

Chapter 7

Sexual selection

Why did humans lose their body hair? Why did they start walking on their hind legs? Why did they develop big brains? I think the answer to all three questions is sexual selection. R. Dawkins

7.1 Why extravagant phenotypes?

So far we have assumed that all individuals in the population were haploid and reproduced asexually. We now relax this assumption and investigate evolution while assuming individuals are diploids who reproduce sexually. Sexual reproduction means that each offspring arises from the fusion of reproductive cells of two parents and thus inherit genes from two distinct individuals. This reproductive strategy usually involves the presence of two sexes, males and females, where “females” are by definition the sex that produces the largest reproductive cell (the egg is larger than the sperm). Sexual reproduction is not only found in animals but in fungi and plants as well.

Competition may arise between the members of the same sex under sexual reproduction, if members of the opposite sex choose their mates. This is the process of *sexual selection*, a concept first articulated by Darwin, who noticed that males in many species have exaggerated traits, such as the tail in peacocks, antlers in deers, or the manes in lions. These traits are not expressed by females and are secondary sexual traits, not directly part of the reproductive system unlike sex organs, which are primary sexual traits. The exaggerated traits usually appear at sexual maturity and Darwin surmised that they may function as a demonstration of the reproductive potential of their bearer (by displaying, for instance, genetic quality or parental investment) over which females may express preferences. As a consequence female choosiness and male ornamentation may co-evolve.

In order to investigate the evolution of a quantitative trait under sexual reproduction

and gain some insights into sexual selection, it is useful to recall the following concepts that were already partly introduced in Chapter 1.

- **Diploid.** A diploid individual has two *homologous* copies of each gene (the *ploidy* is the number of homologous sets of genes an individual has, one for haploids). Under sexual reproduction, the set of genes consist of one maternal gene (obtained through the egg) and one paternal gene (obtained through the sperm) that are paired after fertilization during the formation of the zygote. The genes transmitted by each sex are located on chromosomes, which form the physical basis of inheritance. Under *Mendelian inheritance*, each homologous gene of an individual, the maternal and the paternal copy, are transmitted with equal probability of $1/2$ to an offspring.

- **Heterozygote and homozygote.** An individual is said to be heterozygote at homologous genes if it carries two different alleles, i.e., the maternally and paternally inherited genes are different. An individual is said to be homozygote if its homologous genes are identical and the individual thus carries twice the same allele.

7.2 Phenotypic architecture in diploids

Because a diploid individual carries two homologous genes, the effect of genes on phenotype is more complicated than under haploid reproduction. To understand how genes affect phenotype, let us assume, as usual, that only two alleles segregate in this population: the allele A and the allele B. This implies that each individual can have one of three possible genotypes: the homozygote A (denoted AA), the homozygote B (denoted BB), and the heterozygote (denoted AB).

In diploids, we can thus no longer assume that an allele codes for a single phenotype, since the phenotype of an individual depends on the alleles it has inherited from its father (paternal allele) and mother (maternal allele) and there may be interactions between these alleles. The phenotype of an individual will thus depend on its genotype, and we write y_{AA} , y_{BB} , and y_{AB} , for, respectively, the phenotype of a homozygote A, a homozygote B, and the heterozygote.

The effect of a genotype on a phenotype will depend on the type of gene action; that is to say, how the two homologous genes within an individual interact to produce its phenotype. For instance, if allele A is dominant then the phenotype of the heterozygote, AB, is equivalent to the phenotype of the homozygote AA, namely

$$y_{AB} = y_{AA}. \quad (7.1)$$

In this case, allele B is *recessive*. It may also be the case that the effects of each allele add up. This occurs under additive gene action, which means that the phenotype of the

heterozygote is half-way between the phenotypes of the two homozygotes:

$$y_{AB} = \frac{y_{AA} + y_{BB}}{2}. \quad (7.2)$$

In order to be able to capture various degrees of dominance, we write the phenotype of the heterozygote as

$$y_{AB} = \underbrace{\frac{y_{AA} + y_{BB}}{2}}_{\text{additivity}} + d \underbrace{\left(\frac{y_{AA} - y_{BB}}{2} \right)}_{\text{interactions}}, \quad (7.3)$$

where d is the *coefficient of dominance*, which tunes the deviation from additivity according to the distance between the two homozygotes ($y_{AA} - y_{BB}$). When $d = 0$, we have co-dominance (eq. 7.2), which is also often referred to as additive gene action.

