

BIOL2007 SEX AND SEXUAL SELECTION

EVOLUTIONARY QUESTIONS ABOUT SEX

Sex is fun, but is also still a puzzle for evolutionary biologists. Today we will explore:

A) *The evolution of sex*

- 1) What is the evolutionary advantage of recombination and sex?
- 2) What is the optimal sex ratio?

B) *Evolution of sexual dimorphism - sexual selection*

- 3) Why are there sexually dimorphic "*secondary sexual characteristics*" - Darwin called characters "*secondary sexual*" if they were dimorphic but weren't directly involved in gamete production or transmission.

There are many *OTHER* interesting questions that *could* be asked. For example:

- 4) Why has meiosis evolved to share chromosomes equally between gametes?
- 5) Why are mitochondria and other organelles NOT shared equally between the sexes?
- 6) Why are there only 2 sexes anyway; not 3, 5, or 100?
- 7) Why do different kinds of sex determination evolve (e.g. chromosomes, environment)?

These and similar questions are answered in more detail in Behavioural Ecology and Sociobiology and in Sex, Genes and Evolution in the 3rd year. This lecture is just a sampler of the many areas covered.

WHAT IS SEX?

In mammals, reproduction *requires* sex. In the rest of the animals, plants, and prokaryotes this is not necessarily true. Sex is usually (but not always) associated with reproduction; however reproduction often happens without sex. Sex is actually a smorgasbord of characters:

- *Recombination* - prokaryotes and eukaryotes
- *Meiosis* - eukaryotes only
- *Anisogamy* - unequal gamete size - multicellular eukaryotes
- *Dioecy* - Separate sexes - vs. hermaphroditism and monoecy

All of these are complex traits, and therefore almost certainly adaptations. But for what? Recombination seems to be the lowest common denominator of all sex, and perhaps the key. For example it is hard to imagine sex in *E. coli* with its pili and *F*-plasmids, or meiosis and gamete fusion in eukaryotes evolving unless there was some major use for recombination.

EVOLUTION OF SEX

Costs of sex

Recombination and sex are often costly. Although fun, sex may expose the organisms having it to increased predation and other dangers.

A particularly severe cost has been identified in dioecious organisms, the ***two-fold cost of sex***. Populations grow faster if they consist purely of female *parthenogens*, rather than having 50%

males. Suppose each female produces 2.4 progeny:

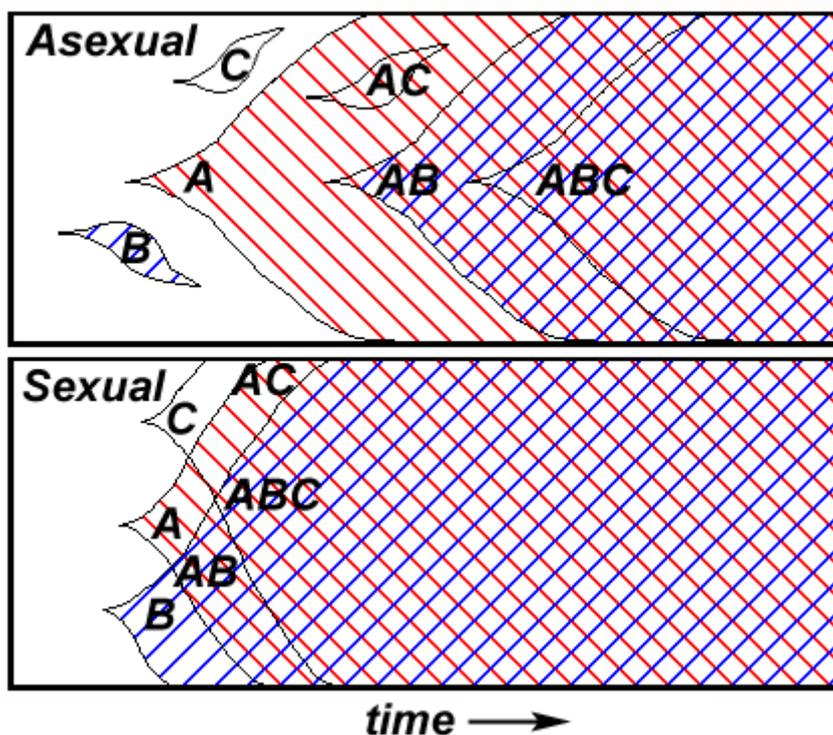
Males only contribute genes to the population, but suck up nutrients from the females; clearly males are useless! In a mixed population, parthenogenetic females increase at twice the rate (2.4x per generation) of sexual females (1.2x per generation). The advantage won't always be twofold, because males are *sometimes* useful: they may help with parental care, nuptial feeding, and so on rather than just standing around looking pretty. Even so, males are almost always a load!

