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)

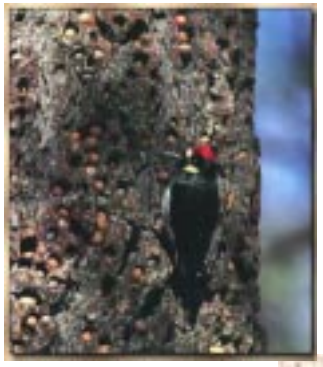
Human bias in thinking about social systems:

- •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 Self	Effect On Neighbor: +	Effect On Neighbor: –
+	Mutually Beneficial	Selfish
–	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)

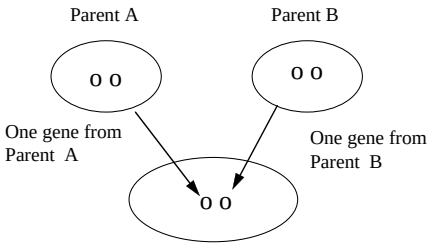
Surprise: In the second case, the expected gain in points is the same for choice (a) and (b).

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

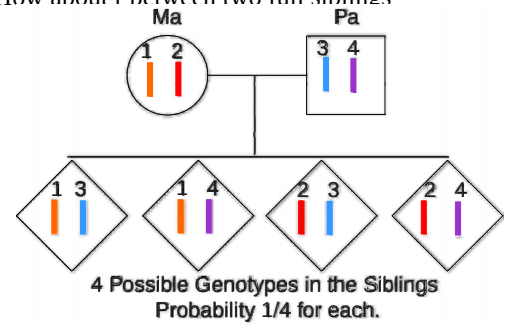
Coefficient of relatedness (r): the coefficient of relatedness between two individuals is the expected proportion of their genes which are identical by descent

Example: r between a parent and an offspring



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

How about r between two full siblings



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.