If $d = 1$, then A is completely dominant and we get $y_{AB} = y_{AA}$ (eq. 7.1), while if $d = -1$, A is now completely recessive and we have $y_{AB} = y_{BB}$. Finally, it is possible that $d > 1$, which is called *overdominance* and it results in the phenotype of the heterozygote individual being larger than that of the two homozygotes. If $d < -1$, we have *underdominance* and it results in the phenotype of the heterozygote being smaller than that of the two homozygotes (see the figures in the lecture slides for an illustration of these concepts).

7.3 Evolutionary invasion analysis in diploids

To study selection in diploids and sexual selection we will make the simplifying assumption that gene action is additive and start by considering females only. As we have been doing for haploids in the previous chapter, we consider the fate (invasion or extinction) of an allele A that arises as a single copy in a population otherwise monomorphic for B. When A arises as a single copy, the individual in which the mutation appears is necessarily heterozygote AB. Hence, to determine whether A is favored by selection at a low frequency, we only need to consider the fitness of a heterozygote female and can neglect homozygotes for the resident allele A.

Let us denote by $w_f(x_f, y_f)$ the fitness of a *single* heterozygote AB female expressing phenotype x_f introduced into an otherwise monomorphic population for allele B, where homozygote BB females express a resident phenotype denoted y_f . A key point (and difficulty) of the model is that fitness is now defined at the **gene level**. Specifically, $w_f(x_f, y_f)$ is the number of successful offspring produced by a female per haploid set of genes she carries (i.e., **per ploidy**). Hence, fitness $w_f(x_f, y_f)$ can also be interpreted as the expected number of gene copies produced over one demographic time step by a single allele A residing in an individual that express phenotype x_f . Thus $w_f(x_f, y_f)$ here corresponds to the number of offspring a AB females produces divided by “2”, since we want to determine the spread of the A allele in the population. We thus refer to $w_f(x_f, y_f)$ as the the **gene fitness** of a mutant individual.

We denote by $w_f(y_f, y_f)$ the gene fitness of a single BB individual in a monomorphic B population, which is assumed to be at its demographic equilibrium (say for number n^* of individuals which implies $2n^*$ genes). Since at a demographic equilibrium each gene just replaces itself, gene fitness must be equal to one (recall eq. 6.2), whereby

$$w_f(y_f, y_f) = 1. \quad (7.4)$$

Hence, allele A is disfavored by selection when

$$w_f(x_f, y_f) \leq 1. \quad (7.5)$$

This says that if an heterozygote individual carrying allele A produces less or exactly one offspring (per ploidy) or one replica gene over a single demographic time period, then selection does not favor the invasion of the B population by allele A.

In complete analogy with the concept of uninvasability seen for haploids (recall eq. 6.4), we say that a resident phenotype y_f is an *uninvasable strategy* if

$$w_f(x_f, y_f) \leq 1 \quad \forall x_f \in \mathcal{X}_f. \quad (7.6)$$

Here, \mathcal{X}_f is the phenotype space in females, that is, the set of feasible alternative phenotypes (or “strategies”) that a female can implement at the heterozygote stage. An uninvasable strategy cannot be invaded by any alternative strategy in the phenotypic space and thus characterizes an evolutionary equilibrium for female trait expression.

