K_{VTD}=\frac{m}{cd}$ . What is the interpretation of this quantity?

13. In this exercise, you will investigate the paradox of enrichment (e.g. A.A. Berryman, The origins and evolution of predator-prey theory, Ecology 73:1530-1535, 1992).

i) For the usual Lotka-Volterra predator prey equations

$$\frac{dV}{dt} = rV(1-\frac{V}{K}) - dVP$$

$$\frac{dP}{dt} = bVP - mP$$

demonstrate the following: if the prey carrying capacity increases from K to a higher value K', the predator steady state population increases but the prey steady state population does not.

ii) Some authors have suggested that a way around this problem is to assume that the per capita rate of change of the predator population is

$$b(1-\frac{P}{qV})$$

If this assumption is used, what is the "carrying capacity" of the predator population.

iii) Find the isoclines for predator and prey populations and show that the paradox of enrichment disappears.

14. Read pg 139 ff in Leopold's **A Sand County Almanac**. Derive predator-prey equations for Wolves, Deer, and Foliage, assuming that i) per capita birth rate of wolves is proportional to deer, ii) per capita death rate of wolves is constant, iii) per capita birth rate of deer is proportional to grass, iv) per capita death rate of deer is the sum of a constant plus a term proportional to wolves, v) foliage grows logistically in the absence of deer, and vi) the per capita removal of foliage is proportional to deer population. Explain how these three predator prey equations could be used to illustrate what happened to the mountain after the wolves were removed.

**COMPETITION**

1. Consider the Lotka-Volterra competition equations

$$\frac{dN_1}{dt} = 2N_1\left(1 - \left(\frac{N_1 + N_2}{125}\right)\right)$$

$$\frac{dN_2}{dt} = 3N_2\left(1 - \left(\frac{N_2 + 4N_1}{200}\right)\right)$$

Population size is measured in grams and time in days.

i) What is the maximum per capita growth rate of the first species?

ii) In the absence of the second species, what is the carrying capacity for the first species?

iii) Which species is the stronger interspecific competitor?

iv) What are the units of the "4" in the second equation?

2. The competition between two species of beetles is studied using DeWitt plots in which a total of 100 individuals are initially placed together. Medium is changed every third day to insure the carrying capacity is constant. The population sizes are measured after 10, 20, 40 and 80 weeks and are shown below:

After t=10 weeks

| X(0) | X(t) | Y(t) |
|---|---|---|
| 0 | 0 | 100 |
| 20 | 15 | 92 |
| 40 | 17 | 85 |
| 60 | 20 | 72 |
| 80 | 23 | 48 |
| 100 | 28 | 0 |

After t=20 weeks

| X(0) | X(t) | Y(t) |
|---|---|---|
| 0 | 0 | 100 |
| 20 | 15 | 92 |
| 40 | 15 | 92 |
| 60 | 16 | 88 |
| 80 | 18 | 76 |
| 100 | 28 | 0 |

After t= 40 weeks

| X(0) | X(t) | Y(t) |
|---|---|---|
| 0 | 0 | 100 |
| 20 | 15 | 92 |
| 40 | 15 | 92 |
| 60 | 15 | 92 |
| 80 | 15 | 92 |
| 100 | 28 | 0 |

i) Construct DeWitt plots for each week.

ii) Interpret the results.

iii) Compare your results for the case in which X is grown with a different species Z, and the results are shown below. That is, what might be different between the two situations, what ecological interactions are suggested by the data?

After t=10 weeks

| X(0) | X(t) | Z(t) |
|---|---|---|
| 0 | 0 | 100 |
| 20 | 38 | 95 |
| 40 | 38 | 88 |
| 60 | 36 | 73 |
| 80 | 33 | 49 |
| 100 | 28 | 0 |

After t=20 weeks

| X(0) | X(t) | Z(t) |
|---|---|---|
| 0 | 0 | 100 |
| 20 | 39 | 96 |
| 40 | 39 | 96 |
| 60 | 38 | 92 |
| 80 | 36 | 79 |
| 100 | 28 | 0 |

After t=40 weeks

| X(0) | X(t) | Z(t) |
|---|---|---|
| 0 | 0 | 100 |
| 20 | 39 | 96 |
| 40 | 39 | 96 |
| 60 | 39 | 96 |
| 80 | 39 | 96 |
| 100 | 28 | 0 |

3. This question deals with the Lotka Volterra competition equations

$$\frac{dX}{dt} = 2X\left(1 - \frac{5X+3Y}{100}\right)$$

$$\frac{dY}{dt} = Y\left(1 - \frac{2Y+4X}{200}\right)$$

where biomass is measured in tons and time in years.

i) What is the maximum per capita growth rate of the first (X) species?

ii) What is the maximum growth rate of the second (Y) species?

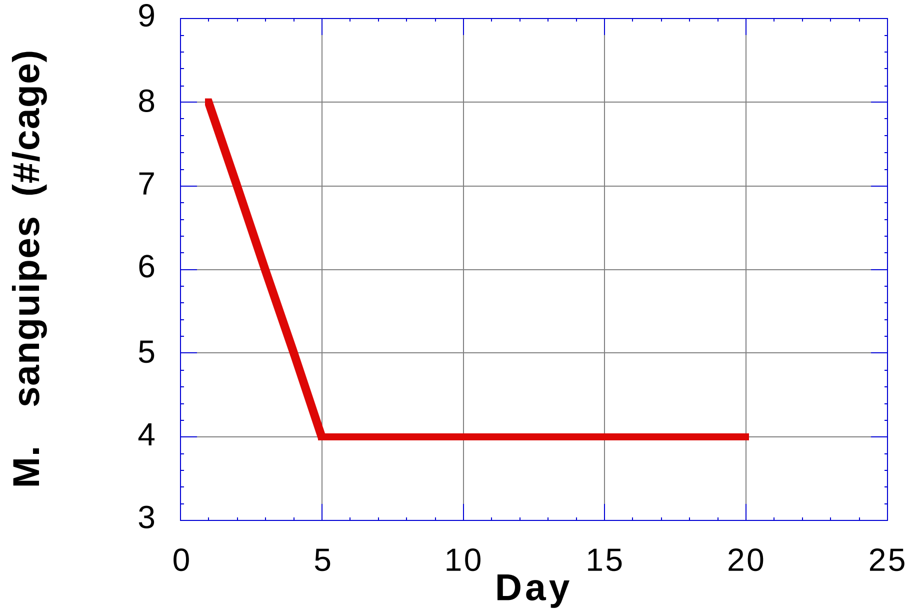
iii) What are the carrying capacities of the two species?

iv) Which species is the stronger intraspecific competitor?

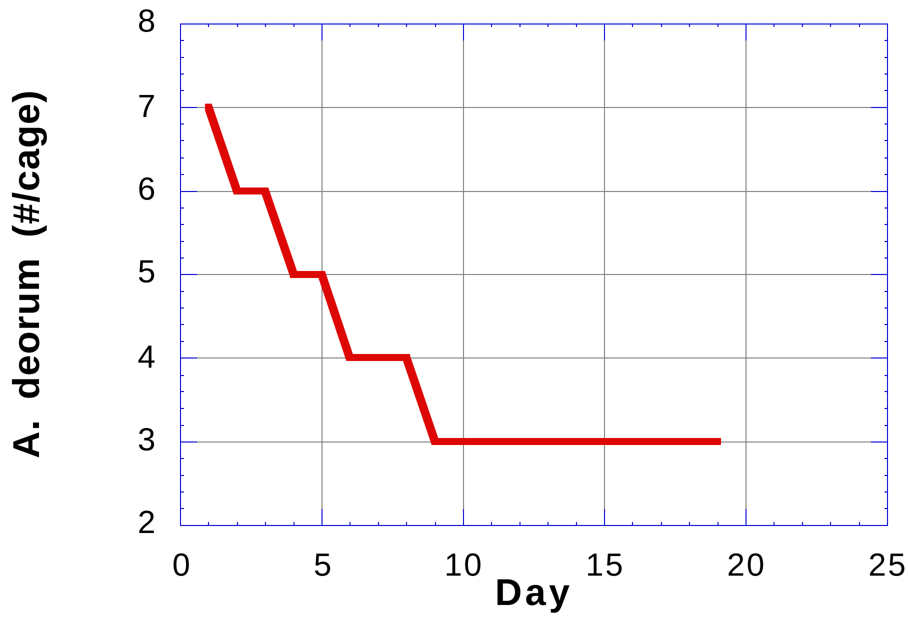
v) Which is the stronger interspecific competitor?

vi) Plot the isoclines for the two species and predict the result of the interspecific competition.

4. J. Chase and G. Belovsky (American Naturalist 143:514-527, 1994) studied the competition between two grasshoppers *Ageneotettix deorum*, which feeds almost exclusively on grasses, and *Melanoplus sanguinipes*, which feeds on both grasses and forbs. Experimental treatments consisted of different densities of grasshoppers in cages with different levels and kinds of food. (This is called the "included niche" competition.). When the two species were alone, the population size versus time curves looked like this:

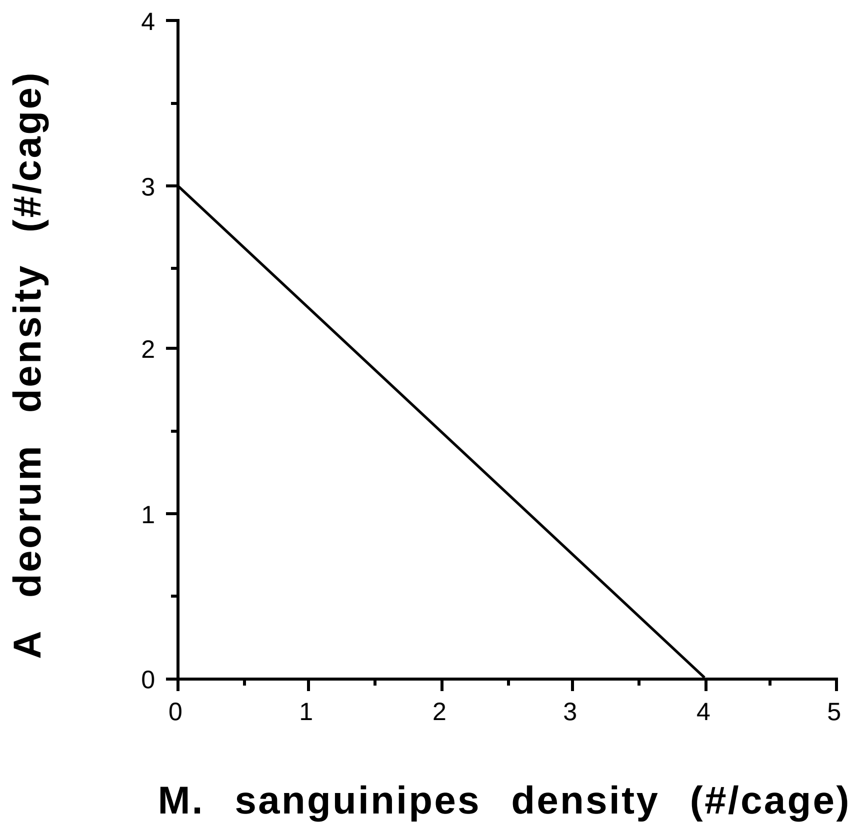

M. sanguipes (#/cage)
9
8
7
6
5
4
3
0
5
10
15
20
25
Day

and

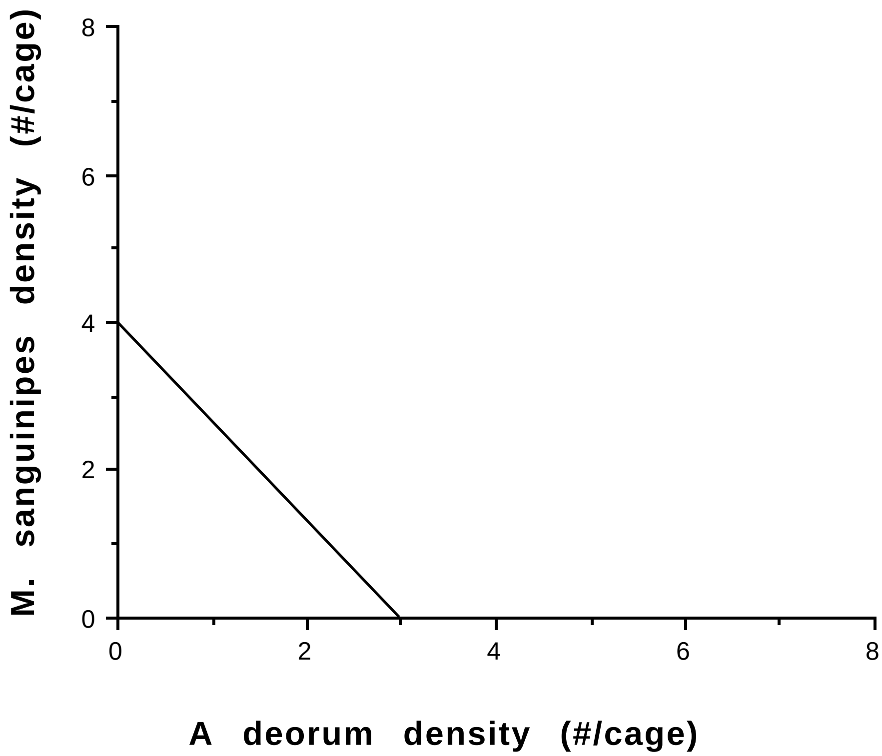

A. deorum (#/cage)
8
7
6
5
4
3
2
0
5
10
15
20
25
Day

i) What are your estimates for the carrying capacities of the two species in these cages (assuming that food is maintained at a constant level) and why?

