Mathematical Models in Ecology & Evolution 2019

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14th July, 2019

Problem 5.4

Problem statement: Including a unidirectional mutation rate mu from allele A to a during reproduction in the haploid model of selection, we want to find system equilibira and examine their stability.

We define the fitnesses of the two alleles A and a as $W_A = 1$ and $W_a = 1 - s$. The recursion equation for allele frequency of A is:

$$p(t+1) = (1-\mu)p' (1)$$

where:

$$p' = \frac{W_A p(t)}{W_A p(t) + W_a (1 - p(t))}$$
 (2)

(a) Determining equilibria

One obvious equilibrium for the system is at p=0, since there is no regeneration of allele W_A . The upper maximum of p must be modulated by the mutation rate of A to a, and thus cannot be 1 as in the simple model.

To find this equilibrium, we set p(t+1) = p(t), and replacing each by \hat{p} :

$$\hat{p} = (1 - \mu) \frac{W_A \hat{p}}{W_A \hat{p} + W_a (1 - \hat{p})}$$
(3)

$$W_A \hat{p} + W_a - W_a \hat{p} = W_A (1 - \mu) \tag{4}$$

$$\hat{p}(W_A - W_a) = W_A(1 - \mu) - W_a \tag{5}$$

and replacing the fitnesses as defined:

$$\hat{p} = \frac{s - \mu}{s} = 1 - \frac{\mu}{s} \tag{6}$$

(b) Biological validity

The non-obvious equilibrium $\hat{p} = 1 - \mu/s$ is only valid between 0 and 1, requiring $\mu/s \le 1$, or the mutation rate to be lower than the selection coefficient.

(c) Mean fitness

The mean fitness of the population at the polymorphic equilibrium is $\overline{W} = W_A \hat{p} + W_A (1 - \hat{p})$, which on replacing \hat{p} with $1 - \mu/s$ yields:

$$\overline{W} = 1 - \frac{\mu}{s} + (1 - s)\frac{\mu}{s} = 1 - \mu$$
 (7)

(d, e) Stability when either A or a is absent

To determine the local stability of each of the two equilibria, $\hat{p} = 0$, and $\hat{p} = 1 - \mu/s$ we differentiate the recursion equation f(p), $p(t+1) = (1-\mu)p'$, with respect to p.

$$\frac{df}{dp} = \frac{d}{dp} \frac{(1-\mu)W_A p(t)}{W_A p(t) + W_a (1-p(t))}$$
(8)

In Mathematica, the command D[p (1 - m)/(p + ((1 - s) (1 - p))), p] on simplification yields the derivative:

$$\frac{df}{dp} = (m-1)(s-1)/(1+(p-1)s)^2 \tag{9}$$

At each of the two equilibria, we obtain the value of $(df/dp)|_{p=\hat{p}}$ by replacing p with \hat{p} and define these values as λ_{eq1} , when allele A is nearly absent, and λ_{eq2} , when allele a is nearly absent: $\lambda_{eq1} = (\mu-1)/(s-1)$, and $\lambda_{eq2} = (s-1)/(\mu-1)$.

These represent the stability conditions at these equilibria, and are dependent on the mutation rate μ , and the selection coefficient s.

(f) Stability conditions

The mutation rate μ and selection coefficient s are constrained between 0 and 1. For the equilibrium $\hat{p}=0$, the value of λ_{eq1} is nearly always positive (or possibly 0 for unreasonable values of μ), and takes values > 1 when $\mu << s$, which may be expected when allele a is rare and $W_A > W_a$. This makes $\hat{p}=0$ an unstable, non-oscillatory equilibrium, and allele A will increase in proportion away from near this equilibrium. For the equilibrium $\hat{p}=1-\mu/s$, λ is nearly always positive and less than 1 (except when $s\approx \mu$), making this a stable and non-oscillatory equilibrium.