EEB 245: Evolutionary Biology
Evolution of Behavior

Conflict & Cooperation: Sexual Selection

Rs: Reproductive success

Sexual Dimorphism: A difference between the male and female phenotypes within a species

- Darwin's attempt to explain exaggerated and potentially disadvantageous traits in terms of selection
  Ex: size dimorphism in elephant seal (males larger) or harlequin crabs (females larger)
  Ex: color dimorphism in mallard duck (males bright/showy, females drab/cryptic)

Sexual Selection: Differential Rs as a result of variation in the **ability to obtain mates**
*if there is *heritable* variation in a trait that affects the ability to obtain mates, then favored variants will become more common over time.

Ex: The long tail of the male widowbird may be disadvantageous in the face of predation (or in terms of energetic costs) and may suggest decrease survival of such individuals. But long tails attract more mates leading to greater reproductive success (more offspring) of an individual with a long tail. If the long tail trait is heritable, male offspring will also display this phenotype and, given higher reproductive success of individual males with long tails, long tails will become a common trait for males in the population of widowbirds.

Parental Investment: Energy and time invested in constructing and caring for offspring

- Variable gamete size (heterogamy): egg: large/sperm: small and numerous
- Eggs are more expensive than sperm: Females typically make a larger PARENTAL INVESTMENT than males

Theory of Sex Differences: Female Rs most likely to be limited by the number of eggs she can produce rather than the number of mates she can obtain and male Rs more likely to be limited by the number of mates he can obtain rather than the number of ejaculates he can produce (*Bateman's Principle*)

A.J. Bateman (1948): *Drosophila* mating experiments suggested that male Rs usually increased with number of mates while female Rs did not change much after a single mating; males were also more variable in the number of mates they could obtain compared to females (i.e. given a certain number of fertilizable females, for every female a male fertilizes, another male loses a mating opportunity/Rs – some males can have many mates and others can have few if any at all. Most females are expected to be fertilized so there is little variation in female reproductive success under many circumstances)
Conclusions:

- Variation in mating success is usually GREATER among males than among females
- Sexual selection (variation in fitness due to variation in success at acquiring mates) is usually STRONGER in males than females

Operational Sex Ratio (OSR): The relative numbers of males and females in the mating pool at any one time

Equation: males prepared to mate /(males + females prepared to mate)
when 0, only females prepared

when 1, only males prepared
given 10 males and 10 females, OSR = 10/20 or ½, a 50/50 sex ratio

OSR often MALE-BIASED because males mate more frequently

- Access to females will be a limiting resource for males but access to males will not be a limiting resource for females
- Variation in mating success will usually be greater among males than among females
- Variation in mating success is often used as a measure of the INTENSITY OF SEXUAL SELECTION, where large variation → intense sexual selection

Ex: monogamous wandering albatross: low variation in mating success, most individuals successfully pair and rear offspring together.

Ex: polygamous plains zebra: high variation in mating success for males. Some males have large harems of females, some males are unable to mate at all.

Sex-role Reversals: When males invest more per offspring than females, access to males will be a limiting resource for females

Ex: Pregnancy in male seahorse (*Hippocampus spp*): Females deposit eggs into a male's brood pouch and males will carry the fertilized eggs until they hatch and become free-swimming fry. Females often court males and males are choosy about mates (Futuyma, pg 344).

Ex: Territorial Female Phalarope (*Phalaropus spp*): Females defend a territory and defend multiple males incubating their eggs from female intruders. Males will not mate with other females if they are guarding an egg and outside females attempt to destroy eggs in order to mate with males (Futuyma, pg 330; Fig 14.5).

*In both cases females can produce eggs faster than males can rear young so that males become the limiting resource.

Table 14.1 Mechanisms of competition for mates and characters likely to be favored (Futuyma, pg 330)

Intrasexual Selection: Selection on traits that increase the ability of one sex to compete for fertilizations; occurs when individual males can monopolize access to females

Male-Male Competition:

- Can favor lg size, strength, weaponry, threat signals

- Direct: via control of females themselves
  Ex: Harems in Elephant Seals (lg male size favored in harem defense and combat)
  Ex: Combat in male deer (antlers as weaponry or threat signal)

- Indirect: via control of some resources important to females
  Ex: Food, Nest sites (Red-winged blackbird uses wing patch as threat signal)

Other types of male-male competition:

- Infanticide

  Ex: When male lions take over a pride they may kill cubs in order to bring females into reproductive condition so that the new males can produce their own offspring. Females are not reproductively active while they are weaning their offspring (Futuyma, pg 345)

- Sperm Competition

  Ex: Male genitalia of damselfly spp. have morphological adaptations that allow males to remove sperm of rival males from a females reproductive tract (Futuyma, Fig 14.7)

Intersexual Selection: Selection on traits that increase the attractiveness of one sex to the other; occurs when males cannot directly control access to females, the males compete by advertising for mates

Female Choice:

- Females often mate preferentially with males that have larger, more intense, or more exaggerated characters
  - Color patterns
  - Ornaments
  - Vocalizations
  - Display behaviors

  Ex: Females of the Trinidad guppy (*Poecilia reticulata*) prefer males with certain color patterns although females themselves are drab

Why female prefer certain traits??

