Evolutionary Fundamentals for Ecology

Principles of Ecology
Biology 472

6/22/99

Objective

Review the basic notions of phenotype, genotype, selection, and evolution. Give an example of the evolution of a simple trait controlled by a single locus (melanism in moths). Then consider quantitative characters influenced by many loci and by environmental factors. This brings us to quantitative genetics. We will try to get through enough of that field to understand what narrow-sense heritability is and we will review heritabilities for the sorts of traits we will be investigating for the first half of the quarter.

Models in Ecology

"All models are false
but some models are useful"

- Sorts of Models (not exhaustive and not necessarily exclusive):
  - Verbal
  - Descriptive
  - Quantitative
  - Predictive
- Something All Models Share: Simplifying Assumptions
  - Robustness: how many assumptions can you violate before the model becomes seriously inaccurate?
  - Depending on the application of the model, the violations of the assumptions might actually be what you are interested in.
- We will concern ourselves primarily with quantitative/predictive models in this course.
- You should always be asking yourself, "What are the assumptions of this model?"

Some Review

$$\text{Genotype} \xrightarrow{\text{environment}} \text{Phenotype}$$

- Genotypes: the genetic "architecture" that the individual carries and which has a chance to be transmitted to offspring
- Phenotype: this is essentially "what you see." The outcome of a melting pot of genetic and environmental factors
- Evolution as change of gene frequencies
- Natural selection operates through fitness differences between different phenotypes
  - Ultimately these are differences in reproductive success
- Differential reproductive success and natural selection "become interesting" when there is a correspondence between phenotype and genotype
- Two situations in which evolution on a trait has a hard time occurring:
  - canalization: many genoytpes $\Longrightarrow$ single phenotype
  - environmental plasticity: when many different phenotypes have the same underlying genotype

A Classic Example of Evolution

- The pepper-moth, *Biston betularia*, and the Industrial Revolution
- Two morphs—dark (melanized) and light
- Melanization controlled by a single autosomal locus (dark = dominant trait)
- Before the Industrial Revolution tree trunks were lighter in color
  - Light-colored morph was better camoflauged
- Dark morphs hide better on soot-covered trees
- Over ≈ 40 generations the freq. of the dark morph increased from about 2% to about 94% in some polluted forests.
- Kettlewell's mark-recapture experiments

- But this is all very simple!!
- The "one-trait, one-locus" paradigm doesn't apply to more complex traits

Two Morphs of the Pepper-Moth

(a) Light on Unpolluted

(b) Light on Polluted

(c) Dark on Unpolluted

(d) Dark on Polluted

Variation, Fitness, and Heritability in More Complex Traits

- Many traits of interest are controlled by multiple genes
- Traits might be continuous
- *Quantitative genetics* is the field that seeks to understand variation, heritability, and fitness of such traits
  - A spectacular achievement of the 20th century
  - But very complex
  - Eagerly accepted since its inception by animal and plant breeders, but ecologists have been slower to appreciate its utility
  - Recently, however, that trend is changing
- For today we want to take home an understanding of:
  - Breeding Values
  - Heritability
  - Additive Genetic Variance
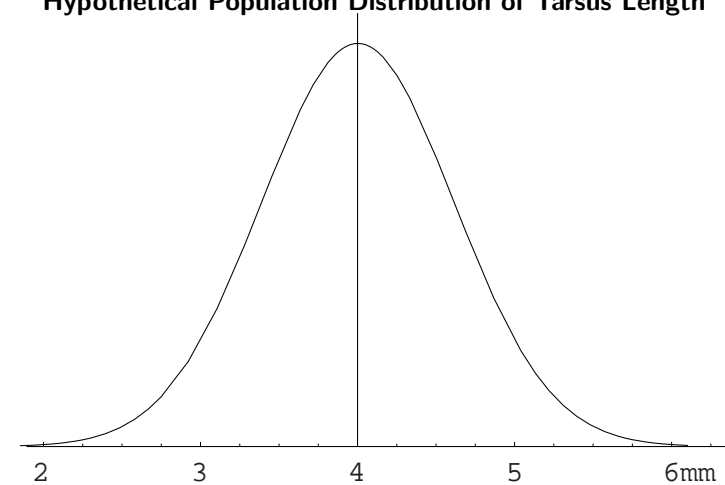
Consider a Quantitative Trait

- How about tarsus length in red-legged grasshoppers

Hypothetical Population Distribution of Tarsus Length

There is variation from **Genetic** and **Environmental** sources

Total Phenotypic Variance $= V_G + V_E$ ($+ 2\mathrm{Cov}_{G,E}$)

The "Breeding Value of an Individual"

- The Breeding Value *of an individual* may be obtained by a thought experiment:
  - Produce many offspring by mating the individual at random with the rest of the population
  - Compute the mean tarsus length of that individual's offspring
  - Multiply by two the difference between that figure and the *population's* mean tarsus length
  - That gives you the individual's breeding value
- Consider doing that with every individual in the population and looking at the distribution of breeding values over all the individuals in the population
- The variance of that distribution of breeding values equals the *additive genetic variance*. This is the most important part of the variance of phenotypes that can be attributed to genetic differences.

$$V_G = V_A + V_D + V_I$$

Additive Genetic Variance

This is the amount of variation in a trait that can be explained by applying to it a very simple model of genetic variation. Namely:

- There are many loci of small effect
- The contribution of each locus to the trait only depends *additively* on the number of alleles (0, 1, or 2) of a particular type at that locus
- Hence this model does not include dominance or epistasis

- The additive genetic variance is, however, that which is most available to alteration by natural selection
- Thus one defines "heritability in the narrow sense," or h^2 as the proportion of the total phenotypic variance accounted for by the additive genetic variance

Estimates of Heritability in Wild Populations

From Mousseau and Roff (1987) as presented in Stearns (1992): Heritability estimates for different types of traits in populations of wild animals.

	Life History	Physiology	Behavior	Morphology
n	341	104	105	570
Mean Heritability	0.262	0.330	0.302	0.461
S.E.	0.012	0.027	0.023	0.004

- In studying evolutionary ecology, we will focus on Behavorial traits and Life-History traits

Using Quantitative Genetics to Study Evolutionary Ecology

In addition to allowing people to estimate heritabilities and selection pressures on traits, a quantitative genetics perspective is available for learning more about the genetic constraints on evolution (genetic correlations between traits that could impede evolutionary progress).

Given this it seems as though it would provide a worthy paradigm for analyzing the evolution of ecological strategies. However, in behavioral ecology the quantitative genetics perspective has been rarely adopted. Rather, people have traditionally used optimality models and game theoretic models. We'll see those starting on Thursday, returning to a more quantitative genetic perspective when we look at the evolution of life-history strategies later in the quarter.

Optimality Models and Game Theory

Principles of Ecology
Biology 472

6/24/99

Historical Backdrop for Optimality Models

- Late 1950's and early 1960's amongst geneticists

  - Well after the appreciation of the Neo-Darwinian synthesis
  - Neutral Theory of Evolution gaining more acceptance

- Mid 1960's amongst ecologists

  - Rapidly increasing interest in role of ecological strategies
  - Sought ways to analyze strategies
  - Developed an adaptation-oriented perspective

Strategies for Successful Reproduction in Salmon

Females establish spawning territory. Males compete with one another for access to females.

- Two distinct strategies for males:

  1. Get big and compete heartily
  2. Mature young and very small and hope larger males won't harass you

- Strategy 1 is adopted by most individuals: much allocation to somatic growth and development of secondary sexual xters (fierce jaws)

- Straregy 2 is adopted by "jacks"—males at least one year younger than most. They allocated much less to somatic growth, and much more energy to the growth and early maturation of their gonads.

  - Sneaking

Evolutionary Ecologists are Interested in the Evolution of Strategies

- Study the fate of different strategies in populations

- Why are some strategies present and some not?

- The classical, genetics-based approach would be to:

  1. Establish strategy heritability
  2. Observe variability in strategies in population
  3. Document fitness differences and hence selection for particular strategies

- Ecologists seldom do this. Instead use Optimality Models or Game Theory

Strategy: a behavior or trait that accounts for energy input into different aspects of life

Growth

Reproduction

Foraging

Survival/Defense
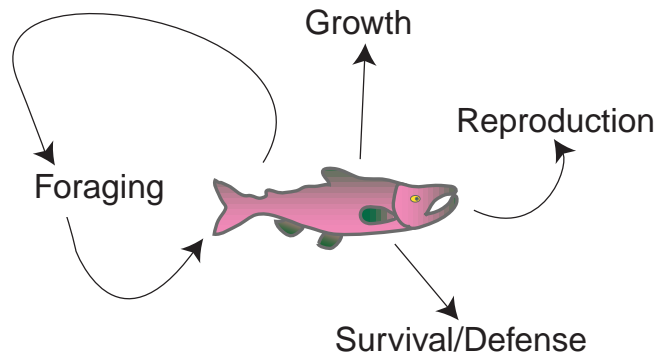
Assumptions for Optimality Models

The Big Assumptions (that are seldom tested)

1. Strategies are heritable

2. The optimal strategy was available for selection long ago in the population

3. The strategy has been subject to a fairly constant selective regime over some time, so the optimal strategy has had a chance to be selected in the population

Steps for Developing an Optimality Model

1. Choose a currency—Should be a limiting resource

   • food, protein, access to mates, (ENERGY or ENERGY/TIME)

2. Quantify the costs and benefits of different strategies in terms of the chosen currency

3. Find the optimal strategy subject to assumed constraints and trade-offs

4. Test to see if individuals in a population are using the optimal strategy

Constraints and Trade-offs

• Constraint: a restriction not subject to change by evolution

• Trade-off: a relationship between two things which is modifiable by evolution

• There may be many genetic constraints, but these are typically assumed not to exist

Criticisms of Optimality Models

- The strategy investigated may not actually be under selection

- It presents a hypothesis that isn't really falsifiable. Consider the interpretive options if optimal behavior is not observed:

  - We chose the wrong currency
  - We chose the wrong cost-benefit function for the strategies
  - We did our experiment incorrectly
  - These critters truly fail to behave optimally

Optimal Foraging in Fine Grained Environments—Macarthur and Pianka (1966) Optimal Number of Prey Items

- The goal was to predict the optimal diet breadth—i.e. how many prey items should an individual exploit

- This was a cost-benefit analysis—finding a balance between:

  - Time Spent Searching for Food
  - Time Spent Handling Food

- Want to maximize long-term food intake per unit time

- The different strategies are "Different Number of Prey Types in Diet"

Assumptions

- The standard optimality assumptions about evolution

- Environmental structure is repeatable (not patchy)

- "Jack of All Trades Assumption"

  - The animal can't be good at handling all food types

- However, assume that the animal can linearly rank prey items in terms of their Energy/Time (i.e. Benefit/Time)

- In addition to Handling Time for items, some time must be spent searching for items as well. The "Jack of All Trades Assumption" does not apply to searching

The Optimal Strategy Minimizes Time Spent per Unit of Benefit From Food

Let:

- $T(n)$ = total time spent searching and handling for a set a given amount of food *when the diet includes n prey types*

- $T_S(n)$ = amount of time spent searching in order to obtain a given amount of food when the diet includes n prey types

- $T_H(n)$ = amount of time spent in handling prey in order to obtain a given amount of food when the diet includes n prey types

- $T(n) = T_S(n) + T_H(n)$

Evidence from the field:

Shore Crabs and Mussels

Elner and Hughes 1978

- Shore Crabs forage for mussels which come in different lengths.
- Different length mussels provide different amounts of energy per second of handling time.
- Elner and Hughes collected mussels of 3 different sizes and measured crab energy gain.

Joules/Sec of Handling

Mussel Length — 4 cm
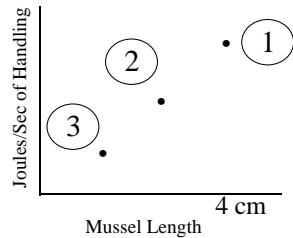
- 3 size classes in rank order of energy gain per unit of handling time. 1, 2, and 3.
- The Manipulation: Fix the proportion of different sized mussels but vary the overall abundance (# of each class in a given area).
- The Observation: Proportion of each size class eaten under different abundances.

Size Class--->	1	2	3
Low Abundance (Available)	2	4	8
Low Abundance (Eaten)	30%	65%	5%
High Abundance (Available)	10	20	40
High Abundance (Eaten)	60%	35%	5%

- The Conclusion: The crabs are foraging in a size-selective manner AND they get more selective at higher abundances.
- Note though, they still sample unprofitable size classes.

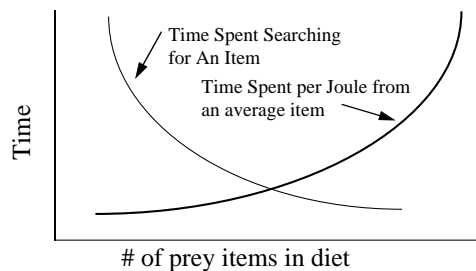Crabs behave somewhat as one would expect:

Comparing to "coin-foraging"

- Our foraging experiment with pennies, nickels, dimes, and quarters was similar:
- The handling times for each coin type were equal, but the "energy-gains" followed the value of the coins.
  - Different gain/time values for different coins
- Under high abundance, participants could be more selective for high-value coins, even when there were many more pennies to be found.

