BIOL2007 EVOLUTION OF SEX AND SEXUAL SELECTION

EVOLUTIONARY QUESTIONS ABOUT SEX

Today:

A) *The evolution of sex*

1) What is the advantage of sex?
2) What is the optimal sex ratio?

B) *Ev. of sexual dimorphism - sexual selection*

3) Why are there "*secondary sexual characteristics*"

OTHER interesting questions *could* be asked:

4) Why has meiosis evolved to share out chromosomes?
5) Why are mitochondria and organelles NOT shared equally?
6) Why are there only 2 sexes?
7) How does sex determination evolve?

See: BIOL2011 (Behavioural Ecology and Sociobiology) and BIOL3012 (Sex, Genes and Evolution).

WHAT IS SEX?

- *Recombination* – all of life
- *Meiosis* - eukaryotes only
- *Anisogamy* - unequal gamete size - multicell eukaryotes
- *Dioecy* - Separate sexes - vs. *hermaphrodites* and *monoecy*

These are complex energy-requiring traits
⇒ ADAPTATIONS.
Recombination seems to be a lowest common denominator of all sex.

EVOLUTION OF SEX

Costs of sex

Recombination and sex is complicated, costly, predation-prone (even if fun).

Two-fold cost of sex. Populations grow faster if pure *parthenogens.* Suppose each female produces 2.4 progeny:

Generation	*Parthenogenetic*	*Sexual*
0	100 females	100 females (+ 100 males)
	↓	↓
1	240 females	120 females (+ 120 males)
	↓	↓
2	576 females	144 females (+ 144 males)
	↓	↓

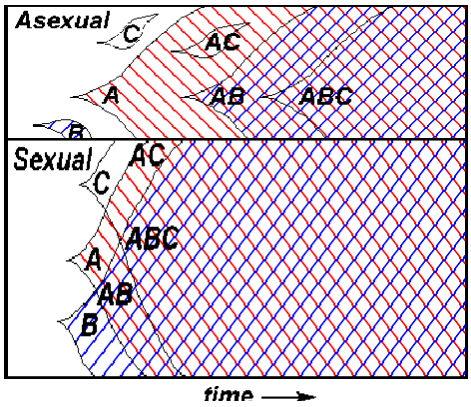
… and so on (but it works for any reprod. rate)

Males contribute little; males are useless! Parthenogens outdo sexual females and increase in frequency.
Advantage not always twofold…
If such strong *disadvantages* to dioecy,
…must be some pretty hefty *advantages*.
Recombination is the primary feature of sex.
Advantages of sex must have something to do with recombination.

Advantages of sex

a) recombination increases ev. rate

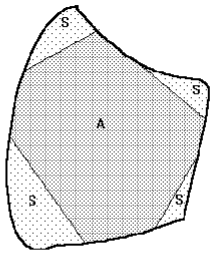
Muller: Recombination allows advantageous mutations to combine in the same individuals.



Species compete, so a higher evolutionary rate can be adaptive for a *species*.
May work against *individual* disadvantages for sex within populations: so a form of *group selection*.
Asexual "cheats" might gain *individual advantage* and spread to fixation within their own species, but cannot spread to other species.
If other species have higher evolutionary rate, may cause extinction of asexual species: one of the few cases where people believe that group selection may actually be operating.

Evidence: asexual species trapped on “twigs” in phylogenies; do not produce many progeny species.
Asexual (clone) lineages, also often seem trapped in some areas where they can compete.
Sexual forms are found in habitats where asexuals cannot invade.
For example, many weeds of human cultivation are asexuals, but sexual relatives live in more complex non-cultivated environments. (e.g. dandelions)

Phylogeny showing how asexual species (A) tend to be scattered rarely within the phylogeny of sexual species (S). This suggests that asexuals do not have a long term advantage, though their scarcity is also clearly helped by the scarcity of asexual mutations in most sexuals.



