

Sexual Selection and Mating Systems



"For crying out loud, Warren ... can't you just beat your chest like everyone else!"

Darwin was perplexed by traits that appeared to impair male survival in some species



The lion's mane or the tusks of the babirousa



The tail of the male widowbird



Darwin also observed that most animals are sexually dimorphic in appearance & behavior



Elephant Seal



Siamese Fighting fish

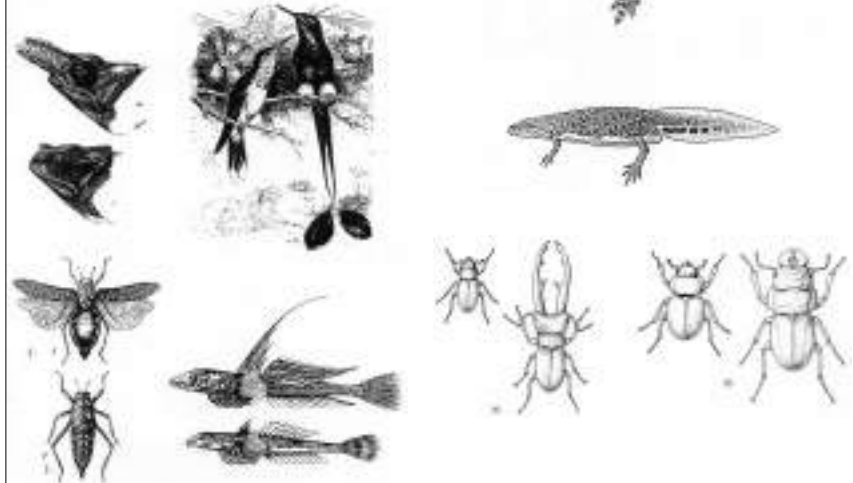
Some species are sexually monomorphic



But sexually monomorphic species are fairly rare, & even in these species, subtle sex differences often exist.



Most animals are sexually dimorphic



Most birds are sexually dimorphic



Most mammals are also sexually dimorphic



Darwin observed that, in many animal species, males are typically

- Larger
- Stronger
- Better armed
- More ornamented
- More aggressive



Male bower birds

Weaponry present in males but not in female conspecifics



Male ornaments impose survival costs but enhance RS



In his 1872 book, *Sexual Selection & the Descent of Man*, Darwin suggested a new form of natural selection

- Sexual selection: a special form of natural selection that occurs when individuals vary in their ability to secure mates
- Sexual selection favors traits that can enhance ability to compete for or attract mates, even if those traits decrease survival

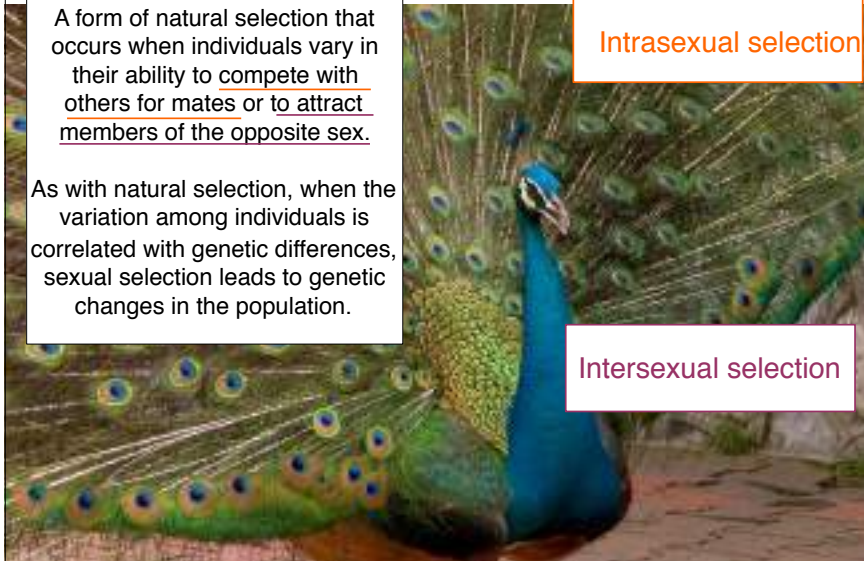
Sexual Selection

A form of natural selection that occurs when individuals vary in their ability to compete with others for mates or to attract members of the opposite sex.