- This phenomenon can be predicted by the graphical analysis we did relating to Mac-Arthur and Pianka's diet breadth model.

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A tidy graphical result:

MacArthur and Pianka revisited

- Thinking in terms of crabs and mussels:
  - Searching and handling are mutually exclusive
  - Call different mussel lengths the "prey types"
  - Energy per handling time greatest by specializing on size class 1. And decreased when more size classes are added.
  - This is equivalent to noting that handling time per unit energy increases when more size classes are added to the diet.


Time Spent Searching for An Item

Time Spent per Joule from an average item

Time

# of prey items in diet

The Effect of Δ-ing Abundance

- The goal of the optimal foager is to minimize time per energy yield which is the dotted line to the right:

# of prey items in diet
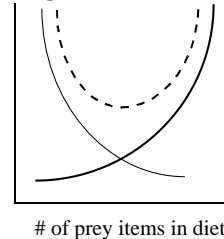
- Increasing the abundance shifts the search time curve down and to the left--decreasing optimal diet breadth. Red = Low Abund. Green = Hi Abund.
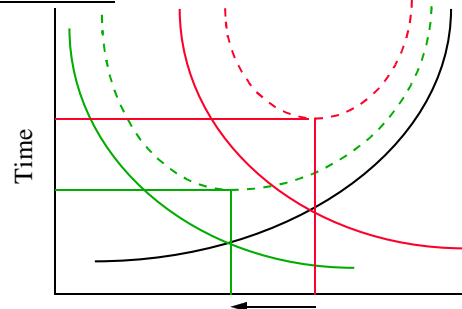
Time

A further experiment:

Brown Trout Prey Selection

Ringler (1979)

Prey Classes:
- Brine Shrimp (15 Joules)
- Small Crickets and Mealworms (104 J)
- Large Crickets and M-worms (230-240 J)

- Aquatic "Conveyor Belt" for food
  - Expmter can manipulate "search times"
  - Fish can't handle two prey items simultaneously
- Manipulation: Different arrival rates and diet qual.

KJoules per day

Low--------->Diet Quality-------->High

A = Optimum predicted on highest quality diet
B = Optimum predicted on low quality diet (only brine shrimp)

- Brown trout never achieved their optimal energy intake at the high quality diet, because they kept sampling the lower quality brine shrimp (and hence missed some high quality food oppotunities.
- Why? Look back at assumptions:
  - Maybe trout can't rank prey quality
    - Perhaps more learning of rank quality is needed
  - "Ambient Background Sampling" may be advantageous if novel prey types appear or if handling times can be decreased through learning:
    - Morgan 1972 with Dog Whelks eating a novel mussel variety. Over 60 days handling time per mussel decreased threefold.
  - Currency assumptions may be wrong---maybe energy isn't the limiting factor.
- There are quite a number of models that try to account for such factors--->complicated mathematics.
- Maybe there are too many constraints/ complexities for evolution to produce optimally feeding trout.

Seabirds and shell-breaking:

Revision of Optimality Hypotheses---Examples

- Three Examples:
  - NW Crows and Whelks
  - NW Crows and Mussels
  - Oystercatchers and Mussels
- Encapsulate the Adaptationist reply to criticism from non-Adaptationists
- Demonstrate what is deemed relevant to the optimal foraging modeler:
  - Finding plausible explanations for behavior
  - <u>Not</u> trying to prove that evolution has made everything the best that it can be.
  - Optimality is the tool---not the hypothesis that is being tested!
  - The hypotheses to be tested are the assumptions made about currencies and cost/ benefit functions relating currencies to fitness.
  - Start with simple assumptions and only make your model more elaborate if necessary

Example 1:

Northwest Crows and Whelks
Zach 1979

- Crows drop whelks on rocks to break them open
- Several Observations:
  - 5 Meter Drop Height
  - Re-Drop Until they break
  - Choose to drop only large whelks

Optimality Assumption: Crows maximize energy gain per energy spent handling whelks.

Hypothesis to be tested:
- Crows behave as they do because their energy gain is highly dependent on getting the whelk to break.

- Tests:
  - Drop whelks from different heights
  - Drop different sized whelks

- Results:
  - Large whelks break more easily
  - (Small whelks almost never break)
  - Probability of breakage the same for each drop
  - Increased breakage minimal above 5 m

Example 2:

NW Crows and Littleneck Clams
Richardson and Verbeek 1986

- Crows must find clams in the sand and dig up
- Once they dig them out, they drop them on rocks to break them
- Mussels of 29 mm are abandoned without even trying to open them 50% of the time.
- Mussels >32 mm are always dropped on rocks

- The obvious Hypothesis, extrapolating from Zach:
  Hyp #1: Large clams break more easily

- <u>The Test:</u> Not true!!

- The Revision:
  Hyp #2 Little clams are left behind because larger clams yield more energy

- Measurement of mussel energy content is consistent with Hyp #2

Example 3:

Oystercatchers and Mussels
Meire and Ervynck 1986

- Oystercatchers eat mussels, but break them with their beaks.

- First M & E only looked at the energy content of mussels that birds successfully opened.
  - Large ones took longer but were still more profitable
    Hyp. 1: Oystercatchers should utilize the largest mussels they can find

Profitability vs Mussel Length (curves A and B)
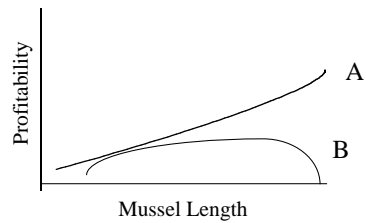
Hypothesis 1 is based on Model A
•OOPS! Reconsidering the data, some large mussels are impossible to open.
•Leads to Model B which yields
  Hyp 2 An intermediate size will be optimal

The Model Predictions didn't quite fit the data:

Finally it was discovered that length was confounded with barnacles. Barnacles interfere with opening, and are more likely to be found on some (but not all) big mussels.
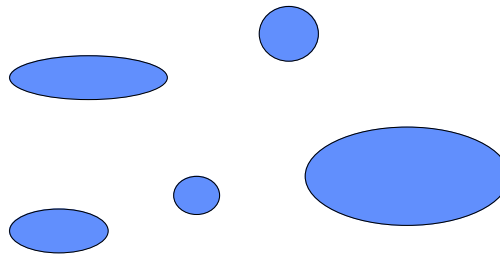

Key Point = Constant Revision of Hypoth.

Moving to a related, but new topic:

Foraging in Patches

•Environments are not always "repeatable" as assumed in MacArthur and Pianka's model
•Food is typically clumped. Examples:
  • Grubs in logs
  • Flowers of particular plant types
  • In Seattle--Lawns for geese and robins
•How a Theoretical Ecologist Might View Patches:

Forager must now search for patches and then decide how long to stay in each patch.

The Patchy Env. Problem

Example: Great Blue Herons and backyard fish ponds

•The Habitat consists of all the fish ponds the GBH can visit
•The Patches are the fish ponds themselves
•GBH seriously reduces fish abundance--- diminishing returns over time in each patch

• Decision that must be made: at which point does the GBH decide that patch profitability has been reduced enough that it is time to move on to a new patch.
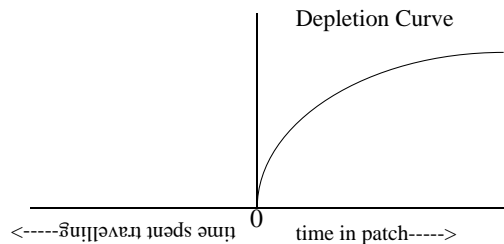

Another classical graphical result
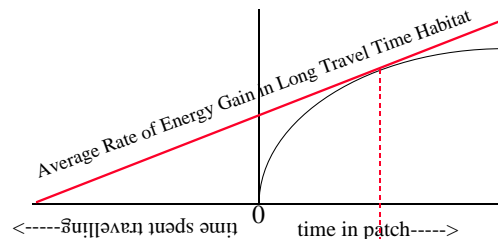
The Marginal Value Theorem

Charnov 1976

Assume:
•Many copies of one type of patch dispersed through the habitat
•All patches have the same "depletion curve"
•Fixed travel time/costs between patches
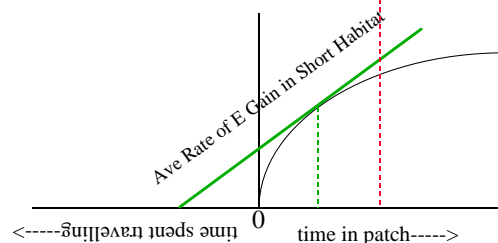•Desire to maximize long-term average energy gain

•Bizarre Axis System:

Depletion Curve

<----- time spent travelling | 0 | time in patch ----->

Long Travel Time Optimum:

Average Rate of Energy Gain in Long Travel Time Habitat

<----- time spent travelling | 0 | time in patch ----->

Short Travel Time Optimum:

Ave Rate of E Gain in Short Habitat

<----- time spent travelling | 0 | time in patch ----->

Basic Results of MVT

• Forager should leave patch when its instantaneous rate of energy (food) gain is equal to the average rate of food gain (averaged over the whole habitat)
•Longer average travel time between patches should lead to longer patch residence times
•Could extend to variable patch quality; foragers should stay longer in better patches

• Empirical work on seeing if animals respond to MVT-based cues is very difficult
• Hard to discriminate which cues the forager is really using to make decisions about staying in patches
•Consider observations on the aardwolf, *Proteles cristatus*, foraging on patches of its favorite termite species, *Trinervitermes bettonianus*, in the Serengeti.

Aardwolf seeking termites
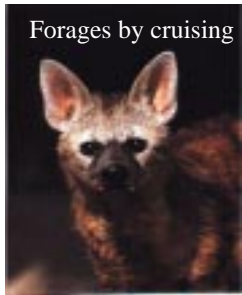
Forages by cruising over the grasslands slowly, Starting 3 hours before dark and continuing until dawn.

Don't seem to use olfactory cues to locate termites

Use their ears instead!

(They cancel all foraging for rainstorms---can't hear the termites!)

When they find a colony of termites they root through the dirt with their noses, and lick up the termites

After they've left though, you can run over there and still find plenty of termites milling around, just there for the taking? Why did they leave the patch?

Answer: Soldier Termites filled with terpenoids.

So, do you say that they are leaving the patch because they have depleted the edible termites, or are they leaving because they can't stand the taste?

SO WHAT? The point is that there are many cues that animals may respond to.

Other issues:
•Is it reasonable that animals can monitor "instantaneous rate of food intake" when prey arrive as discrete chunks?

Simpler explanations for patch-staying behavior?
Could be a simple "turning rule" based on how much food has been obtained in the last few minutes.

Search theory: a well developed field of inquiry into these questions
Computer lab this week asks you to optimize intake of a silicon gopher given simple search/foraging rules.

One arena where MVT ideas/results figure nicely:

Central Place Foraging

<u>Basic Notion:</u> Animals forage outward from a central "home-base" to which they return

Especially germane when animals bring food back:
  • Rodents/Squirrels storing food
  • Bird foragers bringing food back for offspring

<u>Two Classic Experiments:</u>
•Squirrels feeding on manipulated sunflower-seed patches
  • Manipulated distance of different sunflower patches
  • Squirrels spent longer feeding at the more distant seed patches, and filled their cheek pouches fuller
  •Not a great fit with MVT predictions though (Kramer 1982)

•Starlings trained to get food from a "decreasing profitability mealworm dispenser (Kacelnik)

Maximizing energy gain to self? or energy delivered to chicks?

2 different things!

Multiple Foragers at Once

Simple notion that is often invoked:

The Ideal Free Distribution:

Foragers will disperse themselves amongst patches or across habitats so that their individual gains are maximized

In terms of aggregate behavior this means the animals distribute themselves with respect to both the quality of resources and the number of competitors

Example: Milinski and more stickleback experiments.

IFD assumes that animals are <u>free</u> to move where they want to.

 Akin to the <u>ideal</u> gas law

We'll see this again as an assumption in the Cartar paper

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A new topic:

Risk-Sensitive Foraging

Charnov and Stephens

Up until now, the *optimal* in optimal foraging has meant "maximizing the *long-term average* rate of food intake" but consider experiments by Les Real with bumble bees (*Bombus*):

<u>Two Colors of Imitation flower:</u>

all yellows filled with 2 µl of artificial nectar

1/3 of blues have 6 µl
2/3 have 0 µl
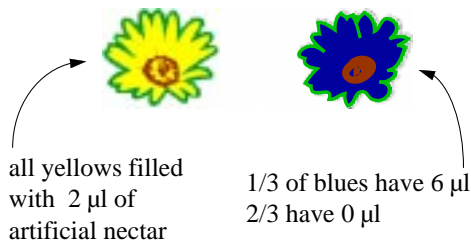
So *long term average rate* of food intake would be the same while visiting either flower color.

However, the bees overwhelmingly prefer the yellow flowers.

Further Manipulations by Real:
  •Swap Flower colors. So that the blue flowers are the constant ones
    •<u>Result:</u> bees prefer blue then!
  • Try a different nectar distribution in "risky" flowers: 2/3 get 0.5 µl
              1/3 get 5 µl
Same result--->Bumble bees don't like to gamble.