Distributions of asexual forms (A) within species often suggests that their advantage is only present in some environments or habitats. Sexual forms (S) may be in the minority but often “hang on” on the periphery of the range.

b) *Individual selection*

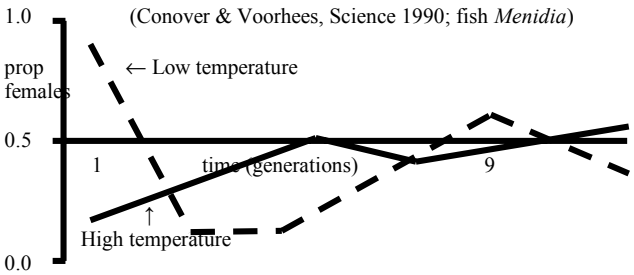
Normally, evolutionists are often suspicious of group selection explanations.
Some species: facultatively asexual, e.g. aphids, or water fleas (*Daphnia*).
Sexuals persist in many lineages in competition with asexuals. --> implies individual selection:

Survival in a coevolutionary "arms race".
If the environment of offspring very different from that of parent, parent's adaptations may not be sufficient.
Sex as a lottery for producing at least some progeny with reshuffled adaptations - a direct individual selection advantage to parents in producing recombined offspring.

Other ideas. There are plenty, but we will leave that to other courses.

EVOLUTION OF THE SEX RATIO

In dioecious organisms, sex ratio usually ~1:1.
Darwin puzzled, and eventually gave up, admitting that the subject was too complicated!
RA Fisher: *frequency-dependent* selection.



Conover & Voorhees' experiment accords with Fisher's frequency-dependent sex-ratio theory:
It isn't the ratio of of *numbers* of the sexes that matters, but the ratio of *investment*.
Females should *invest* about ½ their resources in male production and female production.

EVOLUTION OF SEXUAL DIMORPHISM - SEXUAL SELECTION

Darwin explained *secondary sexual characteristics* as due to a struggle for genetic representation between members of the same sex.
He contrasted *sexual selection* (struggle for mating success) with *natural selection* (struggle for survival and reproduction after mating).
Nowadays: sexual selection as a special form of natural selection, but a very important one.

Why are males more extreme?

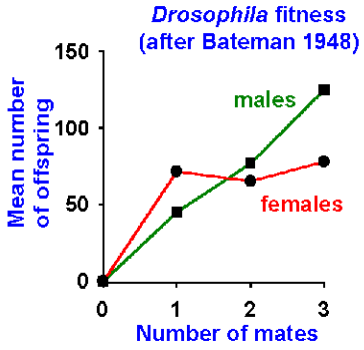
Most often, males are more flamboyant than females, with horns, bright colours, or displays [SHOW SOME EXAMPLES].
Why is it usually this way around? Darwin's view was that males are more "passionate" than females, due to the need for energetic males to seek out females. But why *do* males seek females, rather than the other way round?

Males:
cheap gametes
can produce lots
little parental investment
⇒ potentially father many offspring

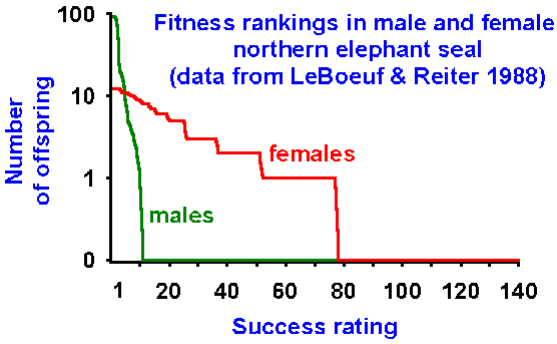
Females:
expensive gametes
often show more parental care, at least as far as nutrients in the egg
⇒ limited number of offspring than males

⇒ *Males:*
compete for access to females
more indiscriminate, less to lose

⇒ *Females:*
plenty of willing males around
worthwhile to be choosy, because number of matings doesn't limit offspring number.



