Laws of Adaptation

Lectures on mathematical models of biological evolution
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Lecture 7

Ways to diversity, or polymorphic LTE

Part I – discrete traits

Tuesday October 16, 15:30-16:30
Adaptive polymorphism in nature

- Sofar we have considered only monomorphic LTE, and have even excluded the possibility of polymorphic LTE in wide classes of selection regimes
- On the other hand, there are many and important examples of adaptive polymorphisms in nature, of which we will show now a few examples
- Thus the question arises whether, and how, long-term evolution theory can account for these situations
Batesian mimicry (Clarke C.A. & Sheppard P.M., Heredity, 1960)

**Mimic Species** (Papilio dardanus)
- male
- female

**Model Species**
- Danaus c. chrysippus
- Amauris crawshayi
- Amauris niavius

**Predators**
- Palatable
- Distasteful
Cryptic colorations (Clarke C.A. et al, Evolution, 1963)

Papilio demodocus

adult  larva  feeds on

Predators

Citrus  Umbelliferae
Predatorial tactics (Hori M., Science, 1993)

Perissodus microlepis

Scale-eating ciclid fish of lake Tanganyika attacks preys from behind

right-handed morph

right side left side

on the left flank

left-handed morph

on the right flank
Predatorial tactics and food types

Haematopus ostralegus  
(oistercatcher)

Hammerers

Stabbers

Worm-feeders

Sutherland W.J., Nature, 1987

Pyrenestes ostrinus

An African finch which feeds on seeds of various Scleria species (Cyperaceae)

Scleria meadow
Pyrenestes ostrinus feeds mostly on large, hard seeds (Scleria verrucosa) and small-billed morph feeds mostly on soft seeds (S. mikawana, S. boivinii). The frequency distribution of lower mandible width (mm) is shown in the graph.
Evolutionary dynamics of dimorphism (Lessard, 1984)

- The only case of polymorphism (dymorphism) we have dealt with so far was within population game theory in the Hawk-Doves game where a polymorphic (mixed) ESS exists whenever H is better than D, against D, but also D is better than H, against H; namely whenever
\[
\nu(H,D) > \nu(D,D) \quad \text{and} \quad \nu(D,H) > \nu(H,H)
\]

- We now consider situations of this type, where only two (ultimate) phenotypes are possible but individuals may differ in the probability of expressing one or the other morph, from the point of view of short- and long-term dynamics

**Short-term dynamics**

- Two morphs: \(C_1, C_2\)
- One gene with alleles: \(\{A_1, \ldots, A_n\}\), of frequencies \(p(t) = \{p_1(t), \ldots, p_n(t)\}^T\) at generation \(t=0,1,\ldots\)
- Expression of morphs: \(h_{ij} = h_{ji}\) = probability that \(A_iA_j\) expresses \(C_1\), so that \(1-h_{ij}\) is the probability that it expresses \(C_2\)
- Frequency of \(C_1\) in the population:
\[
\bar{h} = \bar{h}(p) = \sum_i \sum_j h_{ij} p_i(t)p_j(t) = \sum_i \bar{h}_i(p)p_i(t)
\]
- Probability of survival of individuals is determined by the outcomes of random pairwise contests, with a payoff matrix
\[
F = \begin{pmatrix} f_{11} & f_{12} \\ f_{21} & f_{22} \end{pmatrix}
\]
such that, from the point of view of population game theory, it would admit a mixed ESS, \(C^*\); hence
\[
\nu(C_2,C_1) = f_{21} > f_{11} = \nu(C_1,C_1) \quad \text{and} \quad \nu(C_1,C_2) = f_{12} > f_{22} = \nu(C_2,C_2)
\]
- Remember that in this case the probability, \(h^*\), that the ESS strategy plays \(C_j\) is the unique solution in \((0,1)\) of
\[
\nu(C_j,C^*) = \nu(C_2,C^*) \iff h^* f_{11} + (1-h^*) f_{12} = h^* f_{21} + (1-h^*) f_{22} \iff h^* = \frac{f_{12} - f_{22}}{f_{21} - f_{11} + f_{12} - f_{22}}
\]
The fitness of $C_i$ is:

$$F_i = F_i(\bar{h}) = \bar{h}f_i + (1 - \bar{h})f_{i2}, \quad i = 1, 2$$

the fitness of genotype $A_iA_j$ is:

$$w_{ij} = w_{ij}(\bar{h}) = h_{ij}F_i(\bar{h}) + (1 - h_{ij})F_2(\bar{h})$$

the mean fitness of allele $A_i$ is:

$$\bar{w}_i = \bar{w}_i(\bar{h}) = \sum_j p_j(t)w_{ij}(\bar{h}) = \bar{h}_iF_i(\bar{h}) + (1 - \bar{h}_i)F_2(\bar{h})$$

and the population mean fitness is:

$$\bar{w} = \bar{w}(\bar{h}) = \sum_i p_i(t)\bar{w}_i(\bar{h}) = \bar{h}F_i(\bar{h}) + (1 - \bar{h})F_2(\bar{h})$$

Hence, the recursion equations of the gene frequencies are:

$$p_i(t + 1) = p_i(t)\frac{\bar{w}_i}{\bar{w}} = p_i(t)\frac{\bar{h}_iF_i + (1 - \bar{h}_i)F_2}{\bar{h}F_i + (1 - \bar{h})F_2}, \quad i = 1, \ldots, n$$

Any equilibrium $\hat{p} = (\hat{p}_1, \ldots, \hat{p}_n)^T$ must satisfy the conditions

$$\hat{p}_i(\bar{h}_i - \bar{h})[F_i(\bar{h}) - F_2(\bar{h})] = 0, \quad i = 1, \ldots, n$$

which identify two types of equilibria:

- **Genotypic:** $\hat{p}_i(\bar{h}_i - \bar{h}) = 0$
- **Phenotypic:** $F_i(\bar{h}) = F_2(\bar{h})$

Genotypic equilibria, which are independent of the payoff matrix $F$, are formally equivalent to the equilibria of constant selection dynamics, with the phenotypic expression matrix $H = \{h_{ij}\}$ in place of a fitness matrix. Hence they correspond to points of maximum or minimum of $\bar{h}(\hat{p})$.
Phenotypic equilibria entail that the two morphs, $C_1$ and $C_2$, have the same fitness and that therefore their proportions are identical to those of the ESS, $C^*$, of the game identified by $F$. In fact

$$F_1(\bar{h}) = F_2(\bar{h}) \iff \bar{h}(p) = h^* = \frac{f_{12} - f_{22}}{f_{21} - f_{11} + f_{12} - f_{22}}$$

A Liapunov function for the dynamics of dimorphism

Lessard (1984) provides a rigorous proof in discrete time; here I adopt instead a quicker and rougher proof based on the continuous time approximation of the recursion

Accordingly, replace $t+k$ with $\tau+k\delta$, $f_{ij}$ with $f_{+i}^j \delta\phi_{ij}$ and let $\delta \to 0$; the recursions tend to the differential equations:

$$\frac{dp_i(\tau)}{d\tau} = -\theta p_i(\tau)(\bar{h}_i - \bar{h})(\bar{h} - h^*) , \quad i = 1, \ldots, n \quad \text{where} \quad \theta = \frac{\phi_{21} - \phi_{11} + \phi_{12} - \phi_{22}}{f} > 0$$

Consider the function $\Psi(\tau) = \left[\bar{h}(p(\tau)) - h^*\right]^2$ and compute its time derivative:

$$\frac{d}{d\tau} \Psi(\tau) = -4\theta \left[\sum_i p_i(\tau)(\bar{h}_i - \bar{h})^2\right](\bar{h} - h^*)^2 \leq 0$$

with equality obtaining only at the equilibria; hence $\Psi(\tau)$ is a Liapunov function for this dynamics