Notice: in all of these trials, the *mean* rate of food intake is the same between flower colors, but the *variance* of what the bee gets from any one flower is <u>zero</u> for one of the flower colors (constant 2µl) and <u>positive</u> for the other flower color.

In the jargon of the field we say that these bumble bees are <u>Risk-Averse</u>:
  • They will go for the food that gives them the constant reward rate

• The opposite of Risk Averse is called Risk Prone

• Question? Why would any critter in its right mind be risk prone?

Risk Sensitivity

•Two different meanings for "Risky Foraging":

   •Risk of Predation

      •Example: Another Milinski stickleback epxeriment

   •Risk of variable food payoff*

      •Les Real's bumble bees and paper flowers

•Definitions:

   •Risk-sensitive

   •Risk-averse

   •Risk-prone

•Why be risk-prone?

   •Threshold requirement condition

Z-score model

Provides a way of explaining risky versus non-risky food choices when the sum of all the food items must exceed some threshold (i.e. survival is a *step function* of energy obtained)

   •e.g. energy stores accumulated over the day in order to survive the night

•Assumption that food is obtained in small parcels throughout the "day" and food quality of items is independent from one to the next

   •(This requirement satisfies the Central Limit Theorem assumptions. CLT yields normal distribution)

Total Food Accumulated in the day
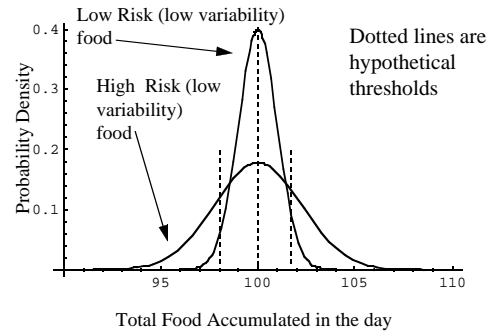
In its simplest form:

   •Discrete choice nature of the model---either predicts risk-averse yes! or risk-prone yes!

•Hunger-level sensitive risk-sensitivity

   •When energy-reserves are depleted animal should be more risk-prone.

•Forms the basis for the hypothesis in Cartar's bumble bee paper. Bees facing energy shortfall

should forage on the more variable (but equal mean) payoff flower type

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Going over Cartar 1991:
Natural History Features

Life on the island: Three summers on Mitlenatch
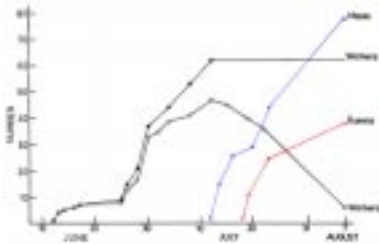•Bee Colonies Transplanted from S-F U. campus
•Cycle of Bumble bee colony

Figure legend: The development of a free foraging B. terricola colony. Cumulative totals of the bees are given by the shaded symbols. The open circles signify the actual number of workers in the colony at that date. source: http://indecol.mtroyal.ab.ca/bumble/

A Laboratory-raised colony

Brood Clump and HoneyPot ---the communal feeding trough
•Hive temp
•Energy reserves

Two types of plants provide nectar for the colonies:
   • Seablush
   •Dwarf huckleberry

The big assumption about nectar levels in flowers is:

The "Null-Hypothesis" is an Ideal Free Distribution type of prediction
•Two flavors of the IFD argument
•Both qualitatively predict that risk-aversion should decrease when energy stores decrease

Estimating profitabilities of flower types:

1. Measure nectar levels at the end of the day
2. Measure time required for bees to forage on the different flower types
(Quite a lot of work!)
3. Combine those estimates into profitabilities

Main result: Same Expected Profitabilities BUT dwarf huckleberry was more variable.

AHA! Two different food types:
High Variance = Risky

and

Low Variance = Not so risky

A Dwarf huckleberry congener

Honey Pot Manipulations
Artificially creating the spectre of energy shortfall

- Between 1430 and 1600 in the afternoon he drained some honey pots and added sugar solution to others
- Scientific Method things to Note:
  - Randomization
  - Minimization of carryover effects
  - Balancing the number of foraging bees

- Results: Counting Color-coded bumble bees

	Treatment	
	Reserves Enhanced	Reserves Depleted
Dwarf H.	24 (47%)	61 (68%)
Seablush	27 (53%)	29 (32%)

*Only late in the afternoon.
*Statistically significant differences in the above table.
- Indicates a preference for the "higher risk" flower when stores are depleted (wow...even with other avenues available to them---more foragers, nectar/pollen switch, etc.)

One final flavor of optimal foraging

Up to now we have considered two different "currencies" that foragers might be optimizing.

1. Long term average intake

2. Probability of meeting minimal requirements

A final currency you should know about is time required to satisfy nutrient requirements (optimization now means "minimization")
- Different than long term average intake
- Overall intake may affect fitness less than, say, avoiding being preyed upon or succumbing to climatic extremes while foraging:
  - Example: desert ant colonies

Bottom line: the proper currency should be intimately linked to fitness!

Applications of Foraging Theory in Conservation and Solving "Ecological Problems"

OK...How can we use this stuff?

There's not an over-abundance of examples

Three though:
- Schmitz (1990): Evaluating supplemental feeding programs for white-tailed deer
- Monaghan (1996): Using seabirds to monitor fish populations
- Luck (long-term programme) biocontrol of citrus pests

Extensive OFT modelling in
White-tailed deer

Schmitz 1990

Majestic beasts and also valuable for sport hunting economy.
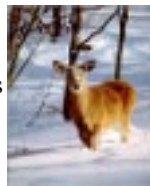
- Truly charismatic megafauna
- Northern latitudes/harsher winters
- Supplemental feeding programs
  "*ad libitum*"

Important question: How effective and efficient are these supplemental feeding programs. Schmitz claims it is not sufficient to just survey food use by deer in supplemented and non-supplemented areas:

"The efficiency of feeding programs can only be judged by predicting diets deer should select in different environments and comparing how well their diets match the predictions." --- Oswald Schmitz

Schmitz's OFT Model

Assume that deer will forage optimally, then develop a model to predict what they ought to be eating.

Optimization of diet types subject to three factors which he calls his three constraints:

1. Processing Constraint

2. Time Constraint (How long can a deer forage per day?

3. Energy constraint (how much is required?)
   - Energy typically limiting in northern environments in the winter....good!

Investigated the optimal diet composition subject to these constraints using two different optimality criteria we've seen before. They were:

Data and Inputs
Brrrrrrrr...a long, cold winter watching deer.

- Rumen volume and turnover times
- Bulkiness of different forage types
- Time deer can spend foraging vs. temp
- Cropping rates (how quickly can they browse)
  - Measured many twigs
- Energy requirement model

Observed Behavior:
- Non-supplemented deer foraged as predicted by the energy-intake maximizing criterion

- Optimal Behavior for supplemented deer would be to "eat nothin' but the good stuff"

- Implication: Supplemented deer not being as efficient as they could be.

- Interpretation and management implications

Feeding stations and such...

Fisheries and Seabirds

•Inextricably intertwined:
•Historical sideshow-->Seabirds Preservation Act of 1869 in Britain

•Fluctuations in fish popns due to fishing has a great impact on seabird populations

•Some background on fisheries stock assessment and the "development" of fisheries

•Monaghan works on Shetland seabird colonies.
•Main fishery = lesser sandeels. Yearly harvests in the North Sea around 10 BILLION kg!
•Small fishery opened for sandeels in 1974, peaked in 1982, then guess what happened?
•Populations of surface feeding birds had greatly reduced reproductive output
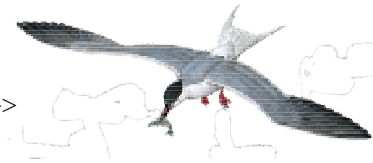•Diving birds not so badly hit

Surface Feeders:

Arctic Tern -->

<-- Kittiwake

Diving Birds:

Guillemots and shags

Bird-Related Indicators for Fish Abundance

Monaghan and colleagues' long term study investigating:
•Colony breeding numbers
•Reproductive parameters
•Body condition
•Diet Composition
•Foraging Behavior*

•First three not very reliable because changes in foraging behavior could compensate for some effects
•Foraging behaviors of diving birds changed noticeably---birds worked harder!
•Surface feeders also changed their behavior:
•Longer foraging journeys when abundance was low (recall central place foraging)
•Could reliably monitor by recording time that both parents remained at the nest
•Diet Composition is potentially useful (clearly) but would require much more work (empirical *and* theoretical) to make it a reliable indicator

On to a new topic:
Territoriality

•How I would like to traverse this topic:
•Definitions
•Varieties of Territorities
•Phyletic perspective on territoriality

•Costs and benefits of territories
•More optimization ideas

•Mechanisms of territory maintenance
•Some game theoretic ideas

•Effects of territoriality on larger ecological issues

Definitions of Territoriality

There are many.
One end of the spectrum---Odum:
•"An actively defended home range"
•"At the risk of offending semantic purists we are including under the heading of territoriality any active mechanism that spaces individuals or groups apart from one another, which means that we can talk about territoriality in plants and microorganisms as well as in animals."

•Huntingford and Turner---A Behaviorally defined notion. Territorial behavior has 4 components:
1. Site attachment
2. Exclusive use of the area
3. Agonistic behavior
4. Attack changes to retreat at the territory boundary

Typically refers to an area in space rather than a mobile resource (for example red deer stag and his harem of does)

Not a Home Range!

Huntingford and Turner's defns are specifically geared toward distinguishing territory from h.r.

Home range is basically just the area in which an individual tends to restrict *itself*

Example of coatis:
Exclusive home ranges but *not* territories.

Varieties of Territory

A bit ad hoc:
1. *Based on Resource* that the owner gets access to:

food

mates

shelter

also nest sites

2. Length of Time defended.
   Ranges from hours to year-round

3. Defended by whom and how many?
Single individuals versus mating pairs, etc.

Phyletic Perspective on Territories

phyletic a. Biol. Of or pertaining to the development of a species or other taxonomic group.

Winn 1954. Territoriality in Darters (fish)

A continuum of territorial behavior across closely related species from "more primitive" to more recent/more specialized:
•*Percina caprodes*---lake dweller, non-territorial
•*Hadropterus maculatus*---drive other males away from females
•*Etheostoma* (2 spp.) defend females and remain near landmarks
•*E. blennoides*---high aggression and fixed territories.

Population-level consequences

A fatal blow for the Ideal Free Distribution concept.

Thus, Natl Seln may act to increase proportion of territorial animals in a population.

Costs and Benefits of Territoriality

Benefits:
   •Food: lasts longer, lower depletion rates, less variability in supply
   •Mates
   •Offspring rearing (female salmon)
   •Lowered predation (due to nest dispersion)
Costs:
   •Acquisition
   •Displays and patrolling
   •Possibility of injury (though not very common!)
   •"Single-Use" Territory
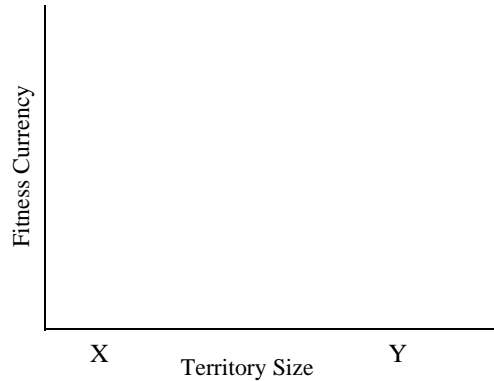   •TTP (Displays and Patrolling really are costly!)

Yarrow's Spiny Lizards on Mt. Graham

Studying the effects of test-osterone implants in male lizards. (Marler and Moore)

How Large a Territory?

Another simple graphical framework:

The optimum occurs where the slopes of the cost and the benefit curves are equal (That is where the *marginal* benefits of a larger territory start to decrease faster than the costs are increasing.)

Curve shapes will depend on environmental quality and population size relative to limiting factors

Conditional Territoriality

Some animals are territorial at times and downright gregarious at other times.

Bellbirds in New Zealand.

Extra 25 kJ/day from switching to terr. behav. under low food density

Rypstra (1989) studying a social spider:
- •Low Food Density---solitary and highly territorial
- •Hi FD---social. aggregations spin webs and individuals are free to go where they will. Fewer insects escape from the group webs.
- •The bee-eater mystery
  - •One would expect that individuals that voluntarily choose to be non-territorial will do so because there is not an energetic advantage to holding the territory.

African Bee-eaters:

Live in mud-bank colonies, but forage in separate foraging terri-tories that they defend against intru-ders

Communal feeding area close to home:
        100 mg insect/hour average
Defended, distant territories
        250 mg insect/hour average!

Yet, some birds abandoned their territory to feed close to home.   Why?!?!

Once again (as in the starling, central place foraging example---bringing food back to chicks

Explanations for Territory Maintenance

Two interesting observations:
1. Most territory owners don't forfeit their territories in conflicts with intruders
2. Things don't often escalate to full-blown fighting

Why could this be? We'll look at three explanations.

1. The "Arbitrary Rule" ESS hypothesis:

Speckled wood butterfly and sunspot territories. (Davies 1978)

The Resource-holding Power Asymmetry Hypothesis

Territory owners are bigger and stronger by nature.