In *Drosophila*, females little extra benefit from fooling around
males' fitnesses are roughly proportional to the number of matings.



Greater struggle for matings among males ⇒ males under greater sexual selection. Females rarely benefit much from more mates; males benefit from virtually unlimited matings.

In elephant seals, > 90% males father no offspring; The fittest male fathered 93. But> 50% females have one or more offspring. Males have higher *variance* in offspring number.

Quite likely that sexual selection may obtain increased matings *at the expense of reduced survival*.
Darwin argued that sexual selection could outweigh natural selection, and explain much conspicuous coloration in the animal kingdom. Sexual selection can *antagonize* natural selection for camouflage.

Darwin: ***two major types of sexual selection:***
Intrasexual selection - male-male competition in which males compete, often by fighting for females. And …
Intersexual selection **-** sexual selection by ***female choice***, in which males compete for the favours of females.

Intrasexual selection - male-male competition

a) *Selection for fighting ability*

Relatively uncontroversial.
But not always appreciated, at least by laymen who believe in “balance of nature”, that serious injury, even death may result from fights between males.
(Not getting mated is genetic death!)

Examples:

- Red deer males: harems of females, defend by roaring, displaying, and finally fighting; injuries and death may result.
- Salmon: males fight to the death with enlarged hooklike jaws, useless for feeding. All males die at the end of season; so competition very severe.
- Fig wasps: in some species, specialized males with huge jaws hatch out and kill other males, before mating with all the females in the fig.

b) *Sperm competition*

Male-male competition: after females mate multiply.
Here, *sexual selection between sperm* of rival males for fertilization of eggs, often in the reproductive tract of females.
In primates, males from species with more *polyandry* have larger testes than males from *monandrous* species.
Gorillas are monandrous, and have smaller testes than human males!
(But chimps have bigger testes than us).

Sperm competition, like other forms of fighting, can have nasty effects on the female too.
Tracey Chapman (UCL Biology) has shown this in *Drosophila*. Mated females age faster than unmated females, due male accessory gland proteins.

Intersexual selection - sexual selection via female choice

Sexually dimorphic traits seem costly.
Costly display traits can evolve if females actively choose males with more exaggerated traits.
Darwin: females have an "aesthetic sense", but few believed him, perhaps understandably.
Wallace, believed most sexual dimorphism not costly; instead due to display in male-male competition.

RA Fisher: theoretical analyses rehabilitated female choice in the 1930s.
Today, an explosion of work showing females do indeed choose, and that sexually selected traits are indeed often costly.
For example: Anders Møller’s barn swallows.

But why SHOULD females choose males with exaggerated and costly traits?
Three major theories:

a) *Sensory bias.* A modern version of Darwin’s hypothesis. Recognition *requires* a preference exaggerated traits. Exaggeration a *supernormal sign stimulus* for the natural male.
Pre-existing preferences: *Physalaemus* frog phylogeny shows that an odd "chuck" sound has evolved in a terminal branch of the genus.
Females of related spp. which lack the "chuck" still like it. (Mike Ryan, University of Texas).
Sensory bias can explain some features of dimorphism but additional ideas to explain why some traits are very costly.

b) *Direct benefits of female choice*

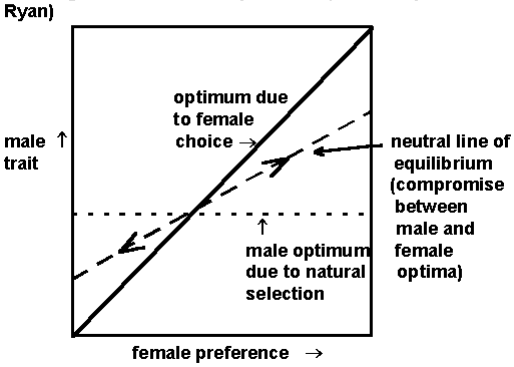
Avoiding disease by mating with uninfected males.

c) *Indirect benefits of female choice* Indirect benefits are passed on to the offspring via genetic contribution from male.

i) *“sexy sons”.*

Mathematical models, by Russ Lande and Mark Kirkpatrick (1980s): *runaway models of sexual selection*.
Imagine male trait evolution and female choice; females *can choose whatever they want*;
males have a *natural-selection* optimum.

