

Laws of Adaptation

Lectures on mathematical models of biological evolution
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Lecture 5

Invading mutants, or the “long-term dynamics” point of view

Part III – frequency dependent selection

Tuesday October 2, 15:30-16:30

Frequency dependent selection: monomorphic LTE

- ❖ There are many forms of frequency dependent selection and a general representation valid for all does not exist. We concentrate on a specific model, inspired to the formalism of population games, that can serve as a good approximation for many ecological conditions including some, as competition for limited resources, apparently quite removed from the situation of direct contests between individuals typical of the game theoretic approach
- ❖ Fitness is determined by random pairwise confrontations between individuals, in which payoff depends on the value of a continuous trait:

$v(x',x)$: payoff to individual of trait value x' confronting opponent of trait value x ; $x',x \in [a,b]$

$\{x_\alpha, \dots, x_\omega\}$: the trait values occurring in a population

$\{p_\alpha, \dots, p_\omega\}$: their relative frequencies

$W(x_\kappa) = p_\alpha v(x_\kappa, x_\alpha) + \dots + p_\omega v(x_\kappa, x_\omega)$: fitness of trait value x_κ , $\kappa = \alpha, \dots, \omega$

- ❖ In this situation, conditions for a LTE occurring at $x^\circ \in [a,b]$ are formally the same as those derived for constant selection, but with a different interpretation of fitness parameters w_α

$$\begin{aligned}\varepsilon_i(t+1) &= \frac{w_{0i}}{w_{00}} \varepsilon_i(t) + \frac{2}{w_{00}} \sum_{j>i} w_{0j} R(i|0j) \varepsilon_j(t) + o(\varepsilon) \quad , \quad \forall g_i \in \mathcal{G}_1 \\ \varepsilon_i(t+1) &= \frac{2w_{0i}R(i|0i)}{w_{00}} \varepsilon_i(t) + \frac{2}{w_{00}} \sum_{j>i} w_{0j} R(i|0j) \varepsilon_j(t) + o(\varepsilon) \quad , \quad \forall g_i \notin \mathcal{G}_1 \\ \text{LTE condition} \\ w_{00} &> w_{0i} \quad \forall g_i \in \mathcal{G}_1 \quad , \quad w_{00} > 2R(i|0i)w_{0i} \quad \forall g_i \notin \mathcal{G}_1 \quad , \quad \forall \mathcal{G}\end{aligned}$$

- ❖ Since the recursions for mutant frequencies are approximated to $O(\varepsilon)$, it is sufficient to approximate the fitness parameters to only $O(1)$; hence

$$\begin{aligned}w_{0i} &= W(X(g_0g_i)) = v(X(g_0g_i), X(g_0g_0)) = v(X(g_0g_i), x^\circ) \\ w_{00} &= W(X(g_0g_0)) = v(X(g_0g_0), X(g_0g_0)) = v(x^\circ, x^\circ)\end{aligned}$$

- ❖ We conclude that $x^\circ \in [a, b]$ is a LTE whenever

$$v(x^\circ, x^\circ) > v(x, x^\circ) \quad , \quad \forall x \in [a, b], x \neq x^\circ$$

- ❖ LTE occur at trait values such that individuals *maximize* their payoff by having the same trait value as their opponents
- ❖ Observe that this condition is *identical* to the first of the two conditions for an ESS, in the case of discrete strategy sets (set of available pure strategies). Here we are dealing with continuous traits (continuous strategy sets), where the second condition would not be very relevant, given that it would apply in the non-generic case that $v(x, x^\circ) = v(x^\circ, x^\circ)$ for some $x \neq x^\circ$.

Frequency dependence: convergence to monomorphic LTE

- ❖ With constant selection the indications are that any LTE is “locally stable”, namely paths from a sufficiently small neighborhood converge to it. *It is not the same with frequency dependent selection*: there is a precise criterion that discriminates between (most probably) stable and unstable LTE

Continuous Stability (Eshel and Motro, 1980; Eshel, 1983)

- ❖ Discovered in the context of population game theory, as a property of ESS in games with a continuous strategy set
- ❖ An example: a game with payoff function of the form

$$v(x',x) = \psi(x', (x'-x)^2) \quad , \quad \text{for } x', x \in \mathbb{R}$$

where $\psi(u,z)$ is a smooth function, \downarrow in z : meaning that, irrespective of their particular aspect, it is always better to be like the others

