Whiptail Lizard
Sexual Selection

Charles Darwin and Alfred Russell Wallace

Noticed that males of many species have highly elaborated traits that seem maladaptive (secondary sexual characters)
Antlers
Irish Elk (extinct)

Hercules Beetle
Male
Female

Horns
Bighorn Sheep

Elephant Tusks
African Lion: Mane is used for protection during male clashes (male-male competition)
Pheasant: Elaborate bright red wattle on cheek

Pheasant: Elaborate spur used in male-male fighting and by females to choose.

(Notice the fake spur on the right. Some males try to trick females, but do not fight.)
Two Types of Sexual Selection

- Male-male competition (intra-sexual selection)
- Mate (female) choice (inter-sexual selection)
Male-male competition

- Within group dominance
- Female-defense polygyny
- Territorial polygyny
- Lekking (competition for a position in the lek)
Within group dominance

Grey Wolves
Female defense polygyny

Northern Elephant Seals
Territorial defense
polygyny

Impala
Waterbucks head butting
Sperm competition
Mate Choice

Two broad categories:
- Resource based
- Non-resource based

In most cases, females are the choosy sex, but not always.

Why?

Grouse, a lekking species
Why are females choosy?

- Investment cost
  - eggs are expensive relative to sperm
  - internal fertilization and carrying young to term is costly
When are males choosy?

(sex-role reversal)

- When their contributions exceed the cost of making eggs
- The chances of mating with multiple females is small (biased sex ratio—many females and very few males)
Example: Sea Horse (males care for the young)
Mate choice

(Why choose in the first place?)

- Mate with correct species
- Better fertilization ability or higher fecundity
- Provides more food
- Better parental ability
- Better breeding territory or defended resource
- Lower risks or hazards (e.g., predation)
- Partner offers higher heritable viability or other heritable qualities that are important
Mate choice

Direct benefits (proximate benefits)

Example: Bush crickets (nuptial gifts)

1. Males provide spermatophores which females feed on. Often consist of up to 30–40% of male body weight (i.e., very costly)

2. More spermatophores allow female to lay more eggs.
Mate Choice

- Indirect benefits (ultimate benefits)
  - Good genes
  - Others (e.g., Fisherian runaway sexual selection, which will not be discussed)
Good Genes

- Females (or males) choose a mate which offers high quality genes influencing survival.
- Mate quality is indicated by a secondary trait.
- Secondary trait must be heritable.
- Must be heritable variation in mate quality.
- No, low, or high cost to males bearing the trait (e.g., bearing the cost is an indicator of good genes..."handicap model").
Good Genes Example

Gray Tree Frog (Hyla versicolor)
Short vs. Long Calls
<table>
<thead>
<tr>
<th>Fitness Measure</th>
<th>High Food</th>
<th>Low Food</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larval growth</td>
<td>LC</td>
<td>LC</td>
</tr>
<tr>
<td>Time to meta.</td>
<td>LC</td>
<td></td>
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<tr>
<td>Mass at meta.</td>
<td></td>
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<tr>
<td>Larval survival</td>
<td></td>
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<tr>
<td>Postmeta. growth</td>
<td></td>
<td>LC</td>
</tr>
</tbody>
</table>
Final Topics

- Lekking and the evolution of leks
- Sensory bias/exploitation
What are leks?

An aggregation of males which females visit only for the purpose of mating.

- No male parental care (only contribution is sperm)
- An area that males aggregate and mate with females that is not associated with feeding, etc.
- Display sites of males contain no significant resources to females (e.g., nesting site)
- Females have the opportunity to choose, or shop, among available males
Evolution of leks

- lower predation risk for males and females
- passive attraction; more males is better
- hotspot model (males congregate in areas that increase the probability of encountering females)
- black hole model (females are not choosy, but wish to avoid dangers associated with mating)
- hotshot model (females choose the “best” male; poor males congregate near good males in the hopes of increasing their chances)
Bowerbirds

An example of sexual selection in a lekking species:
Males build and decorate courtship arenas, called bowers, on leks for the purpose of courting females.

