Behavioral Evolution and Altruism

BIOL 4415: Evolution
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Assuming that genes affect behavior, how can altruistic behavior evolve?

- Geneticists William Hamilton and Robert Trivers developed the concept of *inclusive fitness*.
  - The fitness that we've talked about is *direct fitness*—ultimately based on individuals' chances of successfully reproducing
  - *Indirect fitness*, however, results from the successful reproduction of relatives.
  - The sum of the two is *inclusive fitness*.

Assuming that genes affect behavior, how can altruistic behavior evolve?

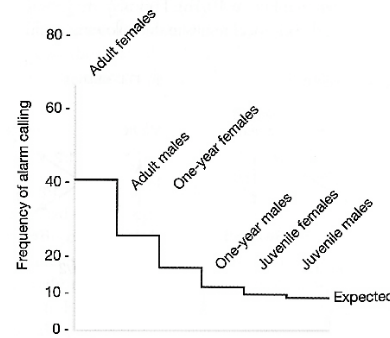
- Imagine a gene that causes individuals that have it to sacrifice some benefits "for the sake of" their relatives
  - Those relatives are probably carrying the same gene. (Why? *Because* they're relatives!)
  - Even if the altruist fails to reproduce, or doesn't reproduce as much as he would otherwise—if he makes it possible for his kin to reproduce, the altruism gene will potentially increase in frequency in the population.
- This is *kin selection*.

W. D. Hamilton proposed *Hamilton's Rule:*

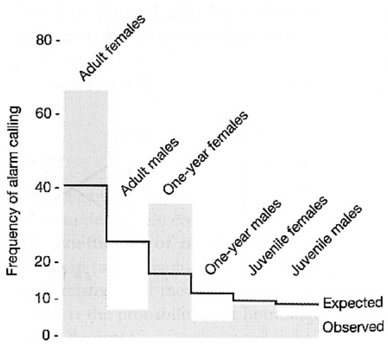
- For altruistic behavior to evolve:
  - Define *coefficient of relatedness* (r) as the probability that any given allele is shared by two relatives. (It's also the fraction of all alleles that two relatives share.)
  - Let B = the benefit to the recipient and c = cost to the donor
  - Then if $rB > c$, altruism is favored
- "I would sacrifice my life for two brothers, or eight first cousins." —(allegedly) J.B.S. Haldane

Case study: Belding's ground squirrel

Belding's ground squirrel (*Spermophilus beldingi*) is native to mountain meadows of the western US and Canada. Ground squirrels feed in groups, with certain individuals standing on "sentry duty" watching for predators. When a predator is sighted, the "sentry" gives an alarm call, and the group runs away. . . but the "sentry" is almost three times more likely to be pursued by the predator, since *she* called attention to herself by giving the alarm. How could this be adaptive?



If every ground squirrel spent an equal amount of time as a "sentry", we would expect to get this graph showing how frequently individuals of different ages and sexes call. Adult females would call the most, because they make up the largest single class of squirrels; adult males would call the next more often, and so on. . .



However, observations of who's actually doing the alarm calling (yellow bars) shows that females are much likelier to give alarm calls than expected —and males are much less likely to give alarm calls.

Why the females? These ground squirrels live in colonies. Grown males usually leave their colony and disperse to other colonies, while females usually stay in the colony where they were born.

Result: Females are related to many members of their colonies; males generally are not.

A female ground squirrel shares many of her genes with other members of her colony. Presumably, she has genes that influence whether she gives alarm calls or not—and those genes are shared with many other members of the colony. Even if a caller puts herself at increased risk of death, such genes may still become more common if the behavior results in saving the lives of the caller's relatives. This is *inclusive fitness*.

Females are more likely to give alarm calls when close relatives are nearby. Ground squirrels apparently use scent and other cues to recognize who their close kin are—which is what these "kissing" squirrels are probably doing. . . .

Case study II: Parasitic wasps

Many wasps are known as *parasitoids*—they lay eggs inside the eggs or larvae of other insects. Parasitoid larvae devour their hosts from the inside and eventually kill them. Here's *Copidosoma floridanum* laying an egg inside an embryo of the moth *Trichoplusia ni*.