A useful quantity to characterize uninvasable strategies is the selection gradient

$$S_f(y_f) = \left. \frac{\partial w_f(x_f, y_f)}{\partial x_f} \right|_{x_f=y_f} \quad (7.7)$$

on the evolving trait at point y_f . The selection gradient is the marginal change in the fitness of a female when she varies her strategy in a population expressing strategy y_f . Therefore, it characterizes the direction of selection on the female trait at this point. A necessary first-order condition for uninvasability is thus that $S_f(y_f) = 0$.

We can now apply exactly the same reasoning to males and introduce the gene fitness $w_m(x_m, y_m)$. This is the number of successful offspring (per ploidy) of a *single* heterozygote AB male expressing phenotype x_m , when introduced into an otherwise monomorphic population of homozygote BB males expressing phenotype y_m . The selection gradient on the male trait is thus given by

$$S_m(y_m) = \left. \frac{\partial w_m(x_m, y_m)}{\partial x_m} \right|_{x_m=y_m}, \quad (7.8)$$

which is the marginal change in the fitness of a male when he varies his strategy in a population expressing strategy y_m . Therefore, this selection gradient characterizes the direction of selection on the male trait at this point.

In general, males and females interact, meaning that the fitness of an individual of any sex will depend on the phenotypes expressed in the opposite sex. Hence, the fitnesses of males and females should be written $w_f(x_f, y_f, y_m)$ and $w_m(x_m, y_m, y_f)$ so as to emphasize that female fitness also depends on the male phenotype y_m and male fitness also depends on the female phenotype y_f .

7.4 Coevolution of female choosiness and male ornament

We now turn to analyzing an example of sexual selection. To that end, we consider the following life cycle. (1) Males compete for access to mating with choosy females. (2) Females fecundity (number of offspring produced) depends on the amount of resources they obtain. (3) All adults die and offspring (male and female) survive to adulthood (possibly involving density-dependent competition) to form the next generation of adults.

We assume that the trait x_f is the level of female choice while the trait x_m is the male ornament size. We consider that ornament size is a honest signal of paternal care levels; that is, male investment into provisioning the mated female with resources to produce and/or rear the offspring. We thus assume that ornament size is correlated to the provisioning of resources, so that larger ornament means a male is more likely to provide parental care. Male paternal care, in turn, increases the amount of resources available to the female it mates with for production and/or survival (stage (2) and (3) of the life cycle).¹ To consider the co-evolution of female choice and male ornament size we now make a number of assumptions about the fitness costs and benefits that these traits generate.

Let us first consider the female side. We assume that the benefit of choosiness for a female expressing trait x_f in a resident population where males have ornament size y_m is $x_f e^{\beta y_m}$. This says that the benefit of choosiness is proportional to the female's level of choosiness x_f and to the benefit $e^{\beta y_m}$ of parental care. The latter is modeled as an exponential function of male ornament y_m , which is thus increasing in y_m since there is a correlation between ornament size and male provisioning of resources to offspring (the choice of an exponential is based on the fact that it allows to simplify the calculations while capturing the biological scenario). The parameter β modulates that effect: the larger β the larger the benefits to females of resource provisioning by males. Note that if $y_m = 0$, then, $e^{\beta y_m} = 1 > 0$. The assumption here is that even if males do not express ornament size (a genetically determined trait), there is still some variation in male resource holdings (due to environmental variation), which benefits females to be choosy about.

¹We are here assuming that male ornament size is a honest signal of male quality, which will be the case if signaling is costly, such that only those males with a larger ornament can afford to effectively exhibit a stronger signal.

We also assume that there is a cost to choosiness (due to time and energy allocated to it), so that it decreases fitness by an amount of x_f^2 (this cost is accelerating, i.e., x_f is squared, which is the simplest way to capture an accelerating cost). Putting cost and benefit together, the fitness of a female with strategy x_f in a resident population where males and females have resident traits y_f and y_m is assumed to be given by

$$w_f(x_f, y_f, y_m) = k_f \underbrace{(x_f e^{\beta y_m} - x_f^2)}_{\text{fecundity}}, \quad (7.9)$$

where the term in parentheses is the female's fecundity (increasing with male provisioning and decreasing with cost of choosiness). The constant of proportionality k_f is a regulating variable taking density-dependent competition into account (thus ensuring that the population is regulated) and that will be considered as fixed and positive (hence we assume density-independent selection).

