

Not Quite Enough Selection (Or Maybe a Bit Too Much)

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1 Introduction

This note summarizes basic results from the theory of natural selection. It develops the conventional algebraic model and uses this to derive a series of qualitative conclusions, which are stated below as “Results.”

2 Basic model

Consider a locus with two alleles A_1 and A_2 , whose relative frequencies in some generation are p and $q = 1 - p$, respectively. Let w_{ij} denote the probability that an individual of genotype A_iA_j will survive to reproduce. This probability is called the fitness of genotype A_iA_j . The genotypic fitnesses and frequencies are shown in table 1. The frequencies before selection are in Hardy-Weinberg equilibrium. The contribution of each genotype to the gene pool of the next generation is proportional to the product of its frequency and fitness. Dividing by \bar{w} , the mean fitness, ensures that the genotypic frequencies after selection sum to unity.

The frequency of allele A_1 is $p = P_{11} + \frac{1}{2}P_{12}$, where P_{11} and P_{12} are the frequencies of A_1A_1 and A_1A_2 .

*EXERCISE 1 Show that $p = P_{11} + \frac{1}{2}P_{12}$.

Applying this to the last row of table 1 gives the frequency of A_1 after selection.

$$p' = \frac{p^2 w_{11} + pq w_{12}}{\bar{w}} \quad (1)$$

Here, p is the allele frequency among the parents and p' is that among the children. Equation 1 tells us p 's value in one generation as a function of its value in the previous generation. Such equations are called *recurrence equations*. They provide recipes for getting from one generation to the next.

Table 1: Genotypic fitnesses and frequencies

Genotype	A_1A_1	A_1A_2	A_2A_2
Freq. before selection	p^2	$2pq$	q^2
Fitness	w_{11}	w_{12}	w_{22}
Freq. after selection	$p^2 w_{11}/\bar{w}$	$2pq w_{12}/\bar{w}$	$q^2 w_{22}/\bar{w}$

Where $q = 1 - p$
and $\bar{w} = p^2 w_{11} + 2pq w_{12} + q^2 w_{22}$

3 The rate of change

How much change occurs between successive generations? To find out, we calculate Δp (pronounced “delta pee”), which equals $p' - p$. Δp is positive when p is increasing, and negative when p is decreasing. When there is no tendency to change, the system is said to be at *equilibrium*, and $\Delta p = 0$. Subtracting p from equation 1 gives (after some algebra)

$$\Delta p = \frac{pq}{\bar{w}} [p(w_{11} - w_{12}) + q(w_{12} - w_{22})] \quad (2)$$

This equation provides a great deal of intuition concerning the dynamics of natural selection, which I summarize in the paragraphs that follow.

*EXERCISE 2 Derive Eqn. 2 from Eqn. 1.

Result 1 *Response to selection is slow when either allele is rare.*

This is because Δp is proportional to pq and is therefore low when p is small or when q is small.

Result 2 *Selection is especially slow when a recessive allele is rare.*

If A_1 is recessive, $w_{12} = w_{22}$, and Eqn. 2 becomes $\Delta p = p^2 q (w_{11} - w_{12}) / \bar{w}$. When A_1 is rare, p^2 is very small, so response to selection is very slow.

Result 3 *Selection is especially slow when a dominant allele is common.*

If A_1 is dominant and common, then A_2 is recessive and rare, so Result 2 implies that $\Delta p \approx 0$.

Result 4 *A rare allele spreads if its heterozygote is fitter than the common homozygote.*

This result is used widely, because all mutations are initially rare, and we would like to know which ones will spread. It holds because when A_1 is rare, p is small, the expression in square brackets is approximately $w_{12} - w_{22}$. Allele A_1 will increase in frequency if this quantity is positive.

Result 5 *If the heterozygote has intermediate fitness, then one allele will increase to fixation.*

To see why, note that if $w_{11} > w_{12} > w_{22}$, then the quantity in square brackets in Eqn. 2 is always positive, and A_1 will increase to fixation. On the other hand, A_2 will fix if $w_{11} < w_{12} < w_{22}$.