This generates predictions:

Beewolf wasps (O'Neill 1983)
Pseudoscorpions (Zeh et al. 1997)
Damselflies, endurance flying, and fat reserves (Marden and Waage 1990)

But note red-winged blackbirds (Shutler and Wetherhead 1991)

The Payoff Asymmetry Hypothesis

There are certain costs to establishing a new territory, initially

but then the payoffs increase over time because you have an "agreement" with your familiar neighbors
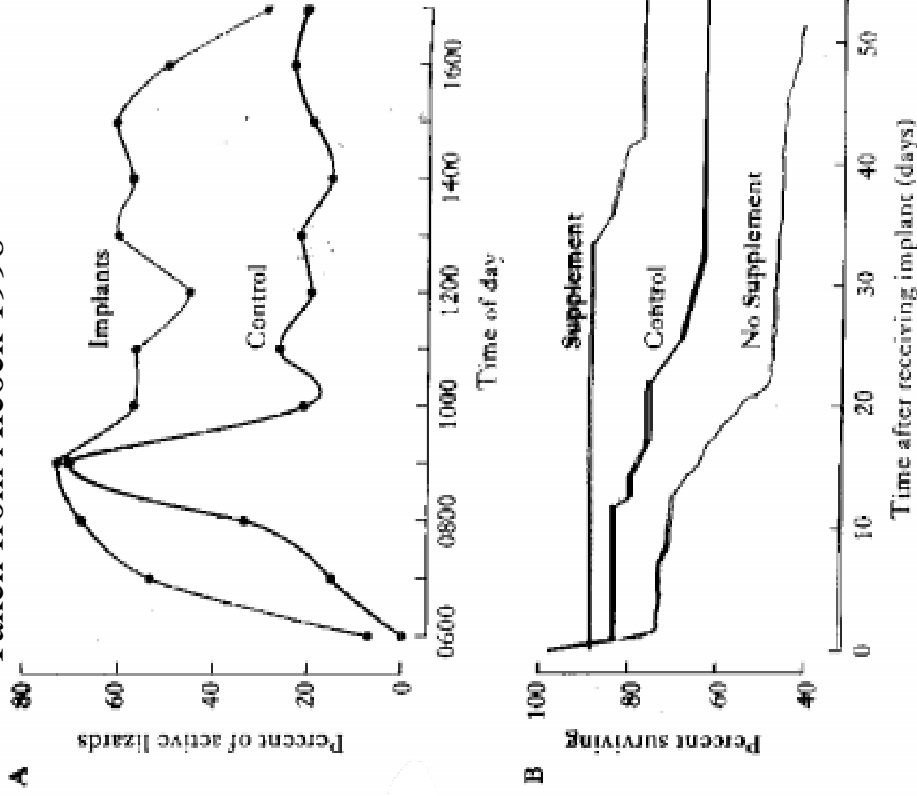
Two testable predictions:
1. If you remove an individual, and let somebody take over his territory, he is less likely to regain his territory if you keep him captive longer
2. The duration of contest to re-gain the territory should increase with increasing time of being away from its original territory
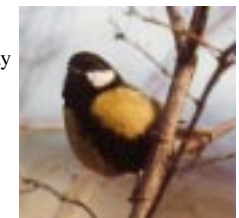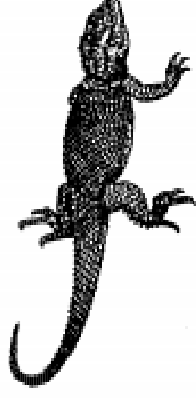
Krebs 1982: found these trends BUT---not a properly controlled experiment
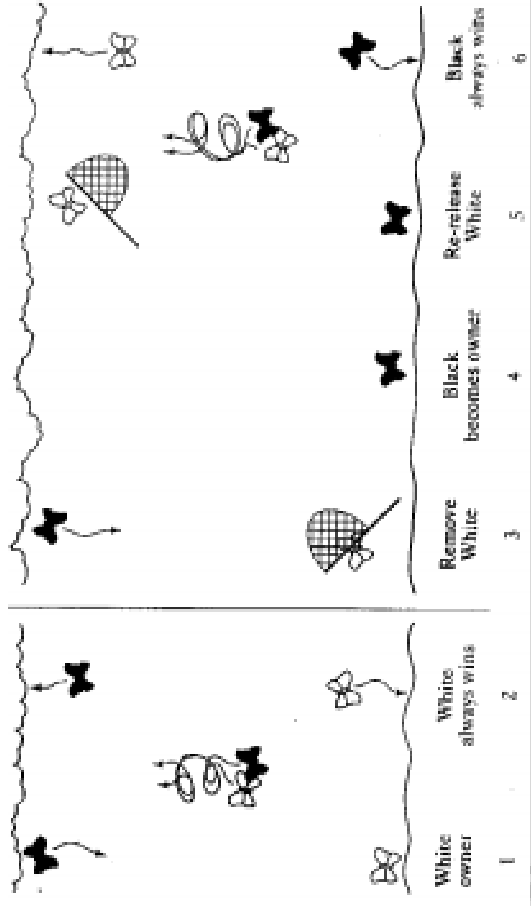
Testosterone enhancement in lizards

Taken from Alcock 1998

A — Percent of active lizards vs Time of day (0600–1600); curves labeled Implants and Control.

B — Percent surviving vs Time after receiving implant (days), 0–50; curves labeled Supplement, Control, No Supplement.

Energetic costs of territoriality. Males of Yarrow's spiny lizards became unusually territorial during the summer when they received an experimental testosterone implant. (A) The experimental males spent much more time moving about than did control males. (B) Testosterone-implanted males that did not receive a food supplement disappeared (and presumably died) at a faster rate than did control males. Testosterone-implanted males that received a food supplement survived as well or better than controls; thus the high mortality experienced by the unfed group probably stemmed from the high energetic costs of their induced territorial behavior. (Source: Marler and Moore 1989, 1991)

The arbitrary-rule hypothesis. Experimental evidence. (Taken from Alcock 1998)

| White owner	White always wins	Remove White	Black becomes owner	Re-release White	Black always wins
1	2	3	4	5	6

The resident always wins? An experimental test of the hypothesis that territorial resident males of the speckled wood butterfly always win conflicts with intruders. When one male ("White") is the resident, he always defeats intruders (1,2). But when the resident is temporarily removed (3), permitting a new male ("Black") to settle on his sunspot territory (4) then "Black" will defeat "White" upon his return after release from captivity. (Source: Davies 1978). But note that this was in a condition when sunspots were plentiful, and unoccupied ones were frequently available nearby.

The Payoff Asymmetry hypothesis test by Krebs on great tits. (Taken from Alcock 1998)
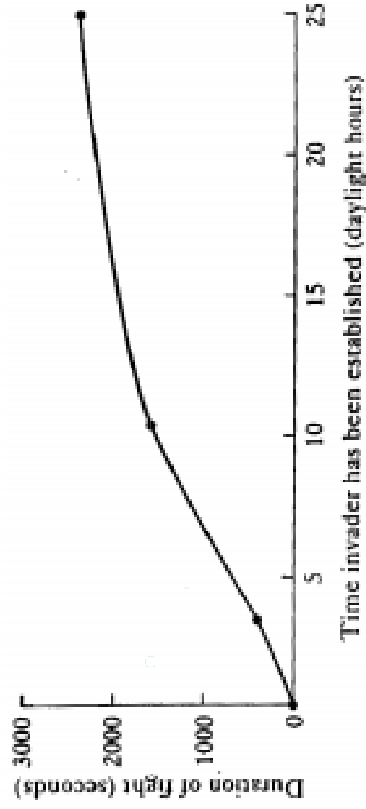
In great tits, the more time a new resident has been on a territory, the longer the fights between that individual and the oringinal resident (which was temporarily removed from his territory by the experimenter). (Source: Krebs 1982)

Duration of fight (seconds) vs. Time invader has been established (daylight hours)

Examples related to the resource-holding power asymmetry hypothesis: taken from Alcock (1998)
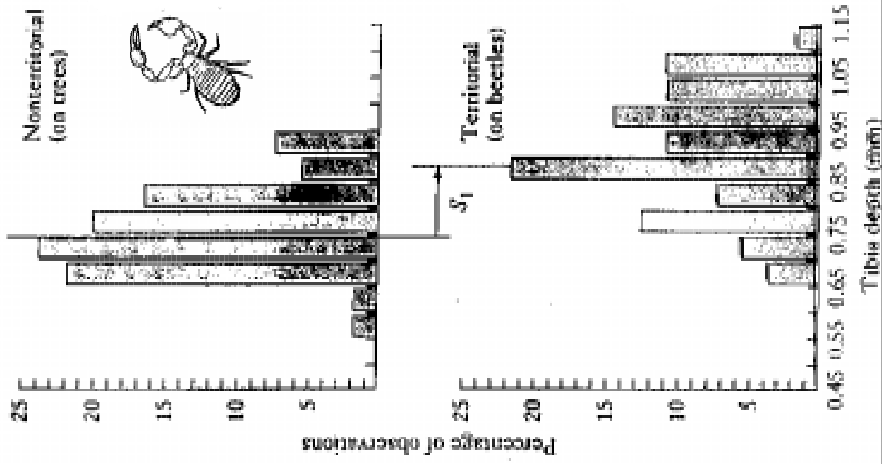
Body size, territoriality and reproductive success in a tropical pseudoscorpion. During the genertions when the pseudoscorpions are living on trees, where males are not territorial, being large carries no reproductive advantage. But when the tiny pseudoscorpions disperse on the backs of beetles, males fight for space, favoring large individuals. As a result, the mean size of males shifts upward during the dispersal generation by an amount shown here as S_1. (Source: Zeh 1997)

Nonterritorial (on trees)

Territorial (on beetles)

S_1

Percentage of observations

Tibia depth (mm)

0.45 0.55 0.65 0.75 0.85 0.95 1.05 1.15

Size of original resident (mm)

Size of replacement (mm)

2.8 3.0 3.2 3.4 3.6

Resource-holding power and the resident advantage in a beewolf wasp. The graph plots the size of the original resident (as measured by head width) agtainst the size of the replacement male that occupied his territory upon his removal. Points that fall above the ascending line represent cases in which the orininal resident was larger than the replacement. (Source: O'Neill 1983)
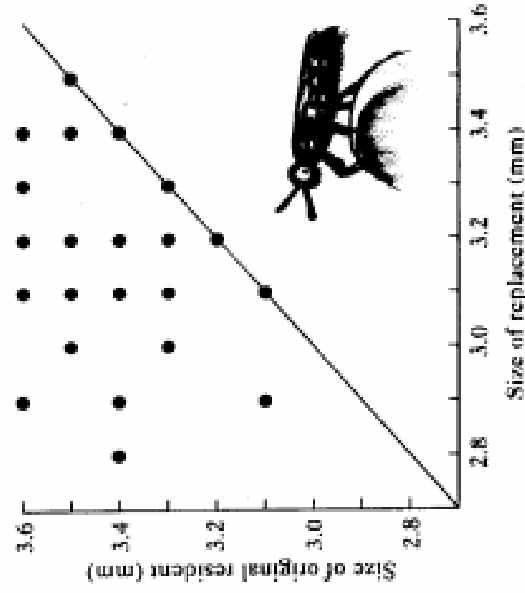
Animal Signalling and Communication

Outline:
1. Purposes and variety of signals
2. Signals in evolutionary context
   - Tactical components
   - Sensory exploitation
   - Unintended receivers
3. Evolutionary thought on signalling
   - •Strategic components
   - •Honest and deceptive signals
   - •Zahavi's handicap principle
4. Specific examples in territorial behavior

Purposes of Signals

1. recognition of species, individuals, neighbors, castes (social insects), kin, or demes
   - •Bird-song differences between species: are they adaptive?
      - •Allopatric Speciation
      - •Hybridization zones
      - •If hybridization decreases fitness, we'd expect greater song differentiation in areas of closely-related species overlap.
- •Gill and Murray (1972): Compared bird songs of golden-winged and blue-winged warbler in areas of species overlap and non-overlap

- •Songs were less varied in areas of overlap, perhaps because it was adaptive to be more specific.
- •But this is a lone study amongst many that suggest bird song is not so important for species recognition.

Golden-winged warbler

2. Sexual ritual or calling behavior between males and females
   - Tungara Frogs
   - Fireflies

3. Establishing territories and/or social status
   - Red deer, red-winged blackbirds

4. Alarm calling
   - Ground squirrels
   - Great tits and other birds subject to raptor predation
      - Convergent evolution in "seet" calls

5. Information in groups of foragers
   - Honey-bee example. The "Waggle Dance"
   - Number of waggles gives info re: distance to food
   - Direction of the straight-run gives info regarding the direction toward a food source.

Fig 1. The Waggle Dance

6. Parental care: offspring/parent recognition

Studholme (1994): Fiordland penguins
Offspring orient to and respond to their parent's calls more than other calls. (But parents seem less responsive to their particular offspring's call.)

Conveying Hunger levels:

Adult birds bringing food back for nestlings. The hungrier nestlings could scream louder.

Signal Components

Tactical Components:
   Features of a signal which are concerned with how easy it is for the signaller to transmit it, for the receiver to receive it and discriminate it from other signals.

