

chapter 13

the evolution of genetic systems

II. some consequences of sex

In this chapter, I assume sexual reproduction, and discuss some consequences.

The sex ratio

It is a familiar fact that, in most dioecious species, there are approximately equal numbers of males and females. Why should this be so? One answer would be that, in most species, sex is determined by the segregation of X and Y chromosomes in the meiosis of the heterogametic sex (usually the male), and that meiosis generates a 1:1 ratio. This is true enough as far as it goes. If it were selectively advantageous to do so, however, organisms would surely have evolved some mechanism that produced a sex ratio different from 1:1. We therefore want a selective explanation for this ratio.

For the present, assume that the sex ratio is determined by genes acting in the parent: for example, genes could act in the heterogametic sex by altering the ratio of male- and female-determining gametes produced, or, in the homogametic sex, by altering the success of the two types of gamete in fertilization. However, I assume that a gene in a parent cannot alter its own likelihood of being transmitted to a gamete.

First, consider a verbal explanation of the 1:1 ratio. Suppose that there were more females in the population than males. Then males will have, on average, more children than females. Therefore, a gene acting in a parent would be transmitted to more descendants if it could cause that parent to produce the rarer sex—that is, sons. Similarly, if there were more males in the population than females, a gene causing parents to produce females would spread. Hence the only evolutionarily stable sex ratio would be 1:1, because only then is the reproductive value of a son equal to that of a daughter. This argument, originally due to R. A. Fisher, is made more precise in Box 13.1. In fact, it is shown that it is not the numbers of males and females that are equal at equilibrium, but the parental expenditure on males and females: if the costs of a son and a daughter are equal, equal expenditure implies a 1:1 ratio.

Box 13.1 The evolution of stable sex ratios

Suppose that a pair can produce m sons and f daughters, where

$$m + kf = C. \quad (13.1)$$

In this equation, C represents the total possible 'expenditure' on offspring, and a daughter costs k times as much as a son.

Consider a random-mating population in which typical pairs produce m^* sons and f^* daughters. A rare dominant gene M causes females to produce m sons and f daughters, and is not expressed in males (an exactly similar conclusion follows for a gene expressed only in males). The frequency of $M/+$ females is P , and of $M/+$ males is p . P and p are small, so we can ignore M/M genotypes, and matings of $M/+ \times M/+$. If we ignore terms in P^2 , Pp , and p^2 , we have the values in Table 13.1.

Table 13.1

Evolution of the sex ratio in diploids

Mating		Frequency	Offspring per pair			
♀	♂		male		female	
			$M/+$	$+/+$	$M/+$	$+/+$
$M/+$	$+/+$	$P(1-p) - P$	$m/2$	$m/2$	$f/2$	$f/2$
$+/+$	$M/+$	$p(1-P) - p$	$m^*/2$	$m^*/2$	$f^*/2$	$f^*/2$
$+/+$	$+/+$	$(1-P)(1-p) - 1 - P - p$	—	m^*	—	f^*

Hence, among the offspring:

$M/+$ males	$Pm/2 + pm^*/2$,
$M/+$ females	$Pf/2 + pf^*/2$,
total males	$m^*(1-P) + mP = m^*$,
total females	$f^*(1-P) + fP = f^*$.

Hence, if P' and p' are the frequencies of $M/+$ females and males, respectively, in the next generation, we have

$$P' = \frac{1}{2}P \frac{f}{f^*} + \frac{1}{2}p,$$

$$p' = \frac{1}{2}P \frac{m}{m^*} + \frac{1}{2}p. \quad (13.2)$$

Adding these equations gives

$$(P' + p') = \frac{1}{2}P \left(\frac{f}{f^*} + \frac{m}{m^*} \right) + p, \quad (13.3)$$

$$= (P + p) + RP,$$

where
$$R = \frac{1}{2} \left(\frac{f}{f^*} + \frac{m}{m^*} \right) - 1. \tag{13.4}$$

Note that when $f = f^*$ and $m = m^*$, $R = 0$; that is, $(P + p)$ neither increases nor decreases. This is as expected, since gene M has no effect.