Result 6 *If the heterozygote has the highest fitness, then A_1 evolves toward an intermediate equilibrium.*

This is the case of “fitness overdominance” or “heterozygote superiority.” In this case, $w_{11} - w_{12} < 0$ and $w_{12} - w_{22} > 0$, so Δp is positive when p is small but negative when p is large.

Result 7 *When the heterozygote has highest fitness, the allele that is most common at the stable equilibrium is the one whose homozygote has highest fitness.*

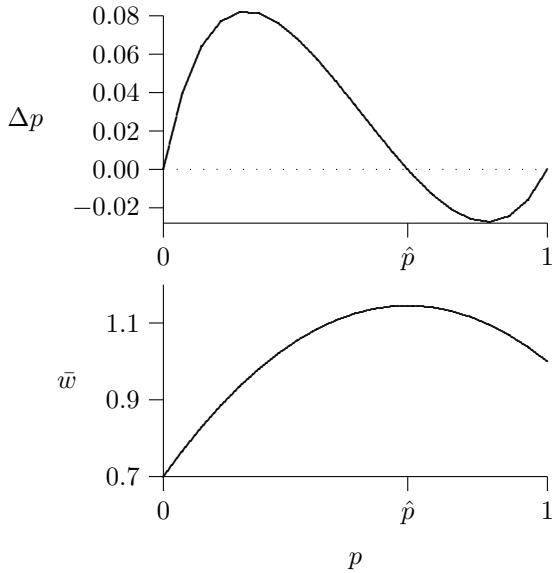


Figure 1: Model of heterozygote advantage. Upper panel: the rate, Δp , of change in p . Equilibria occur where $\Delta p = 0$. The equilibria at $p = 0$ and $p = 1$ are unstable. That at $p \approx 0.64$ is stable. Lower panel: mean fitness, \bar{w} , as a function of p . The equilibrium value, \hat{p} , maximizes \bar{w} and coincides the point at which $\Delta p = 0$.

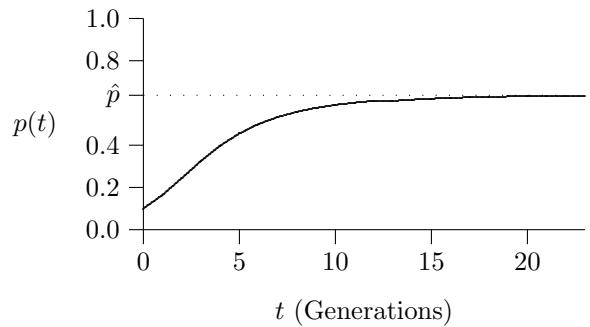


Figure 2: Time path of allele frequency using the same model as Fig. 1. The dotted line indicates the equilibrium value, $\hat{p} \approx 0.64$.

To derive this result, set to zero the quantity in square brackets in Eqn. 2 and rearrange to obtain

$$\frac{\hat{p}}{\hat{q}} = \frac{w_{12} - w_{22}}{w_{12} - w_{11}}$$

where \hat{p} and \hat{q} are the equilibrium values of p and q . On the right side of this equation, the numerator and denominator are both positive, because we are concerned with the case of heterozygote superiority. If $w_{11} > w_{22}$, then the denominator will be smaller than the numerator, and this implies that \hat{p} (the frequency of A_1) exceeds \hat{q} (that of A_2). For example, suppose that $w_{22} = 0.1$, $w_{11} = 0.2$, and $w_{12} = 0.3$. Then

$$\frac{\hat{p}}{\hat{q}} = \frac{0.3 - 0.1}{0.3 - 0.2} = 2$$

and \hat{p} is twice as large as \hat{q} .

Result 8 *If the heterozygote has lowest fitness, then there are two stable equilibria, one at which A_1 is fixed and another at which it is lost.*

In this case, $w_{11} - w_{12} > 0$ and $w_{12} - w_{22} < 0$, so Δp is negative when p is small but positive when p is large.

