10 SEXUAL SELECTION AND BEHAVIORAL EVOLUTION

In this course, you have already discussed how natural selection favors alleles that increase survival and reproduction. However, one can observe traits in some organisms that seem clearly to reduce some aspects of fitness. For example, in social insects, many individuals are sterile workers, and they feed and rear the offspring of other individuals. Another example occurs in many animals in which individuals of one sex have conspicuous traits or behaviors that make them vulnerable to predators, are energetically expensive to produce, and don't contribute to the well-being of offspring. In this lecture, we will concentrate on traits in this second category, the evolution of conspicuous, sexually dimorphic traits.

Darwin was at first puzzled by conspicuous traits such as bright colors, horns, and displays of males of many species—seemingly lower survival of the bearers (predation, energy).

His solution—**Sexual Selection** (he devoted most of a book—*The Descent of Man, and Selection in Relation to Sex*—to this topic).

Definition: Selection that arises from differences in mating success (# of mates that bear progeny over a defined time interval) (Arnold and Wade 1984). It is a kind of natural selection (vs. ecological selection)

Sexual Selection exists because one gender is a limiting resource for the other. In many species, females are a limiting resource for males b/c females produce few, large, gametes that are energetically expensive, while males produce many, small gametes that are not expensive. In some species, females provide more parental care than males, which also makes females a limiting resource.

However, males can be a limiting resource for females in species in which males provide parental care (many insects, fish, birds, and mammals, including primates). Two examples:

1) Female **red phalaropes** lay more eggs than a male can tend, they are more brightly colored than males and compete with other females for mates (Oring 1986).
2) **Pipefish**: eggs deposited in the male's brood pouch, or attached to his ventral surface. Males fertilize eggs, developing embryos are protected, aerated, osmoregulated and nourished by the male brooding structure—males are choosy sex (they prefer females with blue coloration. Berglund et al., (1986), Berglund & Rosenqvist (1993, 1994) Berglund (1991), Rosenqvist(1990).
3) **Midwife Toad**
4) **Giant Water bug**

Also, in many species, <u>it takes two parents</u> to successfully raise offspring, so males and females are equally limiting (many primates, many birds).

10.1 Kinds of Sexual Selection

Darwin proposed two kinds of Sexual Selection:

10.1.1 Intrasexual Selection—

contests between male (females) for access to females (males).

a) Male **blackbirds** defend territories using song, and display (epaulets). Anderson showed that obscuring epaulets led to more trespasses by other males (Andersson 1994).

10.1.2 Intersexual Selection:

Sexual selection via mate choice. Females of many species mate preferentially with males with particular phenotypes (size, color pattern, behavior).

Jumping spider courtship:
http://tolweb.org/tree/eukaryotes/animals/arthropoda/arachnida/araneae/salticidae/++salticidae/movies/tarsalis.mov

Courtship behavior in Japanese crane: see
http://www3.famille.ne.jp/~ochi/eng/kushiro2.html

Striking how numerous and seemingly arbitrary these traits are. In some species, females prefer males with bizarre artificial traits.

WHY would females prefer these strange traits?

Several Hypotheses:
1) Direct Benefits
2) Indirect Benefits
3) Sensory Bias

10.1.2.1 Direct Benefits

Male provides a **resource** that directly benefits the female (food, territory, parental care). Male house finches vary from orange to bright red. Redder males bring food to the nest at a higher rate (Hill 1991), and are preferred by females. Not controversial, but does not explain evolution of ornaments in species in which males provide nothing to females or offspring (except gametes).

10.1.2.2 Indirect Benefits

Most difficult to explain are those species in which male provides no resources to the female, and does not participate in parental care. Male provides only genes. What could be the cause of female preference in such species?

a) **"Good Genes" Models.** Females choose mates of <u>high genetic quality</u> so that their offspring inherit this "quality". Females choose based on some trait that indicates high fitness (both trait and fitness must be heritable, $V_A > 0$). Mutation, changing environments, or parasite and pathogen co-evolution could contribute to long-term maintenance of heritable variation for fitness.

a) **Runaway Sexual Selection.**

First model described by R.A. Fisher (1930), developed mathematically by O'Donald (1962), (in O'Donald 1980), (Lande 1980; Kirkpatrick 1982). Male trait and female preference, once initiated, become self reinforcing. Can lead to continual co-evolution and elaboration of both trait and preference.

