

To compute p_{n+1} , it helps to construct a *Punnett square*, as shown in Table 2.2, which summarizes the frequencies of the alleles in the current generation, and the resulting frequencies of the three different genotypes in the next generation. Thus, the frequencies of the next generation with genotypes WW, Ww (= wW), and ww are p_n^2 , $2p_n(1-p_n)$, and $(1-p_n)^2$, respectively. The frequency of the W allele in the next generation is equivalent to the probability of obtaining a W allele by randomly choosing one allele from a random individual. The probability of obtaining a W allele from an individual with genotype WW is 1; from an individual with genotype Ww it is $\frac{1}{2}$; and from an individual with genotype ww it is 0. Computing a weighted average of these probabilities thus yields the following expression for the frequency of the W allele:

$$p_{n+1} = \frac{1 \cdot p_n^2 + \frac{1}{2} \cdot 2p_n(1-p_n) + 0 \cdot (1-p_n)^2}{p_n^2 + 2p_n(1-p_n) + (1-p_n)^2} \quad (2.28)$$

$$= \frac{p_n}{(p_n + 1 - p_n)^2} \quad (2.29)$$

$$= p_n. \quad (2.30)$$

We see that allele frequencies do not change from generation to generation, provided the assumptions stated above hold, of course. This conclusion is known as the *Hardy-Weinberg law*.

Selection in a population with two phenotypes

The assumptions stated in the previous section imply that there is no selection. What happens when there is selection? For example, suppose that white-winged moths are more conspicuous, and therefore more likely to be eaten by birds than black-winged moths. Will white-winged moths become extinct? What if white-winged moths have the selective advantage instead? Will black-winged moths become extinct?

Let α be the fraction of white-winged moths surviving to produce the next generation, with $0 \leq \alpha \leq 1$. Similarly, let γ be the fraction of black-winged moths surviving, with $0 \leq \gamma \leq 1$. Choosing $\alpha > \gamma$ gives white-winged moths a selective advantage, while $\alpha < \gamma$ gives black-winged moths a selective advantage.

Just before reproduction, the genotype ratio WW : Ww : ww is $\alpha p_n^2 : 2\alpha p_n(1-p_n) : \gamma(1-p_n)^2$. The resulting frequency of W alleles in the next generation then is

$$p_{n+1} = \frac{1 \cdot \alpha p_n^2 + \frac{1}{2} \cdot 2\alpha p_n(1-p_n) + 0 \cdot \gamma(1-p_n)^2}{\alpha p_n^2 + 2\alpha p_n(1-p_n) + \gamma(1-p_n)^2} \quad (2.31)$$

$$= \frac{\alpha p_n}{(\gamma - \alpha)p_n^2 - 2(\gamma - \alpha)p_n + \gamma}. \quad (2.32)$$

Note that when $\alpha = \gamma$, that is, when there is no selective advantage, we recover the Hardy-Weinberg equilibrium, namely $p_{n+1} = p_n$. But when $\alpha \neq \gamma$, we have a nonlinear equation that warrants further investigation.

Let's begin by finding the fixed points p^* of this equation, and determining their stability with a linear stability analysis. First, we look for values of p^* such that $f(p^*) = p^*$, where

$$f(p) = \frac{\alpha p}{(\gamma - \alpha)p^2 - 2(\gamma - \alpha)p + \gamma}.$$

It is easy to show that this equation has two distinct roots, corresponding to two fixed points, namely $p_1^* = 0$ and $p_2^* = 1$. In terms of the genetic problem at hand, $p_1^* = 0$ means that the W allele has become extinct and all moths have black wings, whereas $p_2^* = 1$ means that the w allele has become extinct and all moths have white wings. Intuitively, we expect $p_1^* = 0$ to be stable when black-winged moths have the selective advantage ($\alpha < \gamma$), and $p_2^* = 1$ to be stable when white-winged moths have the selective advantage ($\alpha > \gamma$).

To determine the stability of these fixed points with linear stability analysis, we find

$$f'(p) = \frac{-\alpha((\gamma - \alpha)p^2 - \gamma)}{((\gamma - \alpha)p^2 - 2(\gamma - \alpha)p + \gamma)^2},$$

so that $f'(p_1^*) = f'(0) = \frac{\alpha}{\gamma}$ and $f'(p_2^*) = f'(1) = 1$. The appearance of the ratio α/γ looks promising in light of our intuition discussed above. Let's check the details. When $\alpha < \gamma$, we have $0 < \frac{\alpha}{\gamma} < 1$, and so we conclude that the fixed point $p_1^* = 0$ is stable. That is, when black-winged moths have the selective advantage, the W allele indeed can become extinct if its frequency becomes sufficiently small (since the linear stability analysis only is local, we cannot conclude that the W allele will become extinct per se). Similarly, when $\alpha > \gamma$, the fixed point $p_1^* = 0$ is unstable. Since $f'(p_2^*) = 1$, the linear stability analysis does not yield a conclusion about the stability of the other fixed point, $p_2^* = 1$ (see Theorem 2.1). A graphical stability analysis will be helpful.