4 The same result in terms of genic fitnesses

We can also write equation 2 as

$$\Delta p = \frac{pq(w_1 - w_2)}{\bar{w}} \quad (3)$$

where w_1 and w_2 are the *genic* or *marginal* fitnesses of A_1 and A_2 . The genic fitness of allele A_i is simply the average fitness of copies of A_i .

In diploid organisms, genes occur in pairs. Each copy of the A_1 allele is paired with some other gene. What is the probability that this second gene is also a copy of A_1 ? If mating is at random, then the second gene is (in effect) drawn at random from among all the genes in the population. Since a fraction p of these are copies of A_1 , p is also the probability that the second gene is an A_1 . In this case, the original copy of A_1 resides in an A_1A_1 homozygote with fitness w_{11} . On the other hand, the original A_1 might (with probability q) be paired with a copy of A_2 . If so, then the initial A_1 resides in a heterozygote with fitness w_{12} . The mean fitness of allele A_1 is therefore

$$w_1 = pw_{11} + qw_{12}$$

A similar argument applies if the initial gene is a copy of A_2 and leads to

$$w_2 = pw_{12} + qw_{22}$$

Since pq/\bar{w} is always positive, equation 3 implies that

Result 9 *Selection favors the allele whose genic fitness is highest.*

*EXERCISE 3 Verify that $w_1 - w_2$ is equal to $p(w_{11} - w_{12}) + q(w_{12} - w_{22})$.

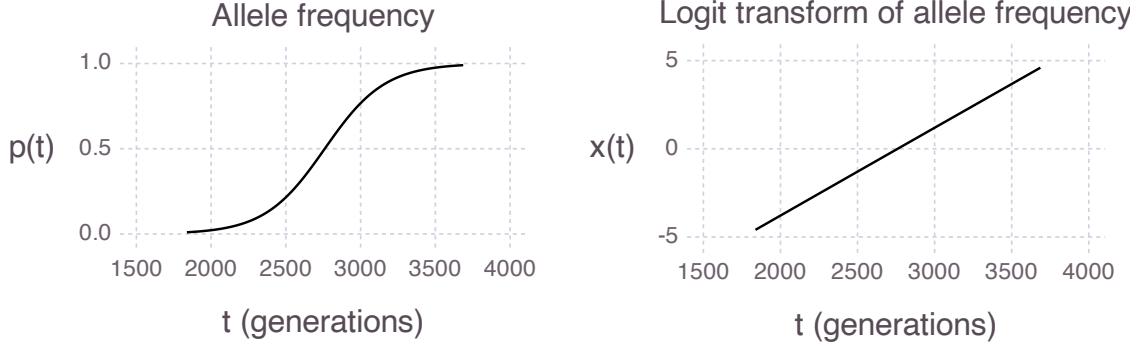


Figure 3: Time path of p , the frequency of an advantageous allele, A_1 , over the range $0.01 \leq p \leq 0.99$. The model assumes that the fitness of the favored homozygote (A_1A_1) exceeds that of the unfavored one (A_2A_2) by $s = 0.01$ and that there is no dominance. Calculations used Eqn. 1.

5 Wright's equation

We saw above that Eqn. 2 is rich in insight about the behavior of natural selection. Most of that insight came from studying the quantity in square brackets. Sewall Wright [4] noticed that this quantity is equal to $\frac{1}{2} \frac{d\bar{w}}{dp}$, where $d\bar{w}/dp$ is the derivative (or slope) of the curve that describes \bar{w} as a function of p . Thus,

$$\Delta p = \frac{pq}{2\bar{w}} \cdot \frac{d\bar{w}}{dp} \quad (4)$$

This equation is equivalent to 2, but provides a different kind of insight. Notice that $pq/2\bar{w}$ is always positive when p is neither zero nor unity. This means that p will increase when $d\bar{w}/dp > 0$ and will decrease when this derivative is negative. Selection pushes allele frequency in a direction that increases \bar{w} , the mean fitness. It pushes the population “uphill” on the function $\bar{w}(p)$. Consequently,

Result 10 *Stable equilibria occur at peaks in the graph of mean fitness against allele frequency.*

The lower panel of Fig. 1 illustrates this principle.