When *M. sanguinipes* was held constant at different levels, the steady level of *A. deorum* looked like this

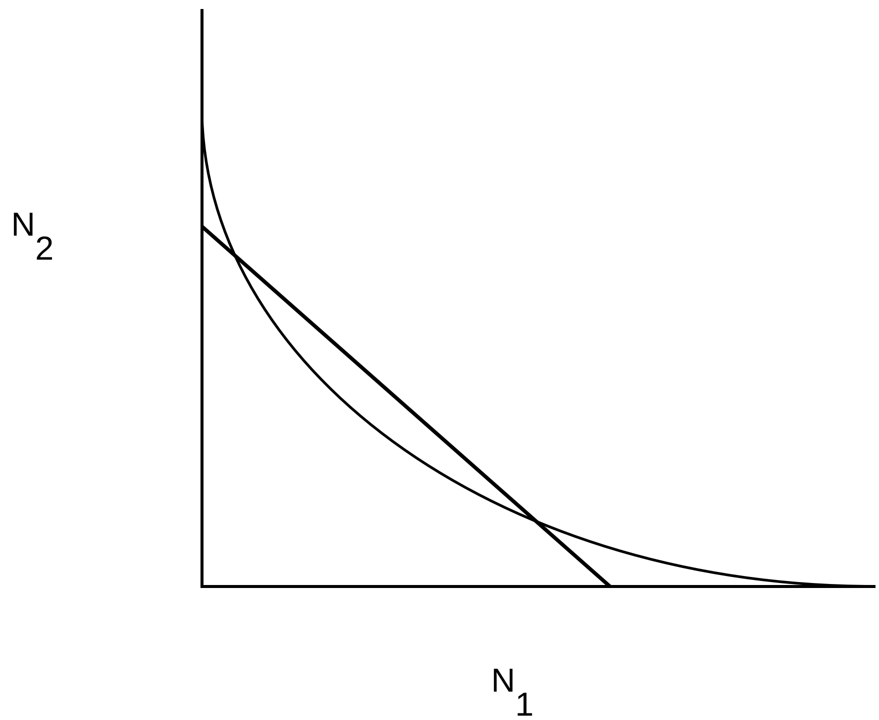



and when *A. deorum* was held constant, the steady density of *M. sanguinipes* was like this:




ii) Use these results to estimate the interspecific competition coefficients, assuming that the populations follow the Lotka-Volterra competition equations.

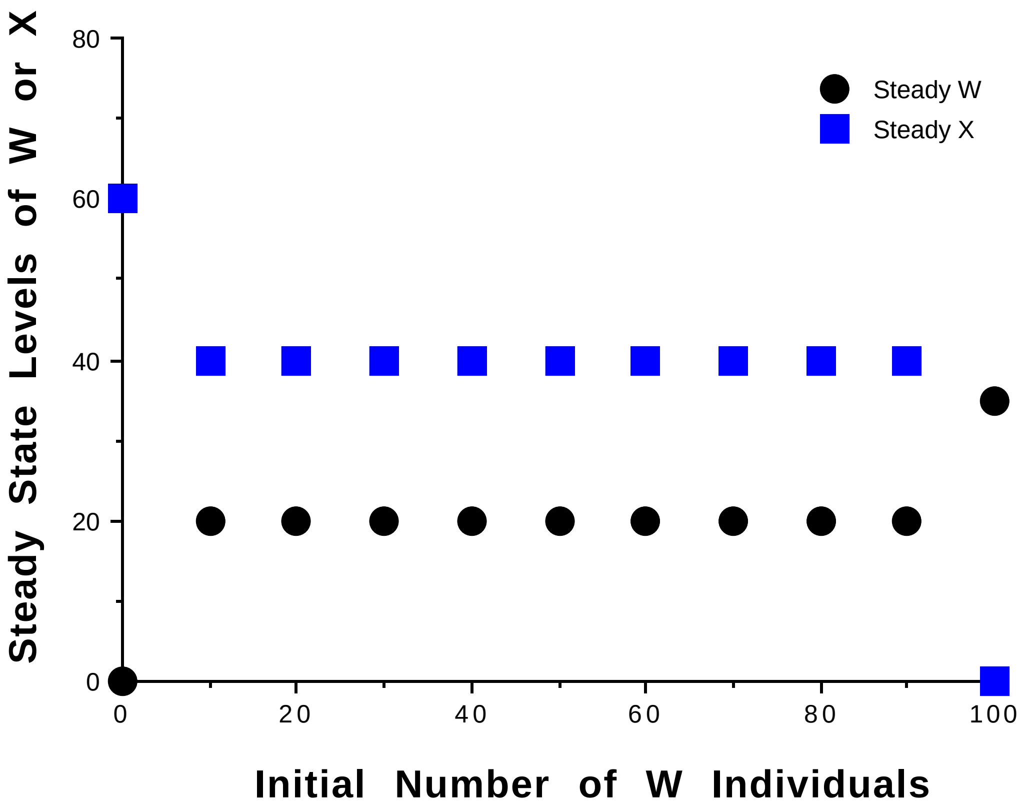
5. In his study of competition and predation, A.D. Bazykin encountered a situation in which the isoclines for the growth rates of the two species were as shown below



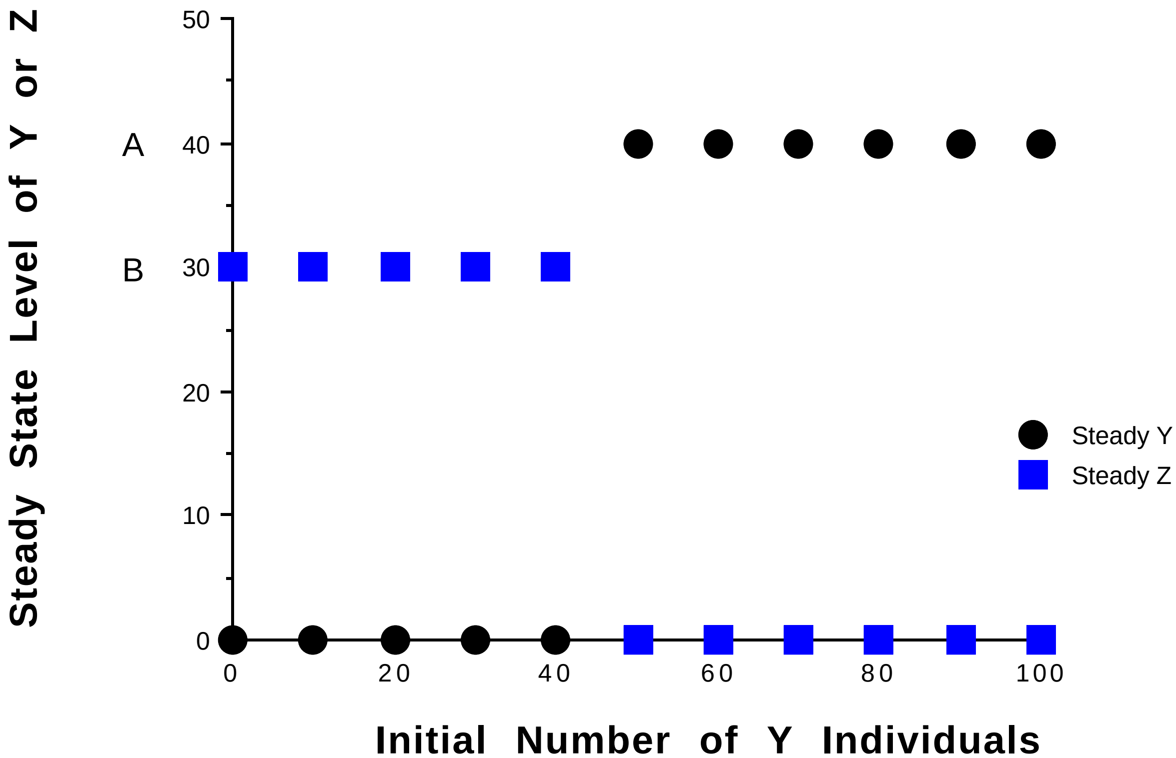

Here the straight line corresponds to the isocline for $\frac{dN_1}{dt}$ = 0 and the curve corresponds to the isocline for $\frac{dN_2}{dt}$ =0. Describe the population dynamics.

6. Friedman (1971) conducted competition experiments on two shrubs (*Artemisia herba-alba* and *Zygophyllum dumosum*) in the Negev desert in Israel. He was primarily interested in how adults of one species affected the seedlings of the other. Propose an experiment to measure competition between the two species taking life stage into account. Make certain to outline what data you will collect and what comparisons you will make.

7. In a study of competition, two species of beetles W and X are placed in large enclosures and allowed to live together until their populations reach a steady level. Each enclosure starts with a total of 100 individuals. When the steady levels are plotted as a function of the initial number of W individuals, the following results are obtained:



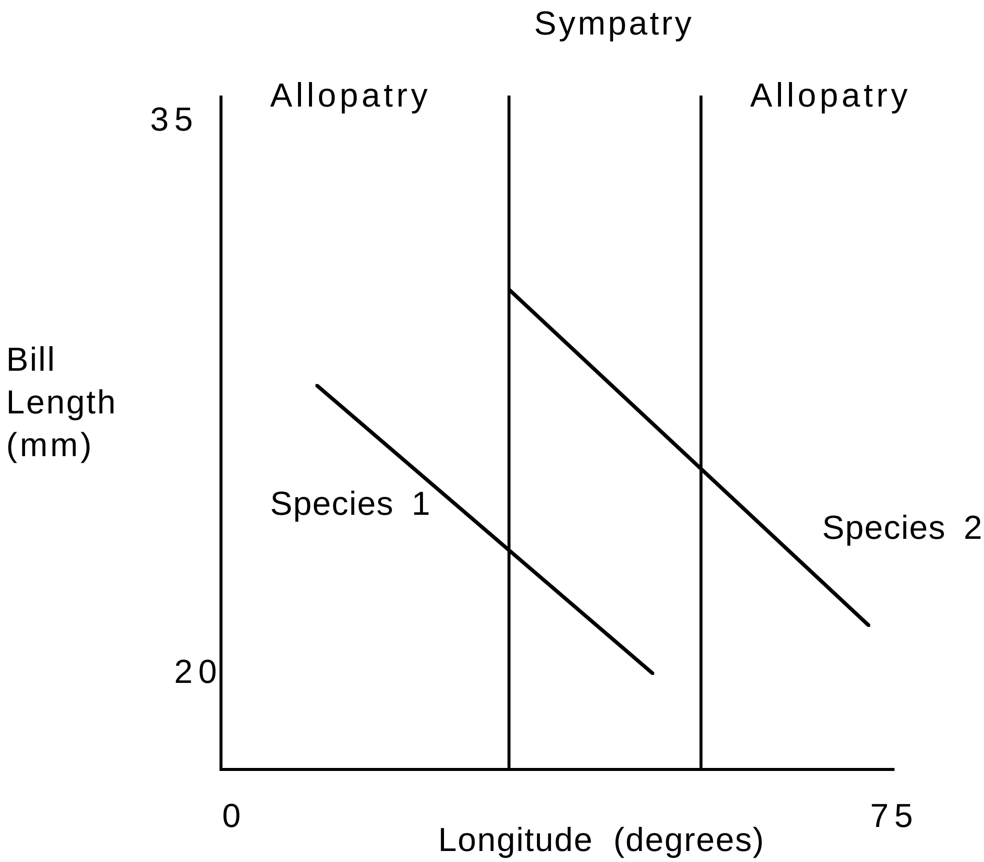

When the same procedure is replicated with two different species of beetles, Y and Z, the following results are obtained:




i) What do the points A and B on the second graph represent?

ii) Interpret the results in both figures. In your answer, include a discussion of how the results relate to the Lotka-Volterra competition equations.

8. In the mid 1970s, Peter Grant studied two species of nuthatches (*Sitta*) that have bill length and plumage traits that vary in the manner shown below:




Provide two explanations for the pattern in these results.

9. Draw results that you would predict if Dewitt plots were made for

i) Predator-prey interactions.
ii) Competitive interactions.
iii) Mutualistic interactions.

10. In his book **Vertebrate Zoology**, Hairston describes competition studies between *Plethodon jordani* and *P. oconaluftee*. He writes the competition equations like this

$$\frac{dN_1}{dt} = r_1N_1\frac{K_1-N_1-a_{12}N_2}{K_1}$$

$$\frac{dN_2}{dt} = r_2N_2\frac{K_2-N_2-a_{21}N_1}{K_2}$$

and gives the following data:

In the Smoky Mountains: $K_1$=45, $K_2$=12, $a_{12}$=2.255, $a_{21}$=.194

In the Balsam Mountains: $K_1$=47, $K_2$=11, $a_{12}$=0.63, $a_{21}$=.14

i) What kinds of organisms are these?

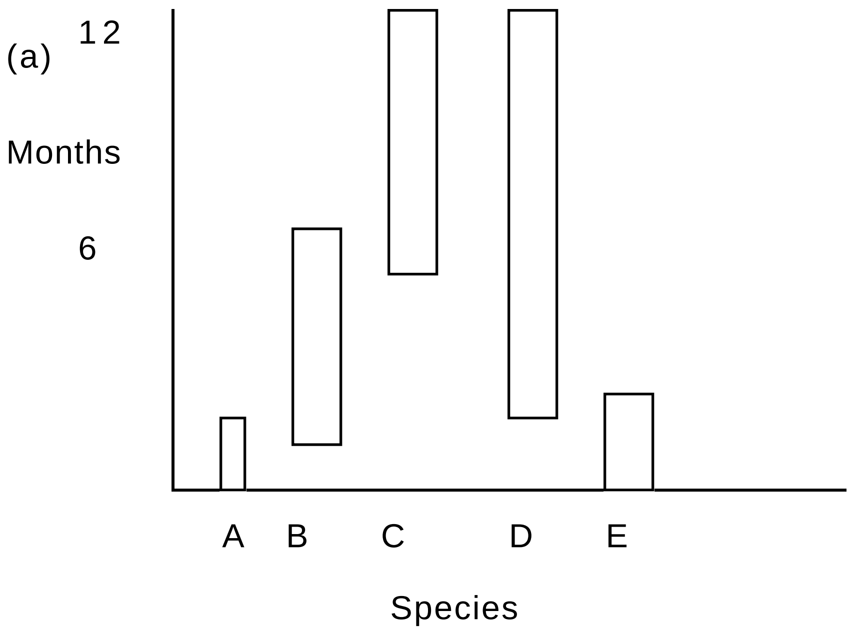
ii) Predict the outcome of competitions in these two different regions.