Let us now consider the male side of the model. We assume that the male benefit of ornament size is to increase its number of matings (mating success), modulated by the function $e^{(x_m - y_m)y_f}$. This is an increasing function of female choosiness and of the difference between ornament size of a male trait x_m when other males in the population have trait y_m . Hence, if a focal male “advertises more” (has a larger ornament) than other males in the population, then he is more likely to be chosen for mating as it makes him more attractive, as long as females are choosy. Note that if $y_m = x_m$, then $e^{(x_m - y_m)y_f} = 1$, and so the fitness of a male is independent of female choosiness. Similarly, if $y_f = 0$, then $e^{(x_m - y_m)y_f} = 1$, and so the fitness of a male is not increased by ornament size.

We also assume that there is a cost to expressing the male ornament, which increases quadratically with ornament size x_m^2 . Putting cost and benefit together, the fitness of a male with strategy x_m in a resident population where males and females have resident traits y_f and y_m is assumed to be given by

$$w_m(x_m, y_m, y_f) = k_m \underbrace{(e^{(x_m - y_m)y_f} - x_m^2)}_{\text{mating success}}, \quad (7.10)$$

where the term in parentheses is the male's mating success. The constant of proportionality k_m captures the fact that (i) males are subject to density-dependent competition and (ii) male fitness is proportional to female fecundity, since the fitness of a male is necessarily linked to that of the female(s) it mates with. But these two biological features do not affect the direction of selection on males ornament, and so for simplicity we do not model them explicitly and subsume them into k_m , which is assumed positive.

In summary, the above fitness models say that selection will affect female fecundity (eq. 7.9) and male mating success (eq. 7.10), but we do not model explicitly the other features as they will not affect the direction of selection. With these two fitness functions, we can compute the selection gradient on each trait. Substituting eq. (7.9) into eq. (7.7),

we find that the selection gradient on female choosiness is

$$S_f(y_f) = k_f (e^{\beta y_m} - 2y_f), \quad (7.11)$$

where $\exp^{\beta y_m}$ is the marginal benefit of choosiness and $2y_f$ is the marginal cost. Substituting eq. (7.10) into eq. (7.8), we find that the selection gradient on male ornament size is

$$S_m(y_m) = k_m (y_f - 2y_m), \quad (7.12)$$

where y_f is the marginal benefit of ornamentation (and equal to the level of choosiness) and $2y_m$ is the marginal cost.

In order to understand the joint evolution of the male and female traits, consider first that $y_m = 0$ and $y_f = 0$. Then, it benefits females to be choosy, since $e^{\beta y_m} - 2y_f = 1 > 0$ in eq. (7.11). Hence, the selection gradient on the female trait is positive, $S_f(0) > 0$, which implies that female choosiness is favored by selection (y_f increases). This in turn, generates a benefit to ornamentation in males, since $y_f > 0$ in eq. (7.11). Hence, the selection gradient on the male trait is positive, $S_m(0) > 0$, which implies that ornamentation is favored by selection (y_m increases from zero). These considerations show that both y_f and y_m are initially jointly favored by selection and the co-evolution of these traits leads to two possible outcomes.

- When β takes on small values, and since the expression of both traits is costly, an *interior equilibrium* is reached where marginal costs and benefits balance out each other. This equilibrium (y_f^*, y_m^*) is computed by setting $S_f(y_f^*) = 0$ and $S_m(y_m^*) = 0$ and solving jointly for (y_f^*, y_m^*) as both selection gradient depend on the two trait values y_f and y_m . The equilibrium is attracting and is thus a convergence stable strategy pair (left panel of Fig. 7.1). At this convergence stable point, female choosiness and male ornamentation are the best responses to each other and so the strategies are also uninvadable.

