

## **Mating: sexual selection**

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- **Sexual selection:** selection that favors traits that increase male success in mating
- Sexual selection is just a kind of natural selection
  - but it is unusual in that it often favors traits that
    - are mostly or only expressed in males
    - and that seem to be useless or even harmful to the males' survival
  - the huge tails of male peacocks, for instance
    - that make it hard for the peacocks to escape predators
    - but make them more attractive to female peacocks
  - sexual selection favors traits like these if
    - if they improve the males' reproductive success by increasing matings
    - more than they harm reproductive success by increasing predation or other costs
- two kinds of sexual selection:
  - **intrasexual selection:** selection that occurs due to differences in success at mating that result from interactions between members of the *same* sex
    - the most common form is **male-male competition**
      - such as males fighting each other for access to females
      - the outcome of the interaction of the males determines which male mates; the female is not involved in the decision
    - classic example: intrasexual selection in baboons
      - led to large bodies and large canines among males
      - because bigger males with larger canines can drive other males away, so they get more access to females, so they leave more offspring
  - **intersexual selection:** selection that occurs due to differences in success at mating that result from interactions between members of *opposite* sexes
    - the most common form is **female choice**
      - such as females picking the most desirable male to mate with, based on some visible trait
    - classic example: intersexual selection among peacocks
      - led large tails among males, because the female peacocks prefer to mate with males with large tails, so the large-tailed males mate more often, so they leave more offspring
- other kinds of natural selection caused by predators, changing food supplies, etc. act more or less equally on males and females
  - but sexual selection acts primarily on the one sex that is competing for the other
    - that is, it mostly affects males
- we tend to think of survival to adulthood as being the biggest factor in natural selection, hence the phrase “survival of the fittest”
  - a phrase that does not even appear in Darwin's *Origin of Species*
- but in fact, sexual selection can exert a much stronger evolutionary effect than selection based on different rates of survival

- males who do not mate frequently may produce absolutely no offspring
  - this means absolutely none of their genes go into the next generation
  - from an evolutionary point of view, leaving no offspring is equivalent to dying in infancy
    - this causes very severe selection against traits that lead to having no offspring
  - yet, it is common for males to have no offspring
- meanwhile, males who mate often may produce many, many offspring
  - very rapidly increasing the representation of their traits in the next generation
  - being successful at mating and having a large number of offspring has a far greater effect than just surviving and having an average number of offspring
- example: imagine a species in which 80% of the males produce no offspring, and the remaining 20% father the entire next generation
  - these are realistic figures for many animals, from lions to baboons
  - the effect of this difference in just one generation would be equivalent to a drought that killed off 8 out of 10 individuals - a very drastic selection event
  - that is, an ordinary, common amount of selection on sexual success has as much effect on the next generation as the most drastic, rare extremes of selection that affect survival
- the same is true even if most males do leave one or two offspring, as long as a few have large numbers of offspring
  - say ten males have one offspring each, and one male has a dozen
  - that one male contributes more genes to the next generation than all the rest of the males combined!
  - the traits that led him to have many children are *much* more common after a single generation!
- Point: the process that has the strongest, most consistent effect on evolution is not “survival of the fittest”, but “reproduction of the sexiest”
- because sexual selection is so strong, it can favor traits that improve mating success even if they have significant costs for survival
  - classic example of sexual selection: peacock tails (on males)
    - the showier the tail, the more successful the male is at mating
    - the tails have gotten so big that they make it hard for the males to hide or get away from predators
    - but the benefit in terms of success in mating outweighs the cost to survival
- intrasexual selection (male-male competition) in primates
  - males try to keep other males away from females
    - this ensures that they are the likely fathers of any offspring
    - this involves hostile encounters or fights
  - so sexual selection favors large body size, large canines, possibly other traits in males that help one male defeat another for access to females
  - but females would not benefit as much from larger body size, canines, etc.
    - they would just have to eat even more to maintain a large body
    - when food is already their limiting factor in reproductive success