Strategic Components:
   Properties of a signal that are concerned with what good they do to the signaller, i.e. how does the signaller benefit from emitting the signal.

Both have been viewed from an adaptationist perspective.

Tactical Components
"Getting the message across"

Example from Johnstone (1997): Anoline lizards and the "assertion display" versus the "challenge display"
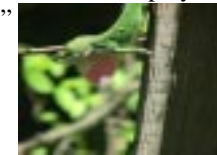
The assertion display is not sent out to anyone in parti-cular. But it "ought" to be noticed by some other lizard.

- •Common features of signals ensuring their appropriate reception:
   1. Conspicuousness
   2. Stereotypy
   3. Redundancy } analogy to electronic signal transmission
   4. Alerting components

Tactical Components and the Environment

Signals' conspicuousness seems to have evolved with respect to the environmental background.
•Marchetti (1993): Plumage patterns of congeneric warblers. Those living in low light environments had brighter plumage.
•Wiley (1991): Comparison of song-birds in North American habitats.
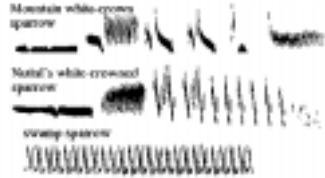   •Rated sonograms of birdsongs for
      •period of repeat of elements
      •buzzes
      •side-bands
   •Categories for habitat type (i.e. grassland versus forest, etc)
   •Songs from birds in open habitat had more reveberation-degradable features than songs from forest habitats.

Some Sonograms of different birdsongs

Back to the Methodology Zone for a moment:
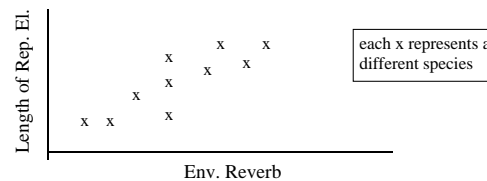
The Comparative Method

•Definition:
   Quite often, the relationship between two traits, OR the relationship between an environmental characteristic and an organismal trait will be explored by comparison of the traits and environments *across species* (or other taxa). The goal is to demonstrate a significant correlation between the two traits in question, or between the environmental conditions and the trait. This, then, might be taken as evidence of adaptation. This process is called the *Comparative Method*.

•Example:
   Studying, for example, the length of a repeated element in bird songs versus the amount of reverberation from the environment

each x represents a different species

The Nasty Statistical Issue:

It is important to know if the observed relationship between the two variables in statistically significant. However a simple linear regression (put a least-squares-fit line through the data and then test to see if the slope of the line is significantly different from zero) is invalid because it assumes that all the observations are independent.

But in the comparative method, the different points are not independent. *They are related by their common phylogenetic history*. Consider:

If the X's and O's are more closely related to one another, evolutionarily, then the observations in the cluster of X's and the cluster of O's are not independent of one another.

A simple linear regression will treat each point (species) as if it were an independent observation.

The Result: too much statistical significance inferred.

In reality, bird species of the "x" cluster may have all inherited a mutation that shortens the length of song elements, and they may live in less reverberative environments, but the two may not be related.

There are methods to try to correct for the non-independence between closely related species (for example Felsenstein (1985)).
   These are what Johnstone is referring to when he uses phrases like "incorporating various measures to control fro the effects of phylogeny."

Tactical Components and the "Audience"

"Color blind organisms should not have colorful displays or signals."

Sensory Exploitation:
   When signalling behavior evolves to take advantage of pre-existing sensory biases.

Proctor (1991): male water mites "tremble" at a similar frequency to prey. The females are acutely sensitive to this (being part of their foraging behavior repertoire).
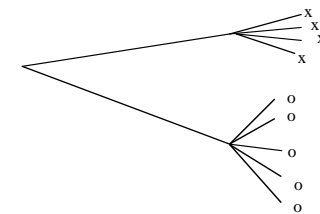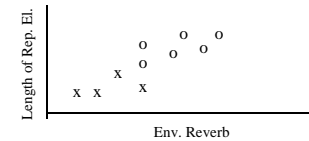

The female grabs at the male who somehow contends with the female's mouth parts, and is able to effectively mate with her.

Was this sensory exploitation? **(Proctor 1992)** and phylogenies.

Tactical Components and Unintended Audiences

Any time an animal is signalling, the message may get picked up by an unintended receiver (for example a predator).

Two types of alarm calls in great tits:
   Mobbing alarm call: loud indiscreet signal to others to mob and molest a *perched* hawk.

   "Seet" alarm call: short, high-pitched, discrete alarm call given to warn others of a *flying* hawk.

   The frequency of the seet call is high enough that hawks cannot hear it very well, but it is well within the range that great tits can hear well.

   (Studies with hawk orientation to recorded seet calls.)

The Evolution of Strategic Components of Signals

Traditional Ethological View (Pre-1970's)
- Signals were there to "facilitate and coordinate social interactions by making information available to be shared."
- Reasonable for cooperative signaling---
  - When both the signaller and the receiver benefit
- Deceit was not commonly considered, even though it was well-known on an inter-specific level, i.e. Batesian mimicry:

Viceroy Butterfly
Basilarchia archipus

Monarch Butterfly
Danaus plexipus

Signalling and Conflict of Interest

Signaller and Receiver don't always stand to benefit in the same way

Examples:
Displays of territory owners

In some species males seek matings with as many females as possible while females seek to mate with the "most fit" males

Early 1970's. Maynard Smith and game theory for signalling---without appropriate controls deceit should abound and signals should evolve to become meaningless.

Since signals are not all meaningless, something has maintained their honesty or utility. What? Two main (and related) types of explanation:
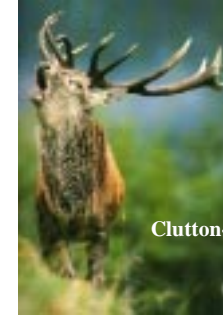- "Honest Signals"
- Handicap Principle

These reflect other evolutionary pressures that may be acting on signalling behavior

Honest Signals

An *honest signal* is one which reflects the true state of the sender by virtue of physical necessity

Examples:
Hill and Montgemorie (1994): Correlation between coloration and nutritional condition of male house finches

Clutton-Brock and red deer roaring contests

Also, frog-croaking tone. Small frogs are unable to croak at the lowest freqs.

Main point = direct link between the ability to generate the signal and the physical condition or foraging ability (taken to be a surrogate for fitness) of the signaller

---

Another way (in theory) to curtail deceit
Handicap Principle
(Zahavi 1975 and later)

- Similar to the Honest Signal notion, but here the link between condition and the *ability to generate* the signal is not so clear.
- Rather, deceit is discouraged because one must have high fitness in order to overcome the handicap of the signal.
- Example: Andersson (1982): Male Widowbirds in central africa. The "signal" is the long tail.
  - Females have a preference for males with long tails
  - The tails don't confer a fitness advantage to the males---if anything they are a handicap.

Male Widowbird

Notion of the handicap principle echoes Veblen (1899): *The Theory of the Leisure Class*, and his idea of "conspicuous consumption"

Condition-Dependent Cost or Benefits

At the heart of the Handicap Principle are

The signal/handicap must cost more for the "low-quality" individual than the "high-quality" individual

Conceptually/Graphically:
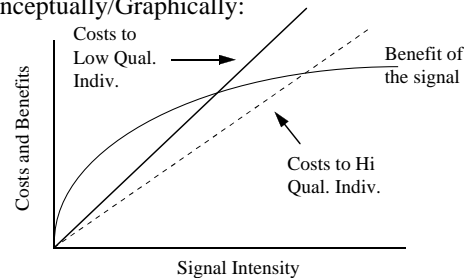
This has made actual testing of the Handicap Principle very difficult. Almost no studies have managed to quantify condition-dependent costs.

Sex & Sexual Selection

Sexual Selection : when individuals differ in reproductive success either because:

1. of competition within one sex for access to mates and their gametes (*intrasexual selection*), or

2. one sex prefers the gametes received from certain members of the opposite sex (*intersexual selection* or *epigamic selection*).

First we must entertain a few ideas about
The Evolution of Sex

The spectrum of reproductive possibilities:
- •Asexual:
  - •Parthenogenetic (eggs developing without fertilization. Oftern females giving rise to females)
  - •Clonal (quaking aspens)
- •Sexual
  - •Self-fertilization (some dioecious plants) though often there are mechanisms for self-incompatibility or partial self-incompatibility
    - •In genera *Petunia* and *Oenethera*:
      - •Single locus with two alleles
      - •pollen and stigma must differ for the seed to develop
  - •Sex-switching: protandrous or protogynous species/individuals
    - •Order often related to which sex has a greater advantage if they are larger
    - •Reef fishes, plants

The Origin of Sex:
   Long ago, given the
   Near ubiquity in eukaryotes
The Maintenance of Sexual Distinction

Both of the above present difficult evolutionary problems with several hypotheses for each.

Why is this so?

Asexual Reproduction
   advantages:

   disadvantages:

Sexual Reproduction
   advantages:

   disadvantages:

Thus, how did the "longer term" benefits of sex evolve and how are they maintained in the face of short-term benefits to individuals of asexuality?

Males, Females, and Anisogamy

What typically distinguishes males from females?

Yeast, protozoa, some green algae:
   Gametes are identical (isogamy)
   Different mating types (but not sexes)

Most multicellular organisms:
   Female gametes:
      Large and few
      Energetically expensive
   Male gametes:
      Small and many
      Energetically cheap
Differentiation of gametes is known as anisogamy.

House Wren:
- •Egg is >15% of body weight
- •Males may have up to 8 billion sperm at any one time

Many mechanisms of:
Sexual Determination

Haplo-Diploid (Hymenoptera)
   Males haploid, females diploid
Chromosomal/Genetic (i.e. XX or XY)
   whether females are heterogametic or homogametic varies across taxa
Environmental Sex Determination
   Nutrition
   Presence of conspecifics of different sexes
      Sex-switching reef fishes
   Temperature-dependent (crocodilians)

Also cominations of above. A difficult mess to untangle evolutionarily.

More bizarre: in parasitoid *Nasonia* wasps:
- •"Paternarnal Sex Ratio Factor" a non-chromosomal element that wipes out the paternal chromosomes in a zygote making it male (recall haplo-diploidy)
- •*Wolbachia*: a maternally transmitted, bacterial factor which kills male zygotes, so most of the female's offspring are females.

A *Nasonia* egg that was stained with lacmoid to visualize the *Wolbachia*. The darkly stained dots are the bacteria.

Fisher's Sex Ratio Theory

R.A. Fisher pointed out that in a sexually-reproducing population, every individual has exactly one mother and one father.
With Further assumptions:
- •Random mating
- •Equal cost to producing sons and daughters
- •Heritability of propensity to produce sons or daughters
Sex-ratio should evolve toward 50-50.

However, non-random mating is standard:
- •Positive assortative mating: like mates with like
- •Negative assortative mating (or disassortative mating)
  - •Drosophila and pheromones, the more dissimilar ones were more likely to mate
  - •"Rare male mating" in Drosophila

A different idea:
Operational Sex Ratio: the ratio of sexually receptive males to receptive females in a population at any given time.
- •Typically quite high for reasons of investment in gametes.

Differences in Parental Investment

Robert L. Trivers coined the phrase "parental investment" and made "Triver's Prediction"

Mate choice should depend on parental investment, i.e.
1. Size and costs of gametes
2. Costs of mating
3. Costs of parental care

For the higher investment sex, choice (intersexual selection) should be more important.

For the lower-investment sex getting more matings should be important

The sex that invests less should be able to tolerate more variation in reproductive success

Trivers' Predictions in the Field Some examples

Rick Howard (1983) while a grad student in Michigan.

Spent almost every night at a pond on campus watching marked bullfrogs
•Recorded who mated with whom then watched which eggs hatched
•Female investment higher
•Male variance in reproductive success is 2 to 3 times greater than for females

With High Male Investment: Gwynne (1981) and katydids.

Male passes a spermatophore (up to 27% of body weight of male)to the female
The female also eats the spermatophore
In high density populations
•Males have access to many mates
•Females readily accept the chance to mount
Males preferentially mate with larger (and more fecund) females
A similar example with an Australian katydid species--- under low food conditions females fight for access to males

Selection for 2° Sexual Characteristics

Epigamic selection appears to be responsible for the maintenance of some very outrageous traits.

Darwin noted this
Peacock is a classic example

Darwin mused that perhaps this was due to the aesthetic whims of females.

Since then theorists have searched for more plausible/rigorous hypotheses.

Three Broad Hypotheses for Intersexual Selection
(when nuptial gifts are not involved)

Healthy Mate Hypothesis: females choose males that appear to be healthy and so will not transmit disease or parasites to the female's offspring (a non-genetic explanation)

The Good Genes Theory: females informed by the courtship process choose healthy, well-conditioned mates because they will produce offspring that are more fit. (a genetic explanation)
•The handicap principle is a subset of this

The Runaway Process (Fisher): Starts with some females having genes that make them selective for a particular trait in a male. They will pass these genes on to daughters who will also prefer males with that trait. At the same time, if the trait is heritable, then the existence of females in the population with a preference for that trait will lead to higer reproductive success of the offspring of males with that trait, and things ratchet ahead like that.