★EXERCISE 4 Verify that equations 2 and 4 are equivalent.

★EXERCISE 5 Define $w_{11} = 1$, $w_{12} = 1.1$, and $w_{22} = 0.8$. Find the equilibria in this system by graphing Δp as a function of p .

6 The time required for a selective sweep

How long does it take for an allele to increase from one value to another, under the influence of natural selection? This question has been addressed by Haldane [3] and several later authors [2, sec. 5.3; 1, sec. 3.1.iii.a]. The model is simplest if there is no dominance, so that alleles contribute additively to fitness. Let’s suppose that genotypes A_1A_1 , A_1A_2 , and A_2A_2 have relative fitnesses $w_{11} = 1 + s$, $w_{12} = 1 + s/2$, and $w_{22} = 1$. The left panel of Fig. 3 shows the time path of allele A_1 over the range $0.01 \leq p \leq 0.99$. As the graph shows, this selective sweep takes more than 1500 generations.

The graph on the right shows the time path of the transformed variable,

$$x = \ln \frac{p}{1-p}$$

This is called the “logit transform” and is often used in statistics. As you can see, the graph of x is a straight line, or very nearly so. Appendix A shows that the slope of this line is approximately $s/2$. Consequently, it is easy to write x as a function of t :

$$x(t) = x_0 + ts/2$$

where x_0 is the initial value of x . Solving for t gives [2, Eqn. 5.3.13; 1, Eqn. 3.3]

$$\begin{aligned} t &= \frac{2}{s}(x(t) - x_0) \\ &= \frac{2}{s} \ln \frac{p(t)q_0}{q(t)p_0} \end{aligned} \tag{5}$$

where p_0 and q_0 are the initial values of p and $q = 1 - p$. This result makes it easy to figure out how long it would take for selection to raise the frequency of an allele from one value to another. It is an approximation for weak selection, but it works remarkably well for values of s up to about 0.1.

Let us use it to ask about the time required for a selective sweep. Equation 5 is deterministic and consequently does not inform us about the initial generations, when the advantageous allele is very rare. Neither does it inform us about the final generations, when the alternate allele is rare. Those dynamics are stochastic and are not captured by our deterministic model. We therefore ignore the beginning and end of the selective sweep and ask how long it takes for the advantageous allele to increase from 1% to 99%. For this case, Eqn. 5 becomes $t \approx 18/s$.

Result 11 *It takes roughly $18/s$ generations for an advantageous allele to increase in frequency from 0.01 to 0.99, if there is no dominance.*

For example, in Fig. 3, $s = 1/100$, so the selective sweep lasts about 1800 generations. If generations are 25 years in length, this corresponds to about 45 thousand years. If there is dominance, the time required for a selective sweep is longer [2, p. 193; 1, Box 3.2].

*EXERCISE 6 How many generations are required for selection to increase the frequency of an allele from 1% to 99%, if the coefficient of selection is $s = 0.001$, and there is no dominance?

*EXERCISE 7 Repeat exercise 6, but this time figure out the time required for the allele to increase in frequency from 25% to 75%.

7 Summary

This note introduces the conventional algebraic model of natural selection. Equilibria occur where $\Delta p = 0$. There are always equilibria at $p = 0$ and $p = 1$. There may also be an intermediate equilibrium at which $0 < p < 1$. Stable equilibria occur at peaks in the graph of mean fitness against p .

When the heterozygote has intermediate fitness, selection favors the allele whose homozygote has the higher fitness. A rare allele will spread if the fitness of its heterozygote is higher than that of the common homozygote. When the heterozygote’s fitness is higher than that of either homozygote, the system evolves toward a stable equilibrium at which p is greater than zero but less than unity. When the heterozygote has lowest fitness, the system evolves away from an unstable intermediate equilibrium and toward either $p = 0$ and $p = 1$.

When gene effects are additive, the selective sweep of an advantageous allele takes roughly $18/s$ generations.

Acknowledgements

I thank Jon Seger for comments and hold him responsible for the title.

