Social Behavior 2

• Costs & Benefits of Social Life
• Evolution of Helpful Behavior
• Inclusive Fitness
• Eusocial Behavior
Kin selection and inclusive fitness

• Behavior that benefits 10 relatives may be worth more or less, depending on how closely related you are to those relatives.

• Coefficients of relatedness ($r$) can be calculated for relatives

• The coefficient is the average genetic similarity between two individuals. For instance, since a parent contributes half of its own genes (alleles) to its own young, the parent-offspring $r$ is 0.5, meaning that they share 50% of their genes.
• When calculating the fitness payoff of an altruistic behavior, we multiply each surviving relative by $r$.

• This gives a measure of *inclusive fitness*, the number of genes that an individual leaves through both direct and indirect reproductive effort.

• Coefficients of relatedness ($r$) allow a cost-benefit analysis of helping. First developed by William Hamilton.

### Table 3  Coefficients of relatedness ($r$) between relatives

<table>
<thead>
<tr>
<th>Relationship</th>
<th>$r$</th>
<th>Relationship</th>
<th>$r$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full siblings</td>
<td>0.5</td>
<td>Parent–offspring</td>
<td>0.5</td>
</tr>
<tr>
<td>Half-siblings</td>
<td>0.25</td>
<td>Uncle/aunt–niece/nephew</td>
<td>0.25</td>
</tr>
<tr>
<td>Cousin–cousin</td>
<td>0.125</td>
<td>Grandparent–grandchild</td>
<td>0.25</td>
</tr>
</tbody>
</table>
Hamilton’s Rule

• For altruistic behavior to be adaptive, the direct cost to the altruist (# of offspring not produced [*c] times the parent-offspring r [r_c]) must be less than its indirect benefit (the added # of relatives that survive due to the altruistic behavior [*b] times the r of the altruist and recipient [r_b]).

  (*c x \( r_c \)) < (*b x \( r_b \))

• The left side reflects the direct costs of the altruistic act
• The right side reflects the indirect benefits
Kin selection in Belding’s ground squirrels

- Belding’s ground squirrels give an alarm call when they spot predators, even though calling squirrels get predated more often.
- Males leave their natal area, whereas females typically stick around.
- Females give alarm calls more than males.
- Are females alarm calling only for their own offspring (direct selection) or also for nondescendant kin (indirect selection)?
- Females with only nondescendant kin around are just as likely to alarm call as females with offspring around, so both direct and indirect forms of kin selection apply.

- Also, see pp. 497-8 (including Table 13.1) about helping behavior in Pied Kingfishers.
Outline

• Costs & Benefits of Social Life
• Evolution of Helpful Behavior
• Inclusive Fitness
• Eusocial Behavior
Eusocial behavior

- **Eusocial** species have a more extreme version of helping behavior – one in which the helpers have very little or no chance to reproduce themselves
  - Obligate altruists vs. facultative altruists

- Have distinct “castes” that are non-reproductive. E.g., an insect colony may have foragers, nurses, soldiers, etc - none of which reproduce. Usually only one queen will produce all of the eggs.

- Many bees, wasps, ants are eusocial

http://www.youtube.com/watch?v=lE-8QuBDkkw
**Haplodiploidy and eusociality in the Hymenoptera**

- In the Hymenopteran insects (bees, wasps, ants), sex determination is unusual
  - fertilized eggs (diploid) become females
  - unfertilized eggs (haploid) become males

- Females are **diploid** (have a set of genes from each parent), but males are **haploid** (only one set of genes from mother).
Unfertilized egg

Haploid son

One of each type of chromosome

Egg + sperm

Diploid daughter

Two of each type of chromosome
Haplodiploidy

• This means that males can only contribute one set of genes (alleles) to their daughters.

• Since almost all insects in a colony are female (regardless of caste) and a large number have the same father, many colony-mates will be full sisters.

• These full sisters have received half of their genes from their haploid father, so the full 50% of the genes received from the father will be identical between sisters.

• Plus, sisters will share an average of half of the genes that they receive from the diploid queen.
(A) Mother–daughter genetic relatedness

Foundress female genotype

Chromosome A
Chromosome B

Female gametes

Male gametes stored within female

Equally probable offspring

(a)  (b)  (c)  (d)

Average $r$ between mother and daughter = 0.5
(B) Sister–sister genetic relatedness

Pick any daughter genotype and compare it with the possible genotypes of her sisters

For example:

(c) Genetic similarity

(a) 75%

(b) 75%

(c) 100%

(d) 50%

Average $r$ between sisters $= 0.75$
• In a eusocial colony, workers (full sisters) have an $r$ of 0.75, but would have an $r$ of only 0.50 with their own offspring.

• So it’s better for workers to produce more workers than to produce their own offspring.

• If you are a worker bee (or ant), it’s better to help the colony than to reproduce yourself!
Eusocial behavior in the absence of haplodiploidy

- Haplodiploidy is not required for eusociality.
- Termites have diploid males and females & are also eusocial.
- Same in a mammal, the naked mole rat.
Eusocial behavior in the naked mole rat

• The naked mole rat has a mating system similar to eusocial insects

• Breeding in this species is restricted to a single large “queen” and several “kings” that live in a centrally located nest chamber

• Females that are not queens do not even ovulate, but act as sterile helpers

• Do the females that are not queens do this helping behavior voluntarily?
Eusocial behavior in the naked mole rat

• Queens bully non-breeding females, and are the most aggressive colony members.

• Behavioral contact with a queen (not just urine pheromones alone) are required for maintaining reproductive suppression in non-breeding females.

• Both non-breeding female and non-breeding male naked mole rats rapidly become reproductively active when socially suppressive cues are removed.
Fig. 2. Urinary progesterone profiles for 3 of the 7 non-breeding females removed from their colonies and paired with a male, or housed singly before pairing with a male. M = observations of mating; B = birth of litter; ▲ = vagina imperforate; △ = vagina perforate.
GnRH in the naked mole rat
Kisspeptin in the naked mole rat
Mutualism

Shared gain of direct fitness
*Example: Prey capture by lion pride*

Reciprocity

Delayed gain of direct fitness
(dependent upon repayment)
*Example: Vampire bat blood exchanges*

Helper

Facultative altruism

Temporary loss of direct fitness
(with potential for indirect fitness gain followed by personal reproduction)
*Example: Florida scrub jay helping at the nest, then gaining parental territory*

Obligate altruism

Permanent loss of direct fitness (with potential for indirect fitness gain)
*Example: Honey bee workers foraging for colony*