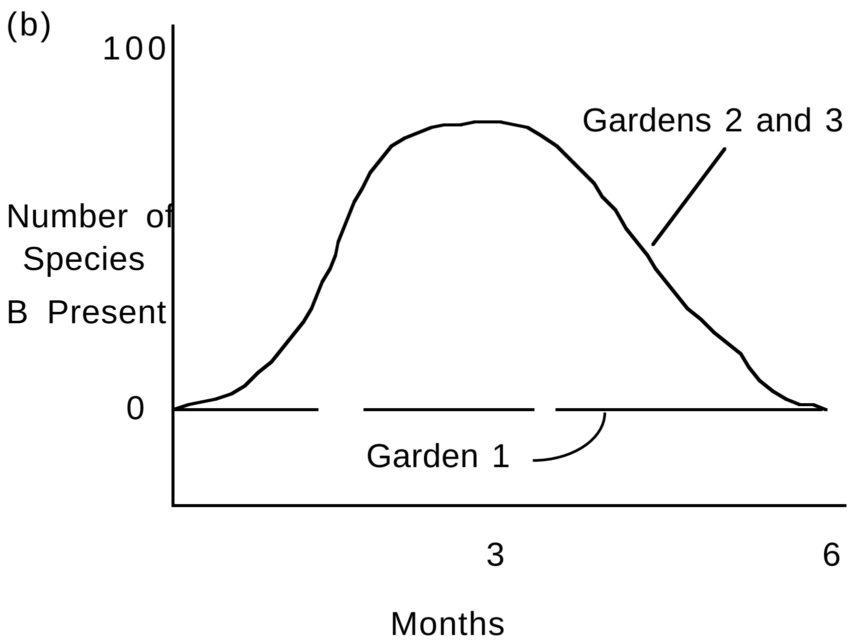
11. B. Two ecologists from different universities (one in Alberta, Canada and one in Oregon) collect large numbers of two species of fish from one lake where the fish have coexisted for a long time. One of the ecologists returns to the lab and finds that regardless of initial population sizes, species 1 always goes extinct in competiton experiments. However, the other returns to the lab and finds that regardless of initial population sizes, species 2 always goes extinct n the competition experiments. In the laboratories, they maintain the fish and do the experiments in large aquaria that have the local algae and plankton.

They have asked you to help sort out what is going on. It is known from previous work that the competition between these two species can be effectively described by the Lotka Volterra competition equations. What do you tell them?

**COMMUNITIES**

1. An ecological study of plant succession involves three different plots. In the first year of the study, all individuals were removed from the three plots. The time course of the presence of species during that first year is shown in panel a. In the second year, once again all individuals were removed from all three plots. However, in addition to that, during the course of the year, all individuals of species A were kept out of garden 1, all individuals of species E were kept out of garden 2, and nothing was done to garden 3, except the initial removal. The time course of the presence of species B in the three gardens is shown in panel b.






i) What type of succession does this represent?

ii) From panel a, what species would you expect to be present in the climax community?

iii) Interpret the results in panel b).

iv) What effect will the frequency (possibly more than one per year) of removal of all species have on the plant species present in the plots?.

2. The famous ornithologist and evolutionary biologist David Lack published the following data on the geographical information about the Lesser Antiles and the number of land birds present:

| Island | Area ($km^2$) | Altitude (m) | Distance from mainland (km) | Nearest island (km) | Number of land species present |
|---|---|---|---|---|---|
| Anguilla | 90 | 300 | 850 | 7 | 11 |
| St. Martin | 85 | 410 | 800 | 7 | 13 |
| St. Barthol-omew | 25 | 300 | 800 | 20 | 12 |
| Saba | 12 | 860 | 750 | 25 | 18 |
| St. Eusta-tius | 21 | 600 | 750 | 15 | 18 |
| St. Kitss | 180 | 1140 | 750 | 3 | 21 |

| | | | | | |
|---|---|---|---|---|---|
| Nevis | 130 | 1100 | 700 | 3 | 19 |
| Barbuda | 160 | 300 | 800 | 45 | 20 |
| Antiqua | 280 | 400 | 700 | 60 | 20 |
| Monserrat | 100 | 910 | 650 | 35 | 22 |
| Guadeloupe | 1500 | 1500 | 600 | 40 | 34 |
| Desirade | 27 | 280 | 600 | 5 | 19 |
| Marie Galante | 24 | 300 | 600 | 35 | 14 |
| Dominica | 800 | 1450 | 550 | 40 | 39 |
| Martinique | 1100 | 1340 | 450 | 30 | 38 |
| St. Lucia | 600 | 960 | 350 | 30 | 42 |
| St. Vincent | 350 | 1240 | 300 | 40 | 35 |
| Barbados | 430 | 340 | 400 | 250 | 16 |
| Bequia | 19 | 300 | 300 | 10 | 19 |
| Carriacoou | 34 | 300 | 200 | 25 | 21 |
| Grenada | 310 | 840 | 150 | 100 | 35 |

i) Do these data accord with the simple theory of island biogeography?

ii) Is there any importance to the information about altitude and distance to the nearest island?

If you use statistical packages, but certain that you can answer any question that a reader might ask about the statistical methods that you use.

3. M.E. Vega-Cendejas, M. Hernandez and F. Arreguin-Sanchez (Journal of Fish Biology 44:647-659, 1994) studied the trophic interactions in a beach seine fishery in Celestun tropical ecosystem in Mexico. A liberal representation of their data is shown below: for simplicity, I use common names, rather than scientific ones, and combine a couple of species, in which case I average the diet composition of the prey type. In addition, whenever a prey component was less than 10% of the diet, I have set that to 0. Finally, I have normalized the remaining components so that the diet composition sums to 100.

| Prey in the diet (%) | Predator | | | | |
|---|---|---|---|---|---|
| | Pigfish | Jenny | Thread Herring | Grunt | Catfish |
| Phyto-plankton | 0 | 0 | 0 | 0 | 0 |
| Zoo-plankton | 0 | 0 | 0 | 0 | 0 |
| Fora-minifera | 0 | 0 | 0 | 0 | 0 |
| Plant material | 0 | 0 | 0 | 22 | 0 |
| Poly-chaetes | 10 | 15 | 0 | 32 | 35 |
| Nematodes | 0 | 0 | 0 | 0 | 0 |
| Molluscs | 12 | 0 | 0 | 0 | 0 |
| Micro-crustaceans | 57 | 70 | 71 | 28 | 17 |
| Decapods | 0 | 15 | 0 | 20 | 16 |
| Other fish | 7 | 0 | 15 | 8 | 15 |
| Detritus | 14 | 0 | 14 | 0 | 17 |

| Prey in the diet (%) | Predator Sardine | Croaker | Cowfish | Pinfish | Seabream |
|---|---|---|---|---|---|
| Phyto-plankton | 0 | 0 | 0 | 0 | 0 |
| Zoo-plankton | 0 | 0 | 0 | 0 | 0 |
| Fora-minifera | 0 | 0 | 0 | 0 | 0 |
| Plant material | 0 | 0 | 52 | 18 | 27 |
| Poly-chaetes | 0 | 0 | 0 | 0 | 23 |
| Nema-todes | 0 | 0 | 0 | 0 | 0 |
| Molluscs | 0 | 0 | 24 | 34 | 35 |
| Micro-crustaceans | 45 | 21 | 24 | 35 | 0 |
| Decapods | 0 | 14 | 0 | 0 | 0 |
| Other fish | 55 | 55 | 0 | 13 | 0 |
| Detritus | 0 | 0 | 0 | 0 | 15 |

i) Draw the food web using individual species and compute the connectance of the web.

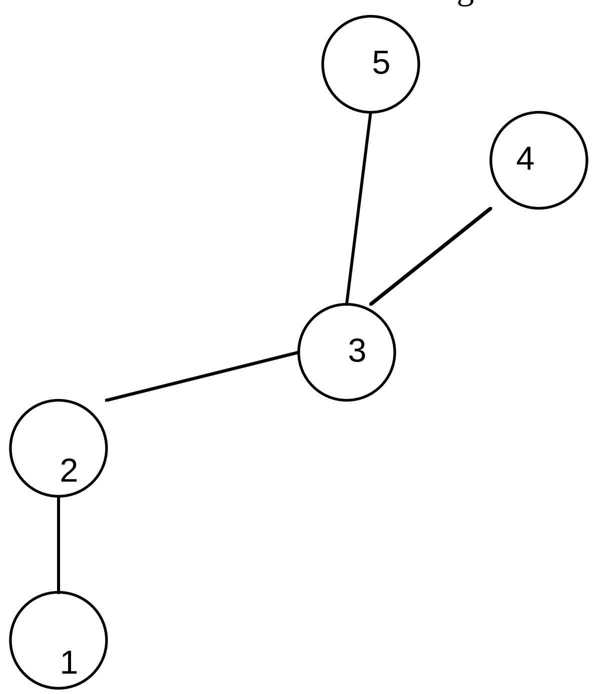
ii) Why do you think the web is so sparce?

4. Imagine two communities, each with the same five species but in different proportions:

| Species | Fraction of Species i in Community A | B |
|---|---|---|
| 1 | .2 | .4 |
| 2 | .2 | .2 |
| 3 | .2 | .1 |
| 4 | .2 | .15 |
| 5 | .2 | .15 |

Compute diversity indices and interpret your results.

5. Suppose that a food web has the following structure:

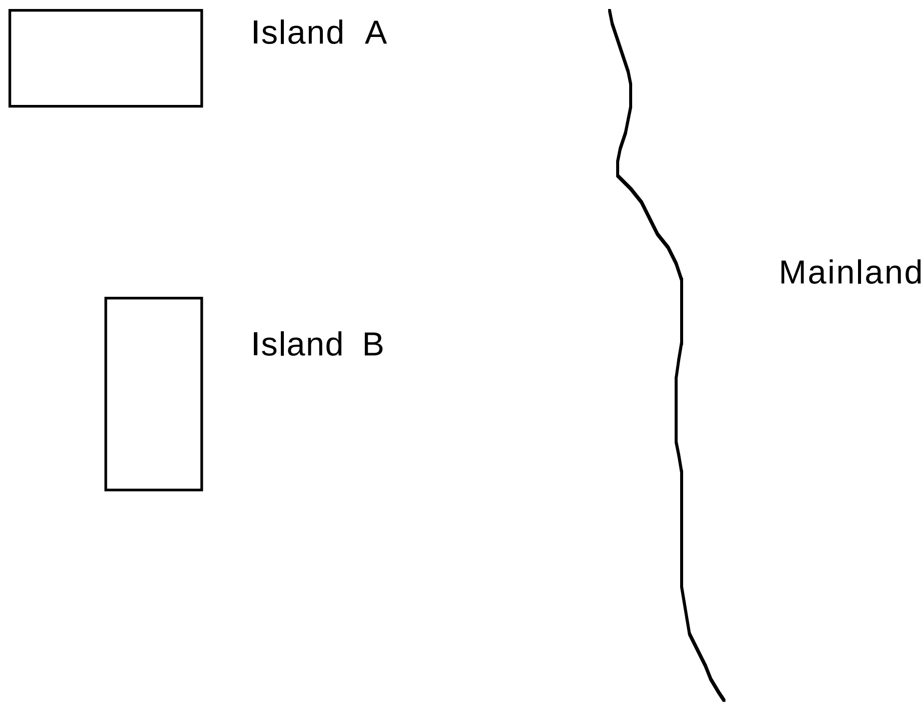



i) Find the connectance of this food web.

ii) Discuss how removal of species one-at-a-time would affect the stability of the web.

6. It is generally true that tropical and deep sea faunas tend to be more diverse than less constant environments. Given this information, sketch the kind of species-area curves that you would predict for i) tropical shallow water, ii) deep sea, and iii) Arctic waters. Label the axes carefully and explain your reasoning for the curves.

7. Two islands of equal area are equidistant from the mainland, as shown in the figure below.




Use biogeographic arguments involving colonization and extinction rates to predict the steady state number of species on each island. Carefully explain your reasoning Suppose now that both islands were completely depopulated. Predict the time dependence of recolonization.

My student Chris Wilcox demonstrated that this kind of analysis is especially appropriate for notenectids.

8. In this exercise, you will collect data that will be shared with the class so that we can estimate the age distribution of cars in Davis.

i) Walk at least a three block transect in your neighborhood and record the number of cars a) with black license plates, b) with blue plates, c) with white plates 2A-2M, d) with white plates 2N-2Z, e) with white plates 3A-3E and with white plates 3E-3Z. Use these data to estimate the frequency of different plates in your transect.

ii) Obtain similar data from three other students in the discussion section and compare the results. Compute alpha and beta diversity levels from these data, treating the different plate types as if they were different species.

9. In 1974, not long after the publication of the work by MacArthur and Wilson on island biogeography, John Terborgh published a paper in **Bioscience** in which he argued that it is more reasonable to expect extinction rates to be proportional to the number of species squared:

$$\text{Extinction rate} = k\ S^2$$

i) What kind of biological justification would you give for using the number of species squared, rather than the number of species.

ii) How would you expect k to depend on island area?

iii) What effect will this assumption have on the predictions of island biogeographic theory?

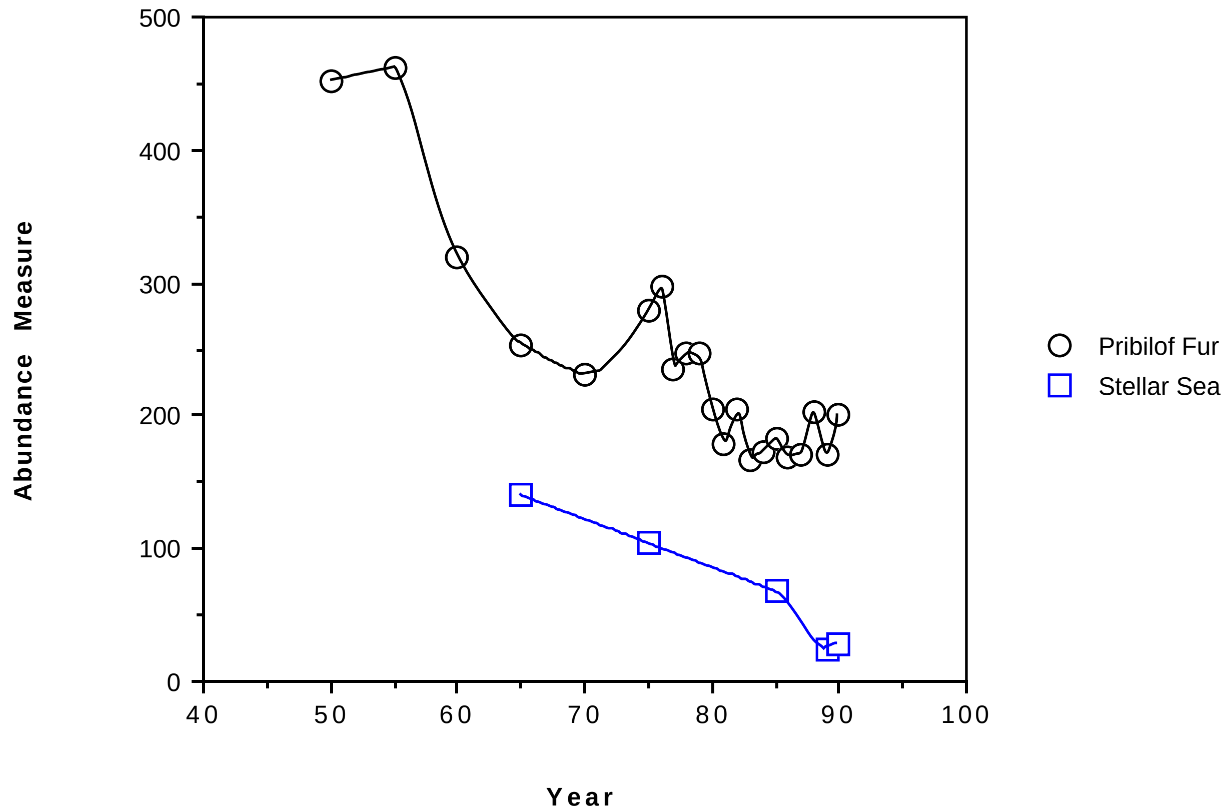
10. There are about 20 species of Tenebroid beetles in Israel. Of these, the biggest species are only found near oasises that contain vegetation.