As with natural selection, when the variation among individuals is correlated with genetic differences, sexual selection leads to genetic changes in the population.

Intrasexual selection

Intersexual selection



Sexual selection favors characteristics that enhance reproductive success

- Primary sexual characteristics
 - Genitalia and organs of reproduction
- Secondary sexual characteristics
 - Morphological differences between the sexes that are not directly involved in reproduction



Ornaments and mate choice in peafowl

- Research question: Are peacock tails an ornament used in mate choice? (Loyau, Saint Jalme, & Sorci 2005)
- Males aggregate on leks, where they display to females

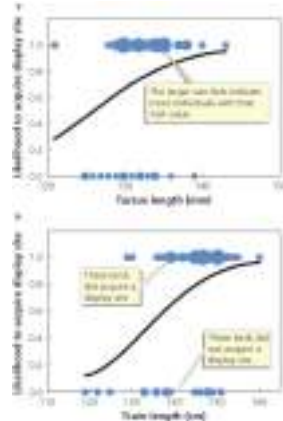


Ornaments and mate choice in peafowl

- Methods:
 - Peacocks (*Pavo cristatus*)
 - Measured:
 - Tail length and male body size
 - Number and duration of tail displays
 - Number of vocalizations and copulations

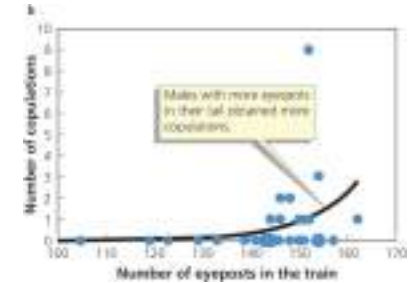
Ornaments and mate choice in peafowl

- Results:
 - Larger males with longer tails were most successful in defending a display site

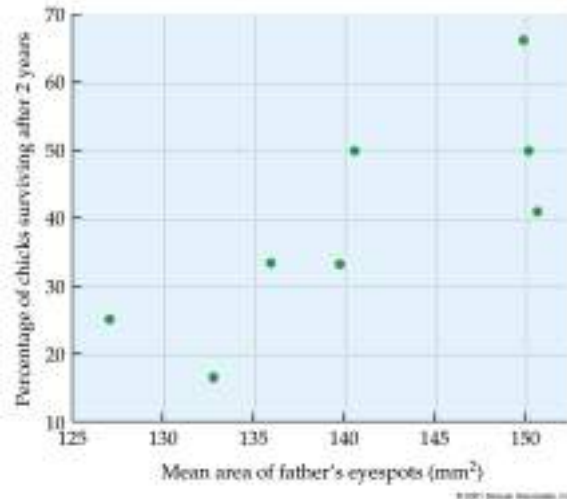


Ornaments and mate choice in peafowl

- Results:
 - Males performing the most displays and with the greatest number of ocelli obtained the most copulations
- Conclusion:
 - Mate competition and mate choice are important in evolution of peacock tail



The number of eyespots on a peacock's tail and quality as a sire



The extent of sexual dimorphism varies among species



What does this suggest about selection pressures?

Sexual dimorphism

- The greater the variability in reproductive potential between the sexes, the more dimorphic males and females are.

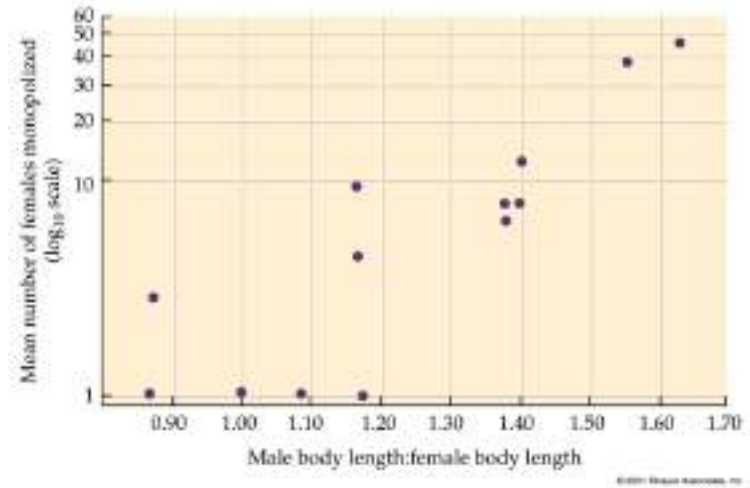


gray wolf



elephant seal

The greater the sexual dimorphism, the greater the male's ability to monopolize many females