We therefore conclude that the population evolves so as to minimize the distance of the frequencies of the two morphs, $C_1$ and $C_2$, from the value requested by the ESS $C^*$. If the current phenotypic expression matrix $H$ permits to attain $C^*$, then the manifold

$$L(h^*) = \{p : \bar{h}(p) = h^*\}$$

is a locally stable continuum of equilibrium points. Otherwise, equilibrium will be achieved at a point of minimum or maximum of $\bar{h}(p)$ that minimizes the distance from $h^*$. Any of such points that lays on the boundary of the simplex of frequency vectors $p$ might coexist, as a locally stable equilibrium, with $L(h^*)$
Long term evolution (at the same gene)

- Consider a population with n alleles, \{A_1, \ldots, A_n\}, of phenotypic expression matrix \( \mathbf{H} \), at the equilibrium \( \hat{\mathbf{p}} = (\hat{p}_1, \ldots, \hat{p}_n) \), so that the frequency of morph \( C_i \) is \( \bar{h}(\hat{\mathbf{p}}) \), that we suppose to be different from \( h^* \).

- Suppose that mutation introduces a new allele \( A_0 \), of frequency \( \epsilon(\tau) = 0 \) at time \( \tau \), so that the frequency of resident allele \( A_i \) is perturbed to \( \hat{p}_i - \delta_i(\tau), i = 1, \ldots, n \), with \( \delta_i(\tau) + \ldots + \delta_n(\tau) = \epsilon(\tau) \); let the mutant genotypes \( \{A_0A_1, \ldots, A_0A_n\} \) have expression probabilities \( \{h_{01}, \ldots, h_{0n}\} \), and let \( \bar{h}_0(\hat{\mathbf{p}}) = h_{01}\hat{p}_1 + \ldots + h_{0n}\hat{p}_n \neq \bar{h}(\hat{\mathbf{p}}) \).

- Then, as long as \( A_0 \) remains rare, the dynamics of its frequency (still using the continuous time version) is adequately represented by this linear approximation

\[
\frac{d\epsilon(\tau)}{d\tau} = -\theta\epsilon(\tau)\left[\bar{h}_0(\hat{\mathbf{p}}) - \bar{h}(\hat{\mathbf{p}})\right]\left[\bar{h}(\hat{\mathbf{p}}) - h^*\right] + o(\epsilon)
\]

- Since by hypothesis \( \theta > 0 \), we see that \( A_0 \) is able initially to increase and invade if and only if

\[
\bar{h}(\hat{\mathbf{p}}) < h^* \quad \text{and} \quad \bar{h}_0(\hat{\mathbf{p}}) > \bar{h}(\hat{\mathbf{p}})
\]

\[
\left[\bar{h}_0(\hat{\mathbf{p}}) - \bar{h}(\hat{\mathbf{p}})\right]\left[\bar{h}(\hat{\mathbf{p}}) - h^*\right] < 0 \quad \Leftrightarrow \quad \bar{h}(\hat{\mathbf{p}}) > h^* \quad \text{or} \quad \bar{h}_0(\hat{\mathbf{p}}) < \bar{h}(\hat{\mathbf{p}})
\]

- In other words, a mutant invades and destabilizes a preexisting equilibrium if and only if it tends to change the phenotypic composition of the population in the direction of the ESS, \( C^* \).

- Once the residents equilibrium is destabilized by an invading mutant, the dynamics follows the direction dictated by the Liapunov function \( \Psi \) and takes the population either on or at least closer to the manifold \( L(h^*) \) that establishes \( C^* \).

- If, on the other hand, \( \bar{h}(\hat{\mathbf{p}}) = h^* \) and the resident population is at equilibrium on \( L(h^*) \), no mutant that takes it away from \( L(h^*) \) can invade. Indeed any mutant is either eliminated or kept in the population, presumably at some small frequency, provided that permanence on \( L(h^*) \) is guaranteed.

- \( L(h^*) \) is therefore the unique (one-gene) LTE of this selection regime.