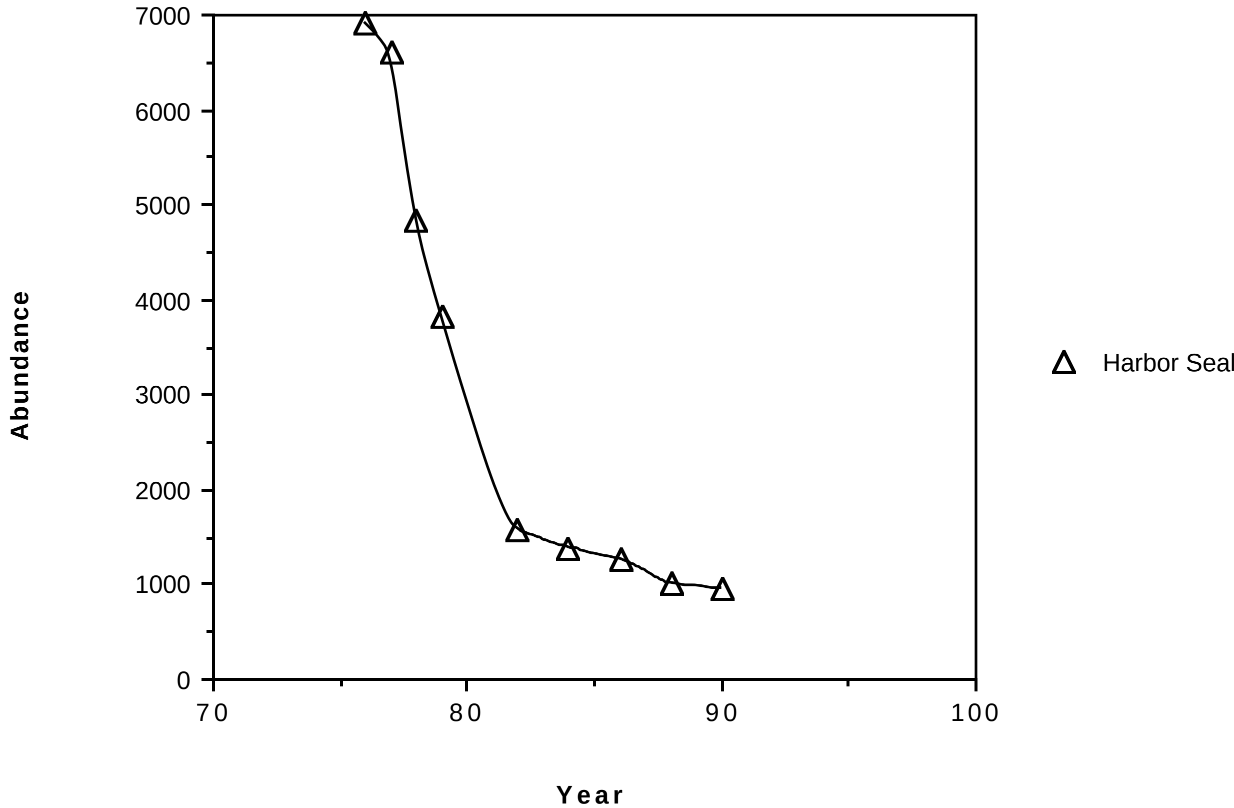
i) Describe a hypothesis for this distribution in terms of survival of predation of the beetles.

ii) Describe a hypothesis for this distribution in terms of reproduction.

iii) Propose an experiment to test one of the these ideas.

11. Population sizes of marine mammals and birds in the Bering Sea have been on steady decline. Below, I show abundance measures for Pribilof fur seals (number of pups born at St. Paul Island), steller sea lions (juveniles and adults on rookeries and haulouts) and harbor seals (haul outs on Tugidak Island). I also show the diet composition of the three species.






| Food Type | Estimated Percent of Diet of Fur Seal | Sea Lion | Harbor Seal |
|---|---|---|---|
| Squid | 33.3 | 4.2 | 1.6 |
| Capelin | 30.6 | 7.4 | 10.4 |
| Pollock | 25.1 | 58.3 | 21.4 |
| Mackerel | 3.5 | 0 | 0 |
| Herring | 2.9 | 20.6 | 6.4 |
| Other | 4.6 | 9.5 | 30.3 |
| Octopus | 0 | 18.3 | 0 |
| Eulachon | 0 | 11.6 | 0 |

i) Interpret the patterns of decline.
ii) Propose an hypothesis to explain the general decline.
iii) Propose an experiment to test the hypothesis.

12. A study of tree species in a forest shows the following:

| Species | % in the Canopy (Mature Trees) | %Seedlings |
|---|---|---|
| Beech | 71% | 10% |
| Hemlock | 20% | 20% |
| Red Maple | 5% | 67% |
| Other | 4% | 3% |

i) In general, what is the definition of a "climax community"
ii) Is this forest at a climax stage?
iii) What assumption(s) do you need to answer the second question?

13. A study of species interactions in a community yielded the following results where the numbers correspond to the percentage of that particular species in the diet of the species in the first column.

| | % of species X in diet | | | | | | |
|---|---|---|---|---|---|---|---|
| Species | A | B | C | D | E | F | G |
| A | 0 | 50 | 0 | 0 | 0 | 50 | 0 |
| B | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C | 30 | 0 | 0 | 60 | 0 | 0 | 10 |
| D | 0 | 30 | 0 | 0 | 0 | 70 | 0 |
| E | 35 | 0 | 0 | 0 | 0 | 0 | 65 |
| F | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| G | 0 | 80 | 0 | 0 | 0 | 20 | 0 |

i) Using true species, draw the food web and find the connectance.
ii) Using trophic species, draw the food web and calculate the connectance.
iii) Interpret the results of parts i and ii.
iv) Using your knowledge of biology, replace the alphabetical names of the species with names of real organisms (e.g. "rabbit") in a manner appropriate for this food web.

14. In his book **Ferox Trout and Arctic Charr**, my colleague Ron Greer describes attempts to improve the conditions for brown trout *Salmo trutta* in Scottish lakes by enhancing their food supplies.

For example, one may add tadpole shrimp *Lepidurus arcticus* to the lake. These zooplankton feed on phytoplankton and the trout feed on the tadpole shrimp.

i) Draw the food web for this interaction.

When the same idea was tried with opposum shrimp *Mysis relicata*, workers discovered major ecological problems. Further investigation showed that although the opposum shrimp were excellent prey items for the trout in the lake, they could outcompete larval brown trout.

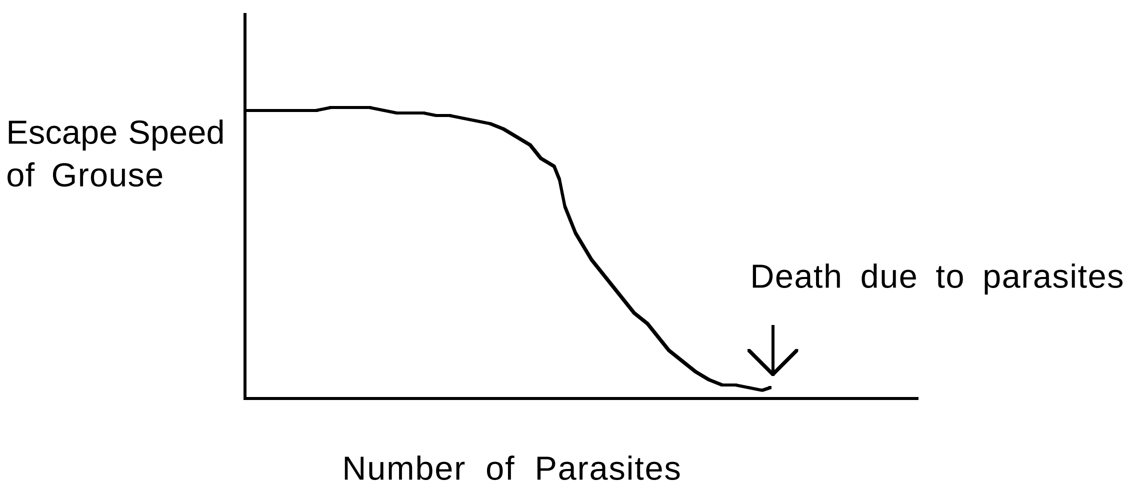
ii) Draw the food web for this interaction.

iii) What inferences do you draw concerning supplementation and enhancement programs?

15. In the 1930s, the red grouse population in Norway was declining, so an effort was made to remove their main predator, a hawk.

i) The grouse eat grass and grains. Draw a food web for the situation just described.

After removal of hawks, the red grouse population declined at an even faster rate. Further examination showed that a parasitic worm infected grouse and that the escape speed of the grouse depended on the number of parasites as shown below.




Hawks were able to only take the slower, more sicly grouse. When the hawks were removed, the parasites spread through the entire population and decimated it.

ii) Change your food web diagram to include parasites, infected and healthy grouse.

iii) What aspects of the problem are missed by the food web?

16. My colleage Tim Wootton studies the food web involving steelhead trout (*Oncorhynchus mykiss*, the migratory form of rainbow trout) on the Eel River.

i) In the simplest description, steelhead eat mayflies and midges, which eat algae. Draw this food web.

Recently caddisflies have been introduced into some streams of the Eel River. It is not clear what the ultimate food chain will be. One possibility is that caddisflies eat algae, but are not preyed upon by steelhead or other fish. However, caddisfly larvae are very senstive to disturbance.

ii) Draw this food web and discuss the implications for the community structure.

Another possiblity is that other small fish and dragonflies eat the caddisflies and that the steelhead trout eat the small fish and dragonflies.

iii) Draw this food web and discuss the implications for the community structure.

17. Raven et al measured the area and distance of islands from the California coast and the number of plant species on those islands:

| Area ($mi^2$) | Distance (mi) | Number of species |
|---|---|---|
| .02 | .25 | 40 |
| .10 | 27 | 12 |
| .20 | 6 | 4 |
| .9 | 3.5 | 62 |
| 1 | 38 | 40 |
| 2.8 | 5.0 | 42 |
| 14 | 26 | 190 |
| 22 | 61 | 120 |
| 56 | 49 | 235 |
| 75 | 20 | 392 |
| 84 | 27 | 340 |
| 96 | 20 | 420 |
| 98 | 165 | 163 |
| 134 | 14 | 205 |

i) Construct a species-area curve using area and number of species.

ii) Construct a species-area curve using log(area) and log(number of species).

iii) A new reserve, on an island of 60 $mi^2$ is going to be set up. Use the results from parts i and ii to predict the number of species that you would expect to ultimately colonize this island.

iv) Use each to predict the number of species that would be lost if half of the habitat on the island in part iii) were lost.

v) What might explain the variation in the species area curves that you have constructed?

vi) Construct a species-distance curve using distance and the number of species. Then do it a second time, without the island that is 165 miles from the mainland. Interpret these results.

**CONSERVATION**

1. In this exercise, you will derive what Colin Clark calls the "Golden Rule of Renewable Resource Economics" by a method using calculus. Imagine a population growing according to the dynamics

$$\frac{dN}{dt} = F(N) \qquad (1)$$

i) If the population were growing exponentially, what would F(N) be? If it were growing logistically, what would F(N) be? Now add a harvest, with harvest rate at time t denoted by H(t), so that the growth rate is

$$\frac{dN}{dt} = F(N)-H(t). \qquad (2)$$

As we have discussed, the discounted value of this harvest is

$$V=\int_0^\infty e^{-\delta t}\ H(t)\ dt. \qquad (3)$$

But note that $H(t) = F(N) - \frac{dN}{dt}$ , so that

$$V=\int_0^\infty e^{-\delta t}\,[F(N) - \frac{dN}{dt}]\ dt. \qquad (4)$$

ii) Integrate the term $e^{-\delta t}\frac{dN}{dt}$ by parts, assuming that $N(0)=N_0$ to show that

$$V = \int_0^\infty e^{-\delta t}[\ F(N)- dN]\ dt + N_0. \qquad (5)$$

iii) Conclude from this that the value is largest when the population is at the size $N^*$ so that $F(N)-\delta N$ is largest.

iv) Assume that F(N) corresponds to logistic growth and use a graph to show the value of $N^*$ when $r > \delta$. Use this same graph to show thatwhen $r < \delta$, it is economically optimal to drive the population to extinction. How does this compare with the result that we derived in class and why do they differ?

2. The Schaefer model was proposed by M. Schaefer in the 1950s for understanding the Eastern Pacific tropical tuna fishery. It is

$$\frac{dN}{dt} = rN(1-\frac{N}{K}) - qEN \qquad (1)$$

where N is the biomass of yellowfin tuna (tons), t is measured in days, E is fishing effort measured in number of vessels and q is called the "catchability coefficient".

i) What are the units of q?

ii) If effort is constant, show that the steady state population size is

$$N_s = K(1-\frac{qE}{r}) \qquad (2)$$

iii) The steady state yield, $Y_s$ is $Y_s = qEN_s = qEK(1-\frac{qE}{r})$. Graph the yield as a function of fishing effort E.

iv) Now introduce economics, by including a price p per ton, so that total revenue is $TR = pY_s$ and a cost of effort c so that total cost is $TC = cE$. The economic rent is Rent = TR - TC = $pY_s - cE$.
H. Scott Gordon calls the "bionomic equilibrium" the value of effort at which the economic rent is 0. What is the interpretation of the rent being 0?

v) Show that this level of effort is $E_b = \frac{r}{q}(1 - \frac{c}{pqK})$ and that the corresponding bionomic population size is $N_b = \frac{c}{pq}$. Interpret the roles that the parameters play in these expressions.

