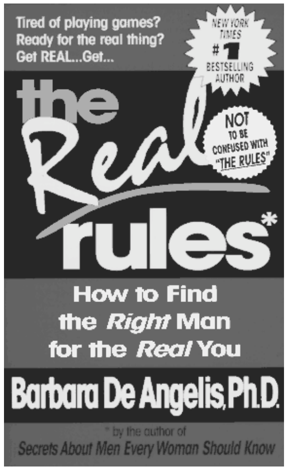
Behavioral Evolution and Sexual Selection

BIOL 4415: Evolution
Dr. Ben Waggoner

The Rules, III

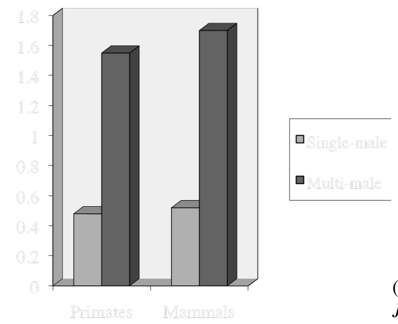
- Male-male competition may be a fight to the death when the stakes are high enough
- But such competition may end up harmful to both competitors!
- Thus, natural selection often favors the evolution of non-lethal "ritual combat" or displays.



In northern elephant seals, successful males have "harems" of females. Fewer than one-third of the males copulate at all, and the top five males may do 50% of the copulating. Male-male competition is vicious and frequently lethal.

In species where not so much is at stake, less lethal forms of male competition may be selected for—such as "neck-wrestling" in these giraffes, or "bugling" and antler fights in elk and deer.

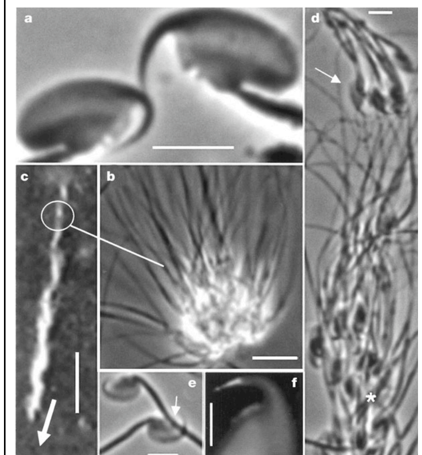
A more subtle form of male-male competition is *sperm competition*. If females mate with several males, selection will tend to favor males who produce more sperm.



This graph shows the mean size of the testes, relative to body size, in both primates and in a wide range of mammals. In species where a female mates with several males, the males have large testes and produce much sperm.

(Source: Kenagy and Trombulak, *Journal of Mammalogy* 67: 1-22)

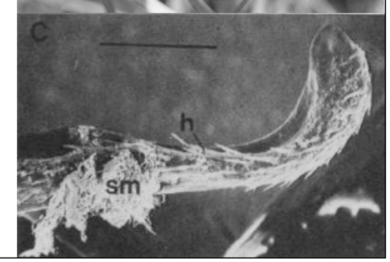
The Cape ground squirrel, *Xerus inauris*, has some of the largest testicles for its body size of any mammal. Females may go into estrus ("heat") at any time of the year, and at these times may mate with as many as ten males in a few hours. Males compete with each other, not only by disrupting each other's copulations (don't ask), but by sperm production as well.



A number of other rodent species have females that mate promiscuously. In many of these species—such as the European wood mouse, *Apodemus sylvaticus*—sperm cells have hooked heads, and sperm cells from the same male chemically recognize each other, hook together, and form "sperm trains" that swim 30% faster than lone sperm. This is altruistic sperm competition!

Selection may favor males who engage in "mate-guarding", staying close to the females that they've mated with—as in these Nebraska tiger beetles.

Selection may also favor males who can scrape out their rivals' sperm with highly specialized, spoon-shaped, bristly penis attachments—as is the case in dragonflies and damselflies.



It gets worse. . .

This is the "intromittent organ" of the bean weevil *Callosobruchus maculatus* (actual size is 0.8 mm). The spines at the tip cause serious wounds inside the female's genital tract.

This tends to discourage the female from mating again. . .

(Source: Crudgington and Siva-Jolly, *Nature* 407: 855-856.)

In many insects and spiders, as well as some rodents, bats, and primates, a male deposits a "mating plug" in the female's oviduct, prohibiting her from mating with another male. . .

. . . but that doesn't stop male bedbugs, who mate by stabbing females in the belly with their unusually sharp and hard phalluses, and directly injecting sperm.

And the semen of some *Drosophila* (fruit fly) species packs a *triple* whammy: it contains chemicals that:

- decrease the female's "libido" (or at any rate, lower the odds that she'll mate with someone else)
- increase her egg production
- kill or disable the sperm cells of other males. (Unfortunately, they poison the female as well.)

Infanticide can be seen as yet another form of male-male competition.

Indian langur monkeys live in groups of one male and several females. A strange male may take over the group; if successful, he will try to kill all infants in the group. . . causing the females to come into estrus ("heat") sooner.

Male lions are noted for infanticidal behavior as well. . . .

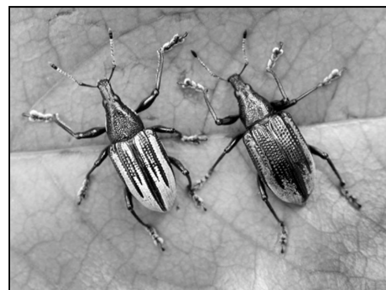
Since a female with a newborn cub won't be in estrus for another eighteen months, males that take over a pride attempt to kill the cubs so that the females are receptive sooner. (However, the females do fight to defend their own cubs. Females actually form "creches", communal cub-rearing groups, so that a creche can defend against a male.)