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 reproductive rate)	

Given such strong disadvantages to dioecy, to say nothing of the cost and danger of meiosis and other forms of sexual liaisons, there must be some hefty advantages to sex, or it wouldn't have evolved. As we have already mentioned, the advantages of sex are probably to do with recombination, i.e. the breakup of disadvantageous linkage disequilibrium.

Advantages of sex

a) Recombination can increase evolutionary rate

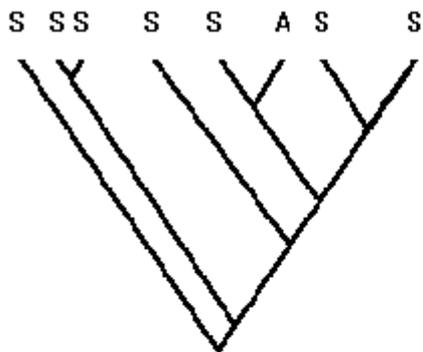


In an asexual population, advantageous genes A,B,C arising in different parts of the population can never get together in the same individual; instead the population must wait until the mutations occur sequentially in the same lineage (top panel). HJ Muller suggested that in a sexual population (lower panel), recombination allows the mutations to recombine in the same individuals. Thus, the evolutionary rate is increased.

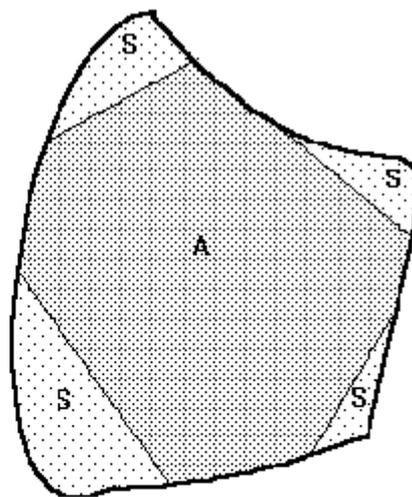
Species compete, so a higher evolutionary rate can be adaptive for a species; but this group advantage must outweigh the individual disadvantages of sex within populations. This would therefore be an example of **group selection**. An asexual "cheat" would gain an

individual selection advantage and spread to fixation, even though this may cause extinction of the species as a whole. This is one of the few cases where people believe that group selection may actually be operating.

Asexual (clonal) species do exist, but they seem to be trapped on "twigs" in phylogenies (below left); they do not seem to produce many progeny species. Asexual lineages are also often trapped in certain parts of a species' range, while sexual forms of the same species are found in a variety of habitats where asexuals do not invade (below right). For example, weeds of human cultivation are often asexuals, but sexual relatives seem to outcompete them in more complex natural environments.



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) "Muller's ratchet". In a similar argument, HJ Muller also suggested that recombination would allow individuals that had accumulated deleterious mutations to produce recombinant offspring without mutations. In an asexual population, this would not be possible; every time a lineage became fixed by genetic drift for a mutation, it could never be reversed, hence the term "ratchet". Because drift is involved, both Muller's mechanisms are important in small populations.

c) Individual selection. However, evolutionists are often suspicious of group selection explanations. Some species are facultatively asexual, for example potatoes, strawberries, aphids, or water fleas (*Daphnia*) - these organisms could presumably evolve asexuality if advantageous to individuals. As shown above in the right hand figure, sexuals persist in species that have one or more asexual lineages. This implies individual selection, but what? One of the most likely is:

Survival in a coevolutionary "arms race". Because of the rapid evolution of predators, pathogens, and predators, - or hosts and prey - the world is a dangerous and unpredictable place. If the environment of offspring is very different from that of their parent (for example, because of rapidly evolving disease epidemics, or predators), their parent's adaptations may not be sufficient for survival. Therefore, sex can be seen as a lottery for producing at least some progeny which may have usefully reshuffled adaptations. This gives a direct individual selection advantage to parents in producing recombined offspring.