3. This problem provides an illustration of the interplay of the discount rate and the intrinsic rate of growth in conservation.

The scenario: Suppose that the discount rate is the same as the interest rate paid on investments and that interest is compounded annually. Suppose that you are the sole owner of a logistically growing resource with parameters r and K and that the resource starts at carrying capacity. Finally, suppose, each harvested animal provides $1000.

The value of extinction. If you drive the stock to extinction in the current year, you collect K $1000. Since interest is compounded annually, the value after y years of driving the stock to extinction is

$$V_{ext}(y) = (K\$1000)(1+\delta)^y \qquad (1).$$

The value of conservation. Since the stock starts at carrying capacity, in the first year you harvest $\frac{K}{2}$ animals, to take it to Maximum Net Productivity. In each subsequent year, you harvest

$\left(\frac{rK}{4}\,\frac{\text{animals}}{\text{year}}\right)$(1 year) = $\frac{rK}{4}$ animals, for which you receive the same \$1000 dollars. Suppose that $V_{cons}(y)$ is the economic value of following the conservation strategy in year y. We can relate two different years in the following manner. First, note that $V_{cons}(1)=\frac{rK}{4}$ \$1000. Second, in any year after the first, there are two sources of value. The previous year's value is incremented by the interest rate (1+d) and there is the new catch. Thus we have

$$V_{cons}(y+1) = V_{cons}(y)(1+\delta) + \frac{rK}{4}\ \$1000 \qquad (2)$$

<u>The relative value of conservation</u>. We can find the relative value of conservation by looking at the ratio $\frac{V_{cons}(y)}{V_{ext}(y)}$ . Do this for K=1000, look 50 years into the future and use r=.07, .12 or .2 and $\delta$=.02, .06, and .1 Interpret your results.

4. The pine borer is a beetle that attacks lodge-pole pine. This beetle has a very high fecundity but very low ability to move through space. Outbreaks of the beetle occur only when the density of trees exceeds a certain level.

i) Given this information, sketch the relationship between the density of trees and the population of the beetle that you would predict. Explain your reasoning.

ii) What kind of management procedure would you recommend in order to prevent outbreaks of the beetle?

5. When I taught ecology in Winter quarter 1992, Mr. D. MacDonald proposed the following harvesting scheme for a population growing logistically: The harvest is composed of a small constant rate $h_0$ and a term proportional to population size qEN, so that $H = h_0 + qEN$.

i) What is the equation for the growth rate of the population under these circumstances?

ii) Use a graphical method to determine the steady states of the population.

iii) Does a Maximum Sustainable Yield exist? If so, how would you find it. If not, why not?

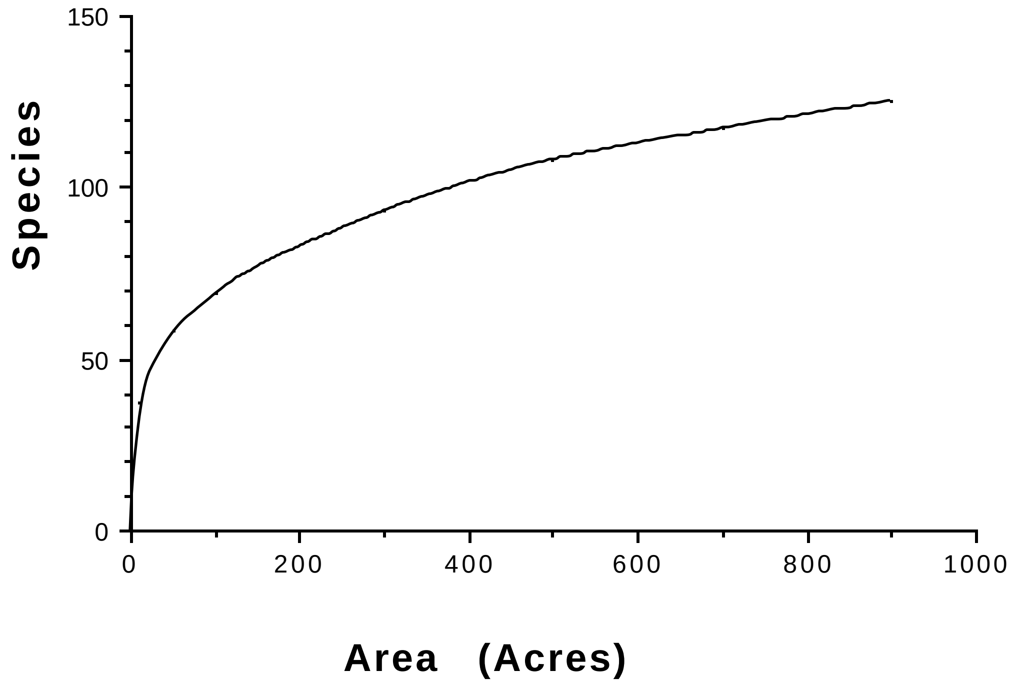
6. There is considerable concern at the present time that dolphins *Tursiops* spp. may be having increasing mortality, due to a mixture of natural and human factors. The main source of data is the "dolphin stranding network", which reports whenever a dolphin appears on a beach. Here are some of the data collected over the last few years in Georgia:

| Observation Number | Day of the Sighting | Interval between Current and Previous Sighting (days) |
|---|---|---|
| 1 | 31 | 31 |
| 2 | 49 | 18 |
| 3 | 68 | 19 |
| 4 | 69 | 1 |
| 5 | 198 | 129 |
| 6 | 358 | 160 |
| 7 | 403 | 45 |
| 8 | 446 | 43 |
| 9 | 605 | 159 |
| 10 | 637 | 32 |
| 11 | 639 | 2 |
| 12 | 651 | 12 |
| 13 | 683 | 32 |
| 14 | 692 | 9 |
| 15 | 700 | 8 |
| 16 | 721 | 21 |
| 17 | 734 | 13 |
| 18 | 778 | 44 |
| 19 | 791 | 13 |
| 20 | 797 | 6 |
| 21 | 799 | 2 |
| 22 | 802 | 3 |
| 23 | 807 | 5 |
| 24 | 808 | 1 |
| 25 | 932 | 124 |
| 26 | 950 | 18 |
| 27 | 952 | 2 |
| 28 | 958 | 6 |
| 29 | 964 | 6 |
| 30 | 966 | 2 |
| 31 | 970 | 4 |
| 32 | 1044 | 74 |
| 33 | 1071 | 27 |

| | | |
|---|---|---|
| 34 | 1076 | 5 |
| 35 | 1083 | 7 |
| 36 | 1083 | 0 |
| 37 | 1098 | 15 |
| 38 | 1110 | 12 |
| 39 | 1113 | 3 |
| 40 | 1133 | 20 |
| 41 | 1146 | 13 |
| 42 | 1149 | 3 |
| 43 | 1154 | 5 |
| 44 | 1154 | 0 |
| 45 | 1174 | 20 |
| 46 | 1176 | 2 |
| 47 | 1178 | 2 |
| 48 | 1181 | 3 |
| 49 | 1191 | 10 |
| 50 | 1193 | 2 |
| 51 | 1202 | 9 |
| 52 | 1286 | 84 |
| 53 | 1298 | 12 |
| 54 | 1299 | 1 |
| 55 | 1310 | 11 |
| 56 | 1316 | 6 |
| 57 | 1318 | 2 |
| 58 | 1356 | 38 |
| 59 | 1371 | 15 |
| 60 | 1395 | 24 |
| 61 | 1403 | 8 |

What do you conclude about the rate of mortality for dolphins from these data?

7. The species area relationship in a certain region is shown below.




You have been asked to make recommendations to the Nature Conservancy about how much land to purchase. There is enough money to purchase 1000 acres. You know that a certain plot of 200 acres is unique habitat that must be purchased. What do you do with the remaining funds if you know that plots will contain unique mixtures of species, but are subject to edge effects? What do you do if plots will contain the same mixture of species?

**Advanced Material**

1. In this problem, you will conduct a simplified version of the analysis that Ray Hilborn and I did in Chapter 10 of our book **The Ecological Detective. Confronting models with data**. You might also want to know that these are the methods that Hilborn and Walters popularized in their 1992 book (cited in the reference list in the reader) and that they go around the world teaching these methods to fisheries managers.

The Namibian fishery for two species of hake (*Merluccius capensis* and *M. paradoxus*) was managed by the International Commission for Southeast Atlantic Fisheries (ICSEAF) from the mid 1960s until about 1990. Your analysis will be concerned with the period up to and including ICSEAF management. Hake were fished by large ocean-going trawlers primarily from Spain, South Africa, and the Soviet Union. Adults are found in large schools, primarily in mid-water. While both species are captured in the fishery, the fishermen are unable to distinguish between them and they are treated as a single stock for management purposes. As the fishery developed, essentially without any regulation or conservation organization, the catch-per-unit-effort (CPUE), measured in tons of fish caught per hour, declined dramatically until concern was expressed by all fishing nations. The concern about the dropping CPUE led to the formation of ICSEAF and subsequent reductions in catch. After catches were reduced, the CPUE began to increase. In the data used in this analysis, CPUE is the catch-per-hour of a standardized class of Spanish trawlers. Such standardized analysis is used to avoid bias due to increasing gear efficiency or differences in fishing pattern by different classes or nationalities of vessels.

Here are the data:

| Year | CPUE | Catch (thousands of tons) |
|---|---|---|
| 1965 | 1.78 | 94 |
| 1966 | 1.31 | 212 |
| 1967 | .91 | 195 |
| 1968 | .96 | 383 |
| 1969 | .88 | 320 |
| 1970 | .9 | 402 |
| 1971 | .87 | 366 |
| 1972 | .72 | 606 |
| 1973 | .57 | 378 |
| 1974 | .45 | 319 |
| 1975 | .42 | 309 |
| 1976 | .42 | 389 |
| 1977 | .49 | 277 |
| 1978 | .43 | 254 |
| 1979 | .4 | 170 |
| 1980 | .45 | 97 |
| 1981 | .5 | 91 |
| 1982 | .53 | 177 |
| 1983 | .58 | 216 |
| 1984 | .64 | 229 |
| 1985 | .66 | 211 |
| 1986 | .65 | 231 |
| 1987 | .63 | 223 |

i) Construct plots of CPUE vs. year, Catch vs. year and cumulative catch vs. year.

You are going to use a Schaefer model without <u>process uncertainty</u> but with <u>observation uncertainty</u> (see our book for more details; otherwise just read on) to analyze the data. That is, if B(t) denotes the biomass (in thousands of tons) at the start of year t and C(t) is the catch in year t, assume that biomass changes in a deterministic manner according to

$$B(t+1) = B(t) + rB(t)\left(1-\frac{B(t)}{K}\right) - C(t) \quad (1)$$

Hilborn and I treat the case in which both r and K is unknown, but here we will assume that r is known from other sources and is r=0.39. However, carrying capacity K is unknown.

We will assume that the index of abundance is catch per unit effort. Since CPUE should be proportional to biomass, we set the predicted index of abundance equal to

$$I_{pre}(t) = qB(t) \quad (2)$$

Where q is the catchability coefficient. As with r, Hilborn and I consider the case in which q also has to be determined. To make life easier for you, assume that q=0.00045.

However, the index $I_{pre}(t)$ is not what we observe. Rather, CPUE involves observational uncertainty. In particular, assume that the CPUE in year t, CPUE(t) is given by

$$CPUE(t) = I_{pre}(t)\ \exp(X_s) \quad (3)$$

where $X_s$ is a normally distributed random variable with mean 0 and standard deviation s. In the calculations that follow, use the value s=0.12 (which is what Hilborn and I determined for the full problem).

ii) Use Eqn 3 to explain why

$$Z(t) = \log(CPUE(t)) - \log(I_{pre}(t)) \qquad (4)$$

will also have a normal distribution with with mean 0 and standard deviation $\sigma$. We say that the index of abundance is log-normally distributed.

This means that the frequency distribution for Z(t) is

$$f(t) = \frac{1}{\sqrt{2\pi\sigma}} \exp\left(-\frac{Z(t)^2}{2\sigma^2}\right). \qquad (5)$$

This is called the likelihood of a deviation Z(t); you can think of it as proportional to the chance that the deviation is Z(t)

In statistical theory, the negative log-likelihood for a single value of Z(t), dentoed by N(t) is

$$N(t) = \log(\sigma) + \frac{1}{2} \log(2\pi) + \frac{Z(t)^2}{2\sigma^2} \qquad (6).$$

Explain how Eqn 6 is derived by taking the logarithm of Eqn 5 and multiplying by -1.

The negative log-likelihood is called the support of a deviation Z(t) between the predicted and observed indices of abundance.

iii) The total negative log-likelihood is the sum of the single time negative log-likelihoods:

$$N_T = \sum_{t=1965}^{1987} N(t) \qquad (7)$$

Compute the total negative log-likelihood associated with different values of carrying capacity K, as K ranges from 2650 to 2850 in steps of 10. To do this, use Eqn 1 to determine B(t) for each year -- assuming that the population started at K in 1965 -- and Eqn 2 to determine $I_{pre}(t)$ for each year. Then finding the total negative log-likelihood by summing up the terms from Eqn 6.

Find the value of K that makes the total negative log-likelihood the smallest. Denote this value by $K^*$ and the associated total negative log-likelihood by $N_T$*; it is the best point estimate. Make a plot of $N_T$ (ordinate) vs K (abcissa) and show K* and $N_T$*.

iv) Also according to statistical theory, the 95% confidence interval for the carrying capacity are the values of K for which the total negative log-likelihood $N_T = N_T^* + 1.96$ and the 99% confidence interval are the values for which $N_T = N_T^* + 3.92$. Use your plot from part iii) to find these confidence intervals.

(Note, if you look in Hilborn and Mangel, you will see that the confidence intervals are much broader. This is caused by admitting uncertainty in r and q and having to determine s as part of the solution. But don' let that worry you now.)

v) At this point, you should have estimates for the 95% and 99% confidence intervals for carrying capacity. Now suppose that the management objective is to keep the population within the optimal sustainable region, in which B(t) > 0.6K from 1988 to 2000 (assume that you were doing this work in 1988). Determine the catch limit that you would apply to achieve this goal. Hint: How do you determine the population size in 1987?

vi) Propose a monitoring and adaptive management scheme, so that you can keep track of the success of the limit that you determined in part v.

2. In fall 1996, Sean Barry gave a seminar in the Environmental Studies program on the San Francisco garter snake *Thamnophis sirtalis tetrataena*. A simplified description of some of his results is the following.

