

LECTURE GOALS:

- Understand that Natural Selection acts on the phenotype of the individual.
- Understand Inclusive Fitness and Kin Selection as a concept.
- Learn to calculate the coefficient of relatedness.
- Appreciate how game theory can be applied in Animal Behavior.

LECTURE OUTLINE:

1. Cooperation, and particularly Altruism presented a puzzle to Darwin
2. *Cooperation* is the process of individual organisms acting together to result in common/mutual benefit though it can also be shown to be “selfish”.
3. *Altruism* is the process of an individual organism behaving in a manner that lower’s its own reproductive success while increasing the reproductive success of the recipient.
4. Some claim that Wynne-Edwards did us a favor by formalizing the theory of “group selection” because it spurred evolutionary biologists George C Williams and William D. Hamilton to refute it theoretically and empirically.
5. *Kin Selection* is one “selfish” **model** based on a “gene-centric” view to explain altruism.
6. *Indirect fitness* is the increased reproduce success an individual gains through the fitness of those with which it shares alleles (i.e. has common genetic material).
7. *Inclusive fitness* is the sum of direct and indirect fitness.
8. Natural selection will tend to increase a genetically based trait that is costly to the individual if that trait influences behavior that provides increased reproductive success to a sufficient number of individuals who share a sufficient amount of genetic material (on average).
9. There are a few simple rules to calculate relatedness:
 - a. Step 1: Identify all common ancestors for the two relatives.
 - b. Step 2: Identify all paths that connect these two relatives.
 - i. -The path must go back against the arrows from one relative to the common ancestor, and then follow the arrows forward to the other relative.
 - ii. - No individual must occur in a single path more than once.
 - c. Determine the proportion of alleles shared in that directional link (parent/offspring or offspring/parent) at each step along the path. (for diploid species this is always 0.5)
 - d. Multiply of these proportions along the path. (for diploid $\frac{1}{2}^n$)
 - e. Add up all of the values calculated for each path you identified.
10. *Dictyostelium*, a single celled slime mold, provides a model in which to study altruism.
11. The Prisoner’s Dilemma is the non-zero sum game used to **model** the evolution of cooperation.
 - a. An Evolutionarily Stable Strategy is one that once established cannot be invaded. Surprisingly, mathematical models showed that under a PD pay off matrix the ESS’s that prevail are “nice”, “retaliatory”, and “forgiving”.
 - b. One can calculate the critical frequency at which natural selection will favor one ESS over another.
12. Allo-grooming can be modeled as an iterative Prisoner’s
13. Inspection behavior can be modeled as an iterative Prisoner’s
14. An example in wrasse suggests that punishment is a used a means of enforcing apparent altruistic behavior.
15. Platt (borrowing from Chamberlain 1897) suggests that the use of multiple alternate hypotheses will advance science more rapidly, a method he terms “strong inference”.
 - a. Devise Alternative hypotheses
 - b. Devise crucial experiment(s) that will support one and exclude another of these hypotheses.
 - c. Carry out the experiment (and get clean results)
 - d. Recycle these steps.
16. Example of Strong Inference in Dom/Sub manakin duet dancing.

HELPFUL FIGURES & NOTES:

(All PowerPoint files will be available on the course website after lecture. The subset of figures and notes here are meant to assist your note taking or studying.)

