

Some traits are difficult to view as adaptations, because they appear to provide a *disadvantage* to the organism

- Structural traits: cumbersome antlers or excessively long tailfeathers (make movement difficult); bright, flashy colors (make the organism more visible to predators)
- Behavioral traits: aggression within a species, particularly among members of the same sex (e.g. fighting among males)

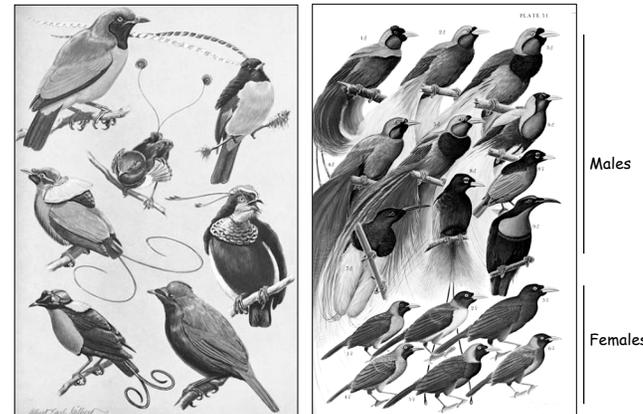
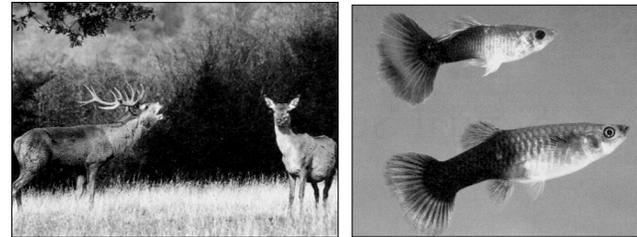
Darwin realized that these and other traits don't make sense under natural selection. They are often: sexually dimorphic (limited to one sex, typically males); expressed only in the breeding season; or not expressed in immature individuals

Some observations

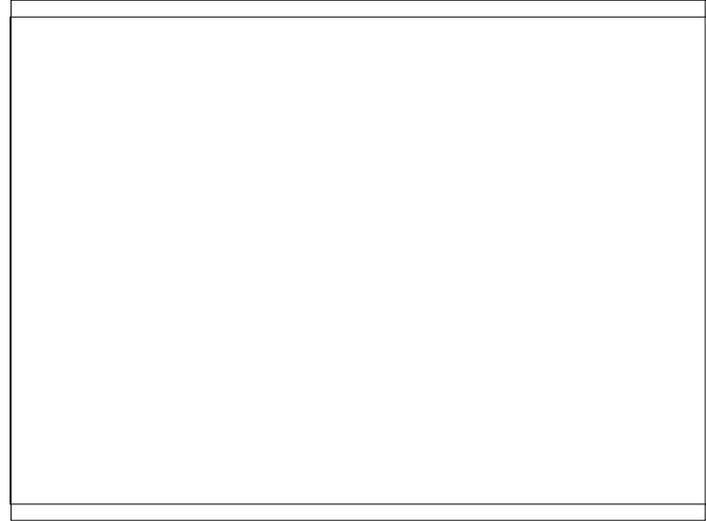
- There are sexually dimorphic traits that don't improve success in survival or copulation
- They are often not expressed outside of the breeding season
- They are often not expressed until maturity

Darwin asked:

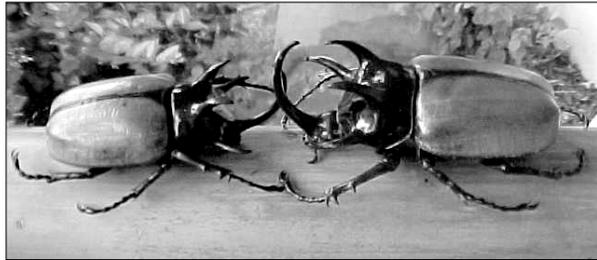
Can natural selection explain these differences?

