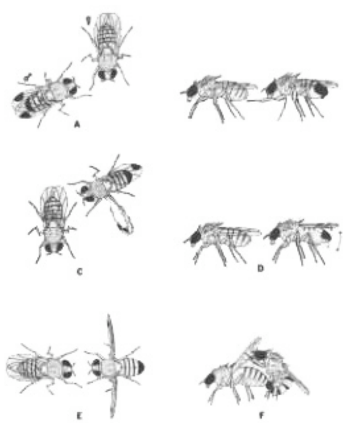
Behavioral Evolution and Altruism

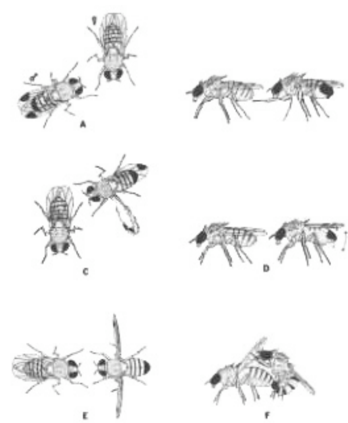
BIOL 4415: Evolution
Dr. Ben Waggoner

Genetics and Behavior

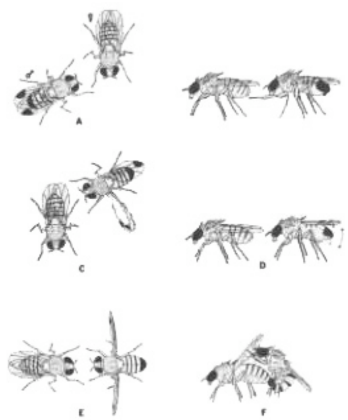
- Do genes control animal behavior patterns? This is an extremely loaded question. . .
- Probably the safest answer is to say that genes influence behavior, and make certain behaviors probable or improbable. . .
- . . . *but* these genes interact with the environment in extremely complex ways—especially in organisms that can learn.
- Genes may not necessarily *control* behavior, but they *affect* it in many ways.



Studies on fruit flies have shown that there are genes that govern circadian rhythms. . . and genes that govern various steps of the flies' rather complex mating rituals (diagrammed at left). Females flies with a mutant allele of a gene that's been named *dissatisfaction* don't respond to males. Males with a mutant allele of the *nerd* gene can't copulate very well. And so on.



In fact, mutant alleles of a gene known as *fruitless*, expressed in fruit fly brain cells, cause males to be unable to recognize females (and court each other!). Female flies with *fruitless* activated show male courting behavior. *fruitless* turns out to be a gene that regulates many other genes involved in courtship and reproduction—a "master switch", as it were.

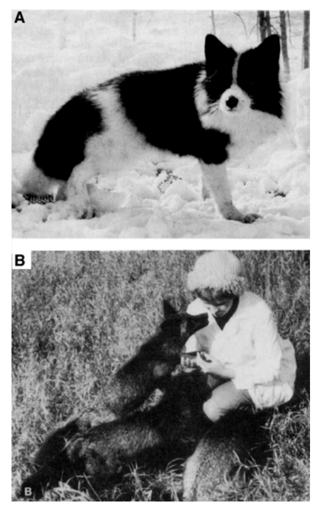


Dr. Trudy Mackay and colleagues at NC State have been able to artificially select for "slow-copulating" fly varieties (with extremely choosy females; copulation may take 2-3 hours) and "fast-copulating" varieties (copulation takes 20 minutes). The two varieties differed in 21% of the genome, suggesting strong epistasis.

Certain behaviors have been selected for in certain dog breeds—herding in sheepdogs, "soft mouth" in retrievers, etc. With the entire dog genome now sequenced, research is underway to find links between dog genes and behaviors.

Case Study: Tame Foxes

- Beginning in 1948, Dmitri Belyaev in the USSR began raising a captive population of silver foxes, and selecting them for tameness.
  - He was interested in how humans domesticated wolves and other animals many thousands of years ago, and wanted to "repeat the experiment"
- The tame foxes became friendly to humans, lost their musky scent, and started showing doglike behaviors (such as tail-wagging, whining, licking, and ear-dropping).
- Tame foxes also show differences in hormones, coat color patterns, and even in skull shape.



A 2005 study showed that, as compared to farm-raised but non-tame foxes, about 40 genes were being expressed differently in the brains of tame foxes.

The Selfish Gene

- Richard Dawkins's 1976 book introduces a powerful metaphor, one that we'll be returning to again and again
  - Some of these ideas had been worked out by, among others, George C. Williams, William Hamilton, etc.
- Genes are the fundamental units of selection (*gene-centered evolution*)

The Selfish Gene

- Genes that are favored by selection are those whose effects on phenotype maximize *their own* probability of replication.
- These effects may *not* always appear favorable to the organism that carries the genes—or even to the species.
- Genes "look like" they are acting to maximize their own replication—*selfish genes*.
  - A gene is a snippet of DNA-encoded information, and as such isn't conscious and can't "try" anything. It's a metaphor. Careful.

The puzzle of altruism

- *Altruism* occurs when two organisms interact in such a way that one receives a benefit and the other appears to give up a benefit.
  - Often the benefit takes the form of a gain in fitness.
- The old explanation was that individuals could somehow evolve to sacrifice themselves for "the good of the species". . .
- . . . but this doesn't seem possible under the standard model of natural selection. How could genes that could block themselves from being passed on ever evolve and become common?