- When β takes on large values, a runaway is observed (right panel of Fig. 7.1). This means that a positive feedback loop emerges, with choosiness selecting ever increasing trait value in males, which in turns boost fitness benefits in females. These benefits always exceed the costs of choosiness, such that choosiness itself is constantly increased by selection. Such a runaway process is thought to be responsible for extreme ornamentation in birds. Interestingly, the runaway can lead to selection-driven population extinction, as the absolute fitness in males decreases over time. Indeed, the $e^{(x_m - y_m)y_f}$ term in eq. 7.10 is always equal to one in a resident population ($e^{(y_m - y_m)y_f} = e^0 = 1$) and thus does not increase over time, while the cost of expressing exaggerated ornaments increases, so that fitness tends to decrease overall. When ornament size evolves to the point where individuals in the population express trait value $y_m = 1$, male fitness reaches zero (since $x_m^2 = 1$ when $y_m = 1$, which implies the term in parenthesis in eq. 7.10 is zero). This illustrates that the relative (competitive) advantage of a male getting a mate is what drives selection on ornament size. The gain in increasing ornament size for a population expressing a given strategy is captured by the the marginal benefit in the selection gradient on male ornament size (eq. 7.12).

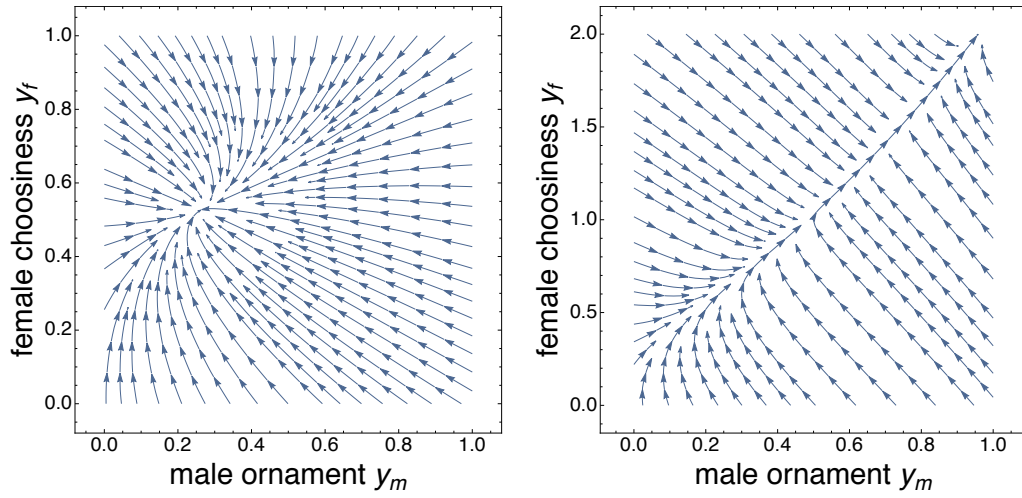


Figure 7.1: Vector field of the selection gradients $S_m(y_m) = k_m(y_f - 2y_m)$ and $S_f(y_f) = k_f(\exp^{\beta y_m} - 2y_f)$ for each combination of trait values y_f and y_m varying between zero and one. Each panel of the figure depicts the direction of selection on the male and female trait; that is, it depicts the vector $(S_m(y_m), S_f(y_f))$ for each combination of trait values y_f and y_m . Left panel $k_f = k_m = 1$ and $\beta = 0.2$, while in the right panel $\beta = 1.5$. For the left panel, we see that all arrows (vectors) point in the direction of a single interior point, which is the convergence stable strategy. For the right panel, the arrows (vectors) point in the direction of ever increasing choosiness and ornamentation.