- since selection favors larger males but smaller females, eventually **sexual dimorphism** arises
  - differences between males and females
  - sure enough, those species with the greatest male-male competition have the greatest sexual dimorphism
    - male-male competition is assumed to be greatest in species whose social groups have the greatest imbalance of females to males
      - because if there are relatively few males in the group, mating with the many females, then there must be lots of males excluded from the group who are not mating at all
      - these **bachelor males** must be constantly driven away by the few **resident males** in the group
  - the evidence:
    - in monogamous species there is very little male-male competition, since each male is paired with one female
      - and indeed, monogamous species have almost no sexual dimorphism
      - gibbons and siamangs are a classic examples; try telling the males from the females at the zoo!
    - in multi-male, multi-female groups, there is considerable male-male competition
      - sexual dimorphism is marked
      - baboons are a classic example
        - note the much bigger bodies of the males, their big canine teeth, and intimidating “mane”
    - in single-male, multi-female groups, male-male competition is the most intense
      - the single resident male has to defend the whole group from circling bachelor males all the time
      - but as long as he can do so, he is rewarded with tremendous reproductive success, compared to the others who don't mate at all
      - species that form single-male, multi-female groups have the most extreme sexual dimorphism
      - gorillas are a classic example
        - gorillas often form single-male groups, but sometimes also include one or even two subordinate males
        - gorilla males are much bigger than females, more robust, aggressive, etc.
- So consider humans...
  - compared to most apes, we have minimal sexual dimorphism
  - human males are only a little larger than human females, and are only slightly better suited to fighting each other
    - no big canines
  - nothing like the difference between male and female gorillas, baboons, etc.
  - so humans presumably evolved in social groups with relatively little male-male competition
  - probably mostly monogamous pairs
    - so monogamy is not a recent, cultural invention for humans

- it is the mating system that must have prevailed for at least the later part of our physical evolution
- humans did not evolve in a social setting like that of baboons or gorillas
- of course, even though the bulk of the matings were probably within monogamous pairs, that would still be just the general rule
  - it does not mean that the membership of these pairs did not shift over time, or that there was no cheating
- mating strategies also affect sperm production
  - in most primates, females only mate during the part of their cycle when they can conceive: **estrus** (the period when they are “in heat”)
  - if there are multiple males around, a female could mate with several males during a single estrus period
    - which one is most likely to father her infant?
      - whichever male deposits the most sperm will have the best chance of being the father of the offspring, just by increasing the odds that one of his sperm will fertilize the ovum
    - so in multi-male, multi-female groups, where multiple males mate with each receptive female, whichever male puts out the most sperm will tend to father the most offspring
      - so in multi-male, multi-female groups, sexual selection favors greater sperm production
        - larger testes
    - this is not an issue in single-male, multi-female groups
      - since the one male is keeping all the other males away
      - so males of species with single-male, multi-female mating patterns tend to have small testes for their body size
      - even though they tend to be the ones with the biggest canines and the greatest dimorphism in body size
    - it is also a minor issue for primates who live in monogamous pairs
      - since only one male is mating with the female
    - but for some reason, males of “monogamous” species tend to have larger testes for their body size than do males of single-male, multi-female groups
      - what might this suggest about the effectiveness of these two strategies for monopolizing access to the females?
    - this is something you might look for at the zoo, especially if you bring binoculars. Compare the size of testes of:
      - male baboons or male chimps, who live in multi-male, multi-female groups
      - to male gorillas (at the SF zoo), who live in single-male groups (or groups in which sub-dominant males do not mate with the females)
      - or male gibbons or siamangs (at the Oakland zoo), who live in monogamous pairs
      - try explaining this to the people standing near you and see what happens!
- intersexual selection (mostly female choice) in primates
  - since receptive females are scarce and males are plentiful, females can be picky about which males they mate with
    - they don't have to mate with any particular male, since there are plenty of others to choose from