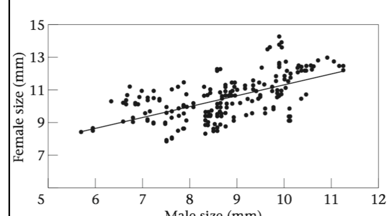
Why does mate choice happen?

- Several hypotheses have been proposed:
  - assortative / dissortative mating
  - direct benefit
  - "good genes" hypothesis
    - "handicap principle"
    - avoidance of hybridization
  - pre-existing sensory bias
  - "runaway sexual selection"
- These aren't mutually exclusive. Real-world cases may be explained by a combination of these causes

Assortative and Dissortative Mating

- *assortative mating*—preference for mates who are similar to oneself
  - Obviously, selection will favor mating within one's own species, since individuals who choose mates that are too much unlike them (e.g. in a different species) have decreased chances to pass on their genes
- *negative assortative mating*, or *dissortative mating*—preference for mates who are different from oneself
  - One example is *inbreeding avoidance*—many species have mechanisms that make inbreeding less likely





Example: In the Caribbean root weevil (*Diaprepes abbreviatus*), assortative mating results from the fact that males prefer large females (who can lay more eggs)—and large males outcompete small males, who are left with only small females to mate with. (Harari et al., 1999)

On the other hand, in the European corn borer moth, *Ostrinia nubilalis*, there are two phenotypes (E and Z) that produce different pheromone blends. Moths mate assortatively, and E-Z hybrids are rare—even though, in this case, hybrids are not at any known disadvantage. The reason for this assortative mating is unclear. (Pelozuélo et al. 2007)

Direct benefit to females

A male hangingfly (Mecoptera) presents a female with a captured prey insect. If she accepts, they copulate, which lasts up to twenty minutes—while the female eats the insect that the male gave her.

- The larger the food insect, the more direct benefit the female gets. (If the insect is too small, the female may refuse to mate.)
- The male benefits, too: The larger the insect, the better-nourished the female is, the more eggs she can produce, the more time he has to transfer his sperm. . . and the less likely that the female will be receptive to another male afterwards.

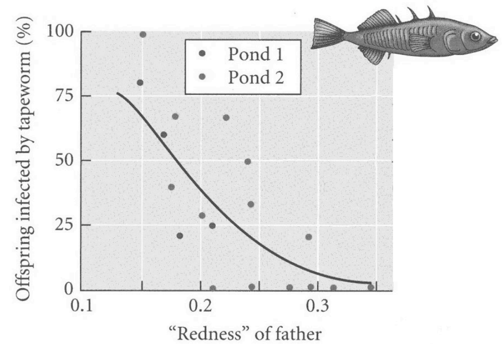
"Good genes": sticklebacks

Threespined stickleback, *Gasterosteus aculeatus*

"Good genes": sticklebacks

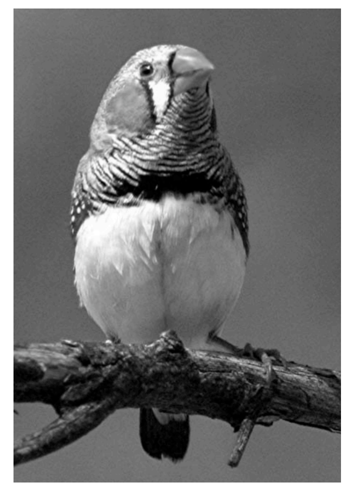
- Sticklebacks (*Gasterosteus aculeatus*) are small freshwater fish with complex courtship and mating behaviors
- 2001 study by Barber et al. showed that the degree of redness of a male stickleback was inversely correlated with the parasite load of his offspring
  - In other words, red males had offspring with few parasites, and drab males had parasitized offspring

This graph gives Barber's data, plotting redness of males against their offsprings' parasite loads.

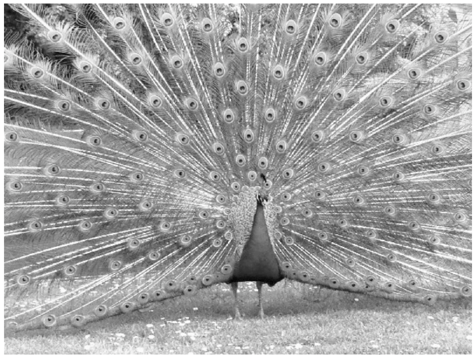


Bright coloration, especially using *carotenoids* (a class of mostly red and yellow pigments) has been linked with low parasite levels in several species of birds and fish. For example, Martinez-Padilla et al. (2007) showed that reducing roundworm infestation in red grouse (*Lagopus lagopus scotica*) boosted carotenoid levels—and the redness of the males' "combs".

Why? The likeliest hypothesis (Lozano 1994) seems to be that carotenoids stimulate the immune system and protect against cancer—in other words, they directly indicate how healthy a potential mate is.
Low carotenoids = stressed immune system!



The handicap principle



Male Indian peafowl, *Pavo cristatus*

The "handicap principle"

- You could consider the handicap principle as a variation of the “good genes” hypothesis.
- Many male traits that are sexually selected would seem to be disadvantageous. (Bright colors, for instance, make an animal more visible to predators.)
- According to the handicap hypothesis, if a male has a disadvantage like this, but still survives, the disadvantage shows that he must have very good genes otherwise. The disadvantageous trait becomes a “mark of genetic quality.”