- Some traits arbitrary and some may decrease male survival!

  Ex: elaborate tails in males of the polygynous African bishop and widowbirds (*Euplectes spp*)

- Proposed functions of female choosiness:
  - Direct Benefits (resources)
  - Sensory Biases (exploited preferences)
  - Indirect Benefits (sexy sons or good genes)

Direct Benefits: Nutrition, superior rearing sites, or parental care for offspring; signaled through male traits

Ex: For A Male Sand Goby, Playing‘ Mr. Mom' Is Key To Female's Heart *ScienceDaily (May 5, 2004)*& Forsgren 1997: Females prefer males who perform more parental care duties during courtship over males who are able to defend their territory from rival males. When males perform behaviors associated with care of offspring during courtship it may signal to a female whether or not a male would be able to care for her eggs.

Ex: Bright red male house finches (*Carpodacus mexicanus*) bring food to nestlings at a higher rate than duller males (Hill 1991)

*In both instances females prefer males who signal ability to provide benefits to a female’s offspring

Sensory Bias: Females prefer a trait because it exploits a bias in the female sensory system, resulting in a preference evolving before the preferred male trait does

Ex: Females in certain species of *Xiphophorus* with and without swords *prefer* swords (Futuyma, pg 333)

In some species males provide NO direct benefits and only contribute GENES:

Lek: A special kind of polygynous mating system where aggregated males display and females attend primarily for the purpose of fertilization

Ex: Displaying male club-winged Manakins (*Machaeropterus deliciosus*) gather at a lek and make loud chirping sounds via wing stridulation (Could this be an energetically costly behavior signaling ‘good genes’ to females?)

Why should females choose males who provide no DIRECT benefit to their offspring?

- Females may benefit INDIRECTLY through mate choice:

  - Alleles affecting female mate choice are expected to increase or decrease in frequency depending on the fitness of the females' offspring, i.e. all that is required for female choice to be beneficial is that offspring are FIT (offspring have high survival and/or Rs)
- Two models proposed:
  - Runaway sexual selection
  - Good genes model

Indirect Benefits: 'Sexy Sons' or viability traits (increase offspring growth rate, increase disease resistance, increase survivorship, increase competitiveness)

Runaway Sexual Selection: Sons of females that choose a male trait have improved Rs because they inherit that trait that made their father appealing to their mother; result is genetic correlation – increase frequency of trait or preference results in an increase frequency of the other (Runaway process)

- AKA "Sexy Son" Hypothesis or Fisherian Model of Sexual Selection
- Genetically variable preferences or trait responses may lead to population divergence!!

  Ex: Lekking stalk-eyed flies (*Cyrtodiopsis dalmanni*): Male stalk-eyed flies defend root hairs near streams and females are attracted to and often mate with males with long eye stalks. Wilkinson & Reillo (1994) found that when female stalk-eyed flies with preferences with longer male eye stalks were mated to males with longer-eye stalks, the crosses produced female offspring with an exaggerated preference for longer eye stalks and male offspring with exaggerated eye stalk length (the heritability (h^2) of trait and preference was high) and selection continued to move towards greater exaggeration of trait and preference across generations.

  *See Futuyma, pg 334 for more examples

Good Genes Model: Preferred male traits indicate viability which is inherited by offspring of females who choose such mates; condition-dependent traits should act as reliable indicators of male quality

- AKA 'the handicap model': male trait indicates viability despite ecological handicap it imposes on survival (Zahavi 1975); it is believed that some male traits are energetically costly and males are only able to bear the cost of the trait if they have high overall health incurred by "good genes"/increased viability
- Viability traits:
  - Increase offspring growth rate
  - Increase disease resistance
  - Increase survivorship
  - Increase competitiveness
- Condition-dependent indicators are important: Must assume male traits are reliable indicators of male quality due to correlation between indicator trait alleles and 'genetic quality' alleles

  Ex: Mate Choice in Threespine stickleback (*Gasterosteus aculeatus*) based on throat coloration as an indicator of parasite resistance (Futuyma, pg 335-337; Fig. 14.11)

Contact Kat (katherine.shaw@uconn.edu) with any questions about the material

Or see Textbook (Futuyma 2005, pgs 329-337) for more details and examples