Adaptive Dynamics Course
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Vienna 2007

Evolution of Anisogamy

Anisogamy is the size difference between gametes (eggs and sperm). In some primitive algae the gametes are of equal size, but in most organisms there is a very marked difference in gamete size between females and males.

> In fact, gamete size provides the *definition* of males and females: Males are the sex which produces the smaller gametes, no matter what the parents' roles are elsewhere. In many species of fish, males rather than females care for the young. In sea horses, the males become pregnant: the female deposits the eggs into a pouch of the male, where the eggs are covered with the male's tissues and are protected and carried until "delivery". Despite of their motherly roles, these parents are the males because they have the smaller gametes.

In primitive plants (where anisogamy evolved in the first place), the life cycle has two distinct stages. The first stage (called the sporophyte) starts with a fertilised egg, called the zygote. We assume that the probability of survival of a zygote is an increasing function of its weight, z, which is in turn the sum of the weights of the two gametes that produced the zygote, for example of x_1 and x_2. If the zygote survives, then it produces $B(N)$ spores (spore number depends on population density in order to prevent exponential population growth, but does not depend on the size strategy). Half the spores carry the allele for weight x_1 and the other half carry x_2. The spores develop into the second life stage (called the gametophyte), which produces the gametes with weights according to the allele brought by the spore. Each individual in this stage has the same amount of resources, R, and hence it can produce R/x gametes of size x. We assume that there is a minimum size x_0 below which the gamete is not viable, and hence the set of possible size strategies is the interval $[x_0, R]$.

Assume first that any two gametes may unite and form a zygote and consider the fate of a gamete of size x_i in a population where gamete types $x_1,...x_k$ occur with frequencies $q_1,...,q_k$. The expected probability of survival of the zygote derived from the focal gamete is

$$\sum_{j=1}^{k} q_j f\left(x_i + x_j\right) \tag{1}$$

where $f(z)$ gives the probability of survival of a zygote of size z. If the zygote survives, then it will produce $B(N)/2$ spores with allele x_i, each of which will, in turn, make R/x_i gametes identical to the focal gamete. The generation-to-generation dynamics of $n_i(t)$, the number of gametes carrying x_i at the beginning of generation *t*, is given by

$$n_i(t+1) = \left[\sum_{j=1}^{k} q_j(t) f(x_i + x_j)\right] \frac{B(N(t))}{2} \frac{R}{x_i} n_i(t) \tag{2}$$

where $q_i(t) = n_i(t) \Big/ \sum_{j=1}^{k} n_j(t)$ and

$$N(t) = \frac{1}{2} \sum_{i=1}^{k} \sum_{j=1}^{k} n_i(t) q_j(t) f(x_i + x_j) \tag{3}$$

is the number of individuals that determine spore production (division by 2 is because two gametes make one individual). It is simpler to concentrate on the relative frequencies of different size strategies,

$$q_i(t+1) = \frac{\frac{1}{x_i} \sum_{j=1}^{k} q_j(t) f(x_i + x_j)}{\frac{1}{x_l} \sum_{l=1}^{k} \sum_{j=1}^{k} q_l(t) q_j(t) f(x_l + x_j)} q_i(t) \tag{4}$$

because then R and the unknown function $B(N)$ is cancelled. The dynamics of relative frequencies depends only on the shape of function *f*.

Investigate what types of functions *f* lead to evolutionary branching or the evolution of a single gamete size. Construct examples such that after evolutionary branching, the population attains an evolutionarily stable dimorphism either in the interior or on the boundary of the product strategy space where the two different strategies can coexist.

Even in algal species where gametes are of the same size, the gametes belong to two mating groups (often denoted by + and -, respectively) and two gametes can unite only if they are of different mating groups. As an extension of the project, consider a species with +/- gametes where two traits evolve simultaneously: strategy *i* is characterised with the vector trait (x_i^+, x_i^-), where the elements are respectively the sizes of + and of - gametes. Assume that initially, x_i^+ and x_i^- are in a small ε-neighbourhood of one another. Explore the joint adaptive dynamics of the two traits under various functions *f*.