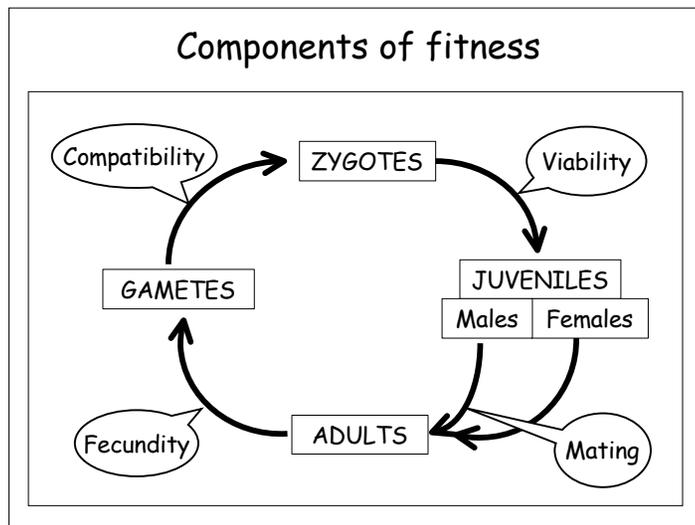
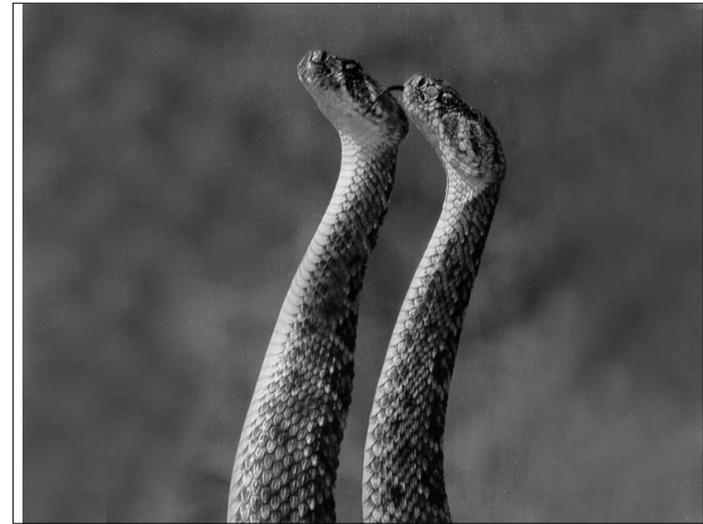


Birds of paradise



Stag beetles





Darwin proposed a theory of **sexual selection**, a special case of natural selection:

Sexual selection is, specifically, selection caused by competition between individuals of the same sex (usually males) for access to mates, resulting in differential reproductive success

Since transmitting genes to next generation requires survival and reproduction, traits can be selected for if they increase mating success, even if they decrease survival

This explains the selection for seemingly disadvantageous traits. In fact, they are adaptations for reproductive success.

Why males?

Operational sex ratio:

The relative numbers of males and females available to breed at a given moment

In the majority of cases, female biological investment in reproduction is greater than that of males; the OSR is male-skewed

Sexual selection helps explain:

- Male-male competition
- Sexual dimorphisms
- Female choice of mates

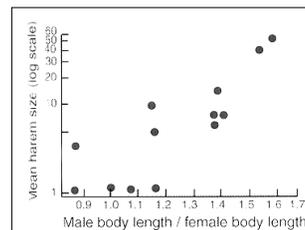
Male-male competition

- Combat
- Sperm competition
- Infanticide

Combat



Elephant seals fight for protected breeding territories that females prefer



Fewer than 1/3 of males ever get mates



Elk (red deer) compete similarly for dominance, and access to females

Risks:

- 23% of mature males injured in fights
- 6% of these injuries permanent

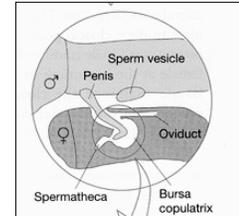


Potential payoff:

- Some males get 10x mean number of matings, increasing fitness

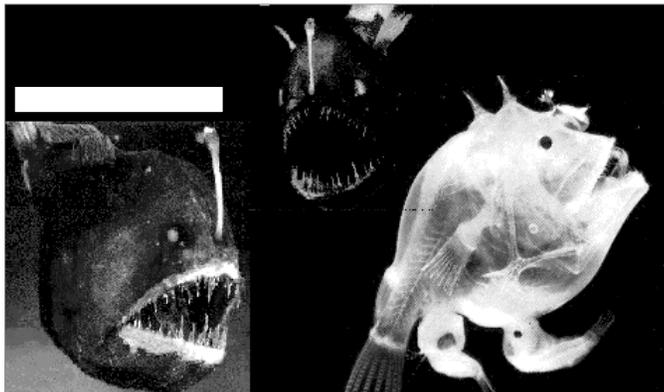
Sperm competition (strategies):

- Make more sperm than other males
- Block other males' sperm (e.g. sperm plugs)
- Kill or remove other males' sperm

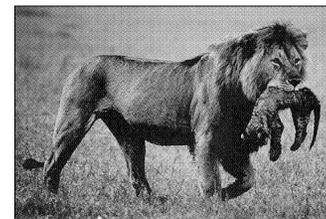


Male damselflies physically remove any previous sperm in a female, before mating

"Parasitic" males in female Angler fish



Infanticide



- Infanticide causes 10% of all lion mortality!
- Infanticide eliminates the genes of competing males
- Infanticide decreases time until females become receptive again
- It's not just lions... many bird and rodent species show infanticide by males -- also some primates, including the closest relative to humans, the chimpanzee

Biologically, males are virtually unlimited in the number of offspring they can sire. Females, however, have a much greater biological investment in their offspring (e.g. egg production, gestation, feeding/nursing, parental care...)

