

LS2201

Evolutionary Biology

Adrika Chaudhuri

***The Horseshoe Crab**

445 Million Years of non-evolution

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Sexual selection

Reproduction is important in that it ensures the passage of genes down the generation, and this ensures that both mating partners have a "genetic" interest in production and maintenance of offspring. However, unless the partners are related. in which case they will share some amount of genetic lineage, neither partner is interested in the survivavl or reproductive success of the other partner.

Darwin proposed two forms of sexual selection:1. contests between males for access to females2. female choice of some male phenotypes over the others

What drives sexual selection?

Females are the *limiting resource* for sexual selection, because they produce large gametes, tend to the young, and invest greater resurces than males in the process of reproduction. This difference automatically creates a need for selection of better quality males; a female's reproductive success can be significantly lowered by inappropriate mate choice.

Male animals often compete for mating opportunities through visual displays of bright colors or other ornaments, many of which make a male look larger. The males of some species fight outright and possess weapons, such as horns or tusks, that can inflict injury.

Directional evolution

Competion between males for being chosen by females often leads to selection of the more extreme traits over time; since the cost of maintenance of these traits usually indicates good genes. However, ecological selection also opposes this evolution when the extreme traits become too costly to maintain. The equilibrium value of the trait is still likely to be greater than it would be if only ecological selection were operating. Another way in which males try to ensure that no other males' sperm wil fertilise a female's eggs is by :

- 1. keeping other males away from their mates
- clasping the females as long as she rpoduces fertilisable eggs (crustaceans & frogs)
- 3. formation of copulatory plug in the vagina or decreased sexual receptivity in the female due components of the seminal fluid.

In many animals, sperm competition occurs when the sperm of two or more males have the opportunity to fertilize a female's eggs. In some such cases, a male can achieve greater reproductive success than other males simply by producing more sperm. This explains why polygamous species of primates tend to have larger testes than monogamous species.

Females often mate preferentially with males that have more exaggerated traits or behaviours, and the preferred male characters are often ecologically disadvantageous. Similarly, choosy females spend a lot of time searching for acceptable males, which reduces reproductive output in several species.

Subject to limits imposed by ecological selection, male traits will obviously evolve to exaggerated states if they enhance mating success. But why should females have a preference for these traits, especially for features that seem so arbitrary and even dangerous for the males that bear them? The several hypotheses that have been proposed include (1) direct and (2) indirect benefits to the choosy female (3) sensory bias (4) antagonistic coevolution.

1. Direct benefits

This applies to species in which the male provides a direct benefit to the female or her offspring, such as nutrition, territory, etc. Females thus prefer to mate with such males and this leads to selection of a distinctive, correlated character that indicates the quality of the male.

2. Sensory bias

Animals frequently show greater responses to supernormal stimuli that are outside the usual range of stimulus intensity, and even artificial neural networks trained to recognize pat- terns show biases for exaggerated stimuli. In some cases, female preference may thus evolve even before the male trait does, due to sensory bias.

3. Indirect benefits

In some cases, the male provides no direct benefit to the females or the offsprings, but only contribues his genes. Why would females prefer such a male?

In such cases, alleles affecting female mate choice increase or decrease depending on the fitness of the female's offspring. Two such hypotheses are the:

a. Runaway sexual selection

The evolution of a male trait and a female preference, once initiated, becomes a self- reinforcing, snowballing or "runaway" process. This is also called the *sexy son* hypothesis.

Figure 14.10 A model of runaway sexual selection by female choice. T_1 and T_2 represent male genotypes that differ in some trait, such as tail length. P_1 and P_2 females have different preferences for T_1 versus T_2 males, as shown in the upper graph. The resulting pattern of mating creates a correlation in the next generation between the tail length of sons and the mate preference of daughters (middle graph). Thus a genetic correlation is established in the population, in which alleles P_2 and T_2 are associated to some extent. Any change in the frequency (t_2) of the allele T_2 thus causes a corresponding change in p_2 . In the lower graph, each point in the space represents a possible population with some pair of frequencies p_2 and t_2 , and the vectors show the direction of evolution. When p_2 is low, t_2 declines due to ecological selection, so p_2 declines through hitchhiking. When p_2 is high, sexual selection for T_2 males outweighs ecological selection, so t_2 increases, and p_2 also increases through hitchhiking. Along the solid line, allele frequencies are not changed by selection, but may change by genetic drift. (Lower graph after Pomiankowski 1988.)

Figure 1.1: Model of runaway sexual selection

In tlle simplest form of the model, haploid males of genotypes T, and T, have frequencies of t l and t2 respectively. T2 has a more exaggerated trait, such as a longer tail, that carries an ecological disadvantage, such as increasing the risk of predation. Females of genotype P2, (with frequency p2,) prefer males of type T2 whereas P1 females exhibit little preference (or prefer T1). It is assumed that alleles Pl and P2 do not affect survival or fecundity, and thus are selectively neutral.

Although the expression of genes P and T is sex-limited, both sexes carry both genes and transmit them to offspring. Because P2 females and T 2 males tend to mate with each other, linkage disequilibrium will develop: their offspring of both sexes tend to inherit both the P2 and T2 alieles. The male trait and the female preference thus become genetically correlated, so that any increase in the frequency of the male trait is accompanied by an increase in the frequency of the female preference through hitchhiking. Perhaps T2 males have a slight mating advantage over T, because they are both acceptable to P1 females and preferred by the still rare P2 females. "Whether for this or another reason, suppose t2 increases slightly. Because of the genetic correlation between the loci, an increase in t2 is accompanied by an increase in p2. That is, T2 males have more progeny, and their daughters tend to inherit the P2 allele, so P2 also increases in frequency. As P2 increases, T2 males have a still greater mating advantage because they are preferred by more females; thus the association of the P2 allele with the increasing T2 allele can increase P2 still further.

b. <u>Good genes hypothesis</u> Because females risk substantial losses of fitness if their offspring do not survive or reproduce, an appealing hypothesis is that females should evolve to choose males with high genetic quality, so that their offspring will inherit "good gcnes" and so have a superlor prospect of survival and reproduction, Any male trait that is correlated with genetic quality, that is, any INDICATOR of "good genes" could be used by females as a guide to advantageous matings, so selection would favor a genetic propensity in females to choose mates on this basis. Female preference for male indicator traits should be most likely to evolve if the trait is a condition-dependent indicator of fitness-as many male display traits indeed are.