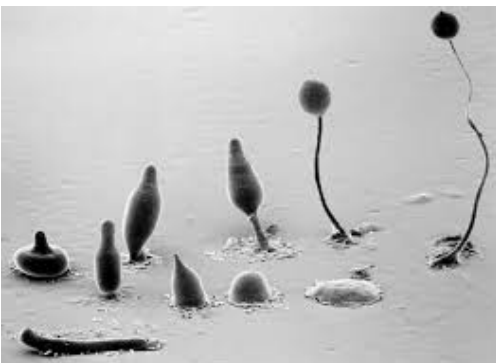
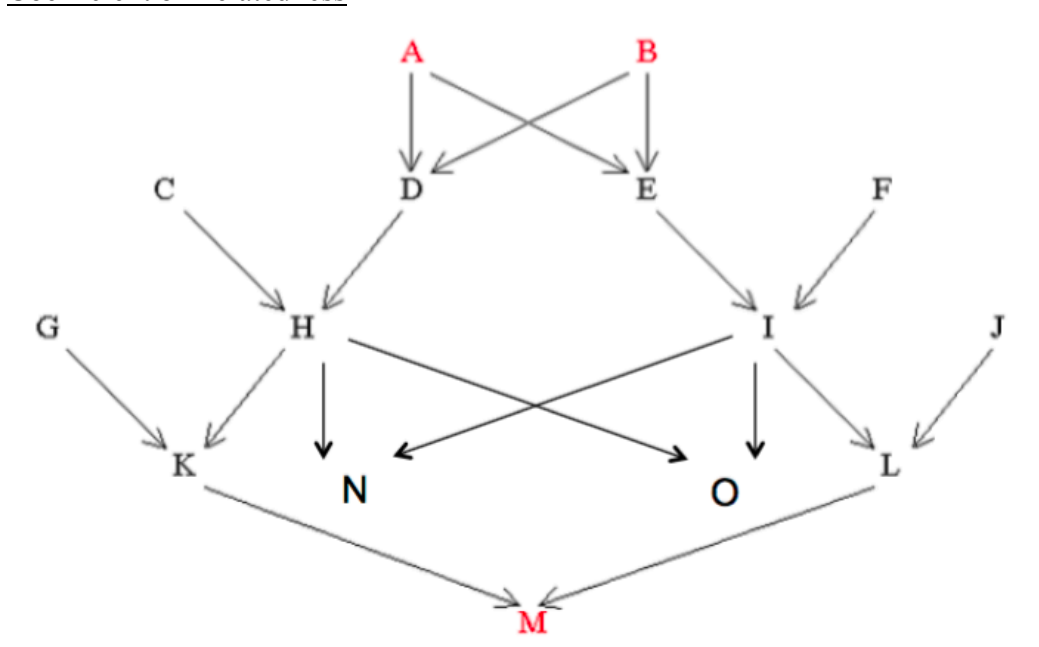
Inclusive Fitness

$$\Sigma r_b B > C$$

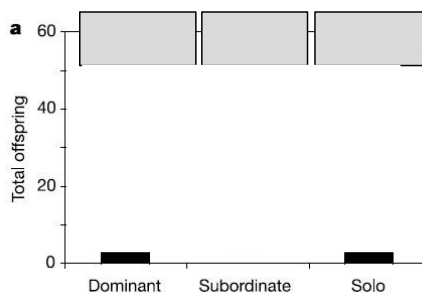
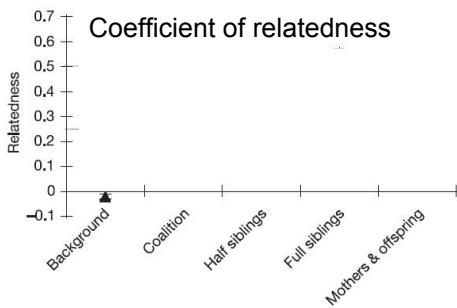
Coefficient of Relatedness

Social Interactions

		Recipient	
		Benefit	Cost
Donor	Benefit		
	Cost		



Think about a mechanism that could explain this apparent Altruistic Behavior



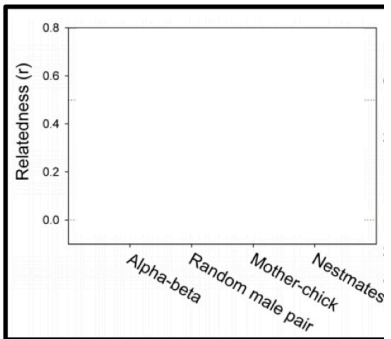
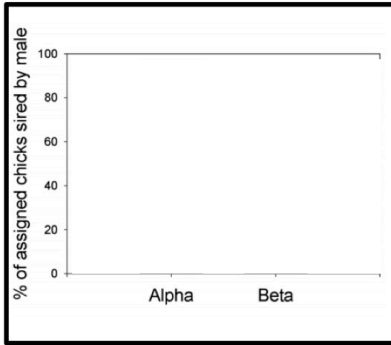
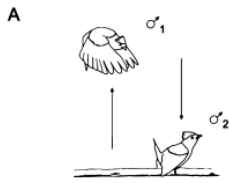
Prisoner's Dilemma

Recipient

Cooperate Defect

		Recipient	
		Cooperate	Defect
Donor	Cooperate	R	S
	Defect	T	P

$T > R > P > S$
 $(T+S)/2 < R$



	Year 2 alpha	Year 2 non-alpha
Year 1 beta		
Year 1 non-dancing male		

VOCABULARY:

(Practice writing interesting, informative sentences that include, and capture the meaning of, 4-5 words from this list. To simply memorize a definition, is not sufficient.)