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

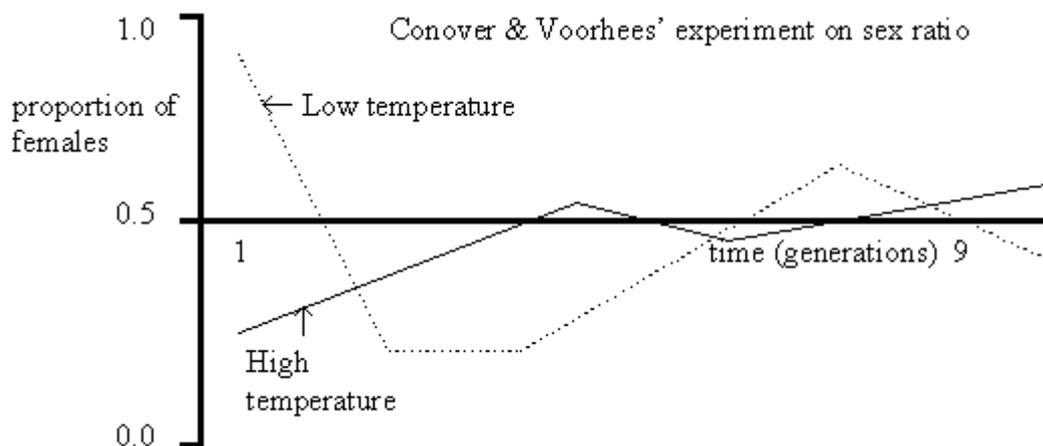
EVOLUTION OF THE SEX RATIO

In dioecious organisms, the sex ratio is often about 1:1. Darwin puzzled why this should be, but [admitted](#) that the subject was too complicated for him (what a great man!).

RA Fisher sorted it out eventually. Under his theory, there should be **frequency-dependent selection** for rarer sex. Think of a population with almost all females. This would be very good for the population, which would have highly efficient reproduction (see [The two-fold cost of sex](#) above) and some very happy males. But now imagine a mutant female that produces more males. She would do much better because each of her male offspring will mate with hundreds of females - she would have many more grandchildren this way than if she produced offspring at the population sex ratio. Similarly, if there is an excess of males, any female would have more

offspring than each male, only a fraction of which can mate and produce progeny.

Fisher's theory has been tested (right). In the fish *Menidia menidia* sex is determined by temperature. In this species, high temperatures produce lots of males, and low temperatures produce lots of females. The exact ratio at different temperatures is under genetic control.



When fish were reared in population tanks at abnormally elevated and lowered temperatures for 9 generations (right), the sex ratios evolved from rather extreme in the first generation of rearing, to a ratio of about 1:1 in the 9th generation, as expected under [Fisher's sex-ratio theory](#).

EVOLUTION OF SEXUAL DIMORPHISM - SEXUAL SELECTION

Darwin explained sexual dimorphism in secondary sexual characteristics as due to a struggle for genetic representation in future generations 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, we recognize sexual selection as a special form of natural selection, but a very potent and important one.

Why are males more extreme?

Most often, males are more flamboyant than females, with horns, bright colours, or displays [SHOW SOME EXAMPLES] that are more prominent in males and females.

Why is it usually this way around? Darwin's view was that [males are more "passionate" than females](#), and noticed that they energetically sought out females. But why *do* males seek females, rather than the other way round?