Typically the runaway process "imagines" that there was some utilitarian purpose (giving rise to the female preference) for the trait in the first place.
Example:
Perhaps primordial peacocks with slightly longer tails were better foragers

However, more explicit theoretical models of the Runaway Process by Lande and Kirkpatrick suggest

•Needn't have a utilitarian genesis
•Even *arbitrary* traits that decrease survival may spread through the population by a runaway process

Discriminating Between the Three Hypotheses

Very, very, very difficult:
•Not mutually exclusive
•Runaway process could start as "good genes"
•Healthy males that don't infect their offspring with parasites may also have "good genes"
•Advanced runaway process leading to handicap principle = "good genes" once again
•Example from peacocks studied by Petrie
•Current evidence suggests "good genes" maintains male feather trains:
•Offspring of highly ornamented (HO) males grow faster, and their sons have higher reproductive fitness
•Peacocks taken by foxes typically have shorter tails and got fewer matings than other males the year before.
•But, can't rule out that the feather train traits originated out of "healthy males" or a runaway process (or both).

It's difficult just demonstrating female choice in peacocks.   Petrie et al. (1991)

Petrie et al. 1991

120 years after Darwin suggested female choice could maintain elaborate plumage:
  First demonstration of female preference for elaborate plumage in males.

Underlying Theory:
  •Intersexual Selection
Specific Hypotheses
  1. Female mate choice depends on male plumage train characteristics (*intersexual sel'n hyp.*) versus
  2. Certain plumage train characteristics confer a competitive advantage to males (*intrasexual sel'n hypothesis*)
Not mutually exclusive hypotheses

Previous Studies (Two)
  •Experimental manipulations
  •Demo'd increased mating success but didn't clearly document the mechanism

Observational Study
  •One lek at Whipsnade Zoological Park (England)

Petrie et al. Observations

•Morphological measurements on males
  •Train features
  •Other body features

•Behavior at one lek
  •Female visits
  •Male courtship attempts (hoot-dash)
  •Male interference and intrusion

•Results
  •High variance in male mating success
    •Displaying males
    •Peripheral displaying males
    •Floating males
  •Males did attempt to interfere with copulation attempts of other males
    •But interference did not seem to alter mating success
  •Successful matings correlated with train morphology
    •Train size and eye-spot number
    •Not correlated with other body measurements or lekking position
  •Data on 11 female visit sequences

Lekking

From Scandinavian word 'lek' for "play"

Males defend small territories of no resource value
  •Typically clumped in a small display area
Females arrive there solely for finding mates

Why do this? Bradbury's hypothesis
  •Should be favored in species with wide-ranging foraging ecology
    •Unpredictable, temporally variable food sources (tropical fruits ripening at different times on different trees)

Big Question: Why do males congregate in small areas?
  •Three Hypotheses:
    •"Hot Spot" hypothesis
    •"Hot Shot" hypothesis
    •Female preference hypothesis

Evidence for "Hot Shot"
  •Great snipes (European sandpipers)
    •Removal of dominant males caused desertion by nearby subordinates
    •Removal of subordinates created rapidly-filled vacancies

Lekking is one example of various

Mating Systems

Inquiry into evolution of patterns of mating systems started fairly recently.

Definitions:
    -gyny --> females
    -andry --> males
    -gamy --> both sexes
Monogamy, Polygyny, Polyandry, etc.
Polybrachygyny --> male "serial monogamy"

Defined in different ways:
    Pair bonds versus ability to monopolize access to mates

Mammals and others: Polygamy far more common---interesting cases are monogamy

Birds: Monogamy quite common---interesting cases are polygyny and polyandry

•Black Grouse
    •Yearly variation in lek sites

Evidence in support of Hot Spot:
    •Multiple species lekking near river confluences

Evidence against female preference hypothesis:
    •Uganda kob (an antelope that leks)
        •Operational Sex Ratio across leks is fairly constant

However, as with all things ecological: Depends heavily on the species.
    •Ruffs (type of sandpiper) exhibit behavior supporting all three hypotheses

        •Located near small ponds on elevated ground
        •Females prefer groups with at least 5 displayers
        •Low-ranking males choose to display near dominant males

Monogamy

Why would males ever be monogamous?
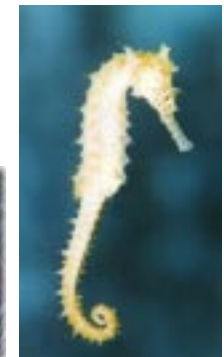
1. Mate Guarding Hypothesis
    •Females may remain receptive after mating
    •Females may be hard to locate
        •Clown Shrimp

2. Mate-Assistance Hypothesis
    •Improvement in offspring survival with paternal care may be dramatic
    •Seahorses
        •Male brood pouches

3. Female-Enforced Monogamy
    •American Burying Beetle

Infidelity in Monogamous Matings

Rationale for extra-pair matings

Male perspective
- Costs: cuckoldry while he's gallivanting about
- Risks of searching for extra-pair copulations and contending with other mates
- Clear benefits

Female Perspective
- Possible Genetic benefits
  - Sufficient sperm quantity
  - Sperm competition (fitter sons if heritable)
  - Genetic variety
    - Sibs less likely to compete ecologically?
- Material benefits
  - Resources on extra male territories
  - Parental care

Male Response on Evolutionary Time Scale:
   Paternity Assurance

Female defense polygyny:
- Pre-existing female clusters
  - Some bat species females forage together and roost together at night a single site in their cave
  - Single male defends these clumps
    - DNA studies: 60 to 90% of matings
    - Up to 50 pups per male!

- Some males form their own female clusters
  - Marine amphipod---constructs "mobile apartment buildings" with up to three females

Male dominance polygyny
- See lekking

Mechanisms of Paternity Assurance/Remating Prevention

Examples:

Dragonfly hitchhikers:
- Fly around on top of the female he's fertilized until eggs are laid

Plugs and cementious semen

Calopteryx spp.

Chemically noxious odorizing

Infanticide

- "Recently promoted" dominant primate males

- Female fetus resorption

The job of paternity assurance is more difficult in species where the female stores semen from previous males

- Solution in *Calopteryx maculata*---the hoooked penis

Polygyny and Polyandry

Monogamy is the norm in birds
- Potential for male reproductive care (mate-assistance hypothesis) seems dominant reason
- Most theory about polygyny and polyandry developed in the context of bird studies

Resource-Defense Polygyny
- Polygyny Threshhold (Gordon Orians)
  - At some point it benefits females to become a second mate of a male with a large territory
  - Lenington with red-winged blackbirds
    - Males arrive first and establish territories
    - Females appear later and choose males
      - Initial choice of unmated males
      - Eventually polygyny was chosen over mating with males on poorer territories
      - Two territory variables
        - Cattail density
        - Food density*

Sociality and Altruism

Overview:
- Some costs of social behavior
    - Imply importance of demonstrating benefits
- Assumption of genetic basis
- Direct selection, Indirect selection
- Types of social interaction in terms of costs/benefits
    - Mutual versus Selfish versus Altruistic behaviors
- Explaining altruistic behavior
    - Quick dispatch of Group Sel'n and Recip. Altru.
    - Kin Selection
        - Inclusive fitness
        - Hamilton's Rule

Sociality and Social Behavior

Broadly-defined: any non-solitary behavior

The Spectrum of social behavior, broadly defined:
- From "simple" conspecific interactions such as encounters between territory owners and intruders
- To highly organized eusocial systems (honeybees)

Human bias in thinking about social systems:
- Highly organized social behavior and social living are "more evolved" in some way
- This is a bias because it is what we do
    - Nothing says evolution should proceed toward greater social organization

- Social Organization may incur high costs:

- Bottom Line: To explain social living and social behavior you must be very clear about the fitness benefits of sociality *to individuals*

Two examples of costly sociality from Alcock 1998

Ovicidal female acorn woodpeckers

Parasite-harboring cliff-swallows

Recalling the Genetic Perspective

Big assumption underlying the evolutionary ecology perspective on social behavior:
- Behaviors in question have a genetic basis
- For behaviors to increase in frequency in populations the genes controlling them must make it to future generations at a higher than average rate
- How do these behaviors "help those genes along" to the next generation? Imagine an individual named Fred:
    - (a) Direct Selection: Fred's genes make him behave in such a way as to increase the chances of passing on his genes (i.e. of having more offspring) **OR** in such a way as to increase the chances of Fred's *offspring* surviving to pass on their genes.
        - This promotes the direct fitness of the genes influencing Fred's behavior
    - (b) Indirect Selection: Fred's behavior promotes the fitness of individuals who are not his offspring, BUT those individuals happen to carry copies of Fred's genes (because they may share a common ancestor)
        - This leads to indirect fitness benefits.

Cost/Benefit classification of social behaviors

Social behaviors can be characterized as interactions between "Self" and "Neighbor"
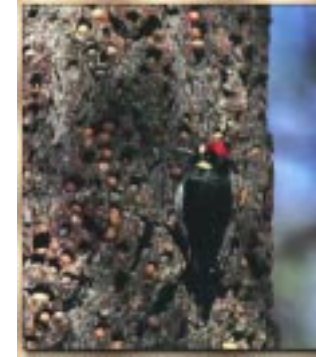- Four main types based on cost or benefit to self or neighbor:

	Effect On Neighbor	
	+	−
Effect On Self +	Mutually Beneficial	Selfish
Effect On Self −	Altruistic	Mutually Disadvantageous

- MB and S are easily explained via natural selection
- MD ought not be very frequent
- Altruistic behavior is the tough one to explain

Note: Altruistic behavior doesn't mean "consciously altruistic" as in "Oh! You're such an altruist!"

Explaining Altruistic Behavior

THE BIG QUESTION: How could a behavior which reduces the fitness of an individual ever evolve in a population?

THREE PROPOSED EXPLANATIONS:
1. Group Selection (a largely discredited hypothesis)

2. Reciprocal Altruism (a game theoretic notion with little empirical support)

3. Kin selection (a fairly widely-accepted hypothesis based on genetic arguments and *indirect selection*)

A Brief History of Group Selection

Basic Premise of Group Selection: the "evolutionary battleground" is the space of all separate populations (groups) of organisms. The "winners" and "losers" in this evolution match are the populations (groups) themselves.

Contrast to Individual Selection within a population

The first Group-Selection Argument was formed by Darwin in his *On the Origin of Species* to explain features of sterile worker bees:

> *How could features of "good" sterile workers be acted upon by natural selection if they don't leave any offspring?*

Darwin: "By the survival of communities with females which produced most neuters having the advantageous modification, all the neuters come to be thus characterized."

This was a widely accepted idea, adopted for many explanations in evolutionary ecology for many years...until the early 1960's.

Wilkinson's data from vampire bats suggests reciprocal altruism in giving food (blood meals) reciprocally between individuals in a group.

There are few other examples, though

Critical Reassessment of Group Selection

Wynne-Edwards (early 1960's) stimulated a great deal of criticism of group selection

Oddly, Wynne-Edwards was a great proponent of GS
•Natural Regulation of Population size
•"Saw its (GS's) magnificent consequences so universally that evolutionary ecologists were forced to consider the argument more carefully." --Ricklefs

Huge Backlash!!

Criticisms of Group Selection:
1. Most organisms don't organize themselves into groups the way that they would have to for Group Selection to be effective
2. The time scale for group selection is slow---much slower than for individual selection within populations. Group selection should be overwhelmed by selfish behavior.

Hamilton (1964) and Maynard Smith (1964) proposed kin-selection which has essentially replaced group selection thinking.

And now:

The Theory of Kin Selection

Kin Selection: A process whereby altruism may be selected for in a population because it increases the *inclusive fitness* of the individual doing the altruistic behavior

Belding's Ground Squirrel

Before getting to kin-selection, however, we investigate

Reciprocal Altruism
(Trivers)

Reciprocity: a mechanism by which altruistic behavior might be maintained by increasing the *direct fitness* of the individual behaving altruistically

Direct Fitness is increased because the recipient of the altruistic behavior "returns the favor later"
"You rub my back and I'll rub yours"

Requires that the cost for the giver is less than the benefit for the recipient

Problem: Single or Few Interactions: Game theory shows cheaters can easily invade a population of reciprocators:
"You rub my back and I'll say I'll rub yours, but I'll really leave town before I do"

Possible Solution: Repeated interaction makes it harder to cheat successfully.

Does reciprocity occur?
Very few examples
Wilkinson (1984) and vampire bats

Imagine you are a contestant on the

Kin Selection Game Show

The Rules:
•You are the contestant
•You are a diploid organism
•two copies of the "locus in question"
•You score points by "putting individuals into a population"
•You get one point for each gene in those individuals that is a copy of one of your genes at the "locus in question"
•Your plays are choices between 2 alternatives

Example: Choose between
(a) putting 50 offspring (from matings with individuals unrelated to you) into the population
(b) putting 100 individuals that aren't related to you into the population

A tougher one: Choose between
(a) 10 offspring (from matings with individuals unrelated to you)
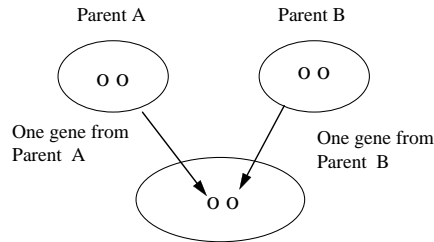(b) 10 full-brothers (i.e. ten more offspring of both of your parents)

Surprise: In the second case, the expected gain in points is the same for choice (a) and (b).

