

## 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


Horns
Bighorn Sheep


Elephant Tusks


African Lion: Mane is used for protection during male clashes (male-male competition)



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.)

Pheasant: Elaborate bright red wattle on cheek


## Two Types of Sexual Selection

- Male-male competition (intra-sexual selection)


## Male-male competition

- Within group dominance
- Female-defense polygyny
- Mate (female) choice (inter-sexual selection)
- Territorial polygyny
- Lekking (competition for a position in the lek)

Within group dominance
Female defense polygyny

Grey Wolves


Northern
Elephant Seals


## Sperm competition



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## Why are females choosy?

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



## Mate Choice

Two broad categories:

- Resource based
- Non-resource based

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

Why?

## 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.

## 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")


## Mate Choice

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

Good Genes Example


Gray Tree Frog (Hyla versicolor) Short vs. Long Calls

## Final Topics

| Fitness Measure | High Food | Low Food |
| :---: | :---: | :---: |
| Larval growth | LC | LC |
| Time to meta. | LC |  |
| Mass at meta. |  |  |
| Larval survival |  |  |
| Postmeta. growth |  | LC |

## 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

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## 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 ${ }_{27}$ prefer neat bowers.


## 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)

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.


Many species of bowerbirds build elaborate bowers, decorate them with colorful objects, and have
elaborate courship displays


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## Fembots



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## Sensory Bias/Exploitation

Latent preferences in females are used by males to gain greater reproductive success.

Physaleumus Frogs

P. coloradum P. postulosum

P. coloradum: Males attract mates by calling using WHINES in males
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.

|  | Female Pref. |
| :---: | :---: |
| WHINE | NO |
| WHINE+CHUCK | YES |




## 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)

| Interaction | Social Donor | Social Recipient |
| :---: | :---: | :---: |
| Mutualism | + | + |
| Reciprocity | + (delayed) | + |
| Altruism | - | + |
| Selfishness | + | - |
| Spitefulness | - | - |

## 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

Groomer helps groomee by removing
parasites \& debris
Favor is returned in baboon females



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."

\author{

- 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."


William Hamilton (1936-2000)

Hamilton, W. D. 1964. The genetical evolution of social behavior, I and II. J. Theor. Biol. 7:1-52.
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## 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.

$$
\begin{aligned}
& \quad B r-C>0 \\
& w_{i}=a_{i}+\sum_{j} r_{i j} b_{i j} \\
& \mathbf{w}=\text { inclusive fitness } \\
& a=\text { direct benefit } \\
& r=\text { relatedness } \\
& \mathrm{b}=\text { benefit }
\end{aligned}
$$

| Direct Selection | $N_{1}$ survive without <br> parental care |
| :---: | :---: |
|  | $N_{2}$ survive because of <br> parental care |
|  | $N_{3}$ survive because of <br> help |



Direct Fitness $=\left(N_{1} \times r\right)+\left(N_{2} \times r\right)$
Indirect Fitness $=N_{3} \times r$

Direct + Indirect Fitness = Inclusive Fitness



## Eusociality

- Overlap in generations between parents and offspring
- Cooperative brood care
- Specialized castes of nonreproductive individuals
- Secondary helpers help an unrelated individual a little, or they can just sit out the year, becoming delayers


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 hymenopterans can alter their investment in colony mates depending on their relatedness.

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## Mueller (1991)

- When a colony is founded by a single female, the asymmetry in relatedness ( $r=3 / 4$ ) persists, and workers invested more energy in females.
- 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 increases.



## 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.