Thus, the females of many species are choosy about the males they mate with. Mate choice may be influenced by:

Increased male visibility (or audibility)

Optimal breeding or nesting territories established by competitive males

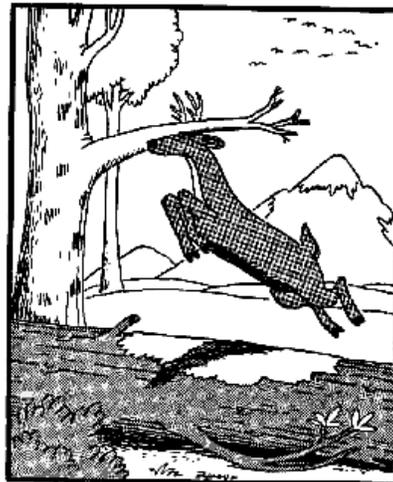
Courtship rituals, nuptial gifts...

Female preference does not require a conscious choice



Was Darwin right? Do male display traits really...

- Decrease survival?
- Increase mating success?



Nature scenes we rarely see

Experimental test: Do male displays decrease survival?



Tungara frogs in Panama make two kinds of mating calls. Females strongly prefer calls that contain a "chuck" element

Whine 

Whine + Chuck 

However, consider the fringe-lipped bat:



Experimental test:
Do male displays increase mating success?



Male

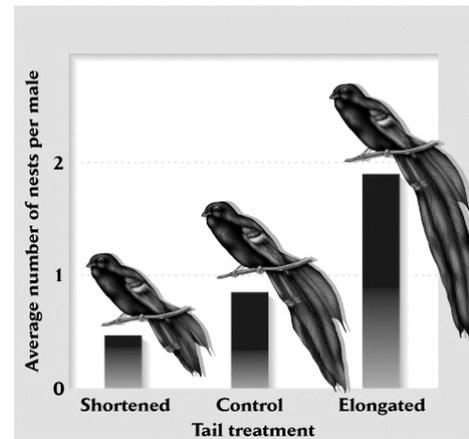
Female

Widowbirds

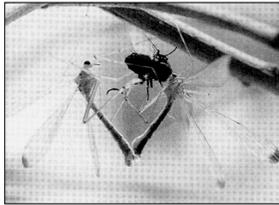
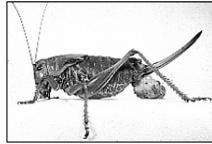


The male widowbird tail is a handicap in flight

Tail altering experiment with long-tailed widowbirds in Kenya

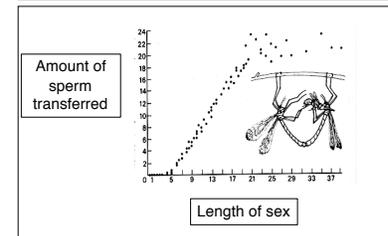
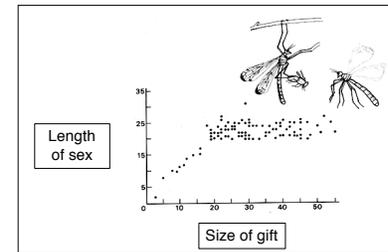


Nuptial gifts



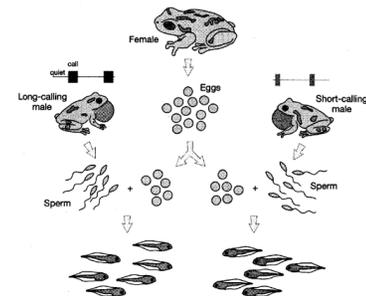
Elizabeth Taylor once possessed a 69.42-carat pear-shaped diamond, dubbed the Taylor-Burton.