Why? To understand why we need a few more concepts.

Identity by Descent: two genes are said to be identical by descent if they are copies of the same ancestral gene

Coefficient of relatedness (r): the coefficient of relatedness between two individuals is the expected proportion of their genes which are identical by descent

Example: r between a parent and an offspring

Parent A   Parent B

One gene from Parent A   One gene from Parent B

Half of the offsprings genes are from either parent. Hence r = 1/2.

How about r between two full siblings

Ma   Pa

4 Possible Genotypes in the Siblings Probability 1/4 for each.

Now Consider the Expected Proportion of IBD between say

and a randomly chosen sibling.

$= (.25)(1) + (.25)(.5) + (.25)(.5) + .25(0) = .5$

So, r between two full siblings is 0.5

Back to the Game Show: Choose between
  (a) 10 offspring (from matings with individuals unrelated to you)
  (b) 10 full-brothers (i.e. ten more offspring of both of your parents)

Either choice a or b will give you 5 points.

How about:
  (a) 4 full brothers
  (b) 4 uncles and 16 first cousins?

Coefficients of Relatedness

Relationship of Self to:	Coeff. of Rel. (r)
Self	1.0
Offspring or Parent	0.5
Full Sibling	0.5
Half Sibling	0.25
Uncle/Aunt or Nephew/Niece	0.25
Grandparent or Grandchild	0.25
First Cousin	0.125

Back to Biology: The points in the gameshow are measured in the units of inclusive fitness of your genes
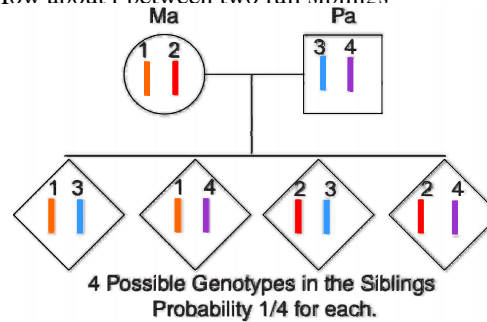
Inclusive Fitness = Direct Fitness + Indirect Fitness
 = (Survival of offspring) x (r for parent-offspring) +
    (Survival of non-descendant kin) x (the proper r for each type of relationship)

Example calculation of inclusive fitness: Imagine you have 29 offspring. Through your diligent parental care 15 survive to reproduce. 5 survive even though you neglected them. You give your life in an heroic deed that saves the lives of 8 cousins, 4 nephews and 2 half-sibs who would have died if you hadn't saved them.

Your inclusive fitness is:
$(5 + 15)(.5) + 8(.125) + 4(.25) + 2(.25) = 10 + 2.5 = 12.5$

Altruism and Inclusive Fitness: altruistic behaviors have costs which are reductions in direct fitness but if they benfit relatives, the indirect fitness benefits to the altruist may offset the direct fitness costs.

Hamilton's Rule

Hamilton's Rule: an altruistic behavior may be adaptive if it results in positive inclusive fitness.

Numerical Example: You save the lives of 5 nephews, but in doing so you lose the opportunity to produce two sons.

Inclusive fitness = $-2(.5) + 5(.25) = .25$
Conclusion via Hamilton's rule: this could be adaptive

Reyer (1984) Pied Kingfisher Study

See the reading from Alcock for details.

Alarm Calls in Ground Squirrels
Sherman 1977

Natural History of Belding's Ground Squirrels
Female sedentism
- Females remain near their natal nest throughout life
- Males disperse after birth.
- Brothers do not congregate elsewhere
- **Females are thus surrounded by kin!**

Foraging and daily behavior habits

Natural predators

Alarm calling

Hypotheses for Evolution of Alarm Calls

1. Predator attention diversion
   - Pandemonium! or ventriloquism

2. Predator discouragement
   - The "I see you!" hypothesis

3. Alerting relatives
   - This is the **kin-selection** hypothesis

4. The Group-selection hypothesis

5. Reduction of probability of later attack
   - Depriving predators of experience

6. The reciprocal altruism hypothesis

The method of competing, alternative, hypotheses...

Observations Made

Audaciously large observation programme since 1969
- Tagging and Kinship studies---pedigrees available

Summers of 1974–1976: 3082 hours of observation

9 ground squirrels observed to be killed in that time
6 adults and 3 juveniles

102 alarm calls heard when a predator was also observed
- Females give alarm calls more often than "expected"
  - Especially females with kin nearby
- Males give alarm calls less often than "expected"
  - "Expected" means "expected at random"

Alarm callers were stalked by predators significantly more often than non-alarm callers

3 of the 6 adults killed were alarm callers (NS)

Confronting the Hypotheses

1 and **2** not supported:
- No pandemonium and predators stalk alarm callers
- Alarm caller not always the closest one to predator

Would not be possible to reject **3** (kin-selection) in favor of **4** (group selection), also
- Anecdotally, no between group differences

5 does not hold water
- Predators don't preferentially return to particular areas
- Older females call more often

6 Reciprocity not supported
- Females don't call as often when they have no living kin. If reciprocity existed beyond kin relationships, this should not be the case
- Presence of non-callers does not deter callers

Left with Hypothesis **3** (kin-selection) being far more intact than the others.

The Reality of Diversity

Kin-selection is not necessarily *the* explanation for all instances of alarm-calling.

Generalizing from one species or study to another is a risky business in ecology

Sentinel Behavior:
Somewhat different than ground squirrel alarm-calling
- Sentinels are self-appointed "lookouts" who take the job of watching out for "the group" while the others forage.

- The "rota" may seem like a highly organized, complex, social behavior.

- An extra tradeoff: sentinels can't forage simultaneously
- But, sentinels may be better at avoiding predators

Bednekoff's Model

The question: Can a simple model (i.e. direct fitness considerations alone) account for the rota.

A discrete time, stochastic model with many individuals

Consider a single individual
- Choice made at *each time step*:
  - Forage or
  - Be a sentinel

- If you forage, you have a certain probability of finding a certain amount of food in that time step
- If you are a sentinel, you have zero probability of finding food in that time step

- However, the probability of being killed by a predator is *lower* if you are a sentinel or a forager **AND** those probabilities depend on how many others in the group are already sentinels

- An individual may die by
  - Starvation
  - Predation

Optimization

Assume: evolution has given animals optimal decision rules
- i.e. Given hunger level and number of other sentinels in the current time step, an animal may choose to forage with probability p or become a sentinel with probability 1-p.
  - There is some p that maximizes the individual's probability of long-term survival

Finding that p, (mathematically)

Simulating groups of animls behaving optimally
- This yields very organized-looking rota behavior!

THE VALUE OF MODELLING:
- Demonstrated that direct fitness arguments could explain sentinel behavior
- Generated testable predictions:
  - Sentinels have reduced predation risk
  - Better-fed individuals are more likely to become sentinels

Clutton-Brock et al. 1999

Checking Bednekoff's predictions in meerkats
- Group Structure of Meerkats
  - One dominant female (75% of litters are hers)
  - One dominant male (fathers most of the litters)
  - Note that the close kinship *is* there
- Foraging: can't watch out for predators while digging
- Sentinels watch for predators and give alarm calls
  - Seldom will an individual take two successive guarding

bouts, but there is not a clearly defined rotation pattern

Nonetheless, because there is some alternation in sentinel behavior; it appears "organized"

Clutton-Brock et al. cont'd

Key Observations:
- No sentinels were killed by predators in 2000 hours of observation (did they see *any* meerkats get killed?)
  - (0.68/year mortality rate amongst adults)
  - More adults killed in small groups than large groups
- Recent babysitters spend less time as sentinels
  - (They ate less the day before)
- Meerkats were more likely to go on sentinel duty if there was currently no sentinel on duty

Manipulation of hunger status:
- Fed some individuals 25g of hard-boiled egg
  - They subsequently spent more time on sentinel duty

All this may be explained by Bednekoff's model

Not necessary to invoke kin-selection.

An application of Occam's Razor:
"one should not increase, beyond what is necessary, the number of entities required to explain anything"

Life History Traits

Brief review of strategies we've seen so far:
- Foraging strategies
- Territorial behaviors
- Signalling behaviors
- Reproductive behaviors
- Mating systems

**We investigated these different behaviors and traits in terms of how they affect fitness of the individual**

Another class of traits have a clear and direct bearing on fitness. These are the life-history traits. The major life history traits are:
- Age at first reproduction
- Number and size of offspring
- Reproductive lifespan and ageing

All of these affect the so-called "Life Table" of an organism

Relation to the "Life Table"

Imagine following a cohort of individuals in a population
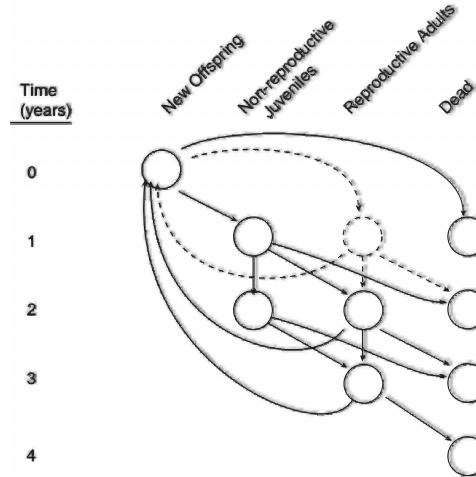
Note, there are more formal representations using matrix algebra

Life History Variation in Pacific Salmon

Fecundity and Age at Maturation, etc.
- Sockeye
- Pink
- Chum
- Chinook
- Coho
- Steelhead

Intraspecific Variation in Fecundity in Chum Salmon
Chum salmon from the Amur River Siberia:

Summer run: 39.8 eggs/cm fork length

Autumn run: 53.5 eggs/cm fork length

Goals of life history theory

To Answer, "Why all this variation?"

and

Ultimately wish to construct models which predict what sorts of traits will be favored in what sorts of environments.

Without constraints, the answer is easy, for highest fitness one would. . . .

The CORNERSTONE (as in other optimality models):
Assumption of limited time and resources and the need to *allocate* these to particular traits

Trade-offs

Evidence for Trade-offs

Four main ways people have tried to demonstrate that these trade-off exist:

1. Phenotypic Correlations within or among populations
   - Example: egg size and egg number between salmon populations of the same species
   - Doesn't really demonstrate direct trade-offs

2. Experimental Manipulations
   - Trade-offs between clutch size and offspring survival.
   - Inspired greatly by the "Lack Clutch" hypothesis of the 1940's
       - Hypothesis regarding latitudinal clutch-size trends
   - Hogsted (1980) Magpie clutch augmentation/ reduction experiments.

3. Correlation of traits between relatives
   - Quantitative genetics approach
   - Maybe useful for demonstrating short-term constraints and trade-offs
   - Long term selection may not be constrained by genetic correlations detected in such studies

4. Correlated responses to selection
   - Artificially select for a trait and see what else changes along the way.
   - Famous experiments by Rose and Charlesworth
       - Squashed fruit flies at an unnaturally young age
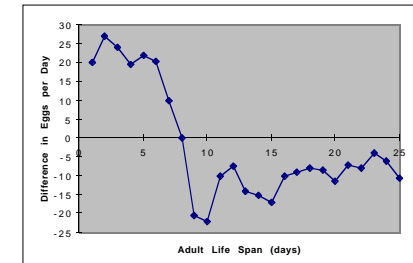
Selection for both shorter life and higher fecundity

Simple Mathematical Models

Perennial vs. Annual Life Histories:

S_0 = Probability of survival in the first year

S_P = Probability of survival in later years

B_a = Seed production rate of annual plant

B_p = Seed production rate of perennial

L = rate of increase

$L \text{ (annual)} = (B_a)(S_0)$

$L \text{ (perennial)} = (B_p)(S_0) + S_P$

What values of B and S lead to the annuals increasing faster than the perennials?

Annuals will be favored when S_0 is high relative to S_P

If not, annual seed production must be high to compete with perennials

Another Model

Relationship between reproductive life-span and reproductive investment.

S_o = Probability of surviving the first year (to reproductive age)

B = number of offspring produced in a season

S_p = probability of surviving adult years
Partitioned into:
S_r = factor of survival probability that is affected by your reproductive investment
S = factor of survival probability unaffected by reproductive investment

$L = (S)(S_r) + (S_o)(B)$

Now, imagine changing B (and hence S_r). Our common trade-off assumption would say that S_r would become smaller as B became larger.

$\Delta L = S(\Delta S_r) + S_o(\Delta B)$

High adult survival favors lower yearly investment in reproduction.