A The slope of the straight line in Fig. 3

In sec. 6, we assumed that genotypes A_1A_1 , A_1A_2 , and A_2A_2 had relative fitnesses $w_{11} = 1 + s$, $w_{12} = 1 + s/2$, and $w_{22} = 1$. With these definitions, Eqn. 2 becomes $\Delta p = pqs/2\bar{w}$, which is approximately $pqs/2$ if selection is weak. Under weak selection, the change in each generation will be small, and we can treat p as a continuous function of time, and Δp as a derivative:

$$dp/dt = pqs/2$$

As we saw above in Fig. 3, the time path is much simpler if we transform p into

$$x = \log \frac{p}{q} = \log p - \log q$$

where $q = 1 - p$. The derivative of x is

$$\begin{aligned} dx/dt &= \frac{1}{p} \frac{dp}{dt} + \frac{1}{q} \frac{dq}{dt} = \frac{pqs}{2} \left(\frac{1}{p} + \frac{1}{q} \right) = \frac{pqs}{2} \left(\frac{q}{pq} + \frac{p}{pq} \right) \\ &= s/2 \end{aligned}$$

Because s is a constant, this result says that the graph of x against t is a straight line with slope $s/2$.

B Answers to Exercises

★ EXERCISE 1 The population contains NP_{11} individuals of genotype A_1A_1 and NP_{12} of genotype A_1A_2 . Each of the former carries two copies of A_1 and each of the latter carries one copy. The total number of copies of A_1 is thus $2NP_{11} + NP_{12}$. Dividing by $2N$ (the total number of genes) gives the relative frequency of A_1 within the population: $p = P_{11} + \frac{1}{2}P_{12}$.

★ EXERCISE 2

$$\begin{aligned} \Delta p &= \frac{p^2 w_{11} + pq w_{12}}{\bar{w}} - p \\ &= \frac{p^2 w_{11} + pq w_{12} - p^3 w_{11} - 2p^2 q w_{12} - pq^2 w_{22}}{\bar{w}} \\ &= \frac{p^2 q w_{11} + pq(q-p) w_{12} - pq^2 w_{22}}{\bar{w}} \\ &= \frac{pq}{\bar{w}} [p w_{11} + (q-p) w_{12} - q w_{22}] \\ &= \frac{pq}{\bar{w}} [p(w_{11} - w_{12}) + q(w_{12} - w_{22})] \end{aligned}$$

★ EXERCISE 3 The calculation is very simple:

$$\begin{aligned} w_1 - w_2 &= p w_{11} + q w_{12} - q w_{22} - p w_{12} \\ &= p(w_{11} - w_{12}) + q(w_{12} - w_{22}) \end{aligned}$$

*EXERCISE 4 Mean fitness is

$$\begin{aligned}\bar{w} &= p^2 w_{11} + 2pq w_{12} + q^2 w_{22} \\ &= p^2 w_{11} + 2(p - p^2) w_{12} + (1 - 2p + p^2) w_{22}\end{aligned}$$

Taking the derivative,

$$\begin{aligned}\frac{d\bar{w}}{dp} &= 2pw_{11} + (2 - 4p)w_{12} + (-2 + 2p)w_{22} \\ \frac{1}{2} \frac{d\bar{w}}{dp} &= pw_{11} + (1 - 2p)w_{12} - (1 - p)w_{22} \\ &= pw_{11} + (q - p)w_{12} - qw_{22} \\ &= p(w_{11} - w_{12}) + q(w_{12} - w_{22})\end{aligned}$$

which equals the quantity in square brackets in Eqn. 2.

*EXERCISE 5 There are unstable equilibria at 0 and 1, and a stable equilibrium at 3/4.

*EXERCISE 6 18,380 generations

*EXERCISE 7 4394 generations

References

- [1] Brian Charlesworth and Deborah Charlesworth. *Elements of Evolutionary Genetics*. Roberts, 2010.
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- [3] J. B. S. Haldane. *The Causes of Evolution*. Cornell University Press, Ithaca, 1932.
- [4] Sewall Wright. *The Theory of Gene Frequencies*, volume 2 of *Evolution and the Genetics of Populations*. University of Chicago Press, Chicago, 1969.