Laws of Adaptation

A course on biological evolution in eight lectures

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Lecture 7

Ways to diversity, or polymorphic LTE

Part I – discrete traits

Wednesday October 18, 15:00-16:00

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)   **Predators**   **Model Species**
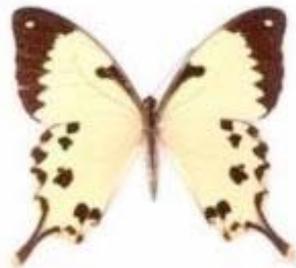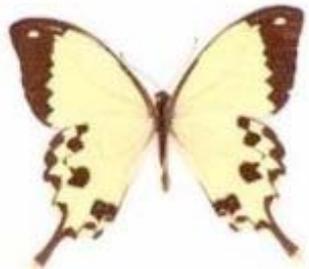
male   female

palatable   distasteful

Danaus c. chrysippus

Amauris crawshayi

Amauris niavius

Cryptic colorations (Clarke C.A. et al, Evolution, 1963)

Papilio demodocus

adult   larva   feeds on

Citrus

Predators

Umbelliferae

Predatorial tactics (Hori M., Science, 1993)

Perissodus microlepis

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

right side   left side

right-handed morph   on the left flank

left-handed morph   on the right flank

Predatorial tactics and food types

hammerers

Haematopus ostralegus

(oistercatcher)

stabbers

hammerer

worm-feeder

worm-feeders

Goss-Custard J.D. et al, J. Anim. Ecol., 1987, 1988, 1993
Sutherland W.J., Nature, 1987

Food specializations (Smith T.B., Nature, 1987, 1993)

Pyrenestes ostrinus

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

*Scleria* **meadow**

Pyrenestes ostrinus

large-billed morph

feeds mostly on large, hard seeds (*Scleria verrucosa*)

small-billed morph

feeds mostly on soft seeds (*S. mikawana, S. boivinii*)
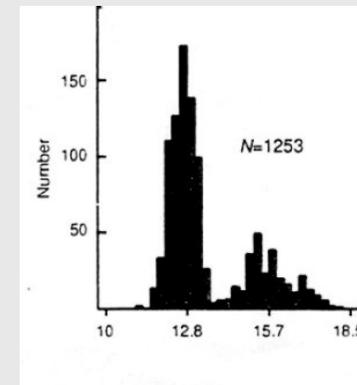
frequency distribution of lower mandible width (mm)

Evolutionary dynamics of dimorphism (Lessard, 1984)

❖ The only case of polymorphism (dymorphism) we have dealt with sofar 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

$$\upsilon(H,D) > \upsilon(D,D) \quad \text{and} \quad \upsilon(D,H) > \upsilon(H,H)$$

❖ 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 $\mathbf{p}(t)=\{p_1(t),\ldots,p_n(t)\}^T$ at generation t=0,1,…

❖ 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:

$$\overline{h} = \overline{h}(\mathbf{p}) = \sum_i \sum_j h_{ij} p_i(t) p_j(t) = \sum_i \overline{h}_i(\mathbf{p}) p_i(t)$$

❖ Probability of survival of individuals is determined by the outcomes of random pairwise contests, with a payoff matrix

$$\mathbf{F} = \begin{pmatrix} f_{11} & f_{12} \\ f_{21} & f_{22} \end{pmatrix}$$

such that, from the point of view of population game theory, it would admit a mixed ESS, C^*; hence

$$\upsilon(C_2,C_1) = f_{21} > f_{11} = \upsilon(C_1,C_1) \quad \text{and} \quad \upsilon(C_1,C_2) = f_{12} > f_{22} = \upsilon(C_2,C_2)$$

❖ Remember that in this case the probability, h*, that the ESS strategy plays C_1 is the unique solution in (0,1) of

$$\upsilon(C_1,C^*) = \upsilon(C_2,C^*) \quad \Leftrightarrow \quad h^* f_{11} + (1-h^*) f_{12} = h^* f_{21} + (1-h^*) f_{22} \quad \Leftrightarrow \quad h^* = \frac{f_{12} - f_{22}}{f_{21} - f_{11} + f_{12} - f_{22}}$$