Hangingflies and the nuptial gift



Indirect selection on preference genes: Preferences for "good genes" in males

1. Preference and courtship display become genetically correlated
2. Display is genetically correlated with "good genes" that increase survival
3. Selection on good genes causes indirect selection on preferences



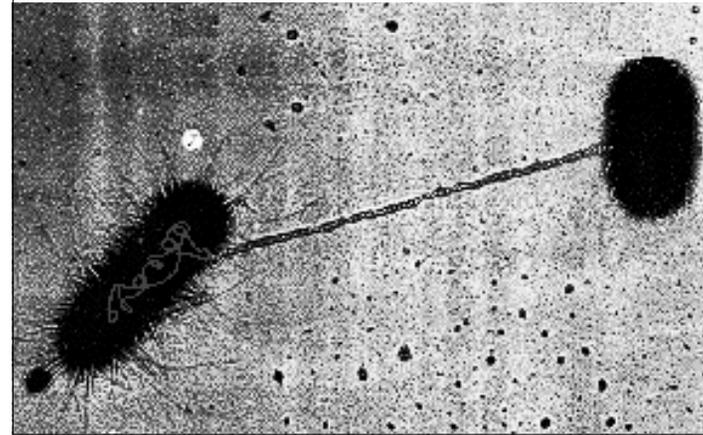
Conclusion:

Females choosing males with long calls have offspring that survive better.
The long call is an "honest signal"

Why would sexual reproduction evolve at all?

Sex is defined as the combination of genetic material from two individuals to produce offspring

Sex-like behavior in bacteria (conjugation)



Sex in insect-pollinated plants

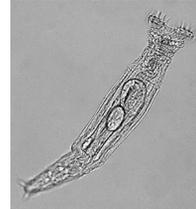


Sex in animals (external fertilization)



Sex in animals (internal fertilization)

What's the alternative to sex? Asexuality... and/or Parthenogenesis



Bdelloid rotifers



Whiptail lizards



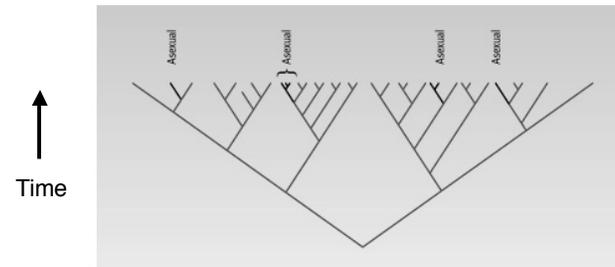
Male bees

Some plants are also asexual...



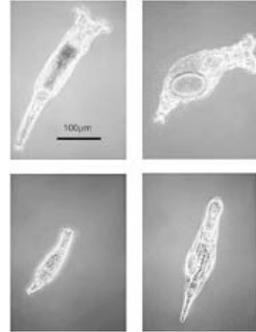
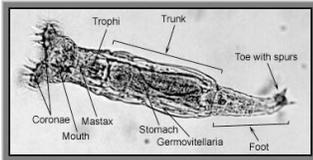
... but it is still relatively rare

Asexual lineages are scattered on the tips of the evolutionary tree



- Their closest relatives are often sexual
- This means that asexual species don't last long

One of the few known ancient asexual lineages:
The bdelloid rotifers (small aquatic animals)



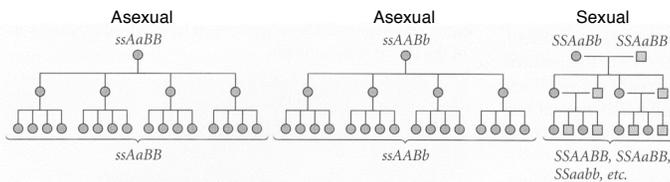
- Over 350 species
- 40 M years with no sex!
- An "evolutionary scandal"

Sex is an evolutionary mystery

Possible reasons not to reproduce sexually
(from an evolutionary perspective!):

- The "two-fold cost" of meiosis
- Finding a partner can be a problem
- Sex breaks up good combinations of genes

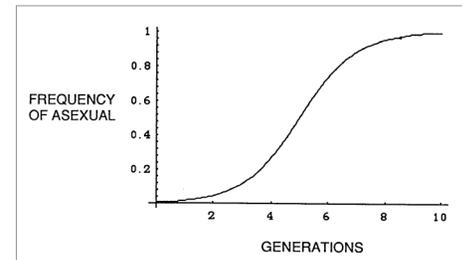
The two-fold cost of meiosis (the cost of having 2 sexes)



Assume constant number of offspring per generation. Asexual females leave *twice* as many descendant genes as those that undergo meiosis and are sexual

□ = male
○ = female
S = sexuality allele
s = asexuality allele

All else equal, you might think the two-fold cost of meiosis should cause an asexual mutation to spread *very* quickly...



So why isn't that happening all the time???

Sex is an evolutionary mystery

Reasons not to have sex (from an evolutionary perspective!):

- The "two-fold cost" of meiosis
- Finding a partner can be a problem
- Sex breaks up good combinations of genes

Asexual species are more common in species that colonize islands and new habitats...