- in contrast to males, who benefit from mating with any female they can find
- but why would pickiness improve a female's reproductive success?
- two general reasons:
  - 1. some males might have genes that, when inherited by the offspring, would help it be more successful (mature faster, be healthier, etc.)
    - any female that tended to choose males with better genes would have more surviving offspring, or ones that would reproduce more
    - these daughters will tend to also get the mothers preference for that kind of male, so the preference will become common
    - so females will tend to develop preferences for any visible traits that indicate beneficial genes
    - for example, large tail feathers might indicate healthier males
    - so females that tend to mate with males with large tail feathers would produce healthier offspring, and their preference would be selected for
  - 2. some males might have parenting traits that benefit the female's survival and that of her infant
    - for example, some males might be more prone to vigorously defend her and her offspring from predators, or to defend a larger territory so that she has more food to eat
    - any tendency of females to select males with these parenting traits will be favored by sexual selection
    - because females who tend to mate with these males will leave more surviving offspring than those that do not
- Whatever the reason, if females prefer some trait in mates, those traits will get into more offspring, and will become more common
- Female choice can get into a positive feedback loop and “run away”, creating bizarre, exaggerated characteristics in males
  - in a process sometimes called **“runaway” intersexual selection**
  - say a few females tend to mate more often with brighter-colored males
    - for some basically unimportant reason
      - for example, maybe the color causes them to look at those males slightly more often
    - this causes the colorful males to mate more often, and leave more offspring
    - so colorful males become more common in the next generation
      - these males also tend to get the preference alleles from their mothers
      - although as males, they don't express the trait
    - the female offspring tend to get the preference alleles from their mothers
      - these females also tend to get the “colorful” alleles from their fathers
      - although as females, they don't express the trait
    - so females who prefer a trait in males tend to leave offspring with alleles for both
      - the preference (from her)
      - and the trait (from the male she preferred)
  - in the next generation, some females again prefer more colorful males
    - so again, more colorful males mate more, and leave more offspring
    - again, colorful males become more common
      - but now, the males get the “colorful” alleles from both parents

- from the father, who is colorful
- from the mother, whose father was colorful
- so males become even more colorful than before
- the males also get the preference alleles from both parents
  - from the mother, who prefers colorful males
  - from the father, whose mother preferred colorful males
- and now, the female offspring become even more picky
  - the get the preference alleles from both parents
    - from the mother, who prefers colorful males
    - from the father, whose mother preferred colorful males
  - so the females develop an even stronger preference for colorful males
- in this way, the trait and the preference for it both just keep getting more and more extreme with every generation
  - the process can spiral on to extremes that have serious costs for survival
  - leading to weirdly exaggerated male characteristics
    - like big peacock tails
    - or huge antlers on elk
    - or the colorful faces of mandrills
- how can we tell if female choice was important?
  - if a visible trait is found only among males and it does not seem to be related to male-male competition
  - example: fleshy noses of proboscis monkeys
- female-choice intersexual selection has been shown to be important in many non-primate species
  - there are some primate species in which it may have played a role, too
    - mandrills, proboscis monkeys, maybe some features of some baboons like the large “mane”
  - but in primates, male-male intrasexual competition seems far more prevalent
- other kinds of behavior are affected by sexual selection, too
  - selection acts differently on males, depending on their mating strategies
- monogamous males
  - little competition for females, so little sexual selection
  - the main option for monogamous males to increase their reproductive success is to invest in their offspring, by carrying them, giving them food, etc.
    - this presumably increases the odds of the offspring surviving to adulthood
    - this could have a big impact on the evolution of a capacity for learned behavior
    - males in some monogamous species care for offspring, others don't
  - another way to increase reproductive success: cheat
    - it increasingly looks like “monogamous” males do in fact mate with other females occasionally
      - although most of the offspring are still from the main mate
  - since males are out there trying to cheat, a male can also increase his r.s. by guarding his mate (ensuring that no other male mates with her)