- | | | |
|------------------|-------------------|-----------------|
| Darwinian puzzle | Indirect fitness | Common ancestor |
| Gene | Inclusive fitness | Haplodiploidy |
| Allele | Group Selection | Mutualism |
| LRF | Kin selection | Altruism |
| Cooperation | Green Beard gene | Dominance |
| Altruism | Coefficient of | Delayed benefit |
| Direct fitness | Relatedness | |

PRACTICE EXAM QUESTIONS:

1. Is Natural Selection necessary for Evolution to happen? (explain)
2. Explain the difference between Life Time Reproductive Fitness and simply the number of offspring and individual has.
3. Based on Hamilton’s rule, we might expect to see behaviors that appear altruistic in species with what type of social structure? And who would we predict would most often be the recipients of the apparently altruistic behavior?
4. In a payoff matrix like that of the Prisoner’s Dilemma, what behavior might you predict if $(T+S)/2 > R$. (rather than less than)
5. Calculate the coefficient of relatedness for two female cousins (daughters of full sisters) in a haplodiploid system.
6. How have “models” helped biologists to understand the evolution of cooperation and altruism?
7. Explain how dominance hierarchies enhance LRF for the individuals involved.
8. Read Ancel et al 2015 in Animal Behavior volume 110 pages 91-98 and re-evaluate Byer’s description of penguin huddling in Chapter 9 of “Animal Behavior: a Beginner’s Guide”. (for future exercises, pay attention to how they record behavior)

Diploid ♀

Haploid ♂

1 vs 0.5

Shared gene proportions in haplo-diploid sex-determination system relationships

Sex	Daughter	Son	Mother	Father	Full Sister	Full Brother
Female	1/2	1/2	1/2	1/2	3/4	1/4
Male	1	N/A	1	N/A	1/2	1/2

Bonus Question: It is thought that haplodiploidy evolved among parasitic species that lay a clutch of eggs in a host because this system allows the female to control the sex-ratio of her offspring by either fertilizing eggs or laying haploid eggs. When would it benefit the female to lay an equal sex ratio? When would it benefit the female to lay a female biased clutch of eggs?

READING FOR TODAY:

Readings in Black are available on the course website.

Those in grey are used in the lecture and you can access them through the Reed library if you are keen to know more detail.

Ryan & Wilczynski pg. 17-25 & 197-212

Beginner's Guide Chapter 9 (I've posted an older version on the course website in the textbook section)

Examples for lecture if you want further reading:

Duval EH (2007) Cooperative display and lekking behavior of the lance-tailed manakin (*Chiroxiphia lanceolata*). *The Auk* 124:1168-1185.

Krakaur (2005) Kin selection and cooperative courtship in wild turkeys. *Nature* 434:69-72.

Queller et al (2003) Single-gene green beard effects in the social amoeba *Dictyostelium discoideum*. *Science* 299:105-106. (understand what the gene is and how this "simple" system can tell us something about animal behavior)

~~Sinervo et al (2006) Self-recognition, color signals, and cycles of greenbeard mutualism and altruism. *PNAS* 103:7372-7377. I'm not using this now but it's a good story~~

Platt (1964) Strong Inference. *Science* 146:347-353.

READING FOR NEXT CLASS:

Martin & Bateson Chapter 1 & 2

Wynne, C.D.L. (2007) What are Animals? Why anthropomorphism is still not a scientific approach to behavior. *Comp Cognition and Behavior Reviews* 2:125-135.

Franco, N.H. (2013) Animal Experiments in Biomedical Research: A historical perspective *Animals* 3(1):238-273.