Females prefer males with lots of blue and yellow objects at the bower. They also prefer neat bowers.
While the female (grey) sights and watches, the male produces an elaborate courship display, including dances, jigs, wingflips, and vocalization. Males, hoping to woo females, will even clasp a yellow flower or feather in the beak.
Males with the best of all these traits get the most matings.
Many species of bowerbirds build elaborate bowers, decorate them with colorful objects, and have elaborate courship displays.
Fembots
Latent preferences in females are used by males to gain greater reproductive success.

Physaleumus Frogs

P. coloradum: Males attract mates by calling using WHINES

P. postulosum: Males attract mates by calling using WHINES and some use CHUCKS
Experiment

Take tape playback unit with recording of *P. coloradum* WHINES with *P. postulosum* CHUCKS to pond. Play and observed, relative to just WHINES, how many females are attracted.

<table>
<thead>
<tr>
<th></th>
<th>Female Pref.</th>
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</thead>
<tbody>
<tr>
<td>WHINE</td>
<td>NO</td>
</tr>
<tr>
<td>WHINE+CHUCK</td>
<td>YES</td>
</tr>
</tbody>
</table>
Swordtails

Platyfish: No swords. When males are modified to have swords, the female Platyfish prefer them.

Swordtails: The males of some species have swords. Females prefer males with long swords.
Helpful behaviors

- Alarm calls (e.g., Belding ground squirrel)
- Sentinel behavior (e.g., meerkats)
- Nest helping
- Eusocial behavior

Actor performs some action that benefits another (the recipient).
How do you explain the evolution of helpful behavior?

- Mutualism (actor benefits)
- Reciprocal altruism (actor eventually benefits)
- Kin selection (indirect selection)
<table>
<thead>
<tr>
<th>Interaction</th>
<th>Social Donor</th>
<th>Social Recipient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mutualism</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Reciprocity</td>
<td>+ (delayed)</td>
<td>+</td>
</tr>
<tr>
<td>Altruism</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Selfishness</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Spitefulness</td>
<td>-</td>
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Mutualism

Groups of lions can bring down larger prey and better defend the prey from other lions and hyenas.
Bluegill Male: Males form nest sites of 50 to 100 males. Mutualistic because predation is lower if your nest is surrounded by others.
Male lions will often cooperate in ousting resident males from a pride, or in defending a pride from other (outside) groups of males. Often, the males in a pride are closely related.
Reciprocal Altruism

Dispense an altruistic (beneficial) act, which is later returned as an equally beneficial act.

Most likely when:

- Repeated interactions between individuals
- Many opportunities for altruism
- Good memories
- Potential altruists interact in symmetrical situations
### Prisoner's Dilemma:

<table>
<thead>
<tr>
<th>Player A</th>
<th>Player B</th>
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<tbody>
<tr>
<td><strong>C</strong> (cooperate)</td>
<td><strong>C</strong> (cooperate)</td>
</tr>
<tr>
<td><strong>D</strong> (defect)</td>
<td><strong>D</strong> (defect)</td>
</tr>
<tr>
<td><strong>R</strong> (both receive light sentence)</td>
<td><strong>S</strong> (suckers payoff)</td>
</tr>
<tr>
<td><strong>T</strong> (reduced sentence for defector)</td>
<td><strong>P</strong> (both receive intermediate sentences)</td>
</tr>
</tbody>
</table>
Prisoners dilemma:

\[ T > R > P > S, \quad R > (S+T)/2 \]

Best strategy is to defect.

However, in the iterated prisoners dilemma, the best strategy is “tit-for-tat”, or “generous tit-for-tat”

Turner & Chao (1999)
Groomer helps groomee by removing parasites & debris

Favor is returned in baboon females
Females hang out together in groups of about 10.

Often fail to feed (on blood!) in a given night.

Will share blood by regurgitating blood meals to others.

Share more frequently with relatives, nestmates, and those that shared with them earlier.
“Would I lay down my life to save my brother? No, but I would to save two brothers or eight cousins.”

— JBS Haldane
“The Creator, if He exists, has a special preference for beetles.”