- in fact, some of the male investment in offspring may pay off more in keeping the female nearby and under the male's control than in increased survival of the offspring
- monogamous male gibbons groom their mates much more than they get groomed back
  - suggesting that this one-sided attention may also be a way of keeping the female from going off and mating with another male
- one-male, multi-female groups:
  - the lone resident male constantly has to fend off bachelor males trying to drive him away
    - in some species, the bachelor males form groups that drive off the resident male in a one-male, multi-female group
      - then the bachelor males fight to replace him
      - in this case, selection could be strong for abilities related to cooperation, good “political” judgment about allies and enemies
    - these conflicts are very serious, often resulting in serious injuries
    - but the payoff is monopoly access to a number of females for a while
    - any given male may not remain in a multi-female group very long
  - some bachelor males employ a different strategy to produce offspring
    - sometimes referred to as the “sneaky f\*\*\*er” strategy
    - they hang around a social group, often alone rather than with other males
    - when the lone resident male is distracted or one of the receptive females is a little away from the group, the bachelor male will take the opportunity to try to mate
    - if some males succeed at this, selection will favor an alternative set of characteristics than those present in the offspring of the lone resident male
      - the lone male is typically a strong, aggressive one able to drive off other males
      - the successful “sneaky f\*\*\*er” bachelor male might be stealthy, observant, smaller, faster, etc.
    - this could maintain more variation in the species, which makes them able to evolve more quickly in response to new environmental pressures, diseases, etc.
- multi-male, multi-female groups:
  - two kinds of male-male competition:
    1. between resident males and bachelor males for access to females
      - bachelor males hang around the edges of the group, trying to mate with the females
      - or bachelor males charge right into the group and confront the resident males
    2. between resident males within the group for access to females
      - males try to drive other males away from females
      - interrupt mating
      - or males may establish dominance relationships through spontaneous confrontations not directly related to access to females
        - these establish which males are dominant over which others
        - confrontations vary from stylized threats, with one male backing down, to real fights
        - the vanquished male typically acknowledges this by a stereotypical gesture of submission
          - sometimes this is a facial expression, or a posture like resting on the “elbows” of the forelimbs in order to lower the head, or a particular kind of sound

- selection favors these signaling behaviors because those that use them are less likely to get beat up in fights - they survive to try again later
- in many cases, the dominance relationships are fairly stable, and a dominance hierarchy is formed
  - similar to the dominance hierarchies among females
    - which give the dominant females better access to resources
  - male dominance probably gives males better access to females
    - but this has only been proven for a few species so far
    - and some studies of captive primates seem to show that dominance does not improve reproductive success
    - sometimes the dominant male spends so much effort fighting to maintain his position that the second-ranked male actually has higher reproductive success
      - why would natural selection lead to this?
- males may form social alliances to get access to females
  - a high-dominance male will form a “**consortship**” with a female in estrus
    - he stays with her, grooms her, mates with her, and keeps other males away
      - this behavior assures that the offspring is his
  - two less-dominant males may team up as a “**coalition**” to challenge the consorting male
    - they can often succeed in driving off the more dominant male
    - and one of the allies becomes the female's consort
- Infanticide
  - In single-male, multi-female groups
  - when a resident male is driven away, the new resident male will sometimes kill some or all of the infants
    - this has now been observed in numerous species
      - Hanuman langurs
      - Red howler monkeys
      - gorillas
      - chimps
    - the females who have lost their infants stop lactating and become receptive quickly
    - so the male can quickly father numerous offspring
    - males that do this leave more of their own alleles in the next generation; so selection favors it
    - this is another example of selection favoring something that is harmful to the group
      - it benefits the individual male's reproductive success
      - while potentially contributing to the decline or extinction of the group
  - this makes the most obvious sense in single-male groups, but it is now clear that infanticide happens in multi-male groups, too
    - for the same reason:
      - if a male is new to the group, or has recently moved up in the dominance hierarchy, few or none of the current infants are his
      - killing an infant causes the female to stop lactating and start ovulating again

