Chapter 10
Sexual Selection
Survival Characters
Non-Adaptive Characters?

Banding variation in *Cepaea nemoralis*. 

*Cepaea nemoralis*

Banding variation in *Cepaea nemoralis*. 
“Deleterious” or “Costly” Characters
• Many animals possess elaborate traits that appear to reduce survivorship.
• Many of these traits are present only in males - **sexual dimorphism** - and they appear to function primarily in mating.

**Q. Why does sexual dimorphism occur in a great variety of organisms?**
Secondary Sexual Characters

Characters that *function* in reproduction but are not *necessary* for reproduction.
Peacock tails have been shown to reduce a male's survivorship:

— they make males more conspicuous to predators
— they reduce a male's mobility, making him less capable of escaping from predators
— they impose a large energetic cost

Given such severe costs, we might expect these tails to be eliminated by selection; yet they are not.
Darwin’s Theory of Sexual Selection
(The Descent of Man and Selection in Relation to Sex, 1871)

• The reduced survivorship of males with elaborate traits is more than compensated for by their increased advantage in mating.

• These traits give males an advantage over other males, not in the struggle for survival, but in the competition for mates.
Darwin indicated two ways in which sexual selection can occur:

1. Intrasexual competition (male-male competition)

2. Intersexual selection = mate choice (female choice)
Why Male-Male Competition and Female Choice?

<table>
<thead>
<tr>
<th>Female Gametes</th>
<th>Male Gametes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Few</td>
<td>Many</td>
</tr>
<tr>
<td>Large</td>
<td>Small</td>
</tr>
<tr>
<td>Costly</td>
<td>Cheap</td>
</tr>
</tbody>
</table>

- The reproductive success of females is limited by resource availability.

- Male reproductive success is thus limited by the number of unfertilized females.
• If sexual selection works primarily on males, we would expect to see more variation in male mating success than in female mating success.

Bateman (1948) proposed that sexual selection should be strongest in males. Here data are provided from *Drosophila* that plots the number of offspring versus the number of mates for males (top) and females (bottom).

Evolution of Traits due to Male-Male Combat

- Sexual selection by male-male competition occurs when individual males can monopolize access to females
- Males may monopolize females through direct control or indirect control
Direct competition involves fighting over resources necessary to attract females, or directly over females themselves.

— Territories
— Females
— Mate guarding

Fighting bull elephant seals
Direct competition cont.

Male marine iguanas in combat
Although iguanas can grow to different sizes on different islands, on any given island males are larger than females.
Medium sized iguanas survived at higher rates than either small or large iguanas – stabilizing selection
• The maximal sizes at which iguanas could sustain their weight are close to the maximal sizes for survival
• The largest females in the populations are near the optimal size for survival, but the largest males are much larger than the optimal size
Reproductive Strategies of Male and Female Iguanas

Prior to the mating season, males stake out territories on the basking rocks.

There is extreme variation in the number of copulations among male iguanas on the mating territories; larger males are participate in more copulations than smaller males.

Figure 10.10 - Mating success in male marine iguanas
Evolution of Traits due to Male-Male Combat cont.

**Indirect competition** involves competition that doesn't include fighting between males.
Indirect competition cont.

Fig 10.14 - Sperm competition in damselflies
Indirect competition cont.

Figure 10.15 - Lion infanticide
Female Choice

• Many secondary sexual characters appear to play no role in male-male competition
• Darwin suggested that these characters exist because females preferred to mate with males possessing these characters

The mating advantage of males with these traits will compensate for the corresponding amount of reduced male survival
General comments about Darwin’s Theory of Sexual Selection:

1. It was a comparative argument
2. Female choice had difficulty gaining acceptance
A.P. Møller’s work with barn swallows

(Møller 1989, Nature 332: 640-642)

— Captured and banded 44 males that established territories, but that had not yet mated
— He divided them into 4 groups:

1. Shortened tail feathers
2. Mock-altered (control 1)
3. Unaltered (control 2)
4. Elongated tail feathers
**Prediction:** If females prefer males with longer tail feathers, then the males with elongated tails would a) attract mates sooner, and b) fledge more young, than either control 1 males or control 2 males.
The control males should, in turn, be more successful than the shortened males.