Cobwebbing diagrams for the allele frequency equation (2.32) are shown in Figure 2.17. In Figure 2.17(a), the case $\alpha < \gamma$ is shown. Indeed, any initial condition p_0 with $0 \leq p_0 < 1$ leads to the fixed point $p_1^* = 0$. We conclude that $p_1^* = 0$ is stable, and $p_2^* = 1$ is unstable (for any $0 < p_0 \leq 1$, which are the only biologically sensible initial conditions). In Figure 2.17(b), the case $\alpha > \gamma$ is shown. Here, the situation is reversed. The fixed point $p_1^* = 0$ is unstable, and $p_2^* = 1$ is stable (again, for any $0 < p_0 \leq 1$).

In summary, selection on the level of phenotype (white-winged versus black-winged), when one allele is dominant and the other recessive, eventually leads to extinction of one of the alleles. How fast the allele is driven to extinction depends on the relative strength of the model parameters α and γ . The larger the difference between α and γ , the faster the approach to extinction.

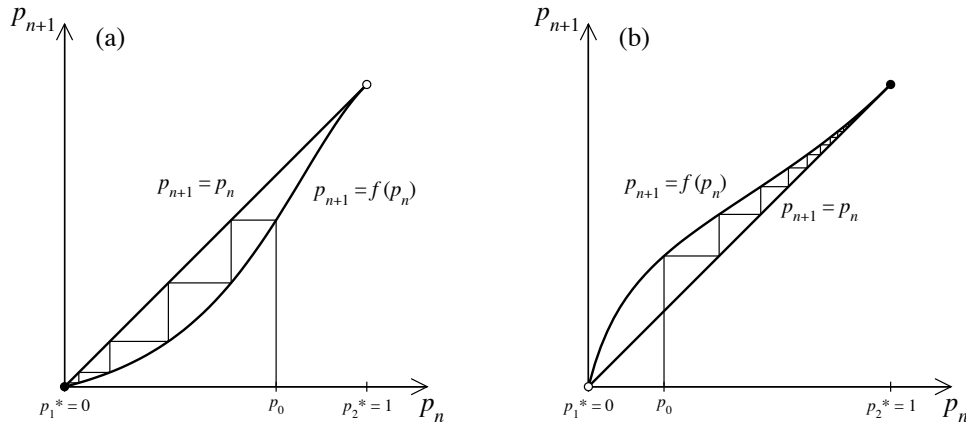


Figure 2.17. Cobwebbing diagrams for allele frequency equation (2.32). (a) $\alpha < \gamma$ ($\alpha = 0.2$ and $\gamma = 0.8$); (b) $\alpha > \gamma$ ($\alpha = 0.8$ and $\gamma = 0.2$).

Selection in a population with three phenotypes

Let's generalize this investigation into the effect of selection one more step. Suppose that the W allele no longer is dominant, and that the three genotypes, WW, Ww, and ww, give rise to three distinct phenotypes. For ease of discussion, we will assume that individuals with genotypes WW and ww will develop white and black wings, respectively, as before, and that individuals with genotype Ww will develop gray wings. Furthermore, introduce the parameter β to represent the selective pressure on gray-winged moths, with $0 \leq \beta \leq 1$. Just before reproduction, the genotype ratio WW : Ww : ww is $\alpha p_n^2 : 2\beta p_n(1 - p_n) : \gamma(1 - p_n)^2$. Questions of interest now include: under which conditions will all three phenotypes co-exist? Similarly, can grey-winged moths be driven extinct? If so, will white-winged moths or black-winged moths survive?

As before, it suffices to study the iterative map for the frequency of W alleles, which is

$$p_{n+1} = \frac{1 \cdot \alpha p_n^2 + \frac{1}{2} \cdot 2\beta p_n(1 - p_n) + 0 \cdot \gamma(1 - p_n)^2}{\alpha p_n^2 + 2\beta p_n(1 - p_n) + \gamma(1 - p_n)^2} \quad (2.33)$$

$$= \frac{(\alpha - \beta)p_n^2 + \beta p_n}{(\alpha - 2\beta + \gamma)p_n^2 + 2(\beta - \gamma)p_n + \gamma}. \quad (2.34)$$

This more general allele frequency equation looks a bit more intimidating than the previous one, but doing the analysis is still quite reasonable. In particular, fixed points p satisfy $p^* = f(p^*)$, where

$$f(p) = \frac{(\alpha - \beta)p^2 + \beta p}{(\alpha - 2\beta + \gamma)p^2 + 2(\beta - \gamma)p + \gamma},$$