- so the new male has a chance of fathering her next infant
- evidence that supports this explanation of infanticide
  - new males kill infants only when they first arrive; they stop killing infants before any of their own can be born
    - Boyd and Silk express this same concept in a different way, noting that in numerous studies, males are shown to kill primarily infants that must have been conceived before they joined the group
      - as determined both by the date of arrival of the male versus the age of the infant
      - and by DNA tests of the males and the dead infants
    - note that this does not necessarily mean the males can recognize their own infants
      - it may just mean that they tend to kill infants when they first arrive, then taper off
  - new males mostly kill the young infants that are nursing, whose deaths will make their mothers become receptive quicker
    - they don't bother with older juveniles who are no longer impeding their mother's fertility
  - observations in several species show that the infanticidal males frequently do mate with the females whose infants they have killed
- infanticide plays a major role in evolution of some primates
  - in several species, up to a third of all infant deaths are infanticides
  - this has a big effect on r.s. of the mothers, and of the fathers
- selection presumably would favor female behaviors to minimize infanticide
  - mothers in some species form “friendships” with certain males after they give birth, staying near them and grooming them frequently
    - these males may defend the infant from other males
    - note that this is the exact opposite from the grooming behavior in monogamous primates, where it is males who do most of the grooming
    - presumably these “friendships” pay off for the males’ r.s. in some way
      - they benefit a little from the grooming, but not much
      - but mostly, such friendships may tend to be between individuals who have recently mated, meaning that the infant is be more likely to the male’s own offspring
        - in that case, the male is increasing his r.s. by helping his own infant to survive
        - this investment by the male is called **parenting effort**
      - friendships may also increase the likelihood of mating in the future
        - this investing by the male is called **mating effort**
- females mate with multiple males, even during pregnancy, when the male can’t actually become the father
  - this reduced the males’ clues about whether or not they are the father
  - it increases the odds that any given male in the group is the father
  - so it increases the costs to a male of killing infants, since they might be his own
- consider humans
  - human females are unusual in that they have “**concealed ovulation**”
  - males cannot generally tell when females can actually conceive an offspring
  - and females are receptive to sex throughout their cycle
    - they don’t have obvious periods of estrus (being “in heat”)

- this makes it hard for males to know who the father of the female's offspring is
- it also makes it even more important to a male's reproductive success that he keeps an eye on the female, to keep other males away
- so concealed ovulation, benefits the female's r.s.
  - reduces likelihood of a male committing infanticide
    - since he can't know that the infant is not his own
  - increases the likelihood that the male will stay nearby most of the time, not just occasionally when the female is in estrus
    - since he can't tell when the female can actually conceive, he has to mate frequently to increase the odds of the offspring being his
    - for the same reason, he has to keep other males away all the time
    - in hanging around, he may improve the female's access to food patches
    - he may defend the infant from other males
- female choice may also play a role in multi-male, multi-female groups
  - in some species, females prefer dominant males
    - apparently because dominant males have better access to food, and males allow their own offspring to feed near them
    - so the offspring of a female that mates with a dominant male have better access to food, grow faster, etc.
  - in others, such as some macaques, some females prefer unknown, lower-ranking males to dominant ones
    - since the dominance hierarchies are long-lasting, this may be beneficial to a female's reproductive success because it adds different genes to her offspring -- increases variability
- Point: Sexual selection can explain how a lot of physical traits and complex social behaviors evolved
  - many aspects of sexual selection may have favored individuals who were more able to make complex judgments about dominance, mating opportunities, etc.
    - generally more complex than behaviors related to getting food or avoiding predators
  - this in turn would favor physical and behavioral traits that promote abilities and opportunities to learn, to come to correct conclusions, and to remember relevant information about many different individuals in the group
  - that is, sexual selection probably played a major role in the evolution of our big brains and complex behavior
- Points for specifically human evolution: Our ancestors probably evolved in monogamous social groups
  - based on our minimal sexual dimorphism
  - and testes size relative to body size in the intermediate range - not as big as in multi-male, multi-female groups, but not as small as in single-male, multi-female groups
  - so male-male competition was probably *not* a big factor in the evolution that led to humans
  - nor is there evidence of drastic female-choice sexual selection
    - human males have no weird, functionless features like mandrills or proboscis monkeys do
    - at least in this male's opinion!

- but selection for behaviors related to monogamy probably did play a major role in our evolution
  - mate guarding among monogamous males would be a kind of intrasexual selection
    - but not direct male-male competition
  - parental investment among monogamous males would be a kind of intersexual selection
    - in that increases the likelihood of fathering the female's next offspring
    - but not quite what we usually mean by female choice
- Many of these sexual selection arguments apply to modern humans, too
  - but remember, we are talking about biologically evolved tendencies, not specific behaviors or individuals, and it is all conditioned by a lot of learned behavior, including cultural norms
  - but still, can you see why the following observations make good sense in light of sexual selection?
    - there are a lot more male customers for female prostitutes than vice versa
    - most bars are said to attract a lot of men, but not as many women (I wouldn't know, myself)
    - stepchildren and adopted children are far more likely to be subject to domestic violence than are children living with their biological parents
      - if you immediately think of social and emotional reasons for this, stop and think: why do we have those emotional responses that make this seem like an unsurprising fact?