A single eggs of *Copidosoma floridanum* can produce over 3000 larvae (this is called *polyembryony*). What's weirder is that each egg produces two types of larvae. *Precocious larvae* (top) never develop into adults, but have huge jaws, and hunt down and kill other parasitoid species' larvae. *Reproductive larvae* (bottom) are the ones that develop into adults.

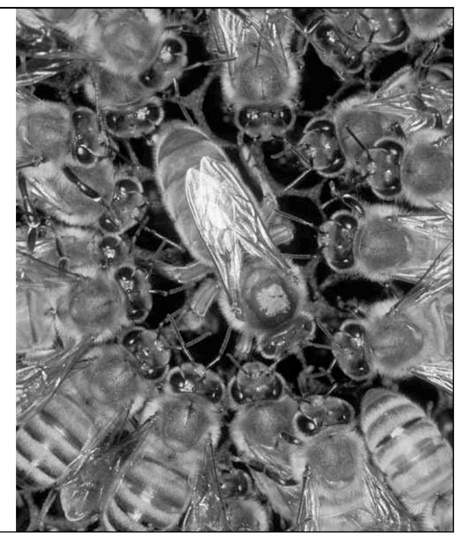
Here's a precocious larva (right) attacking reproductive larvae from an unrelated wasp mother (left). This works because all the larvae from one egg are clones (i.e. their coefficient of relatedness is 1.0)

Eusociality

- *Eusocial* organisms live in colonies in which only one female member (the "queen") is reproductive.
- All others serve the colony and the queen, but do not reproduce. There are separate *castes* of individuals (workers, soldiers, etc.) with overlapping generations.
- Best known examples are insects in the classes Hymenoptera (ants, bees, wasps—11 known species) and Isoptera (termites)
  - Two species of mole rat are the only examples of eusocial mammals.

Hymenopteran insects share a unique method of sex determination: *haplodiploidy*. A diploid, developing from a fertilized egg, is female; a haploid, developing from an unfertilized egg, is male. That's a male honeybee on the left, a female worker on the right.

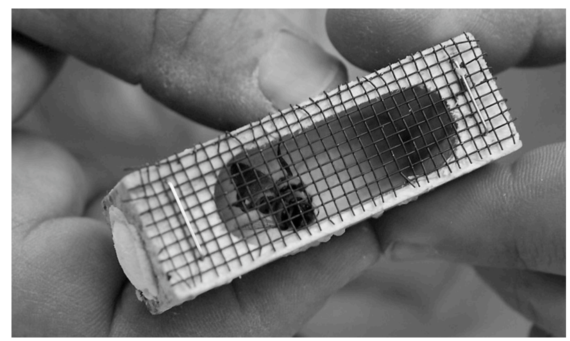
These worker bees surrounding the queen are all full sisters. In fact, they share more genes with each other (0.75) than they would with their own offspring (0.5), since their haploid father put his entire genome into each of his sperm.



When the old queen fails in a colony, the workers will take a larva—one of their sisters—and rear her to be the next queen. The idea is that worker bees pass on more of their genes by raising sisters than they would by reproducing on their own. Thus, genes for eusociality are actually favored.

Problem: These termites aren't haplodiploid. Neither are mole rats, gall aphids, *Synalphaeus* snapping shrimp, or the Australian eucalyptus weevil—yet all of these are eusocial.

Besides**,** the vast majority of hymenopterans are haplodiploid, but not eusocial. *And,* since queen bees mate with several males, worker bees aren't even necessarily all full sisters—two workers with different fathers will share only 0.25 of their genes.



In fact, it is possible for beekeepers to introduce a completely unrelated queen into a hive and get the workers to accept her. And workers sometimes stray into colonies where they aren't related at all to any bee, and they do fine. So this neat explanation for eusociality is probably wrong.

But all known eusocials have a common lifestyle: close quarters, with rich shared resources that require active defense. Kin selection, and possibly *group selection* (selection on the level of colonies, not individuals), may still explain eusociality.