- ❖ The fitness of C_i is:

$$F_i = F_i(\overline{h}) = \overline{h}f_{i1} + (1 - \overline{h})f_{i2} \quad , \quad i = 1,2$$

the fitness of genotype A_iA_j is:

$$w_{ij} = w_{ij}(\overline{h}) = h_{ij}F_1(\overline{h}) + (1 - h_{ij})F_2(\overline{h})$$

the mean fitness of allele A_i is:

$$\overline{w}_i = \overline{w}_i(\overline{h}) = \sum_j p_j(t)w_{ij}(\overline{h}) = \overline{h}_i F_1(\overline{h}) + (1 - \overline{h}_i)F_2(\overline{h})$$

and the population mean fitness is:

$$\overline{w} = \overline{w}(\overline{h}) = \sum_i p_i(t)\overline{w}_i(\overline{h}) = \overline{h}F_1(\overline{h}) + (1 - \overline{h})F_2(\overline{h})$$

- ❖ Hence, the recursion equations of the gene frequencies are:

$$p_i(t+1) = p_i(t)\frac{\overline{w}_i}{\overline{w}} = p_i(t)\frac{\overline{h}_i F_1 + (1 - \overline{h}_i)F_2}{\overline{h}F_1 + (1 - \overline{h})F_2} \quad , \quad i = 1,\dots,n$$

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

$$\hat{p}_i(\overline{h}_i - \overline{h})\left[F_1(\overline{h}) - F_2(\overline{h})\right] = 0 \quad , \quad i = 1,\dots,n$$

which identify two types of equilibria:

genotypic: $\quad \hat{p}_i(\overline{h}_i - \overline{h}) = 0$

phenotypic: $\quad F_1(\overline{h}) = F_2(\overline{h})$

- ❖ Genotypic equilibria, which are independent of the payoff matrix $\mathbf{F}$, are formally equivalent to the equilibria of constant selection dynamics, with the phenotypic expression matrix $\mathbf{H} = \{h_{ij}\}$ in place of a fitness matrix. Hence they correspond to points of maximum or minimum of $\overline{h}(\hat{\mathbf{p}})$

- ❖ 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

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

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 $f+\delta\phi_{ij}$ and let $\delta \to 0$; the recursions tend to the differential equations:

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

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

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

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

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

is a locally stable continum of equilibrium points. Otherwise, equilibrium will be achieved at a point of minimum or maximum of $\bar{h}(\mathbf{p})$ 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*)

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

Long term evolution (at the same gene)

❖ Consider a population with n alleles, $\{A_1,\ldots,A_n\}$, of phenotypic expression matrix **H**, at the equilibrium $\hat{\mathbf{p}} = (\hat{p}_1,\ldots,\hat{p}_n)$, so that the frequency of morph C_1 is $\overline{h}(\hat{\mathbf{p}})$, that we suppose to be different from h*

❖ Suppose that mutation introduces a new allele A_0, of frequency $\varepsilon(\tau)\approx 0$ at time τ, so that the frequency of resident allele A_i is perturbed to $\hat{p}_i - \delta_i(\tau)$, i=1,\ldots,n, with $\delta_1(\tau)+\ldots+\delta_n(\tau)=\varepsilon(\tau)$; let the mutant genotypes $\{A_0A_1,\ldots,A_0A_n\}$ have expression probabilities $\{h_{01},\ldots,h_{0n}\}$, and let $\overline{h}_0(\hat{\mathbf{p}}) = h_{01}\hat{p}_1 + \ldots + h_{0n}\hat{p}_n \neq \overline{h}(\hat{\mathbf{p}})$

❖ 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

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

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

$$\left[\overline{h}_0(\hat{\mathbf{p}}) - \overline{h}(\hat{\mathbf{p}})\right]\left[\overline{h}(\hat{\mathbf{p}}) - h^*\right] < 0 \quad \Leftrightarrow \quad \begin{array}{c} \overline{h}(\hat{\mathbf{p}}) < h^* \quad \text{and} \quad \overline{h}_0(\hat{\mathbf{p}}) > \overline{h}(\hat{\mathbf{p}}) \\ \text{or} \\ \overline{h}(\hat{\mathbf{p}}) > h^* \quad \text{and} \quad \overline{h}_0(\hat{\mathbf{p}}) < \overline{h}(\hat{\mathbf{p}}) \end{array}$$

❖ 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 Ψ and takes the population either on or at least closer to the manifold L(h*) that establishes *C**

❖ If, on the other hand, $\overline{h}(\hat{\mathbf{p}}) = h^*$ 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