Figure 10.17 - Reproductive success and tail length in male barn swallows.
Table 9.2  Extra-pair copulations in Møller’s barn swallow experiment

The numbers reported are rates, measured as extra-pair copulations per hour. $P$ values give statistical significance of variation among groups. From Møller (1988).

<table>
<thead>
<tr>
<th>Extra-pair copulations</th>
<th>Shortened tails</th>
<th>Control I</th>
<th>Control II</th>
<th>Lengthened tails</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>By males</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.040</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>By their social pair-mates</td>
<td>0.036</td>
<td>0.014</td>
<td>0.017</td>
<td>0</td>
<td>&lt; 0.01</td>
</tr>
</tbody>
</table>
Choosy Females may get Better Genes for Their Offspring

• This idea suggests that male displays are indicators of genetic quality
• If this is the case, then choosy females will secure better genes for their offspring
Preferences of Female Gray Tree Frogs

Figure 10.20
Table 10.3  Fitness of the offspring of long-calling male frogs vs. short-calling male frogs

NSD = no significant difference; LC better = offspring of long-calling males performed better than offspring of short-calling males; − = no data taken. The overall result: Offspring fathered by long-calling males had significantly higher fitness than their maternal half-sibs fathered by short-calling males ($P < 0.0008$).

<table>
<thead>
<tr>
<th>Fitness measure</th>
<th>High food</th>
<th>Low food</th>
<th>High food</th>
<th>Low food</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td></td>
<td></td>
<td>1996</td>
<td></td>
</tr>
<tr>
<td>Larval growth</td>
<td>NSD</td>
<td>LC better</td>
<td>LC better</td>
<td>LC better</td>
</tr>
<tr>
<td>Time to metamorphosis</td>
<td>LC better</td>
<td>NSD</td>
<td>LC better</td>
<td>NSD</td>
</tr>
<tr>
<td>Mass at metamorphosis</td>
<td>NSD</td>
<td>LC better</td>
<td>NSD</td>
<td>NSD</td>
</tr>
<tr>
<td>Larval survival</td>
<td>LC better</td>
<td>NSD</td>
<td>NSD</td>
<td>LC better</td>
</tr>
<tr>
<td>Postmetamorphic growth</td>
<td>−</td>
<td>−</td>
<td>NSD</td>
<td>LC better</td>
</tr>
</tbody>
</table>
The Handicap Principle (Zahavi 1975)

Zahavi’s model predicts that sexually selected traits are elaborate because they tend to lower the survivorship of the individuals having them. The more elaborate the character, the more severe the test, and the better the male must be to have survived such a handicap.

**Assumption**: The choosing sex (usually females) is better able to discriminate quality in members of the chosen sex (usually males) when members of the chosen sex display elaborate traits.
Sexually selected traits can handicap males,

A Tungara frog getting nabbed by a bat. Bats like tungara calls with a chuck. So do female frogs -- life is complicated.
Brightly colored male guppies are chosen more often by females, but are also more obvious to predators (blue acara cichlid fish).
Honest Advertisement Models

• But many traits that are preferred by females will not put males at greater risk.
• Zahavi’s Handicap principle is now considered a subset of the “honest advertisement model” which merely states that females choose males on the basis of a male’s honestly advertised characters.

Q. What gets honestly advertised?

— Good genes
— Good current conditions
— Good resources
Choosy Females may Benefit through the Acquisition of Resources

In many species, males provide food and parental care for female and her offspring. Perhaps females are capable of distinguishing between good providers and inferior ones.
Courtship and mating in hangingflies

*Bittacus chlorostigma*

Fig 10.22
The females preference for males with large gifts is beneficial to her in 2 ways:

- It provides her with more nutrients, allowing her to invest more in reproduction
- It saves her from the need to hunt for herself
Choosy Females may have Preexisting Sensory Biases

Sensory exploitation hypothesis (e.g. Ryan & Rand 1990) suggests that female preferences do not coevolve with male sexual signals.