Males

- cheap gametes
- can produce lots
- little parental investment

⇒ can potentially father many offspring

⇒ Males:

- may compete for access to females, because not all mated
- more indiscriminate with mating, less to lose

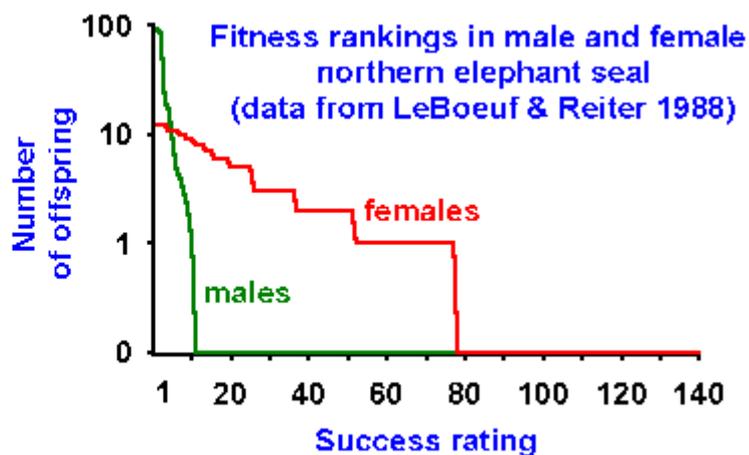
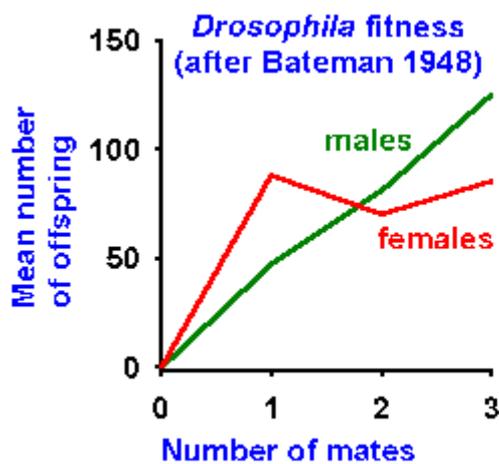
Females

- expensive gametes
- more parental care (e.g. nutrients in egg)

⇒ potentially have a more limited number of offspring than males

⇒ Females:

- plenty of willing males, no problem getting mated
- more choosy, no. of matings doesn't limit offspring



In *Drosophila* (above left), females get little benefit from fooling around, whereas males' fitnesses are roughly proportional to the number of matings they obtain.

This greater struggle for matings among males shows that males will be under greater sexual selection than females. Females may sometimes get a few extra offspring as a result of one or two further matings, but males would continue to benefit from virtually unlimited matings. In nature, many males obtain few matings, and some males can obtain a very large number; whereas females usually have an intermediate number. In the rather extreme example from elephant seals (above right), over 90% of the males father no offspring at all, while the fittest male fathered 93; in contrast, over half of the females have >1 offspring. Males have higher *variance* in offspring number

This powerful logic for sexual selection also predicts that males should risk reduced survival to obtain matings. Darwin argued that sexual selection could outweigh natural selection, and explain much conspicuous coloration in the animal kingdom which would normally be prohibited by natural selection for camouflage. Sexual selection can *antagonize* natural selection. This factor alone may explain dangerous and costly weapons like the antlers of the Irish Elk, or extraordinarily cumbersome display organs like the peacock's tail.

Darwin recognized **two major types of sexual selection**:

Intrasexual selection - male-male competition - 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 - sexual selection via male-male competition

a) Selection for fighting ability

Relatively uncontroversial, almost everyone agrees this happens.

It is not always appreciated, at least by laymen who believe in the balance of nature, that serious death and injury may result from fights between males. For example:

- Red deer males have harems of females, defend by roaring, displaying, and finally fighting; injuries and sometimes death may result.
- Salmon: males fight to the death with enlarged hooklike jaws, useless for feeding. All males die at the end of the season, so competition is very severe; a male that doesn't achieve mating loses everything.
- 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

Although [sperm competition](#) has been recognized for some years, it is increasingly realized that a great deal of male-male competition occurs after multiple mating by females. Here, the competition is between sperm from different males for access to eggs in the reproductive tract of females.

Intersexual selection - sexual selection via female choice

As we have discussed, many sexually dimorphic male display traits seem costly. Costly displays will evolve if females actively choose males with brighter or more exaggerated traits.