Phenotypic Plasticity

Noted in many other types of traits as well, but has received much attention in the study of life history traits.
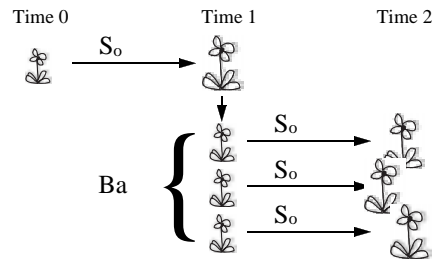
Back to our first day:

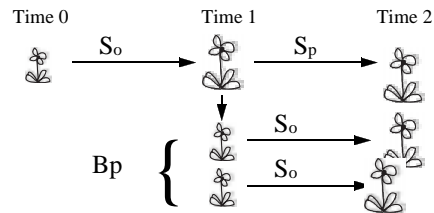$$\text{Genotype} \xrightarrow{\text{Environment}} \text{Phenotype}$$

Reaction Norms.

Selection for phenotypic plasticity itself

Reaction norms

Genetically determined---may be an item under selective pressure.

Annual vs. Perennial

Annual Life History

Time 0   Time 1   Time 2

S_o

Ba { S_o S_o S_o

Perennial Life History

Time 0   Time 1   Time 2

S_o S_p

Bp { S_o S_o

Broad Patterns of Plant Life Histories

Desert floras dominated by annual plants---> Few adults can survive the dry seasons, but seelings are seldom space limited and may grow well (low S_p/S_o ratio)
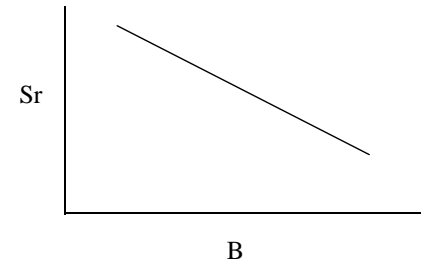
Tropical rain forest zones: seedling survival is low due to competition for space and light from other plants. Mostly peren-nials. (High S_p/S_o ratio.)

Reproductive Life-span vs reproductive investment

Time 0   Time 1   Time 2   Time 3   Time 4

S_o $S(Sr)$ $S(Sr)$ $S(Sr)$

B
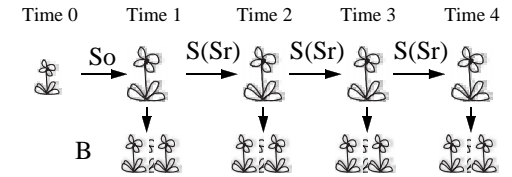
Assume a negative relationship between Sr and B

Sr

B

Semelparity vs. Iteroparity

Salmon survival schedule:
- **egg to fry**: abysmal!
- **fry to smolt**: lousy!
- **smolt to adult**: poor
- **pre-reproductive adult**: much better

So, why not have a more "perennial life history?"
- Hypothesis: massive expenditure on reproduction.

Agave:
Semelparous reproduction
Hypothesis: environmental cond-
itions seldom suitable
for seedling survival.

Many broad predictions, but with greater detail things become much more complicated...

Semelparity versus Iteroparity in Scarlet gilia
Paige and Whitman 1987

Ipomopsis aggregata in Arizona typically exhibits a semel-parous pattern, but is facultatively iteroparous, depending on the environmental conditions!
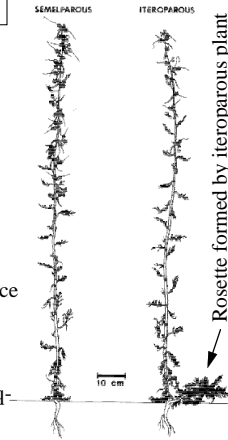
genotype --------- environment ---------> phenotype
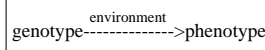
Three Manipulations:
1. Pollinator exclosures
2. Flower chopping
3. Herbivory simulation

Results:
1 and 2 increased incidence of rosette production 5 to 7-fold

3 did not increase the freq-uency of iteroparity.

SEMELPAROUS   ITEROPAROUS

Rosette formed by iteroparous plant

10 cm

Scarlet gilia

Phenotypic Plasticity
Some terms and defns

Canalization: one genotype produces a single phenotype, regardless of environment

Phenotypic plasticity: a general term covering all types of environmentally induced phenotypic variation

Polyphenism: a type of phenotypic plasticity in which the change is between two or more *discrete* phenotypes:
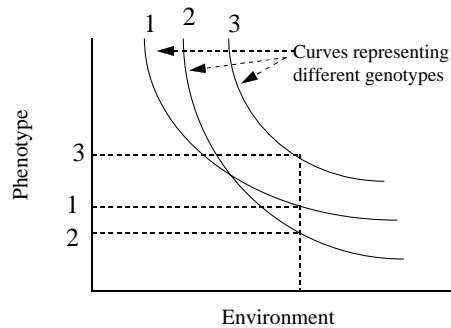- environmental sex determination
- castes of social insects
- locust behavior (isolated/sedentary vs. gregarious)
- semelaparity or iteroparity in *Gilia*

Reaction norm: the continuous relationship between a trait changing due to phenotypic plasticity, and some feature of the environment.
    "A mirror that reflects environmental effects into phenotypes"

With all this phenotypic plasticity, how can natural selection "grab onto" different genotypes?

Predator Induced Phenotypic Plasticity

Daphnia grow thicker and spinier helmets in the presence of compounds associated with their predators

Helmet

0.5 mm
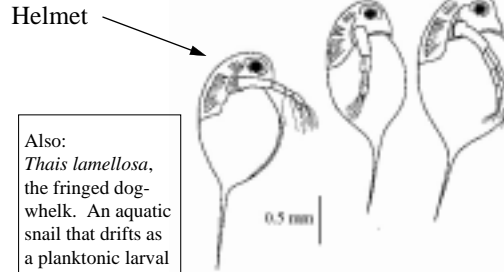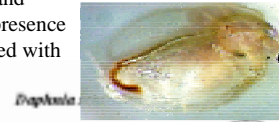
Also:
Thais lamellosa, the fringed dog-whelk. An aquatic snail that drifts as a planktonic larval veliger. If it "lands" in an area with *Cancer productus* (a crab predator) it develops a thicker shell.

Chaoborus, a *Daphnia* predator

Prey-induced plasticity

Cichlid fishes fed different diets developed different jaw morphologies. These changes were reversible.
(Meyer 1987)

Grasshopper mandible morphology changes in response to diet.
- Soft leaves versus hard leaves
- Having the right man-dibles makes a difference in energy accumulation.
(Thompson 1988)

Reaction Norms

1 2 3

Curves representing different genotypes

Phenotype

3
1
2

Environment

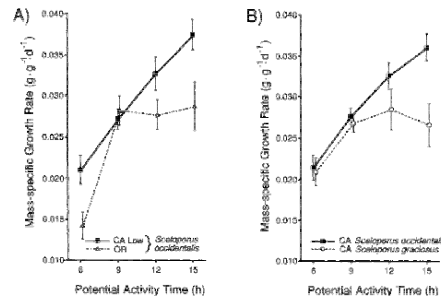**G x E interaction**: when reaction norms for different genotypes cross
- Expected to be pervasive (Stearns 1989)
- Are commonly observed
    - Due to trade-offs?
The reaction norm itself is under genetic control!
This is how natural selection can "grab" the genotype, even in the presence of phenotypic plasticity

Comparative Study of Reaction Norms in Lizards

2 lizard species   **Sinervo & Adolph 1994**
    Sceloporus occidentalis
    Sceloporus graciosus
- Taken from three different elevations (low, med, high) in CA and one population from OR.
- High elevation/latitude populations have fewer active hours
    - Activity = body temp high enough for growth to occur
- Hatchlings raised in 4 expmtal condns: 6, 9, 12, and 15 hours of potential activity time. (Incandescent light bulb)
- Results: 1) Short-day specialists (high altitude/latitude lizards) growth rate did not increase with >9 hr of potential activity
    2) Lower elevation lizards could capitalize on longer potential activity days in the laboratory
    3) Among family variation in reaction norms
    4) Family x treatment interaction-->G x E interaction

A)   B)

Mass-specific Growth Rate (g·g⁻¹·d⁻¹)

CA Low *Sceloporus occidentalis*
OR

CA *Sceloporus occidentalis*
CA *Sceloporus graciosus*

Potential Activity Time (h)   Potential Activity Time (h)

Evolutionary Theories of Aging and Senescence

Some observations:
Raised under **good** conditions with **no predation risk**:
- Birds typically live longer than mammals
- Bats typically live longer than terrestrial rodents
- Flightless birds live shorter than flying birds
- Thick-shelled bivalves live longer than other molluscs
- Tortoises live longer than other reptiles

Interesting Features:
    - Death occurs, eventually with certainty
    - Ideal-condition lifetimes vary greatly across taxa

An Early Explanation for "Programmed Death" (by Wallace)
    "...when one or more individuals have provided a sufficient number of successors they themsleves, as consumers of nourishment in a constantly increasing degree, are an injury to those successors. Natural selection therefore weeds them out, and in many cases favours such reaces as die almost immediately after they have left successors" (quoted in Rose 1991).

Senescence

- If you survive to a ripe old age:
  - Shouldn't your extra experience increase your probability of survival into the future?
- Maybe so, but it doesn't work that way.
- <u>Senescence</u> = greater susceptibility to injuries, disease, and death as one grows older
  - Neural degeneration
  - Reduction in kidney filtration
  - Decreased respiratory capacity, etc

Environmental (proximate) causes
  - Sure, but senescence is still inevitable, it seems

An evolutionary/genetic explanation: Medawar (1946)
  "What is important from our point of view is that the contribution which each age-class makes to the ancestry of the future decreases with age"

The key is reduced selection on older age classes. This could lead to senescence by two mechanisms:
  1) antagonistic pleiotropy
  2) accumulation of late-acting mutations

Antagonistic Pleiotropy

Basic Premise: "Senescence later in life is the price of youthful vigor."

pleiotropy = when one gene affects two or more traits

Williams (1957) "Selection of a gene that confers an advantage at one age and a disadvantage at another will depend not only on the magnitudes of the effects themselves, but also on the times of the effecgts. An advantage during the period of maximum reproductive probability would increase the total reproductive probability more than a proportionately similar disadvantage later on would decrease it."

Experimental Evidence:
  - Quantitative genetic correlations between early fecundity and longevity (sib analysis, line crosses)
  - Mendelian inherited, pleiotropically acting mutations:
    - *C. elegans* age-1 mutant (Friedman and Johnson 1988)
    - *D. subobscura* grandchildless mutation--- female offspring have much longer lifespan, but no ovaries!

Mutation Accumulation

Basic Premise: new, deleterious mutations build up in the genome. Such early-acting mutations are weeded out by selection, but late-acting ones basically fill a "genomic garbage can" that never really gets emptied.

Experimental Evidence: Difficult to come by. Some *Drosophila* selection studies show accumulation of deleterious alleles without a cocnomitant change in early life reproductive fitness.

Overall, it is very difficult to distinguish between antagonistic pleiotropy and accumulation of late-acting, deleterious mutations.

Much research directed in the area of evolution of senescence, however, due in part to the medical interest in the subject.

Phylogenetic relations between adult mortality rate and life-span under "ideal conditions"

A 5-Minute Review

Evolutionary Ecology covers themes from many different disciplines (which overlap themselves). Notably:
  <u>Evolution</u>:
  - Quantitative genetics, natural selection, sexual selection, phenotypic plasticity, kin-selection, life-history theory
  <u>Behavioral Ecology</u>:
  - Foraging theory, signalling, and reproductive behavior
  <u>Sociobiology</u>
  - Kin-selection, mating systems, territoriality

We've encountered four main methods for interpreting variation in strategies in an evolutionary context:
  1. Optimality modeling (optimization ideas are ubiquitious in the field)
    - Most notable in Optimal Foraging Theory, but elements of it appear everywhere
  2. Game theoretic perspective (ESS's)
  3. Comparative method
  4. Population/Quantitative genetic perspectives

Regarding the Exam

- Covers everything from the first day of class.
- It will be closed book, closed notes, closed handouts, etc.
- Readings versus lectures:
  - You are expected to have done the readings, but won't be asked questions of exasperating detail from them.
The readings have been of two types:
1) "textbook" type readings---sections of texts or edited volumes that describe general themes or methodologies. Typically in my lectures I have covered the aspects of those readings that I find most important and relevant. The lectures are a good indication of which parts of those readings to focus on. These readings serve to supplement lectures. Also, if it was a reading that you discussed in section, you should be quite comfortable with its general content.

2) research articles---we've read quite a few of these. It's good to read these to get a sense of how research in evolutionary ecology is done and how its results are transmitted. Some of the articles were not discussed in lecture. Nonetheless for each article you should be able to tell me:

(a) which of the general topics we have covered it is relevant to
(b) the hypotheses that the authors were trying to test
(c) the general methods---for example whether it was an observational study or a manipulation, what animals were studied, and what variables were observed
(d) the general results; especially how the results relate to the general theory that the study is relevant to

You should pay particular attention to those articles about which I talked at length in lecture.

Regarding the lecture notes:
  - A good resource for studying
  - Note: some of the titles and the bottoms of the slides might get chopped off by some printers. You may want to add those back in pen (everything appears correctly on screen in Acrobat Reader)
  - The lectures often contain material that won't be found in the required readings

  - One study strategy: be able to tell the story behind each of the pictures in the lecture notes. The examples make the theory come alive a bit more. Have fun while studying---tell your friends about the natural history items you've learned; tell your significant other about the American burying beetle, etc.