Sexual Selection

Intrasexual Selection

- Subterfuge
- Direct confrontation
- Dominance hierarchies
- Alternative mating strategies
- Sperm competition



Intersexual Selection

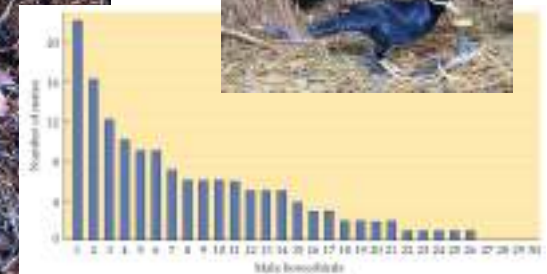
- Mate choice
 - Based on material benefits
 - Without material benefits



Undermine the efforts of competitors

Intrasexual Selection

Members of one sex compete with one another for access to the other sex





Sexual Selection

Intrasexual Selection

- Subterfuge
- Direct confrontation
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Intersexual Selection

- Mate choice
 - Based on material benefits
 - Without material benefits



Infanticide



Intrasexual Selection: Direct Confrontation

- Direct control of mates
- Control of a resource
- Fighting to gain access to mates

- traits often evolving in this context:
 - size and weaponry
 - aggressive behavior
 - honest signals to avoid costly conflicts



Dominance Hierarchy

social ranking system within a group, wherein some individuals concede limited resources to others without a fight



A close-up photograph of a baboon's face, showing its characteristic blue and white fur. Overlaid in the top-left corner is a bar chart with the following data:

| Rank | Percentage of total copulations |
|--------|---------------------------------|
| 1 | ~45 |
| 2 | ~35 |
| 3 | ~25 |
| 4 | ~20 |
| 5 | ~15 |
| 6 | ~10 |
| 7 | ~5 |
| 8 | ~3 |
| 9 | ~2 |
| 10 | ~1 |
| Others | ~10 |

Correlation between male dominance rank and quality of reproductive success

In many species, dominant males can monopolize access to fertile females.

A photograph of two large male seals with reddish-brown fur competing for a female. A rainbow is visible in the background. To the right is a bar chart showing the percentage of total copulations for each rank in a male dominance hierarchy:

| Rank | Percentage of total copulations |
|--------|---------------------------------|
| 1 | ~38 |
| 2 | ~18 |
| 3 | ~10 |
| 4 | ~12 |
| 5 | ~8 |
| 6 | ~4 |
| 7 | ~2 |
| 8 | ~2 |
| 9 | ~2 |
| 10 | ~2 |
| Others | ~5 |

Rank in male dominance hierarchy

In some species, females will even incite competition.

Alternative Mating Tactics

1. Consortships of low-ranking males w/ females
2. Coalition formation b/w low-ranking males
3. Satellite males (female mimics & fringe matings)

olive baboon

Great plains toad

bluegill sunfish



Intrasexual selection can also occur after mating

- Mate guarding
 - When a male follows his mate to prevent her from mating with rivals
- Extra-pair young
 - Offspring of a pair-bonded female produced outside the pair bond by a third-party male
- Sperm competition
 - Competition between sperm of different males to fertilize eggs
- Cryptic female choice
 - When female influences the fertilization success of sperm from one male over that of others

Mate guarding in warblers

- Research question: How effective is mate guarding? (Chuang-Dobbs, Webster, & Holmes 2001)

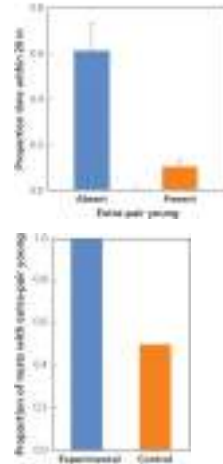
Mate guarding in warblers

- Methods:
 - Black-throated blue warblers (*Dendroica caerulescens*)
 - Observations:
 - Followed focal males and measured distance between them and their mates
 - Experiment:
 - Removed some males for one hour during female's fertile period



Mate guarding in warblers

- Results:
 - Males who spent more time mate guarding had fewer extra-pair offspring
 - Experimentally removed males had more extra-pair offspring
- Conclusion:
 - Mate guarding can be an effective strategy for increasing paternity assurance



Sperm Competition



When females are sexually promiscuous, there is competition among males with respect to the fertilization success of their sperm.