Darwin proposed the idea that females of dimorphic animal species have an "aesthetic sense", and choose the most beautiful males. Few believed Darwin, perhaps understandably. To Darwin, sexual selection via female choice seemed a nice counterintuitive example of his theory of natural selection: exaggerated, costly male traits evolved simply at the whim of females, rather than because they were useful as in ordinary natural selection. Even Wallace, who understood the argument very well, came to believe that most sexually-dimorphic traits were for display in male-male competition rather than evolved for choice by females. But Darwin's idea was rehabilitated by Fisher in the 1930s, and there has been an explosion of work since the 1970s showing that females do indeed choose certain kinds of males, and that sexually selected traits are indeed often costly. For example: Anders Møller's barn swallow work: [SHOW Møller OVERHEADS SHOWING COSTLINESS AND FEMALE CHOICE]

But why SHOULD females choose males with exaggerated and costly traits? this has generated much discussion. There are three major theories around:

a) Sensory bias. Essentially this is a modern version of Darwin's hypothesis. "Neural net" computer models suggest that an organism trained to recognize a particular shape may, after training, prefer an exaggerated version of that trait. For example, if a female recognizes her species by red colour, she may prefer a redder colour than present in the species, just because of the nature of recognition itself, and even if there are no redder males around. This sets up a **sensory bias** which males can exploit by becoming redder; redder males are in fact a **supernormal sign stimulus** for the natural male.

There is plenty of evidence for supernormal sign stimuli in nature, for all sorts of perceptual modalities. With respect to female choice, there is also some evidence for pre-existing preferences; for example, *Physalaemus* frog phylogeny shows that an odd "chuck" sound present in the otherwise "whine"-like male call has only evolved in a terminal branch of the genus. Strangely, females of related species whose males lack the "chuck" preferentially orient to taped calls that have the "chuck", as shown by Mike Ryan at the University of Texas. Clearly the preference for the "chuck" evolved before the chuck itself was incorporated into the song. (Also true of elongated "swords" in swordtail fish - *Xiphophorus*).

Once a new characteristic has evolved, females then train (evolutionarily speaking) on the new signal; in doing so, they may develop a further sensory bias, which then has an evolutionary tendency to become even more biased, and so on; leading to a *runaway coevolution* between male trait and female choice, but all initiated by sensory bias.

Although sensory bias can explain some features of sexual dimorphism, we need additional ideas to explain why some traits are very costly. Sensory bias may in general be adaptive, in that recognition may require a simple "caricature" memory. This will save storage space for the image; however, it may be highly non-adaptive to choose mates that have fraudulent or costly, exaggerated signals.

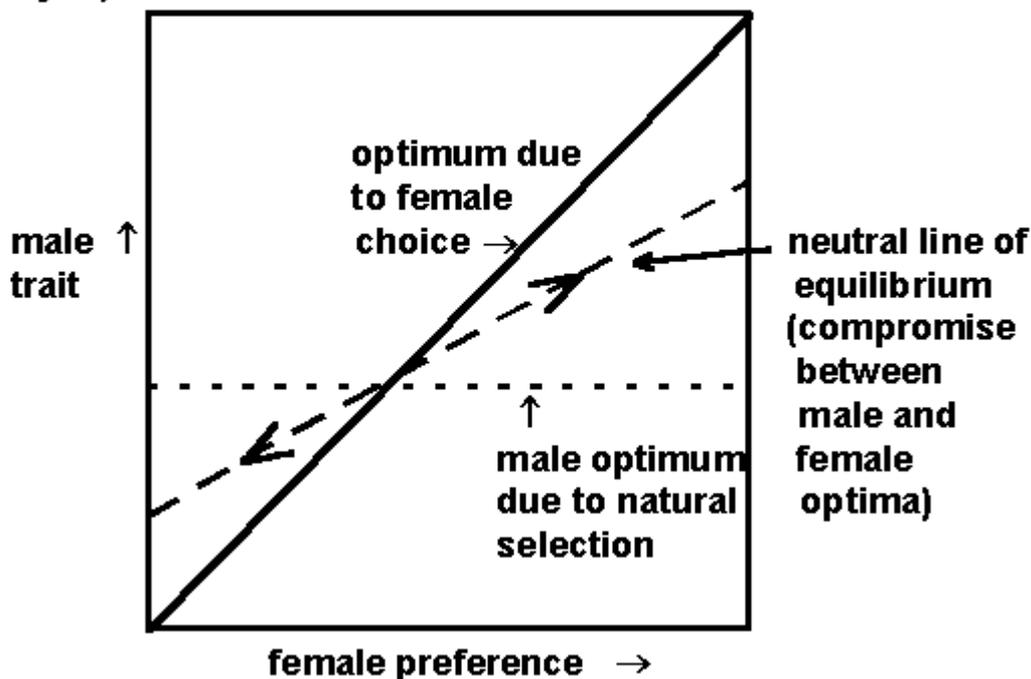
b) Direct benefits of female choice. It is fairly likely that females often choose healthy, larger males in order to gain a direct benefit. Females may be simply avoiding disease by mating with uninfected males; while female birds, for example, often need help from a healthy male to rear the offspring or defend territory.