According to this model, the male trait is favored simply by virtue of its manipulative effect on a pre-existing bias in the sensory system of females.
Courtship Behavior in Water Mites

Figure 10.23
Hypothesis: Male leg-trembling during courtship evolved in this mite because it mimics the vibrations produced by copepods and thereby its elicits a predatory behavior in females.

Experiments

Measured the frequency of vibrations produced by trembling males and compared it to the frequency produced by copepods.

Observed the behavior of females during “net-stance” when they were alone, when they were with copepods, and when they were with males.

Observed the responses of hungry females and well-fed females to the presence of males.
Males probably benefit from leg trembling behavior:

— They use the female response to trembling to determine if a female is present (male more likely to deposit spermatophores if a female clutches him)

— Trembling allows males to distinguish between receptive versus unreceptive females

— They use female response to trembling to determine which direction the female is facing
A key predication of the sensory exploitation hypothesis is that “net-stance” evolved before male trembling.

Figure 10.24 - A phylogenetic hypothesis for *Neumania papillator* and other closely related species.
Runaway selection (R.A. Fisher, 1958)

- An initially naturally selected trait in males accompanies preference for that trait in females.
- Thus, all elaborate traits once had a naturally selected component, no matter how small.
- The trait may become further elaborated for reasons of sexual selection alone.

**Figure 11.5** (a) Early stage in the evolution of a bizarre character such as the peacock’s tail. Before females preferred to mate with long-tailed males, a positive correlation might have existed between tail length (then much shorter than in their descendants) and male fitness. (b) Full relation between the degree of exaggeration of character (tail length) and survivorship. An intermediate optimum exists as well. Modern species like the peacock lie toward the right of the graph.
Stalk-eyed Flies and Runaway Sexual Selection

A male Malaysian stalk-eyed fly
Figure 9.22 Runaway selection illustrated with stalk-eyed flies  

(a) Variation in eyestalks and preferences should lead to assortative mating:

(b) Assortative mating should produce genetic correlations between sons and daughters within families:

(c) Selection on male eyestalks should produce a response in female preference:

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Runaway selection illustrated with stalk-eyed flies

(a) Assortative mating. Females with different tastes choose among males with different eyestalk lengths. If both traits are heritable, then offspring receiving genes for long eyestalks also tend to receive genes for “long” tastes. (b) A genetic correlation between male stalk length and female preference. Each point represents the average value of the offspring of a male mated with each of a number of randomly chosen females. Males whose sons have long eyestalks also tend to have daughters that seek long eyestalks in their mates. After Figure 4.6 in Arnold (1983). (c) Female preference evolves as a correlated response to selection on male stalk length. Each circle represents the stalklength and preference, respectively, of a father-daughter pair. The fathers are also represented by diamonds on the horizontal axis, and the daughters by diamonds on the vertical axis. If we select the longest-stalked males as breeders (red diamonds on the horizontal axis and red circles), we should see a response in the daughters. The arrows indicate the selection differential and predicted response (see Chapter 7). The gray diamond below the horizontal axis marks the average of all fathers in the population, and the red diamond marks the average of selected fathers. The gray diamond to the left of the vertical axis marks the average of all daughters, and the red diamond marks the average of daughters of selected males. After Falconer (1989).
Paired Choice Tests for Female Preference among Stalk-eyed Flies
Runaway selection cont.

Bower bird nests with blue ornaments
The Parasitic Theory of Sexual Selection

• Hamilton’s 1979 parasite theory of secondary sex characters is a refinement of the “good current condition” model of honest advertisement.
• It suggests that parasite load is being assessed by females.