Sperm Competition 1st male advantage

- Mate guarding
- Copulatory plugs & anti-aphrodisiacs



Emasculation serves as a copulatory plug in the golden orb web spider



Figure 1
Male *Aphidius jessense* spider, ventral view. Eggs removed. The conductor (C) is located on the right pedipalp (see missing on the left side (pedipalp)). Scanning electron microscope image.



Figure 2
Genital region of male *Aphidius jessense* spider. Each genital opening is plugged by a conductor (C) and its corresponding embolus (E). Scanning electron microscope image.

(Fromhage & Schneider 2006)

Anti-aphrodisiacs

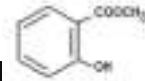
- In some species, males transfer chemicals to females during mating that render them unattractive to future males



fruitfly



green-veined white butterfly



methyl salicylate

Sperm Competition

2nd male advantage

- Removal
- Dilution



Argentine Lake Duck



Brush-like tip to remove previously deposited ejaculate



Muscovy Duck Penis Everting-main slowed 10x

Removal



black-winged damselfly



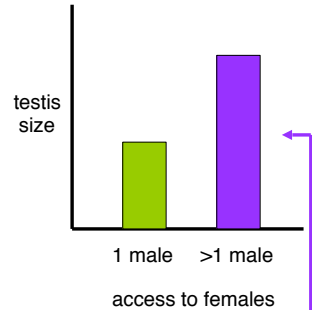
Competitor's sperm is removed with 'sperm scoop' before deposition

Dilution

In general, the male that introduces more sperm into the female has a fertilizing edge over his competitors.



bighorn sheep



1 male >1 male
access to females

Rate of spermatogenesis is determined by gonadal mass

(Pizzari 2006)

Dominant ram cannot always control access to the female, so mates with her as soon as reunited

Dilution



dunnock



After male returns from foraging, he pecks at female's cloaca until she everts it, sometimes ejecting sperm bundle. The male then reinseminates the female.

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Cryptic Female Choice

the ability of a female who has received sperm from multiple donors to choose whose sperm fertilize her eggs



Sexual Selection

Intrasexual Selection

- Subterfuge
- Dominance hierarchies
- Alternative mating strategies
- Sperm competition



Intersexual Selection

- Mate choice
 - Based on material benefits
 - Without material benefits
 - Including cryptic female choice



Intersexual Selection

Females decide:

- Who will get the opportunity to contribute sperm
- Which sperm will fertilize each egg
- How much to invest in each egg/offspring

Males affect female decisions by:

- Providing females with resources
- Demonstrating their good condition



Females select males to obtain direct material benefits

- Direct material benefits
 - Material resources obtained by a female from mating with a particular male
- Nuptial gift
 - A physical resource such as a food item that a male provides to a female to enhance his mating success

Mate choice based on material benefits

(provision of resources)

Male hangingfly w/
nuptial gift



Male redback spider about to sacrifice his life for love



Mate choice based on material benefits

(permit utilization of resources; e.g. feeding grounds, nest sites)



Male great grey shrikes give extrapair mates more food

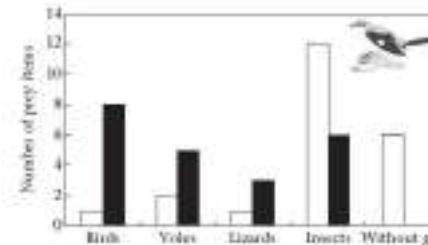


Fig. 1. Number of nuptial gifts offered by males to females in within-pair (□) and extrapair (■) copulations. Prey are shown by taxonomic groups. G test: $G_{1,2} = 22.87$, $P = 0.026$.

(Tryjanowski & Hromada 2005)



Copulation is more likely if high energy foods are offered. The only investment in extrapair copulation is food.

Mate choice based on material benefits

Good Parent Theory

- Mate selection is based on male color, ornamentation, and courtship behavior because they are indicators of a male's capacity to provide paternal care.