c) Indirect benefits of female choice. However, it is likely that exaggerated traits are often chosen because they have heritable traits that are of value to their offspring. These are called indirect benefits because the benefits are passed on to the offspring via a genetic contribution from the male.

c.i) "Sexy sons". There are other ways in which runaway coevolution between male traits and female preference can occur, even without sensory bias. These mathematical models, by Russ Lande and Mark Kirkpatrick, are all recent (early 1980s), and the term *runaway models of sexual selection* were first applied to them; although, as we have seen, sensory bias can cause a similar effect.

Imagine a very simple model of male trait evolution and female choice. Assume that females can choose whatever they want (no costs for choice), but that males have a naturally-selected optimum. Female preference is cost-free (to the female), so the male optimum from her point of view is simply the same as her preference, whatever that is at the time. On the other hand, stabilizing selection affects the male trait. For instance in a bird, tail length has an optimum for aerodynamics. Obviously, the male's tail will evolve to some point that is a compromise between sexual and natural selection (dotted line between the male and female optima). The interesting thing about this compromise line is that in theory it is a *line of neutral equilibrium*, along which populations may drift.

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



What happens if the population is NOT on the line of neutral equilibrium? The answer depends on precise details of the selection. In some cases, there will be coevolution of male trait and female choice towards the line of neutral equilibrium, whereupon evolution will stop. In other cases, the direction of evolution can angle AWAY from the line of neutral equilibrium, in which case it leads to a potentially unending *runaway evolution*. (The Lande/Kirkpatrick models are interpreted to be what Fisher meant in a verbal argument for exponential coevolution of male trait and female preference. However, it is also possible he meant something along the lines of a sensory bias

coevolution).

This runaway involves an association, or *linkage disequilibrium* between genes for female choice and male trait: when a female with extreme preference mates with a male with an extreme trait (as her genes dictate her to), she ensures that her progeny (and their descendents) will have genes both for extreme female choice and for extreme male trait. Females are selected to mate with extreme males, essentially, because, by doing so, they are more likely to produce "sexy sons" (a term you will find in the literature) other females want to mate with. Eventually, the runaway will probably be terminated by natural selection against totally silly female preferences: it would be silly to mate with males who seem sexy, but simply cannot fly at all and always get nabbed by predators. In other cases, cost to the population may be so great that the population goes extinct because of the extreme exaggeration. We don't know of any good example, (maybe the Irish Elk? See main hall of Darwin Building); but it should be true in theory, because evolution maximizes relative fitness, not population fitness!.

c.ii) "Good genes hypothesis". Another possibility is that females choose males with exaggerated, costly traits, but because these traits are "badges", or cues to high fitness. Here females are selecting exaggerated males, not (just) because their sons will thereby be sexier, but because their progeny will be fitter, or have "good genes". Obviously, this must be true at some level; sickly males rarely get chosen for mating purposes. And sickly development means it is more difficult to produce exaggerated traits.

A well-known variant of this idea is the *parasite hypothesis* of Hamilton and Zuk. Many male bird and mammal displays involve bare patches of skin (think of baboons' bottoms and the wattles on cockerels). When these animals are ill or parasitized, the illness is often visible as changes in the colour of blood just under the skin of these displays. Diseases of chickens are often diagnosed in this way. These bare skin patches may be prime examples of "honest displays" which reveal the health status of the male. If disease resistance is heritable, females are making sure they have healthy offspring if they choose such healthy looking males. Hamilton & Zuk supported their theory by showing that sexually dimorphic species of birds tend to suffer more from parasites.