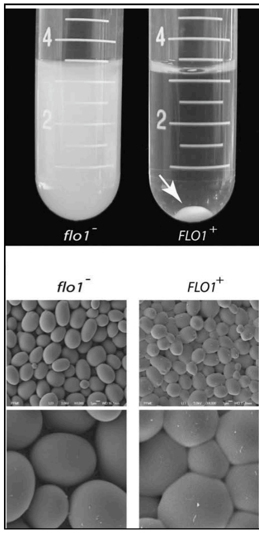
Assuming that genes affect behavior, how can altruistic behavior evolve?

- One explanation is "making the best of it"
  - Seemingly altruistic behaviors may be the only way that young or weak individuals have any chance to survive in a social group
  - This is especially common when the population has a *dominance hierarchy*, and also when the environment is harsh

The Galápagos hawk (*Buteo galapagoensis*) is polyandrous; stable groups of unrelated males mate with single females and share parental care. The environment is harsh, and these hawks are territorial. A group of males can defend a high-quality territory better than a lone pair could.

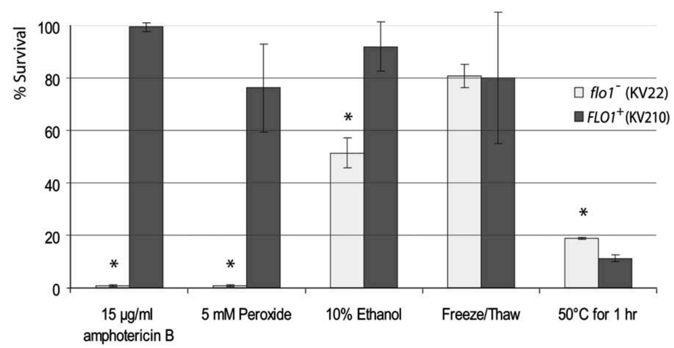
Assuming that genes affect behavior, how can altruistic behavior evolve?

- Another way is the *green beard effect*.
  - Imagine a gene (or conceivably a pair of tightly linked genes) that has both of the following effects:
    - It confers a trait on individuals that have it, which those individuals can recognize
    - It causes individuals that have the trait to behave altruistically towards other individuals that have it
  - Richard Dawkins explained it thus: Imagine a gene that gives people green beards AND makes them want to help other people with green beards. Hence the funny name.

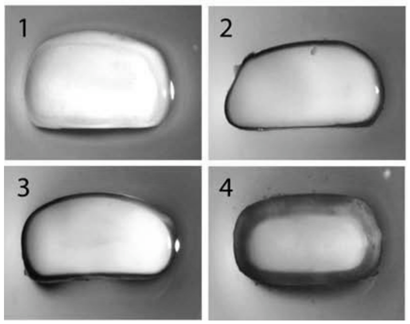


"Green beard genes" were once thought to be theoretical possibilities only, but several real-world examples have been found recently. *Saccharomyces cerevisiae* (brewer's yeast) comes in flocculent strains, in which the cells clump together into little lumps or *flocs* (on the right), and non-flocculent strains, which do not clump (on the left). Flocculation is mostly governed by a single gene called *FLO1*, which codes for a cell surface protein that binds to cell wall polysaccharides.

Flocculent yeast (*FLO1*$^+$, shown by blue bars) survive chemical shocks much better than non-flocculent yeast (*flo1*$^-$, yellow bars), because *FLO1*$^+$ yeast shield each other. A few "cheating" *flo1*$^-$ yeast may end up protected inside a floc, but this is rare: somehow *FLO1*$^+$ yeast stick to each other almost exclusively.



When flocs were chemically shocked (1, control; 2, antifungal drug; 3, 70% ethanol, 5 minutes; 4, 70% ethanol, 45 minutes), cells on the outside of the floc died (stained blue), but cells at the center of the floc survived (unstained).



Smukalla et al., 2008, *Cell* 135: 726-737.

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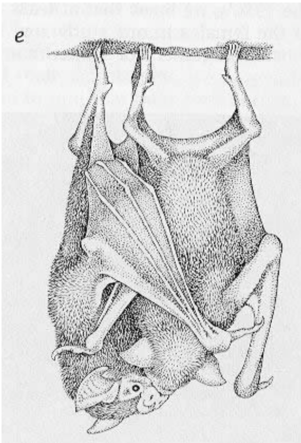
- Yet another way is through *reciprocity.*
  - If an organism that helps another can be reasonably sure of getting helped later on, the benefits of altruism may outweigh the risks—and altruistic behavior will be favored by selection. "You scratch my back and I'll scratch yours."
  - What favors the evolution of reciprocity?
    - Long associations among individuals
    - Individuals can recognize and avoid "cheaters"
    - Role reversal (individual can be either donor or recipient)
    - Benefit to recipient outweighs cost to donor

Case study I: Vampire bats

Vampire bats roost in small colonies, flying out at night to feed. A vampire bat that fails to find a blood meal within 60 hours of its last meal is in imminent danger of starvation. Vampire bats have been observed feeding each other by means of regurgitation: a hungry bat can get a neighbor who has fed to regurgitate some blood for the hungry bat to feed on. . .

70% of all blood sharing happens between mothers and their offspring, and is considered parental care. But the rest may happen between related or unrelated bats—usually between close neighbors in the colony.

A colony with no blood sharing would be expected to lose 82% of its adult members per year. The actual adult mortality is only 24% per year—everyone's fitness increases in a population with this altruistic behavior.



Bats are capable of recognizing other individual bats. Unrelated bats often form "buddy systems": two bats will take turns as needed feeding only each other. This avoids problems with "cheaters". . .

In this case, this form of altruism is an *evolutionarily stable strategy*, or *ESS*

- The *ESS* is a concept from mathematical game theory, applied to evolutionary biology by John Maynard Smith in 1972
- An ESS is a strategy that will persist within a population.
  – Even if some individuals develop a "mutant" strategy, the ESS will persist and the "mutant" will eventually disappear

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*.