The carrying capacity of these snakes is determined by two factors (actually more, but this is the simplified description): the amount of cover around a pond and the number of red-legged frogs around the pond. The measure of frogs, denoted by F, is the number of frogs per 10 m linear survey and ranges from about 0 to 25. The measure of cover, C, is bush area per 50 $m^2$ and ranges from 0 to 20. The measure of snakes, S, is snakes per 100 $m^2$.

i) Both frogs and cover are essential for the snake to exist. Explain why a definition of carrying capacity as the weighted average

$$K = pF + (1-p)C \qquad (1)$$

where p is the weighting factor does not make sense.

ii) In a situation like this, many authors propose that one should use the geometric mean

$$\frac{1}{K} = \frac{1}{2}\left(p\frac{1}{F} + (1-p)\frac{1}{C}\right) \qquad (2)$$

Explain why this would make sense as a means of combining two essential components of habitat.

iii) How would you generalize Eqn 2 for more than two components of habitat?

Some of the habitats for these snakes are reservoirs which fluctuate from year to year.

iv) Now assume that the snakes follow a logistic equation

$$S(t+1) = S(t)\exp\left(r(1-\frac{S(t)}{K(t)})\right) \qquad (3)$$

where r=0.15. Consider two situations

a) C=12 and F = 15

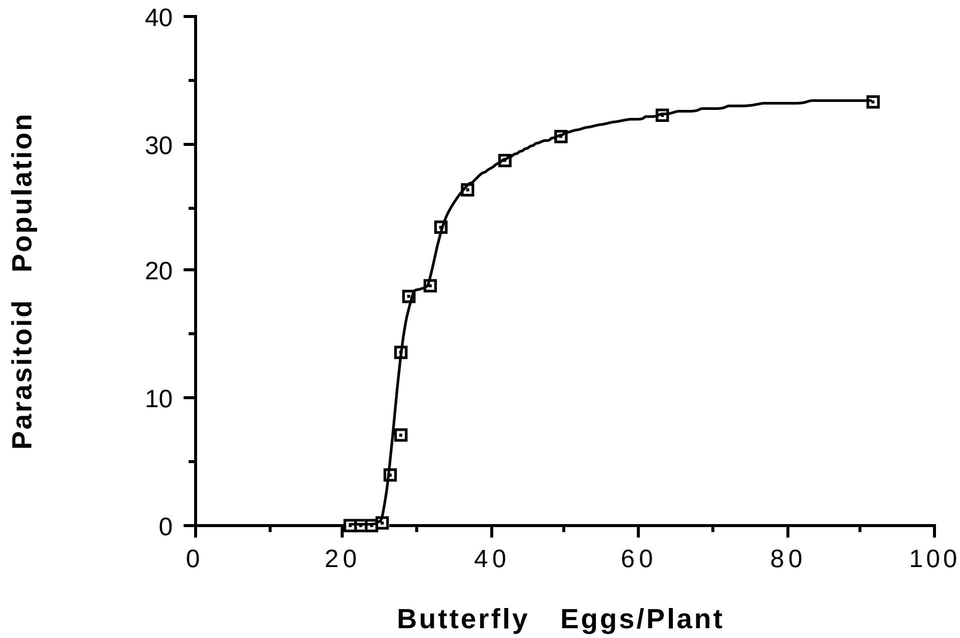
b) C=12 and F=10 in even years and F=20 in odd years.

Investigate the effects of fluctuations in frog level on the population dynamics of the snakes.

3. Jeremy Thomas works on a plant-ant-butterfly-parasitoid system in which ants tend the butterfly larvae. Without ants, butterflies cannot exist.

In the course of her life, each adult butterfly lays her entire egg complement randomly across plants, with no attention to the presence or absence of other eggs. Parasitoids emerge after the butterflies, randomly search for butterfly eggs across host plants and never never superparasitise.

Thomas finds no relationship between area of the habitat (he works in about 9 different patches) and parasitioid population, but a striking relationship between parasitoid population and the number of butterfly eggs per plant:




i) Given your knowledge of the biological system, propose a mechanism that generates this kind of relationship.

ii) Assume tha the conservation objective is to maximize the biodiversity in the entire system. What is the main recommendation that you would make?

4. In 1994, amid some (or considerable, depending upon viewpoint) controversy, Norway resumed the harvest of minke whales in the North Atlantic. In this question, you will explore some of the ideas that could be associated with the resumption of whaling.

The 1996 quota was 425 whales, but only 388 were taken. The 1997 quota is 580 whales.

To begin, assume that the north Atlantic stock is panmictic, with a carrying capacity of K = 60,000 whales and maximum per capita growth rate r=0.04.

i) What is MSY?

ii) In principle, is a quota of 580 whales a sustainable harvest (in principle)?

iii) Assume that the population is indeed panmictic and that growth can be characterized by the logistic equation. Thus, if N(t) is the number of whales at the start of year t and H is the harvest (580 whales)

$$N(t+1) = N(t) + 0.04N(t)\left(1 - \frac{N(t)}{60000}\right) \quad (1)$$

Assume that N(0)= K and use Eqn 1 to construct a plot of whale population size versus time for the first 30 years, assuming a harvest quota of 580 whales.

iv) But actually, there is concern that the north Atlantic may contain a number of different stocks. In the simplest case, we can envision two stocks, with population sizes denoted by $N_1(t)$ and $N_2(t)$. Assume that each of these stocks has a carrying capacity of $\frac{K}{2}$ = 30,000 whales. Furthermore, assume that the harvest need not be apportioned equally between the two stocks, so that if $H_i$ is the harvest on stock i,

$$H_1 + H_2 = H = 580 \text{ whales} \quad (2)$$

Finally, assume that there is migration from the population with the larger size to the population with the smaller size, where a fraction m of the difference in population migrates from one stock to the other.

Under these circumstances, explain why the population dynamics are now

$$N_1(t+1) = N_1(t) + 0.04N_1(t)\left(1 - \frac{N_1(t)}{30000}\right) - H_1 - m(N_1(t)-N_2(t))$$

$$(3)$$

$$N_2(t+1) = N_2(t) + 0.04N_2(t)\left(1 - \frac{N_2(t)}{30000}\right) - H_2 - m(N_2(t)-N_1(t))$$

v) In the extreme case, all of the harvest effort is directed to one-sub-stock, which might be described as $H_1$= H and $H_2$=0; and there is no migration (m=0). As before, plot the population sizes versus time for 30 years. Is the harvest sustainable? Compare your results to the case in which $H_1=H_2=\frac{H}{2}$ and m=1.0.

vi) Explore how migration and the allocation of harvest between the two stocks affect the conclusions one might draw from part v).

**SYNTHETIC QUESTIONS**

1. You are supposed to have read **A Sand County Almanac** by Aldo Leopold. Provide examples from the book that deal with two of these topics:

- Individual behavior
- Single populations
- Predator-prey interactions
- Competitor interactions
- Multi-species interactions

and evaluate Leopold's treatment and understanding of the topic in terms of modern ecological thinking.

2. There is often discussion about whether it is better to control population growth by reducing fecundity per individual or by delaying the age at first reproduction. Create a simple life table (i.e. choose $l_x$ and $m_x$ wisely) to evaluate the two options for a multi-generation time horizon.

3. Choose an example discussed in the textbook and analyze the process of science in regard to this example if one took the approach of Popper, Kuhn, Polyani or Lakatos.

4. At the banquet address of the 10th Biennial Conference on the Biology of Marine Mammals, Alexi Yablokov, said the following:

> Learn to distinguish essential things from the not-so-essential ones...There are four essential "golden rules" of ecology, formulated in the 1970s by Professor Commoner:
>
> 1. Everything is connected to everything else.
> 2. Everything must go somewhere.
> 3. Nature knows best.
> 4. There is no such thing as a free lunch...
>
> I repeat to you four crucial principles that will be useful to all of us:
>
> 1. Learn to distinguish essential things from the not-so-essential.
> 2. Usually there exists an unpredictable solution, even with an unsolvable problem.
> 3. All scientific results are positive; they just need proper interpretation.
> 4. Strive to understand science with simple solutions.

Comment on these points in terms of material that we have discussed in class or that you have read in the textbook

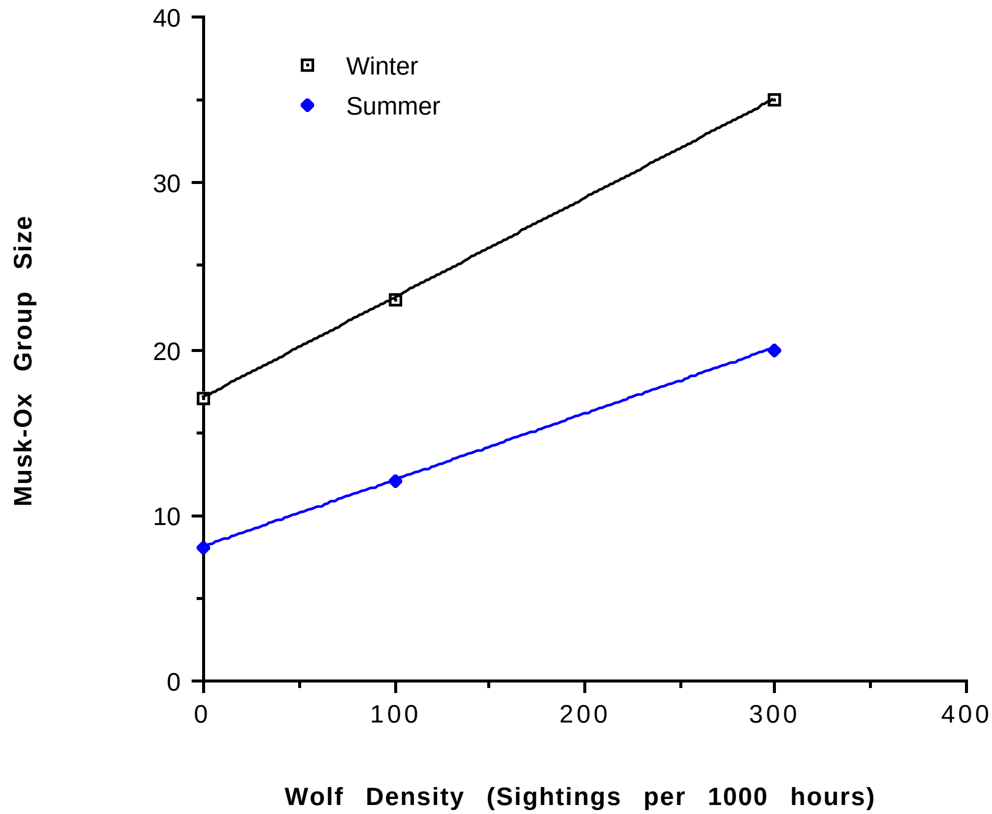
5. In her work on the symbiosis between lycaenid butterflies and ants, Naomi Pierce has developed the following understanding . First, the lycaenids supply nutrients to the ants, increasing the size of the ant colony. Second, the ants protect the immature stages of the butterfly population, thus increasing the growth rate of the butterflies. Pierce and her colleague W.R. Young have proposed a description of population dynamics with the following characteristics.

•The ant population grows logistically. The carrying capacity for the ants is composed of two terms. One is independent of the size of the butterfly population and the other is directly proportional to the size of the butterfly population.

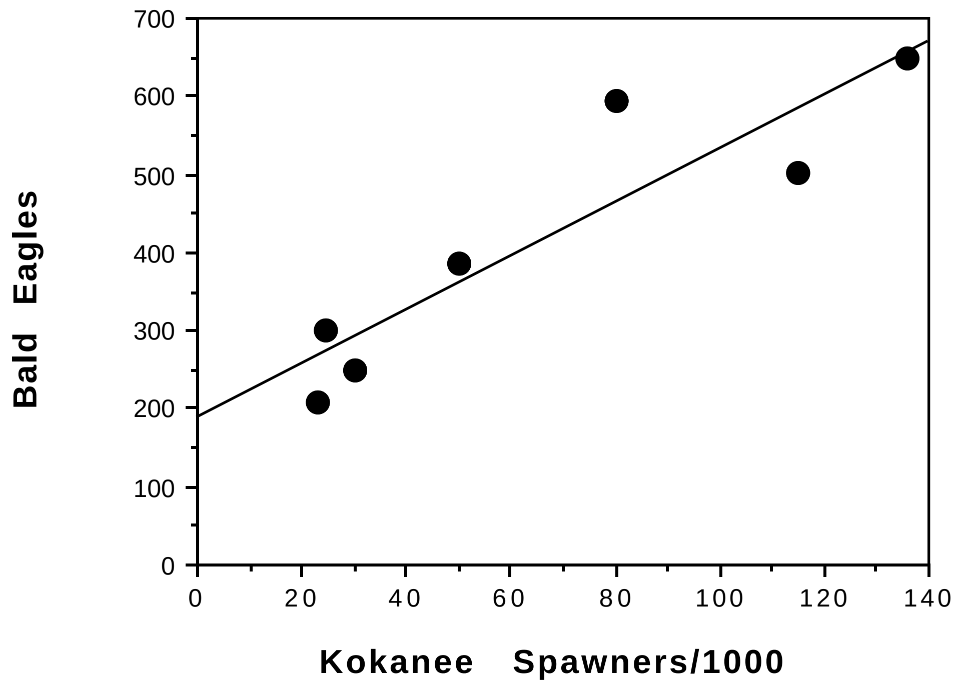
•The butterfly population has a per capita growth rate which is directly proportional to the ant population size and a per capita death rate proportional to the size of the butterfly population.

Convert these verbal statements to equations for the growth rates of ants, butterflies and analyze the resulting population dynamics.

6. In a paper published in the **American Naturalist** in 1992, D. Heard presented the following data concerning the group size of Musk-ox in summer and winter, in relation to the density of wolves, which are their predators. Interpret these results.



7. C. Spencer, B.R. McClelland and J. Stanford studied shrimp, eagles and salmon on McDonald Creek, Montana (Bioscience 41:14-21, 1991). They found the following relationship between eagles (predator) and kokanee salmon (prey).




The line in this picture is given by

$$\text{Eagles} = 189 + 3.4 \text{ Kokanee spawners}$$

i) What is a kokanee salmon?

ii) What does it mean that the number of eagles is greater than 0 when the number of spawners is 0?

iii) Use these data to estimate how many kokanee are needed to "make" a bald eagle?