Another variant is Zahavi's *"handicap principle"*. Zahavi pointed out that a cheap male badge would be prone to cheating: a cockerel might mate if its cockcomb were pigmented red, rather than red due healthy haemoglobin flowing in the blood. Zahavi suggested that only a demonstrably costly trait, such as an energetic dancing display, or a tail so long that it causes flight inefficiency, would create an uncheatable signal. Essentially, a costly "handicap" would be selected as a male trait, paradoxically, because it is a guarantee of "honest signalling" for high fitness.

Tests between ideas for the evolution of costly traits

As we have seen, both the "good genes" and "sexy sons" ideas produce almost exactly the same outcomes: costly, exaggerated male traits which females strongly prefer.

At the moment, none of the above three ideas for explaining costly male traits can be ruled out. There seems evidence for all of them. The most recent idea, "good genes", has perhaps the edge, because it makes clear empirical predictions about the fitness of the progeny of males with extreme traits, which have often been verified. For example, Anders Møller showed that females choose longer-tailed male barn swallows; these males also had fewer blood-sucking mites, and the mite load was heritable. Females are choosing parasite-free males, and enhancing the parasite resistance of their own descendents. However females will also gain a direct benefit, by directly avoiding infection of themselves and their brood, even before the inherited advantage.

There are also semantic problems with the handicap principle. How can a trait which by definition has to be nonadaptive (i.e. costly) be at the same time adaptive (an honest signal of high fitness). Don't the adaptive and the non-adaptive cancel out?

I personally have a lot of admiration for the more non-adaptive "sexy sons" idea, even though it is more difficult to prove (you need to show that a trait has no direct or future "good genes" benefit, and this is hard to do). The logic of the neutral line of equilibria seems inescapable, regardless of whether or not fit males are chosen (and perhaps they frequently are, but they needn't be). Natural selection will not always lead to greater adaptation; in many cases, natural, and especially sexual selection can drive us beyond and away from a naturally selected optimum.

Anyway, though evolutionists haven't yet resolved these arguments, they are fun to think about.

Sexual selection in humans

It is no accident that Darwin's main treatise on sexual selection was called "The Descent of Man and Selection in Relation to Sex". Darwin felt that many human sexually dimorphic traits were under strong sexual selection, and that sexual selection, in the form of standards of beauty, explained many of the extraordinary racial differences in humans. More recently, a spate of popular authors (Desmond Morris, Jared Diamond) have proposed similar theories, and evolutionary psychologists are also coming to similar conclusions.

Features like:-

- bare skin
- lips
- breasts in females
- sex when not in oestrus
- weapons, war?
- music?
- art?
- ... etc.

... are uniquely human. These apparently non-adaptive features can be explained if mate choice, literally titillation, has caused their evolution. In humans, there seems to be a lot of mate choice by both sexes for such traits (mate choice by both sexes is also quite common in animals - we have simplified here). Can you think of a reason why certain kinds of human males might be in short supply, and why human males, as well as females, might therefore be choosy? The brain is, of course, used to further our survival. But the brain also produces literature, music, art, science, and humour; is it possible that the brain and its cultural output evolved in part as a secondarily sexual characteristics which enhance mating success?

We started with the idea that selection for representation in future generations via mating success (sexual selection) is just as important as success in reproduction and survival (fertility and viability natural selection). This course is not primarily about humans, but it is worth realizing that the ideas of sexual selection should apply to humans (but with the added complications of cultural inheritance) as well as to animals.

TAKE HOME POINTS

- Evolution of sex:
 - The basis of sex is recombination; but a lot of other interesting traits are associated.
 - Separate sexes are costly through lost reproduction; asexuality should be favoured
 - ... but separate sexes may exist because
 - lineages without sex go extinct (group selection against asexuality)
 - variability of sexual offspring may be directly important (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 benefit to descendents
 - sexy sons
 - good genes

These ideas are hard to test; but all seem probable.

FURTHER READING

FUTUYMA, DJ 1998. Evolutionary Biology. Sexual selection: chapter 20 (pp. 586-594). Evolution of sex: chapter 21 (pp. 606-617).

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