“Four stages of acceptance: i) this is worthless nonsense; ii) this is an interesting, but perverse, point of view; iii) this is true, but quite unimportant; iv) I always said so.”

“Now my own suspicion is that the Universe is not only queerer than we suppose, but queerer than we CAN suppose.”

— JBS Haldane
William Hamilton (1936–2000)

Kin Selection

Hamilton’s rule: A gene for altruistic self sacrifice will spread through a population if the cost to the altruist is outweighed by the benefit to the recipient devalued by a fraction representing the genetic relatedness between the two.
\[ Br - C > 0 \]

\[ w_i = a_i + \sum_{j} r_{ij} b_{ij} \]

- \( w = \) inclusive fitness
- \( a = \) direct benefit
- \( r = \) relatedness
- \( b = \) benefit
<p>| | |</p>
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<td><strong>Direct Selection</strong></td>
<td><strong>N_1</strong> survive without parental care</td>
</tr>
<tr>
<td></td>
<td><strong>N_2</strong> survive because of parental care</td>
</tr>
<tr>
<td><strong>Indirect Selection</strong></td>
<td><strong>N_3</strong> survive because of help</td>
</tr>
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### Direct Selection

| \( N_1 \) survive without parental care |

### Indirect Selection

| \( N_2 \) survive because of parental care |
| \( N_3 \) survive because of help |

**Direct Fitness** = \((N_1 \times r) + (N_2 \times r)\)

**Indirect Fitness** = \(N_3 \times r\)

**Direct + Indirect Fitness** = Inclusive Fitness
Half-siblings
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Actor → Shared → Recipient

r = 1/4

Full-siblings
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Actor
Mother × Father
Recipient

r = 1/2
Pied Kingfisher
Year-old males that fail to find a mate can become primary helpers, secondary helpers, or delayers.

Primary helpers help their mother raiser her nestlings, really throwing themselves into the job.

Secondary helpers help an unrelated individual a little, or they can just sit out the year, becoming delayers.

Eusociality

- Overlap in generations between parents and offspring
- Cooperative brood care
- Specialized castes of nonreproductive individuals
Haplodiploidy

Mother (diploid) × Father (haploid)

Sister \( r(\text{sister-sister}) = \frac{3}{4} \)

Brother \( r(\text{sister-brother}) = \frac{1}{4} \)

r(\text{mother-daughter}) = \frac{1}{2}

r(\text{mother-son}) = \frac{1}{2}
Because sisters are highly related, a female worker should bias her help towards reproductively competent sisters, rather than toward her brothers.

The queen is equally related to sons and daughters, and favors equal investment in each.

Conflict between queen and daughters (parent-offspring conflict).
Sisters share three times more genes with each other than with brothers. This favors a stable investment ratio of 3:1 in favor of sisters.

Queen wants a 1:1 investment.
Are hymenopteran colonies biased in their allocation of resources to males/females?

Yes:

(1) Trivers and Hare (1976) found the expected 3:1 investment ratio (weight of all female reproductives vs. male reproductives).

(2) Mueller (1991) showed that worker hymenopteranans can alter their investment in colony mates depending on their relatedness.
When a colony is founded by a single female, the asymmetry in relatedness \((r=3/4)\) persists, and workers invested more energy in females (57% of colony weight).

If queen is removed, a worker takes over her role. Now workers are helping raise their nieces \((r=0.375)\) and nephews \((r=0.375)\). The investment in males changes (males 63% of reproductives weight).
Evolution of Eusociality

- Probably ecological (eusociality has only evolved in groups that build complex nests and care for their larvae for extended periods).

- If young are dependent upon parental care and predation is high, it is difficult for a female to breed on her own.

- Cooperation/eusociality might have evolved as a best-of-a-bad-job situation (like the nest helping example given earlier).
Naked mole rat

- Live underground in groups of up to 200 individuals
- Breeding restricted to a single “queen” and to several “kings”
- Others are non-reproductive and act as workers
- Diploid, but colonies composed of closely related individuals (inbred, $r$ is about 0.81)
- Up to 85% of all matings are between parents and their offspring, or between full sibs.