Lande/Kirkpatrick model of male trait and female choice, showing a line of neutral equilibrium (after Kirkpatrick & Ryan)



A *line of neutral equilibrium* (neither stable or unstable) along which populations may drift.
Coevolution of male trait and female response;
Sometimes; evolves *towards* the line of neutral equilibrium, whereupon evolution will stop.
In other cases evolution can angle *away* from the line of neutral equilibrium; a *runaway process of evolution*.

The Kirkpatrick/Lande runaway involves *linkage disequilibrium* between genes for male trait and genes for female choice.
Females are selected to mate with extreme males; and produce males that are themselves favoured, i.e. "*sexy sons*".
Runaway eventually stops via natural selection; alternatively, the population could go extinct because of the extreme exaggeration. Like the ?Irish Elk.

ii) *"good genes hypothesis".* Females choose males with exaggerated, costly traits as "badges" which indicate high fitness.
Here females are selecting exaggerated males because *all* of their progeny will be fitter; they have "good genes".
Sickly development means it will be more difficult to produce exaggerated traits.

The ***parasite hypothesis*** of Hamilton and Zuk. Male bird and mammal displays often involve bare patches of skin (e.g. baboons' bottoms, wattles on cockerels).
Blood diseases, parasitism: changes the colour of blood (e.g. diseases of chickens).
These displays are *honest signals* of health.
Hamilton & Zuk: sexually dimorphic species of birds tend to suffer more from parasites.

Another variant of "good genes" idea is Zahavi's "***handicap principle***".
Non-costly male badges prone to cheating
Zahavi: only a very costly trait uncheatable
A costly "handicap" is selected, paradoxically, because it guarantees "honest signalling".

Tests between ideas for the evolution of costly traits
None of the three ideas ruled out.
"Good genes" makes clear empirical predictions about fitness of progeny.
Anders Møller: longer-tailed male barn swallows chosen by females, but also fewer blood-sucking mites
Mite load heritable. However, females also directly benefit, by avoiding infection, even before any indirect advantage for offspring.

Non-adaptive *"sexy sons"* idea appealing, but difficult to prove. Need to show that trait has no direct or future *"good genes"* benefit. (Hard!)
Neutral line of equilibria seems inescapable.
Sexual (or natural) selection is competition, and may not always give greater adaptation; selection can drive us away from optimum.
Semantic problems with *handicap principle*: How can a trait which is nonadaptive (i.e. costly) also be adaptive (signal of high fitness)?
Anyway, though evolutionists haven't yet resolved these arguments, they are fun to think about.

Sexual selection in humans
Darwin: "The Descent of Man and Selection in Relation to Sex". Sexual selection explained the extraordinary racial differences in animals *and* humans.
Desmond Morris, Jared Diamond, "evolutionary psychologists": similar conclusions.
Human features like:

- lips
- hair colour, skin colour
- breasts in females, beard in males
- copulation when not in oestrus
- weapons, war?
- ornaments, jewellery?
- music?
- art?

... etc.

TAKE HOME POINTS

Evolution of sex:

- The basis of sex is recombination.
- Separate sexes may be costly
- Separate sexes may exist because:
    - group selection against asexuality
    - offspring variability (individual selection)
- Sex ratios stabilize near 1:1, a form of frequency-dependent selection

Sexual selection for exaggerated male traits:

- Male-male competition
    - fighting
    - sperm competition
- Female choice
    - sensory bias
    - direct benefit to self or offspring
    - indirect, inherited benefits
        - sexy sons
        - good genes

FURTHER READING
Douglas J. Futuyma. 2005. Evolution.
Ch 14: 329-339, Ch 17: 417-426.

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