... which suggests there is a disadvantage to sex when the species is rare (requires finding a partner)

Sex is an evolutionary mystery

Reasons not to have sex (from an evolutionary perspective!):

- The "two-fold cost" of meiosis
- Finding a partner can be a problem
- Sex breaks up good combinations of genes

What does sex do genetically?

- Segregation
- Recombination

Both of these break up combinations of genes

So what's the good news
about sex?

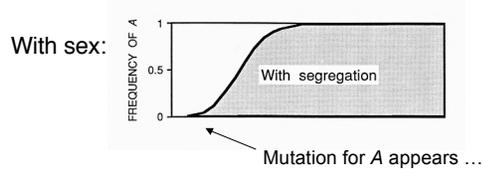
(After all: 15,470,117 sexually-reproducing
species can't all be wrong!)

Evolutionary advantages to having sex

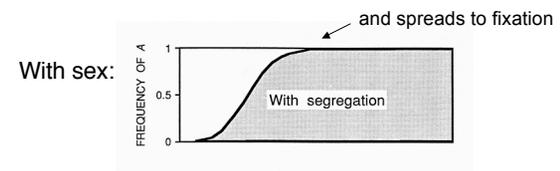
It can speed up adaptations

- By bringing together good mutations
- By freeing good mutations from bad ones

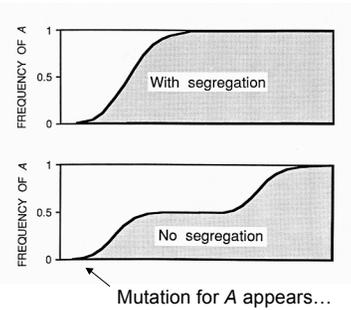
Segregation can bring together two copies
of a good mutation at a single locus



Segregation can bring together two copies
of a good mutation at a single locus (AA)



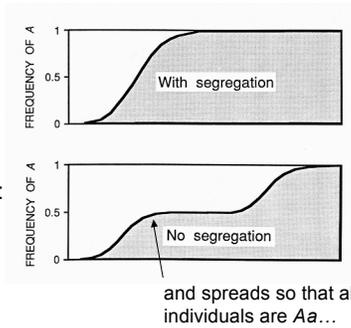
Segregation can bring together two copies of a good mutation at a single locus (AA)



Without sex:

Mutation for A appears...

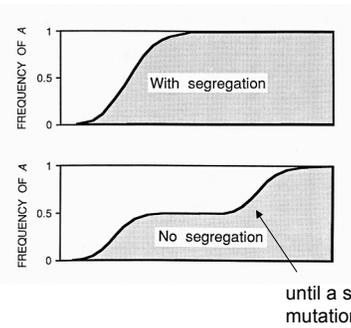
Segregation can bring together two copies of a good mutation at a single locus (AA)



Without sex:

and spreads so that all individuals are Aa...

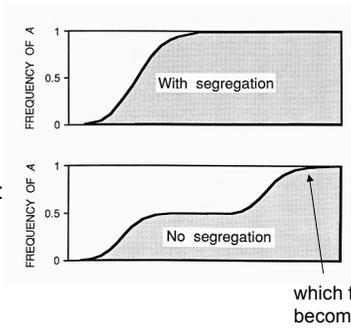
Segregation can bring together two copies of a good mutation at a single locus (AA)



Without sex:

until a second A mutation appears...

Segregation can bring together two copies of a good mutation at a single locus (AA)

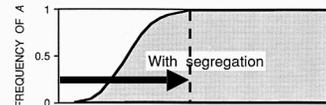


Without sex:

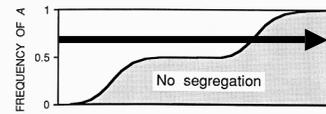
which finally lets the locus become fixed for AA

Segregation can bring together two copies of a good mutation at a single locus

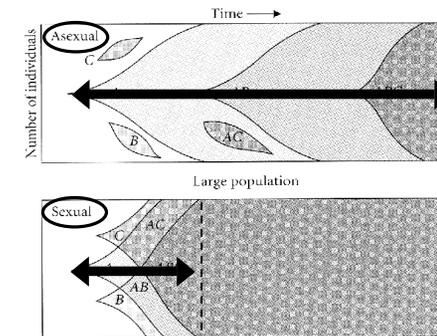
With sex:



Without sex:



Recombination can also bring together good mutations at two different loci



Evolutionary advantages to having sex

1) It can speed up adaptation

- By bringing together good mutations
- By freeing good mutations from bad ones

(via recombination)