From Equation 13.1, $f = (C - m)/k$, and $f^* = (C - m^*)/k$. Substituting in Equation 13.4 and rearranging gives.

$$R = \frac{(C - 2m^*)(m - m^*)}{2m^*(C - m^*)}. \tag{13.5}$$

Now if $R > 0$, the mutant M increases in frequency. Hence, if $m^* < C/2$, the mutant M increases in frequency if $m > m^*$, and if $m^* > C/2$, M increases in frequency if $m < m^*$. That is to say, if $m^* < C/2$, mutants increasing m^* will invade, and if $m^* > C/2$, mutants reducing m^* will invade. Hence the evolutionarily stable sex ratio is $m^* = C/2$. This implies that $m^* = kf^*$, and hence that expenditure on sons and daughters is equal. The best way of seeing what this means in practice is to work through the examples at the end of this chapter.

The stable sex ratio for a haplo-diploid species can be found in the same way. Table 13.2 lists the possible matings. Hence, in the next generation,

$$P' = \frac{P}{2} \frac{f}{f^*} + p,$$

$$p' = \frac{P}{2} \frac{m}{m^*}.$$

Table 13.2

Evolution of the sex ratio in haplo-diploids

Mating		Frequency	Offspring per pair			
♀	♂		male	+	female	+/+
			<i>M</i> /+		<i>M</i> /+	+/+
<i>M</i> /+	+	$P(1-p) = P$	$m/2$	$m/2$	$f/2$	$f/2$
+/+	<i>M</i>	$p(1-P) = p$	—	m^*	f^*	—
+/+	+	$(1-P)(1-p) = 1 - P - p$	—	m^*	—	f^*

Hence, among the offspring:

<i>M</i> males	$Pm/2,$
<i>M</i> /+ females	$Pf/2 + pf^*,$
total males	$m^*,$
total females	$f^*.$

Adding these equations gives

$$(P' + p') = \frac{1}{2}P\left(\frac{f}{f^*} + \frac{m}{m^*}\right) + p.$$

This is identical to Equation 13.3, so we again conclude that, at equilibrium, expenditure on sons and daughters is equal.

Exceptions to the rule are of particular interest. In some populations of the mosquito, *Aedes aegypti*, there is a great excess of males, caused by a Y-linked gene, *M*. Males carrying this gene produce an excess of sons, because X chromosomes are broken during meiosis, and sperm carrying deficient X chromosomes degenerate. If this were the whole story, natural populations of *Aedes aegypti* would consist mainly of males, and would be close to extinction. However, there are resistant X chromosomes, able to suppress the action of *M*. As one would expect, X chromosomes from Africa and central America, where *M* is commonly found, tend to be resistant.

In this example, Fisher's prediction of a 1:1 ratio fails, because one of its basic assumptions does not hold: the gene *M* does affect its own likelihood of being transmitted. This is an example of **meiotic drive**. Another assumption of Fisher's argument is that all males have an equal chance of mating, as do all females. If this assumption is false, this too can lead to a distorted sex ratio. The phenomenon, first described by Hamilton (1967), is the case of **local mate competition**. Consider a parasitic insect that lays several eggs in a host caterpillar. These eggs hatch and develop within the host, and pupate there. They then emerge and mate with one another before dispersing. If only one female lays eggs in each host, then females are mated by their brothers. What sex ratio should a female produce if she is to maximize the number of genes she transmits to future generations? Clearly, she should produce one son, and the rest of her offspring should be female.

Do parasitic animals with this life history produce female-biased sex ratios? The question has been studied mainly in haplo-diploid organisms, for two reasons. First, many haplo-diploids (particularly hymenoptera, and some mites) have the appropriate life history. Secondly, females of haplo-diploid species can choose the sex of each offspring, by fertilizing, or not fertilizing, each egg. Hence haplo-diploids are ideal for testing ideas about sex ratio evolution. In fact, parasitic haplo-diploids often produce highly female-biased sex ratios, as the theory predicts. The extreme example is a mite, *Acarophenax*, in which the female produces live young: the single male in the litter hatches, mates with his 15 or so sisters, and dies before he is born.

Before we accept these data as confirming theories about local mate competition, we must be satisfied that the biased sex ratios are not a direct adaptation