r Selection

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The adaptive dynamics formulation works well for K selection in the canonical Verhulst equation

$$\frac{dN_i}{N_i\,dt} = r_i\left(1 - \frac{N_i}{K_i}\right).$$

Typically, r selection is discussed as the other main scenario, in qualitative terms without a rigorous mathematical model to justify it. Can I make such a model?

The main assumption is that population densities are low. This could be, as in the Lenski experiments, because populations are sampled before they become large and reseeded in empty environments over and over, or because of frequent disturbances replacing inhabited by uninhabited spaces. In the latter scenario, disturbance must be frequent enough to keep density from gradually growing, but not enough to cause extinction. This seems hard unless we use a chemostat scenario. What about the Lenski scenario?

Here we sample and restart the population – presumably this restarts them proportionally to their frequency in the population rather than absolute numbers. So this will also turn out to look like a chemostat equation.

That is modeled by the replicator equation, something like this. If the unaltered population dynamics is

$$\frac{dN_i}{dt} = N_i f_i(N_i)$$

the replicator equation is

$$\frac{dN_i}{dt} = N_i f_i(N_i) - \frac{N_i}{\sum_j N_j}\sum_j N_j f(N_j).$$

Let's derive it ourselves. We can think of reseeding as removing things at a constant rate:

$$\frac{dN_i}{dt} = N_i f_i(N_i) - CN_i$$

In the logistic case, this is

$$\frac{dN_i}{dt} = r_i N_i\left(1 - \frac{N_i}{K_i}\right) - CN_i.$$

This is formally equivalent to the other formulation where habitat is destroyed frequently. But if the destruction rate C is a fixed large constant, less fecund communities will go extinct, and if r_i gets larger the populations will stop being small. So this makes more sense as Lenski's reseeding process or a chemostat than as natural habitat destruction, as the destruction rate must change with the evolving characteristics of the population.

Under the assumption that C is controlled to keep the population at a fixed small density $N_i \ll K_i$, the rest should follow, including the conclusion that selection increases r and ignores K.

To maintain fixed total size in multitype model, we remove at the same rate as total production.

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i}\right) - CN_i$$

This requires the total change in population to be zero:

$$\begin{aligned}\sum_i CN_i &= \sum_i r_i N_i \left(1 - \frac{N_i}{K_i}\right) \\ C &= \sum_i r_i N_i \left(1 - \frac{N_i}{K_i}\right) / \sum_j N_j\end{aligned}$$

Thus we recover the replicator/chemostat equation. This maintains the total population constant at whatever size we start with. We suppose that it's very small, such that the N_i/K_i terms are negligible. In the limit we have

$$\frac{dN_i}{dt} = r_i N_i - N_i \sum_j r_j N_j / \sum_j N_j,$$

which should certainly yield the desired selection.

Here is the replicator version of Masel's $3n$ model (with two types):

$$\begin{aligned}\frac{dX_0}{dt} &= -X_0 r_0 \left(\frac{\frac{X_0 c_0}{K_0} + \frac{X_1 c_1}{K_1}}{c_0} - 1\right) \\ &\quad + \left(X_0 r_0 \left(\frac{\frac{X_0 c_0}{K_0} + \frac{X_1 c_1}{K_1}}{c_0} - 1\right) + X_1 r_1 \left(\frac{\frac{X_0 c_0}{K_0} + \frac{X_1 c_1}{K_1}}{c_1} - 1\right)\right) X_0 \\ \frac{dX_1}{dt} &= -X_1 r_1 \left(\frac{\frac{X_0 c_0}{K_0} + \frac{X_1 c_1}{K_1}}{c_1} - 1\right) \\ &\quad + \left(X_0 r_0 \left(\frac{\frac{X_0 c_0}{K_0} + \frac{X_1 c_1}{K_1}}{c_0} - 1\right) + X_1 r_1 \left(\frac{\frac{X_0 c_0}{K_0} + \frac{X_1 c_1}{K_1}}{c_1} - 1\right)\right) X_1\end{aligned}$$

And here is the small-population limit of that (generated by taking $K_i \to +\infty$):

$$\frac{dX_0}{dt} = -(X_0 r_0 + X_1 r_1) X_0 + X_0 r_0$$
$$\frac{dX_1}{dt} = -(X_0 r_0 + X_1 r_1) X_1 + X_1 r_1$$

And the adaptive dynamics of one type:

$$\frac{dr_0}{dt} = \hat{X}_0 \gamma$$
$$\frac{dc_0}{dt} = 0$$
$$\frac{dK_0}{dt} = 0$$

perfect.