Kirkpatrick's genetic model of Fisher's Runaway process:

	Genotypes	
Females	P1 (no preference)	P2 (preference)
Males	T2 (no trait)	T2 (trait)

P2 females tend to mate with T2 males. P1 females mate randomly. P1 females mate randomly. Offspring of P2 females inherit both the T2 trait and the P2 preference—generates a genetic correlation between preference and trait. Since T2 males have higher mating success, on average, trait increases in frequency in population. Preference increases in population b/c of genetic correlation. Other genes affecting trait and preference behave similarly. Can lead to elaboration of trait and preference until the mating advantage of trait is outweighed by survival cost of the trait.

c) Sensory Bias Models. Female preference for a trait may be a by-product of the female sensory system that has adapted to be sensitive to certain kinds of signals for reasons that are unrelated to mating. Also, some species display preferences for novel stimuli for reasons that are not understood (e.g., grass finches prefer artificial crests). Platyfish and swordtails are related species of Poecillid fish, both in genus *Xiphophorus*. Swordtails (obviously) have sword-like extensions on their caudal fins. Basolo (1990; 1995) attached artificial swords to the tails of platyfish, and showed that female platyfish preferred males with the artificial swords over those that had normal platyfish tails. So the preference for swords exits in female platyfish, even though the sword trait does not exist in this species!

10.2 Sexual and Ecological Selection

Sexual selection is a powerful concept that can explain traits that would otherwise seem maladaptive. But even when sexual selection is strong, organism must cope with other problems in addition to the problem of finding mates. The effort expended to acquire mates may incur a cost in terms of decreased survival. That is, sexually-selected traits are subject to <u>life-history tradeoffs</u>.

A cost of sexually selected traits has been demonstrated experimentally in both laboratory and natural populations. Male Tungara frogs call to attract mates, but the calls also attract a predator (a bat), so males must risk being eaten in order to obtain mates. Female frogs have been shown to prefer males with a particular feature of the call, called a "chuck". But bats are also attracted to this feature of the call.

A similar thing happens in male field crickets, which again, must call (stridulate) in order to attract females. Parasitoid flies use the mating calls to locate male crickets, in order to lay eggs on them. The eggs hatch into fly larvae, which eventually kill the male crickets.

10.2.1 A "Natural Selection" Experiment (This example will be covered in a Laboratory exercise).

In 1980, John Endler published the results of a study that has become a classic example of the interaction between sexual and ecological selection in guppies (Endler 1980).

In nature, guppies co-occur with different suites of predators. There are "high predation" populations, where the guppies co-occur with large, visually oriented cichlid preditors (*Crenicichla alta*), which voraciously consume both juvenile and adult guppies. These populations also co-occur with smaller piscivorous killi fish (*Rivulus hartii*)that consume mainly juvenile guppies. In low predation site, male guppies are very brightly colored, with lots of orange, yellow, green, blue and purple patches. In high predation sites, male guppies are still colorful, but much less bright than their relatives in the low predation sites. The interpretation of this pattern had been that female guppies prefer brighter males, but that these males were more conspicuous to predators. So when predators are absent, the males evolve brighter color patterns than when predators are present.

In order to test this hypothesis, John Endler set up several artificial stream habitats in his lab at UC Santa Barbara. The streams were designed to mimic a natural habitat as closely as possible. Multi-colored gravel was used as the substrate, and guppy predators (Crenicichla) were present in some of the treatments. In some of the ponds, a large grain size was used for the gravel, and in other ponds, a small grain size was used.

Male guppies are most conspicuous (visible) when they have many spots and when those spots are different than the grain size of the gravel background.

Endler set up an experiment in which two different Treatments (predators and grain size

			Predators	
		No predators	*Rivulus* (small)	*Crenicichla* (large)
Substrate	Large grain size			
	Small grain size			

And then he just let the populations evolve for many generations. This is a <u>"natural selection" experiment</u> as opposed to an "artificial selection" experiment, because no one was choosing parents: In this case, natural selection includes both ecological selection and sexual selection. Selection was just proceeding on its own, albeit in an artificial environment.

Question 1: Predict the number of spots (few or many) and the spot size (large or small) that evolved after ~9 generations in each of the six different combinations of predator treatment and gravel treatment.

Question 2: If brighter coloration is favorable because of female preference what different kinds of selection can you identify in this example (e.g., ecological, inter-sexual selection, intra-sexual selection).