Supplementary material to:

Chapter 3: Deriving Classic Models in Ecology and Evolutionary Biology

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Supplementary Material 3.1: Translating between numbers and frequencies in the diploid model of selection

Here, we examine how selection alters the numbers of individuals within a diploid population and show that these changes are consistent with the allele frequency recursion, (3.13a). Let's begin at the gamete pool stage and assume that the frequency of allele A among gametes is $p(t)$. Immediately after gametes unite randomly to form zygotes, let the number of each genotype be $n_{AA}(t)$, $n_{Aa}(t)$, and $n_{aa}(t)$, and let the total population size be $n(t) = n_{AA}(t) + n_{Aa}(t) + n_{aa}(t)$. The probability that genotype AA survives to adulthood times its fertility (the number of individuals that it contributes to the next generation) is measured by W_{AA}. This represents the absolute fitness of AA. Similarly, the absolute fitnesses of Aa and aa are W_{Aa} and W_{aa}, respectively.

According to these definitions, the total number of individuals contributed to the next generation is $n(t+1) = W_{AA}\, n_{AA}(t) + W_{Aa}\, n_{Aa}(t) + W_{aa}\, n_{aa}(t)$. We can also find the average value of the absolute fitness by summing the absolute fitness of each genotype times the frequency of that genotype:

$$\overline{W} = W_{AA}\frac{n_{AA}(t)}{n(t)} + W_{Aa}\frac{n_{Aa}(t)}{n(t)} + W_{aa}\frac{n_{aa}(t)}{n(t)} \tag{S3.1.1a}$$

Equation (S3.1.1a) can be rewritten as:

$$\overline{W} = \frac{n(t+1)}{n(t)}, \tag{S3.1.1b}$$

which demonstrates that the population changes in size by a factor equal to the average value of the absolute fitness.

Assuming that each genotype contributes to the gamete pool in proportion to its absolute fitness, the frequency of allele *A* in the gamete pool at the next generation will equal:

$$p(t+1) = \frac{W_{AA} n_{AA}(t) + \frac{1}{2} W_{Aa} n_{Aa}(t)}{W_{AA} n_{AA}(t) + W_{Aa} n_{Aa}(t) + W_{aa} n_{aa}(t)} = \frac{W_{AA} n_{AA}(t) + \frac{1}{2} W_{Aa} n_{Aa}(t)}{\overline{W}\ n(t)}. \qquad \text{(S3.1.2a)}$$

Assuming that the zygotes at time t were formed by random union of gametes, they will be in Hardy-Weinberg proportions (Table 3.2), and the numbers of each genotype will equal the Hardy-Weinberg proportions times the population size: $n_{AA}(t) = p(t)^2\, n(t)$, $n_{Aa}(t) = 2\, p(t)\, q(t)\, n(t)$, and $n_{aa}(t) = q(t)^2\, n(t)$. This allows us to rewrite the mean fitness as $\overline{W} = W_{AA}\, p(t)^2 + 2 W_{Aa}\, p(t)\, q(t) + W_{aa}\, q(t)^2$ and equation (S3.1.2a) as:

$$p(t+1) = \frac{W_{AA}\ p(t)^2 + W_{Aa}\ p(t)\, q(t)}{\overline{W}}, \qquad \text{(S3.1.2b)}$$

Equation (S3.1.2b) is the same as equation (3.13a) of the text.

We can also describe the dynamics in terms of the change in allele frequency over the course of a generation:

$$\Delta p = p(t+1) - p(t) = \frac{p(t)\, q(t)\, \big(p(t)\, (W_{AA} - W_{Aa}) + q(t)\, (W_{Aa} - W_{aa})\big)}{\overline{W}}. \qquad \text{(S3.1.2c)}$$

This is similar in form to the haploid difference equation; in both cases, the change in allele frequency is proportional to $p(t)\, q(t)$, indicating that evolutionary change slows whenever one of the alleles is rare ($p(t)$ or $q(t)$ near 0).

As was the case with the haploid model, it is relative fitness (measured as the ratio of W_{ij} to some standard) that determines the evolutionary dynamics of allele frequency. Thus, we can multiply or divide all of the fitnesses (S3.1.2b) by any common factor and this will not affect the evolutionary dynamics. Multiplying or dividing the fitnesses by a common factor will, however, alter the equation for the population dynamics. In particular, equation (S3.1.1b) reveals that

$$n(t+1) = \overline{W}\, n(t). \tag{S3.1.3}$$

Therefore multiplying the fitnesses by a common factor σ, will cause the dynamics of the population size to be altered by a factor σ.

In summary, the recursion equation (S3.1.3) for the population size always depends on the genetic composition of the population, unless the genotypes are equally fit. But the recursion equation (S3.1.2b) for the allele frequency does not depend on the size of the population *as long as the relative fitness of each genotype is independent of the population size*. If, however, the genotypes differ in their sensitivity to competition and to population size (e.g., if the fitness of *AA* declines exponentially with population size, $W_{AA} = e^{-\alpha\, n(t)}$) then both equations (S3.1.3) and (S3.1.2b) are necessary to predict the outcome of selection (e.g., Problem 3.17).

Supplementary Material 3.2: A discrete-time version of the Lotka-Volterra predator-prey model.

Here we derive the discrete-time Lotka-Volterra predator-prey model; the equivalent continuous-time model is described in the text by equations (3.18). The key difference in the discrete-time model is that we must specify an order to the events that occur within a time unit. Arbitrarily, we assume that each time unit consists of a census, followed by prey births, predation, predator births, and finally predator deaths.

As in the exponential model, we assume that the prey have a per capita reproductive output of R individuals per time unit in the absence of the predator. Following prey reproduction, a predator has a contact probability of c of finding any one of the prey per time unit, so that the total expected number of contacts between predators and prey within the community is $c\, n_1(t)\, n_2(t)$. At each contact, the probability that the predator successfully attacks the prey is a. Next, we assume that reproduction of the predator is entirely dependent on the number of prey it consumes and that one prey item is the resource equivalent of ε predator offspring. Finally, we assume that a fraction, d, of predators die per time unit. These assumptions are described in the form of a flow diagram in Figure S3.2.1. We now derive the recursion equation by applying Recipe 2.1 to both species after every event in the life cycle:

$n_1'(t) = n_1(t) + (R-1)\, n_1(t)$ $\quad n_2'(t) = n_2(t)$ $\quad$ after prey births

$n_1''(t) = n_1'(t) - a\, c\, n_1'(t)\, n_2'(t)$ $\quad n_2''(t) = n_2'(t) + \varepsilon\, a\, c\, n_1'(t)\, n_2'(t)$ $\quad$ after predation

$n_1'''(t) = n_1''(t)$ $\quad n_2'''(t) = n_2''(t) - d\, n_2''(t)$ $\quad$ after predator deaths

Substituting each line into the next, we get a discrete-time version of the predator-prey model:

$$n_1(t+1) = R\, n_1(t) - a\, c\, R\, n_1(t)\, n_2(t) \tag{S3.2.1a}$$

$$n_2(t+1) = (1-d)\big(n_2(t) + \varepsilon\, a\, c\, R\, n_1(t)\, n_2(t)\big) \tag{S3.2.1b}$$

As a check, if there were no contacts between predators and prey ($c = 0$), the prey should grow according to the exponential growth model (3.1b), and the predators should die off by a factor of $(1 - d)$ each time unit, which is indeed true for equations (S3.2.1).

Figure S3.2.1: A flow diagram for the Lotka-Volterra predator-prey model in discrete-time.