• Female choice of healthy males is a special case of female choice for good genes
A comparative look at the parasite theory of sexual selection

Hamilton and Zuk (1982) reasoned that some bird species will suffer from parasites more than other species. Parasitism will then set up selection on females to choose resistant mates, and the selection will be stronger in species suffering from high parasite loads than in species suffering lower loads.
An experimental look at the parasite theory of sexual selection

• Møller (1994) measured the health of male swallows by counting the numbers of a bloodsucking mite on the bird’s heads
• He found that males with longer tails had fewer parasitic mites

Q. But, is the male’s health (resistance) passed on to his offspring?
What happens when males invest the same or much more per offspring than do females?

When males invest more per offspring than females, access to mates will be a limiting resource for females.
Reverse Sex Roles among Pipefish

• Pipefish in kelp beds.
• The males have a brood pouch where they brood the eggs.
• Males are choosy with whom they mate.
• Females do not differentiate between males of different size.
Mate Choice in Pipefish

(a) Experimental design for paired choice tests

- Male’s aquarium
  - Researchers record whether male spends more time near, for example, the larger or smaller female

- One-way mirror allows male to see females

- Female’s aquarium
  - Screen prevents females from seeing each other

Nerophis ophidion

(b) Female body size

<table>
<thead>
<tr>
<th>Choice frequency (% males choosing each type of female)</th>
<th>Large</th>
<th>Small</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>9</td>
<td>1</td>
</tr>
</tbody>
</table>

(c) Female skin fold size

<table>
<thead>
<tr>
<th>Choice frequency (% males choosing each type of female)</th>
<th>Large</th>
<th>Small</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>7</td>
<td>0</td>
</tr>
</tbody>
</table>

Figure 10.28
Mate Choice in Pipefish cont.

*Syngnathus typhle*

(d) Female spots (caused by parasites)

(e) Female spots (tatoos)

<table>
<thead>
<tr>
<th>Choice frequency (males choosing each type of female)</th>
<th>Few</th>
<th>Many</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>18</td>
<td>5</td>
</tr>
</tbody>
</table>

|                                                        | Few   | Many  |
|                                                        | 12    | 2     |
Sexual Selection and the Mating Mind

What selection pressures favored our large brains, our creative intelligence, and our unique capacities for language, art, music, humor, romantic love, and moral commitment?

Australopithecus afarensis
400 cc

Homo sapiens
1400 cc
Why did we need to become so intelligent?

— Natural selection
— Sexual selection
Machiavellian hypothesis

Richard Alexander in the 1970s suggested that the main evolutionary pressure for human beings to increase in intelligence was competition with other people, in particular, sexual competition between individuals of the same sex.
Runaway Sexual Selection

Being intelligent, witty and entertaining was sexy to our ancestors!

This hypothesis requires only that there was an initial preference for more intelligent mates that drove the process from then on.

— The initial preference was quite arbitrary and only came about by chance. This may explain why an equivalent preference never arose in the other apes.

— The human mating system is unique among apes in that it is characterized primarily by monogamous pair bonding (with occasional polygamy) and shared parental effort in child rearing.
There is a least one caveat:

— The lack of sex differences in human mental capacities becomes a strong argument against the runaway brain theory.

— Fisher’s model is too simple to explain a situation in which both sexes are choosy, and both display their mental traits during courtship.
Recent Ideas about Sexual Selection and the Human Mind

• Many of the traits we're selecting when we choose a mate are not just arbitrary traits; they are actually powerful indicators of things that matter in reproduction:

  — a lot of beauty is really an indicator of health and fertility
  — a lot of traits that are *psychologically attractive* to us, like kindness, warmth, creativity, intelligence, imagination, are indicators of somebody's ability to get along in the world
Universal Mate Preferences

• David Buss’ survey of sexual preferences in 37 cultures all around the world revealed that in every culture, the top two most desired traits in a mate, for both sexes, were **kindness** and **intelligence**.

• Interestingly, two of the major traits that distinguish us from other primates are the same traits that we search for in a mate, and they are under the strongest sexual selection.
Mating Mind Hypothesis

• If sexual selection drove human mental evolution, it must have been a form of sexual selection that could work given mutual mate choice.

• The human mind may have evolved through some combination of:
  — runaway sexual selection
  — sexual selection for fitness indicators
  — psychological biases favoring certain details of ornament design