8. Mansour et al. (Acta Oecologica/Oecologia Applicata 1:225-232, 1980) studied biological control of the apple pest *Spodoptera littoralis* by spiders. A simplified version of their results are shown below, measured at the end of the five day trial.

| | Spiders Present | | Spiders Absent | |
|---|---|---|---|---|
| | Trial 1 | Trial 2 | Trial 1 | Trial 2 |
| Egg mass destroyed | 18/20 | 27/27 | 6/20 | 5/26 |
| Number of leaves with no larvae | 20/20 | 27/27 | 6/20 | 6/26 |
| Number of leaves with no feeding | 17/20 | 20/27 | 6/20 | 6/26 |

That is, there were two trials with spiders present in which either 20 or 27 leaves with one egg mass were observed and two trials with spiders absent in which either 20 or 26 leaves with one egg mass were added to leaves. In the former case, 18 of 20 or 27 of 27 egg masses were destroyed. In the latter, 6 of 20 or 5 of 26 were destroyed

i) What is *Spodoptera littoralis* ?

ii) Draw as many conclusions as you can from these data.

9. Mansour (Phytoparasitica 15:31-41, 1987) studied the effects of spiders on the larvae of the Egyptian cotton leafworm, which preys on cotton plants. After larvae emerged from egg masses on plants, spiders were removed from four plants and left on four others. A simplified version of the results are shown below:

| | Spiders | |
|---|---|---|
| | Present | Removed |
| Number of leaves observed | 233 | 184 |
| Percent of leaves damaged | 23 | 51 |
| Number of larvae on damaged leaves (frequency) | | |
| Absent | .10 | 0 |
| 1-5 | .65 | .11 |
| 6-10 | .25 | 0 |
| 11-20 | 0 | .51 |
| >20 | 0 | .38 |
| Damage to leaves (how much of the leaf is chewed up) | | |
| 0-20% | 0 | 0 |
| 21-40% | .82 | .19 |
| 41-60% | .08 | .33 |
| 61-80% | .07 | .38 |
| >80% | .03 | .10 |

i) What percentage of the leaves in the two treatments had no larvae? What percentage had less than or equal to 10 larvae?

ii) Draw a histogram of larvae present and leaf damage.

iii) Draw a simplified food web for this system.

iv) Evaluate the effectiveness of the spider in controlling this pest.

10. Louda (Oecologia 55:185-191, 1982) studied the interactions between the green lynx spider *Peucetia viridans*, its different insect prey, and the shrub *Haplopappus venetus*, which the prey eat and on which the spider forages for the prey. A simplified version of the results are shown below in which the quantities refer to branches of the shrub.

| Quantity | Spiders | |
|---|---|---|
| | Absent | Present |
| Total number of flower heads | 79 | 82 |
| Number of damaged flower heads | 68 | 46 |
| Number of pollinated flowers per head | 5 | 4 |
| Number of viable seeds produced per branch | 243 | 286 |

i) Draw a food web for this system.

ii) Evaluate the effect of the spider on insect damage.

iii) Evaluate the effect of the spider on reproduction of the plant.

iv) Are there other inferences that you can make from these data?

11. Spiller and Schoener (Oecologia 83:150-161, 1990) studied the effects of lizards on the rate of prey capture by the spider *Meterpeira*. A simplified version of their data is shown below:

| Treatment | Vegetation Height | Number of Spiders Present | Biomass of prey (g x $10^{-6}$) consumed per spider per day |
|---|---|---|---|
| No lizards | Low | 15 | 178 |
| | Medium | 27 | 91 |
| | High | 16 | 120 |
| Control | Low | 6 | 70 |
| | Medium | 5 | 29 |
| | High | 8 | 49 |

Interpret these results.

12. The following essay appeared in the **Sacramento Bee** on Thursday, September 8, 1994 page B7; it was republished from the **Los Angeles Times**. Read the essay and then evaluate it in light of what you have learned in this course.

Little science or precision in 'population science'

By George Weigel
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Ethics and Public Policy Center
Washington, D.C.

We all know that chemistry grew out of alchemy, just as astronomy developed from astrology and medicine from witchcraft. What, one wonders, will grow out of "population science"?

The question is not flip, nor the analogy irrelevant, considering the United Nations International Conference on Population and Development that opened in Cairo on Monday. The conference's U.N. managers, like the Clinton administration and private-sector population controllers who dominated pre-Cairo U.S. policy planning, will insist that their prescription for radically expanding coercive state power in the name of "population stability" and "sustainable development" is scientifically grounded. But given what population science does not know about the present and cannot tell us about the future, doubts on this score are not merely obscurantist. Consider:

•Population science cannot predict the growth rate of human populations over long periods. Because there is no scientific method for predicting birth or death rates with precision, past projections often look ludicrous (one U.N. study famously misprojected India's population by 100 million).

But population projections may become even more difficult in the future. Public health improvements can change mortality rates rapidly, even if countries remain poor. Birthrates can drop quickly and sharply, even absent anti-natalist governmental policies (as in Japan between 1948 and 1958).

•Population science cannot tell us when (much less how) fertility rates will decline, not least because serious scholarship has determined that the relationship between lower fertility rates and economic, social and cultural conditions is extraordinarily complex.

Does fertility decrease as income increases? In some cases, yes. But then why does Tajikistan have both a birthrate and a per-capita output rate twice that of Sri Lanka? Yet another myth - that high levels of health correlate with low fertility - is contradicted by the fact that life expectancy in Kenya today (with a fertility rate of 6.5 births per woman) is about the same as in Germany in the 1920s (fertility rate: 2.3).

•The pretense that Harvard demographer Nick Eberstadt calls "false precision" helps explain why projections in population studies are so difficult. According to Eberstadt, only one-tenth of the Third World's population is covered by reliable registration systems for vital statisitcs.

Somalia, for example, never had a national census until 1985 and has no system for registering births. Yet the World Bank's prestigious World Development Report blithely claims a 2 percent margin of error for its Somali population and birthrate statistics. Given such hard realities, as Eberstadt notes, numbers such as these are simply "guesses dignified with decimal points."

Finally, population science has no scientifically precise definition of "overpopulation" - a shibboleth invoked repeatedly at Cairo. How would we know when a society was overpopulated? When its natural increase (birthrate minus death rate) was unusually high? Then the United States between 1790 and 1800 had serious overpopulation problems. What about high birthrates as a measure of overpopulation? That won't work, either: the U.S. birthrate in the 1790s was 25 points higher than the latest World Bank estimates for India, Indonesia and the Philippines.

Does "population density" - the ratio of people to land - define overpopulation precisely? By that measure, and using 1991 U.N. figures, France is more overpopulated than Indonesia, Japan is much more overpopulated than India, and Singapore (whose government is trying to raise its birthrate) is far more overpopulated than Bangladesh. Then what about the "dependency ratio": the proportion of people under 15 and over 65 to the "working age" population? On that index, Ireland and Nepal are about equally overpopulated and the least overpopulated places on Earth are Hong Kong and Singapore.

Can overpopulation be determined by rates of emigration? Then Mozambique, Angola and Cuba are overpopulated today, as East Germany would have been before the Berlin Wall went up in 1961.

> The images connoted by overpopulated - disease, hunger, overcrowding - are not phantoms. But they describe realities that are more accurately denoted as poverty and material deprivation. The Cairo conference might have helped alleviate those problems and the human suffering they cause. It seems unlikely to do so - it may even make matters worse - because its planners are in thrall to population science.
>
> Which suggests that the policies proposed in its name should be treated precisely as we would treat the fantasies of any contemporary astrologer or alchemist.

13. The following essay appeared in the **Sacramento Bee** on Thursday, April 13, 1995; it was republished from the **Washington Post**. Read the essay and then evaluate it in light of what you have learned in this course.

## Fishermen are responsible for destruction of world fisheries

Jessica Mathews is a senior fellow at the Council on Foreign Relations.

**By Jessica Mathews**

NATO Allies with guns pointed at each other, darkly hinting at breaking off relations. Unthinkable? Not if they're also NAFO members. If you want to know where new international fault lines are emerging, you have to master a new alphabet soup - in this case, Northwest Atlantic Fisheries Organization.

Acting out of desperation as it saw yet another fish stock collapsing (though with an eye to the audience gathered in New York to negotiate a global fisheries agreement), Canada imposed a moratorium on turbot fishing in its 200-mile offshore zone. It then took off after Spanish trawlers fishing outside the line, cut their nets and arrested one boat and its crew. Spain sent naval vessels and threatened retaliation.

Spain was fishing illegally, said Ottawa, in violation of NAFO quotas and with fine mesh nets that snag fish before they're old enough to reproduce. NAFO quotas are voluntary, spat back Madrid, and Spain had legally rejected the turbot limit. Moreover, Canada's actions on the high seas violated international law, so any evidence it had collected could not be considered. Maybe not, responded Ottawa, but here's the proof, and it sailed the 7,000-pound illegal net up New York's East River to the United Nations' doorstep.

Suddenly, fish conflicts are erupting all over the place, many of them violent. Norway and Iceland, Indonesia and Taiwan, Russia and China, Thailand and Malaysia, Russia and Japan, France, Britain and Spain, and Indian fishermen against all foreign fleets, among many others.

The reason is simple. As one marine biologist puts it, with less than the usual scientific precision but compensating straight-forwardness, "Any dumb fool knows there's no fish around." The U.N. Food and Agriculture Organization pins it down: More than 70 percent of the world's fish are fully exploited, in decline, seriously depleted or under drastic limits to allow a recovery.

Despite a veneer of international agreements and a growing scientific effort to monitor the fisheries, the prevailing ethos is still, "Get it while it lasts."

Though the problem is obviously too many boats with too much technology, governments respond to falling catches by competing to build more and higher-tech boats to grab whatever they can, pouring an estimated $50 billion of subsidies into a grossly overcapitalized industry and supporting fishermen who could not otherwise stay afloat. Fisheries that lasted for hundreds of years can now peak and crash in less than a decade. The turbot fracas was caused by a drop in the quota from 60,000 tons to 27,000 tons, which sounds pretty drastic until you realize that the catch grew from 4,000 tons in just five years and only began at all because the cod, redfish and flounder before it had been fished out. Spanish boats are in the area in part because of declines in European waters. Overfishing is an infectious disease: So long as there is a too-large global fleet, it can spread anywhere, almost overnight.

Governments may not, as Adlai Stevenson said, be able to read the handwriting on the wall until their backs are against it, but the collapse of stock after stock and the spreading conflicts over fish seem finally to have focused their attention. A year ago a binding global fishing treaty was a long shot - now one seems achievable within months.

Canada's excursion beyond the bounds of international law has helped to cement the shift by convincing most countries that if they don't act together there will be more unilateral moves until the oceans - especially areas just outside the 200-mile zones - descend into chaos and the law of the jungle replaces the hard-won Law of the Sea.

An effective treaty is by no means a sure thing, however. It requires both strong conservation measures and the means to enforce them - inside countries' exclusive zones as well as on the high seas. Countries with coastal fisheries (led, ironically, by Canada) are loath to surrender their sovereignty to this degree, though all of them - the United States and Canada, in particular - have grossly abused their own resources. Countries that operate distant-water fleets far from their own shores won't accept regulation unless the coastal nations do. The split between the two groups could still block an agreement strong enough to save the fish.

Effective global management will impose real pain. There are too many fishermen in the world. Many will have to find other work. Many catches will have to be cut back. But there are compensations. Once under protection, fish stocks do rebound. And the U.N.'s Food and Agriculture Organization estimates that under sustainable management, global fisheries could yield $15 billion to $30 billion more worth of fish each year. That's the cost of the catch-all-you-can mentality measured in pure waste. Most important, there is no alternative if this vital part of the human diet is to survive.

Every approach to managing marine resources so far has failed miserably. An unmanaged global commons didn't work. Protection within national jurisdictions hasn't worked. Governments proved to be too greedy and too unwilling to accept domestic unemployment.

Swimming fish make a mockery of the human idea of drawing fixed boundaries in the oceans. Voluntary international restraints - as in NAFO - haven't worked. The only option left is a binding global agreement that, at some cost to national sovereignty, forges a better match between nature's needs and humans'.

There isn't a lot of time left, but with sufficient wisdom, there's enough.

# Questions Based on Reading Krebs **Ecology** (4th Edition)

<u>1. Read pages 3-34 and answer the following:</u>

i) What are three definitions of ecology and to whom are they attributed?

ii) If the population of carrion flies describes in these pages doubles every year, what does this tell you about the survivorship from eggs to adults?

iii) What is the essential feature of Malthusian growth?

iv) Diversity can exist at genetic, organism, population and community levels. Give an example describing each.

v) On page 15, Krebs writes "For example, in North Carolina forests, pine seedling abundance (per square meter) is linearly related to incident light in summer". Graphically illustrate what this means.

vi) On the same graph, draw cases of stabilizing selection for survival that are strong or weak, where the trait is wing length in a bird.

vii) In his arguments about clutch size, David Lack treated all birds as semelparous (breeding only once in their lives), while many are really interoparous (breeding many times). Suppose that adult survival decreases with clutch size. How would this affect predictions about optimal clutch size. Explicitly consider the case in which a bird lives only one breeding season compared to a case in which the bird lives exactly two breeding seasons. What predictions do you make about clutch size?

<u>2. Read pages 37-60 and answer the following:</u>

i) The Mediterranean fruit fly *Ceratitus capitata* seems to have two genetically determined forms of dispersal. As long as fruit is present, most individuals move only a short distance from their emergence site while a small percentage make large movements, regardless of the fruit density at their emergence site. What implications does this have for the effectiveness of fruit stripping programs on controlling the med fly?

ii) Why might acclimation temperature affect lethal temperature in salmon and bullhead?

iii) Who was Liebig?

iv) The pine borer is a beetle that attacks lodge-pole pine. This beetle has a very high fecundity but very low ability to move through space. Outbreaks of the beetle occur only when the density of trees exceeds a certain level.

• Given this information, sketch the relationship between the density of trees and the population of the beetle that you would predict. Explain your reasoning.

•What kind of management procedure would you recommend in order to prevent outbreaks of the beetle?

v) Estimate the rate of spread (km/yr) the California sea otter in north and south directions. Would you expect them to be different? Are they different?

vi) What effect would you expect the Panama and Suez canals to have on the ecologies of the regions that they link? What are these regions?

vii) What conclusion can you draw from Figure 4.5 about the rate of colonization of the sponges? Can you infer that the species mix is the same once the number of species is constant?

3. Read pages 61-91 and answer the following:

i) Sir Richard Southwood once wrote a paper in which he described habitat as the "template" for ecology. What do you think is meant by that.

ii) Suppose that snakes eat both *Perognathus penicillatus* and *Dipodomys merriami* but prefer the larger animal and that bush and trees provide protection from snakes. How would habitat usage shift? Assuming that the reverse is true about cover, what would you predict?

iii) Draw an example in which there are two habitats but the habitat suitability curves cross exactly once. What predictions would you make about the distribution of animals as a function of density.

iv) How can the breeding success of herring gulls be constant across habitats if the habitats differ considerably in quality?

v) What do the data on page 78 tell you about the competition between urchins and algae?