15-spined stickleback



humans?

Good Parent Theory

- Male pigmentation is carotenoid-based
- Females prefer to mate w/ redder males
- Redder males feed young more often & their chicks survive better



house finch

(Hill 1991; Navara et al. 2006)

Which of the following *is* an example of intrasexual selection?

- a. a male black-winged damselfly removes a competitor's sperm from the female's sperm-storage organ before depositing his own
- b. two female phalaropes (shorebird in which males provide all parental care) fight over access to a potential male mate
- c. a group of male elephant seals establish a dominance hierarchy that has profound effects on the reproductive success of individual males
- d. two low-ranking male baboons form a coalition against a dominant male, preventing him from monopolizing access to a fertile female
- e. all of the above are examples of intrasexual selection

In what situation can cryptic female choice enhance the fitness of a female?

- a. When she mates with males that differ in quality
- b. When she mates with one male relative
- c. When she mates with a single low-quality male
- d. When she mates repeatedly with the same male
- e. When she must hide from predators while mating

Mate choice without material benefits

Healthy Mate Theory

- Mate selection is based on male color, ornamentation, and/or courtship behavior because they are indicators of a male's health & parasite load

Brighter the plumage, more disease resistant & parasite-free. Less likely to infect female or offspring.



Healthy mate and immune system function in birds

- Research question: How does parasite load affect mate choice? (Zuk et al. 1990)
- Hypothesis: Hamilton-Zuk hypothesis
 - Parasites and pathogens play an important role in sexual selection when secondary sexual traits are costly and condition-dependent
- Predictions:
 1. Females should prefer to mate with males that have the greatest expression of secondary sexual traits
 2. High parasite loads will reduce that expression in males

Healthy mate and immune system function in birds

- **Methods:**

- Red jungle fowl (*Gallus gallus*)
- Infected half the males with intestinal nematode
- Measured size and color intensity of comb
- Conducted mate choice trials with infected and controls (uninfected) males



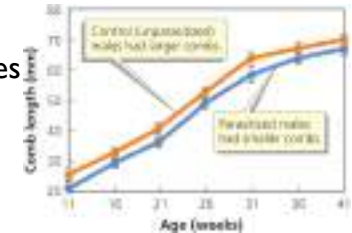
Healthy mate and immune system function in birds

- **Results:**

- Parasitized males had smaller, duller combs than controls
- Females preferred control males

- **Conclusion:**

- Support for Hamilton-Zuk hypothesis



Mate choice without material benefits Good Genes Theory

- Mate selection is based on male color, ornamentation, symmetry and courtship behavior b/c they provide honest information about the possession of viability-enhancing genes, which will be passed on to offspring
- Developmental homeostasis (e.g. symmetry)
- Immune competence
- Survivability
- Heterozygosity and/or MHC complex that complements that of female



Mate choice for good genes in frogs

- **Research question:** How do females assess male quality? (Jacquiéry et al. 2009)
- **Hypothesis:** Females select males for genetic benefits based on their vocalizations
- **Prediction:** The most attractive males provide the best gene alleles (fitness) to offspring

Mate choice for good genes in frogs

- Methods:

- European tree frogs (*Hyla arborea*)
- Captured and identified males from four ponds
- Observed number of matings
- Collected egg masses and reared in lab
- Measured tadpole growth rate and survival
- Genotyped tadpoles to determine parentage



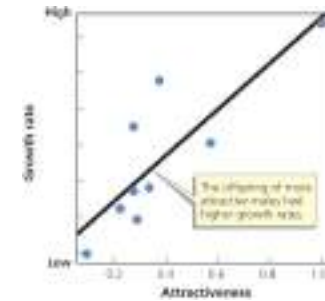
Mate choice for good genes in frogs

- Results:

- Only 10 of 15 males sired offspring
- Males that sired more offspring produced tadpoles with higher growth rates

- Conclusion:

- Females select males for genetic benefits



Mate choice without material benefits

Runaway Selection Theory ('Sexy Sons')

- Discriminating females acquire sperm with genes whose primary affect is to influence daughters' preference for same traits mom found attractive & to endow sons with traits preferred by females
- Traits may reduce survival
- Trait may have arisen arbitrarily