4. Read pages 93-137 and answer the following:

i) What functional relationship would you use to describe the relationship between timberline (A, m) and degrees north latitutde (N)? Propose an equation and interpret the parameters in it.

ii) What are major differences between the phenotype and genotype.

iii) Use the data in Table 7.1 to plot a) longest stem vs. elevation and b) survival vs. elevation, regardless of the origin of the plants. What interpretations do you make from these data?

iv) What kind of functional relationship might you use to describe the temperature data in Figure 7.15c? Interpret that parameters in the functional relationship that you use.

v) Explain Figure 8.2b

vi) What are the differences between $C_4$ and $C_3$ plants? Why are there any $C_3$ species left, if the photosynthetic rate of $C_4$ plants exceeds that of $C_3$ for all light intensities (see Figure 8.4).

5. Read pages 138-165 and answer the following:

i) What differences (genetic, physiological, behaviorial) would you expect in animals with very large geographic ranges when compared to those with very small geographic ranges.

ii) Use the data in Figure 10.1 to determine the allometric relationship between body mass and animal denisty.

iii) Explain how to use the Petersen estimate to determine the number of turtles in the pond by Mrak Hall.

iv) What are the survival advantages of modular organisms over unitary organisms.

v) An organism has the following distributions of size and mortality:

| Size (mm) | Frequency | Mortality |
|---|---|---|
| 10 | 4 | .8 |
| 20 | 12 | .73 |
| 30 | 18 | .65 |
| 40 | 22 | .5 |
| 50 | 26 | .3 |
| 60 | 22 | .2 |
| 70 | 18 | .15 |
| 80 | 12 | .1 |
| 90 | 4 | .1 |
| 100 | 2 | .1 |

a) Plot a histogram showing the size frequency distribution before mortality occurs. b) Plot a histogram showing the expected size frequency distribution after mortality.

6. Read pages 168-197 and answer the following:

i) How would you include immigration in a life table?

ii) There is often discussion about whether it is better to control population growth by reducing fecundity per individual or by delaying the age at first reproduction. Create a simple life table (i.e. choose $l_x$ and $m_x$ wisely) to evaluate the two options for a multi-generation time horizon.

iii) I presume that you know the life history pattern of Pacific salmon. Which of the migration patterns (to sea from freshwater or from the sea back to freshwater) would you consider to be obligatory? Sometimes migration disappears entirely (e.g the sockeye salmon has a land-locked form called kokanee). What do you think is going on?

iv) In many passerine birds, the number of eggs laid is proportional to body size and survival from one winter to the next is also proportional to body size. Assume that both proportionalities are linear and make sketches of clutch vs. body size assuming that a minimum size is needed for reproduction and of survival vs. body size assuming that a minimum size is needed for reproduction. Use these to make a plot of survival vs. clutch size. If you had only made the latter measurement, what would you conclude about the cost of reproduction?

<u>7. Read pages 199-227 and answer the following.</u>

i) Suppose that a population has only two age classes. The number of immature individuals in year t, $N_0(t)$, is a constant b times the number of adults in the previous year. The number of adults in year t, $N_1(t)$, is a constant s times the number of young in the previous year. Write these population dynamics as a matrix equation.

ii) My colleague Paul Smith estimated the following data on the life stages of northern anchovy *Engraulis mordax*:

| Stage | Survival | Duration |
|---|---|---|
| Egg | .79 | 3 |
| Yolk sac | .92 | 4 |
| Early larvae | .87 | 13 |
| Late larvae | .95 | 45 |
| Juvenile | .98 | 156 |
| Prerecruit | .99 | 287 |
| Early adult | .997 | 1000 |
| Late adult | .997 | 1250 |

Construct a stage matrix model for the life history of the anchovy. How would you compute the population growth rate?

iii) List five things wrong with the logistic equation.

iv) When he first moved from theoretical physics to ecology, R.M. May believed that an appropriate discrete time version of the logistic equation

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) \qquad (1)$$

would be

$$N(t+1) = N(t) + rN(1- \frac{N}{K}) \qquad (2)$$

•Explain why this is a natural interpretation.

•Equation (2) is now called the <u>logistic map.</u> Assume that N(0)=60, K=100 and plot N(t) for t=1 to 50 for r=0.4,. r=2.5 and r=2.7 The case of r=2.5 is called a "period 2" map and the case of r=2.7 is called "deterministic chaos". What justifies these words?

•Make plots of N(t+1) vs N(t) for the case in which r=2.7. What does this tell you that the time series did not?

v) Do problem #5, page 227.

vi) Do problem #6, page 228.

vii) Do problem #7, page 228.

viii) Do problem #9, page 228.

<u>8. Read pages 230-259 and answer the following:</u>

i) For a single species, Tilman's description of resource based competition goes as follows. One envisions that the biomass N of the species depends upon a resource R and that the two are linked by the growth equations

$$\frac{dN}{dt} = [\frac{vR}{R+K} - m]N$$

$$\frac{dR}{dt} = r_0R - vNR$$

Interpret each of the terms on the right hand sides of these equations. Determine the steady levels of biomass and resource and interpret the results.

ii) Explain how to use the Lotka-Volterra competition equations for the study of competition between *Saccharomyces cervisiae and Schizosaccharomyces kephir*.

iii) Investigate and explain the ecology of the two species mentioned in part ii).

iv) What can you conclude from Figures 13.11 and 13.12?

v) What are niche and habitat?

vi) How would predation affect competition?

vii) Plot the data on the bottom of page 253 and interpret the results.

9. Read pages 263-298 and answer the following:

i) Explain Figure 14.7 in terms of Lotka-Volterra predator prey equations.

ii) Why do prey reach their peak before predators?

iii) What might cause the population dynamics in Figure 14.2?

iv) Do problem 4, page 293.

v) Do problem 1, page 292

10. Read pages 295-321 and answer the following:

i) What are the three hypotheses for secondary plant chemicals and what experiment might separate them?

ii) What tradeoffs could be involved with inducible defenses?

iii) Why might the protected areas described in Figure 15.11 decline?

iv) Use the data in Figure 15.18 to estimnate the frequency of invasions by common crossbills. What is the mean rate of invasions? What is a good way to describe the variation in this mean rate?

11. Read pages 322-347 and answer the following.

i) For flower beetles *Tribolium*, my colleagues and I have used birth rates given by $(b_0n + b_1)e^{-cn}$ and death rates $d_0n$ where n is population size and $b_0$, $b_1$, c and d are constants. Choose values of the constants and make plots of birth rate and death rate vs. population size. Do the plots on the same axis.

ii) Is there a balance of nature?

iii) Give examples of facultative agencies, catastrophic agencies, density independent factors and density dependent factors.

iv) Is Chitty's hypothesis consistent with the Darwinian paradigm?

v) Make sketches of a response that you would expect to be density dependent, inverse density dependent or density vague.

vi) Describe a situation, other than the one in the book, where you could use key factor analysis.

vii) Could self thinning occur in fish populations?

viii) There is a notion of "good viruses" as ones that have reduced virulence so that the host is not killed. What do you think of this idea?

12. Read pages 349-378 and answer the following:

i) In a dynamic pool model of fisheries, it is often suggested that fishery mortality should be set according to F = kM, where k is a constant. What do you think of this idea?

ii) What connotation do the words "surplus yield" or "surplus production" have in regard to logistic-based models of fisheries?

iii) If one assumes that catch is proportional to population size, so that C = qEN, then catch per unit effort, CPUE = $\frac{C}{E}$ , is a measure of abundance. Suppose, however, that catch is really given by $qEN^a$, where a >0 is a parameter. What is the implication of this for CPUE as a measure of abundance?

iv) Krebs suggests that the Ricker recruitment curve (Figure 17.7) is appropriate for short lived species and the Beverton Holt recruitment curve is appropriate for long lived species. Is this a reasonable idea? What is its likely basis?

13. Read pages 379-399 and answer the following:

i) Porcupines are an agricultural pest in many countries. They forage at night and only eat the border of a field, going no more than about a meter into the field. How would you redsign agricultural practice to minimize porcupine damage?

ii) For three of the examples given in the book, list the pest, the ecological situation, and two potential causes for the outbreak of pests.

iii) What is required for successful biological control?

iv) The Sterile Insect Technique can be described as follows. Many insect pest populations have one generation per year, a 50-50 sex ratio and grow exponentially so that if F(t) is the number of females in generation t, the dynamics are

$$F(t+1) = r\, F(t)$$

•What kind of growth will the population exhibit if it follows this equation? If one releases many sterile males (e.g. sterilized by radiation while in the pupal stage), thus "diluting" the population of reproductively active males. The proposed equation is

$$F(t+1) = r\, F(t)\left(\frac{F(t)}{F(t)+ S(t)}\right)$$

where S(t) is the number of sterile males released in generation t.

•Explain the form of this equation.

•If S(t) = constant, describe the population dynamics of F(t).

v) Has biological control been successful?

14. Read pages 402-428 and answer the following.

i) Conservation biology has been defined as the science of scarcity and diversity. Why would somebody choose this definition.

ii) Elephant tusks, unlike many other valuable animal products which reach an asymptotic size as animals age, increase in size as elephants age.

•Make a sketch showing a product that reaches an asymptotic size as the animal ages.

•Make sketch showing tusk that continue to grow at an increasing rate as the animal ages.

•How might this information help you design anti-poaching strategies involving local peoples?

iii) The model of Robert MacArthur and Ed Wilson in their famous book *The Theory of Island Biogeography* is based on the following

Birth rate when the population size is N

$$= \begin{cases} b_0 N & \text{if } N < K \\ 0 & \text{if } N \geq K \end{cases}$$

Death rate when the population size is N is

$$= d_0 N$$

where $b_0$, K and $d_0$ are constants.

•Interpret these parameters.

•Evaluate the biological attributes of this model.

iv) How would you evaluate whether the causes of a decline of a population are more likely demographic or more likely genetic?

v) I am particularly interested in the ways that catastrophes (e.g. hurricanes, mudslides, extremely harsh seasons, disease) affect populations. Are there any general conclusions we can draw about the value of corridors when populations are subject to catastrophes?

15. Read pages 431-455 and answer the following:

i) E.W. Fager defined communities as "recurrent groups" of organisms. Evaluate this definition.

ii) One way of studing association between species is through a presence-absence table. Over the habitat we measure if the species are found alone, together or not at all and construct the following table

| | | Species 1 | |
|---|---|---|---|
| | | Present | Absent |
| Species 2 | Present | a | b |
| | Absent | c | d |

Many indices of association have been proposed, for example L.R. Dice (1945) suggested that associated be measured by $A_1 = \frac{a}{a+\frac{1}{2}(b+c)}$.

On the other hand, R.R. Sokal and his colleagues proposed a number of indices, one of which is $A_2 = \frac{a+d}{a+b+c+d}$. What are the range of values that these association indices can take? Many authors have argued that d should not be included in a measure of association. Why do you think this would be the case?

iii) What are five measurable attributes of communities?

iv) What do you conclude from the index of similarities on page 448?

v) Do problem 6 on page 457.

<u>16. Read pages 459-481 and answer the following:</u>

i) Many people, myself included, argue that plant structure and morphology is analogous to animal behavior. Why would this be the case?

ii) Does an optimal environment exist?

iii) Explain Figure 21.8

iv) What are the implications of Figure 21.11 for estimating krill abundance from net trawls or from acoustic methods?

v) Why would natural selection reduce the overlap shown in Figure 21.15?

<u>17. Read pages 483-513 and answer the following:</u>

i) Find and describe an example of succession on campus.

ii) What are vernal pools? Are they examples of succession?

iii) Why are random models needed to describe succession?

iv) Suppose that a succession proceeds according to

A ---> B ---> C or A ---> B ---> D.

Construct a matrix showing what kind of information you would need to obtain to describe the succession.

v) Why are gaps so important.

18. Read pages 514-539 and answer the following:

i) What are the levels of biodiversity and which are most important.

ii) What needs to be explained in the patterns shown in Figure 23.6?

iii) What are the two kinds of data needed to measure biodiversity and what factors affect them?

iv) What are the patterns of North American mammals?

v) What are alpha and beta diversity?

19. Read pages 543-569 and answer the following:

i) What are the main equilibrium theories of community organization?

ii) Would you expect to find equilibrium communities in nature? If yes, why? If no, why study equilibrium communities at all?

iii) What are the connectances of the food webs in Figures 24.3 and 24.4?

iv) Why would connectance decrease as the number of species increases?

v) What are guilds and keystone species?

vi) What data are needed to compute a dominance index?

20 Read pages 572-602 and answer the following:

i) Why is disturbance important?

ii) What are the main non-equilibrium theories of community structure?

iii) Interpret Figure 25.2.

iv) Interpret Table 25.4.

v) What is the connectance of the food web in Figure 25.9?

vi) What do the data on page 593 tell you?

21 Read pages 603-632 and answer the following:

i) What measurements could be used to define relative importance in communities?

ii) What controls the rate of primary production?

iii) What are the five ecosystems with the highest productivity and what is the source of the productivity?

iv) If intensity of light satisfies $\frac{dI}{dx} = -kI$, where I is intensity in lux/$m^2$, x is distance from the surface in m, and $k=.05\ m^{-1}$ is the extinction coefficient, and the intensity at the surface is 3 lux/$m^2$ , what is the intensity at 2 meters, including units?

v) Which way does the North Pacific Gyre flow?

vi) Interpret Figure 26.15.

viii) Why is there saturation in Figure 26.19b, but not in Figure 26.19a or Figure 26.18?

22. Read pages 633-658 and answer the following:

i) Explain Figure 27.1d.

ii) What are the problems in estimating secondary production?

iii) What are the implications of Figure 27.3 for food webs?

iv) What limits secondary production?

v) Estimate the productivity of US grasslands from the data on page 646.

vi) What are the different kinds of grasslands?

vii) Is there a relationship between precipitation and herbivore biomass in Table 27.4?

23 Read pages 659-689 and answer the following:

i) Some oceanographers have argued that we should simply think of life in the sea as particulate carbon. How do you respond to that?

ii) What are the broad divisions of nutrient cycles?

iii) What is the importance of nutrient turnover?

iv) Interpret Figure 28.7.

v) What are the main patterns of forest productivity?

vi) Explain acid rain.

viii) Are global warming and climate change the same things?