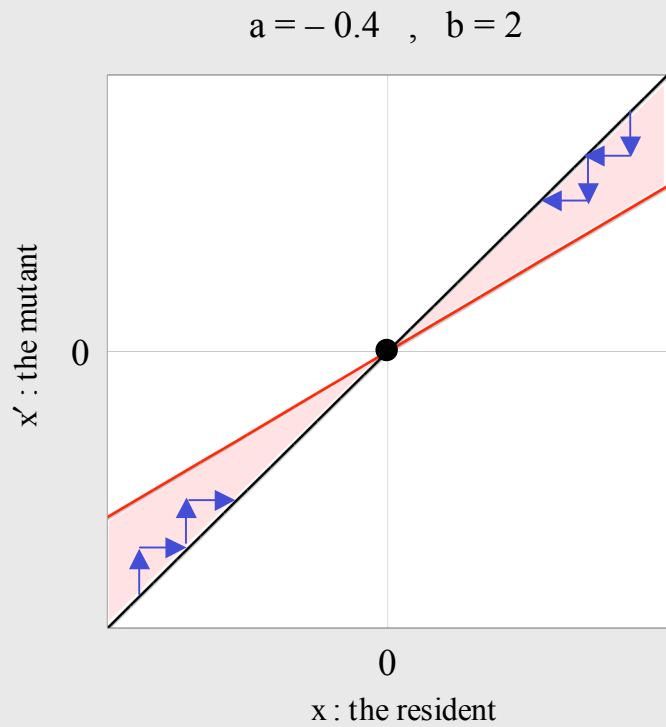
- ❖ In particular choose

$$v(x',x) = (1 + ax'^2) [1 - (a+b)(x'-x)^2] \quad , \quad b > 0, a + b > 0$$

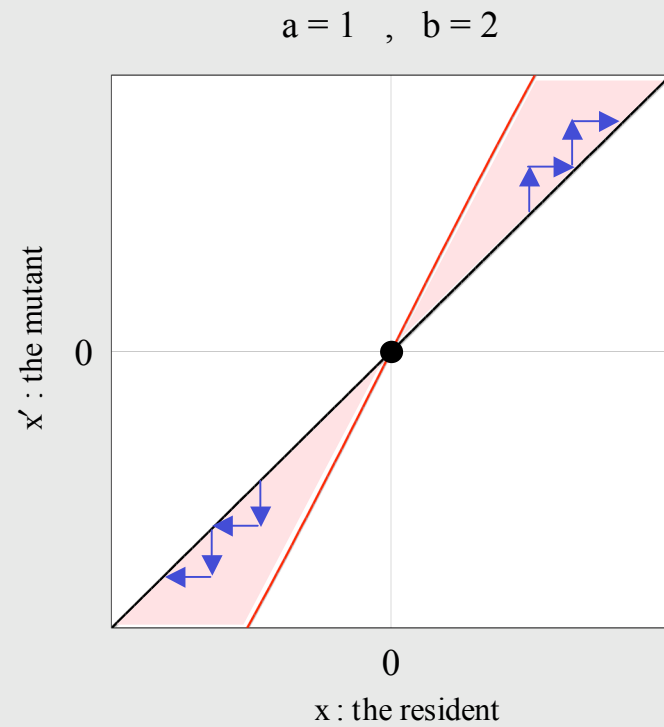
- ❖ The condition for ESS (and LTE) is

$$\left. \frac{\partial v(x',x)}{\partial x'} \right|_{x'=x} = 2ax = 0 \quad ; \quad \left. \frac{\partial^2 v(x',x)}{\partial x'^2} \right|_{x'=x} = -2b < 0$$

- ❖ Hence the unique LTE occurs at $x^o=0$, $\forall a \neq 0$ and $\forall b > 0$; but convergence to this LTE depends on the sign of a , as shown by two the following numerical examples



x° is “continuously stable”



x° is not “continuously stable”

- $x' = x$
- $v(x', x) = v(x, x)$, $x' \neq x$
- $v(x', x) > v(x, x)$

Definition of Continuous Stability

- ❖ An ESS x° , from a one-dimensional, continuous strategy set with payoff function $v(x',x)$, is continuously stable when, for any resident strategy $x \neq x^\circ$ sufficiently close to it, any mutant strategy $x' \neq x$ satisfies $v(x',x) > v(x,x)$ only if x' is on the same side of x as the ESS x° ; formally:

$$v(x',x) - v(x,x) > 0 \quad \text{only if} \quad (x - x')(x - x^\circ) > 0$$

- ❖ Since the condition for monomorphic LTE, with frequency dependent selection of the type we are considering, is identical to that for continuous ESS, this definition is equally applicable to LTE

A local condition for Continuous Stability

$$v(x', x) - v(x, x) > 0 \quad \text{only if} \quad (x - x')(x - x^\circ) > 0 \quad (*)$$

- ❖ Consider a smooth payoff function $v(x', x)$ in a neighborhood of a unique monomorphic LTE (or ESS), x° , so that

$$\left. \frac{\partial v(x', x)}{\partial x'} \right|_{x'=x=x^\circ} = 0, \quad \left. \frac{\partial^2 v(x', x)}{\partial x'^2} \right|_{x'=x=x^\circ} \leq 0$$

Assume mutations of small effect. Then, for $|x - x^\circ|, |x' - x^\circ| < \varepsilon \approx 0$, by a second order Taylor expansion around (x°, x°) , we can approximate $v(x', x) - v(x, x)$ as

$$v(x', x) - v(x, x) \cong [A(x' - x) + 2(A + B)(x - x^\circ)](x' - x)$$

where

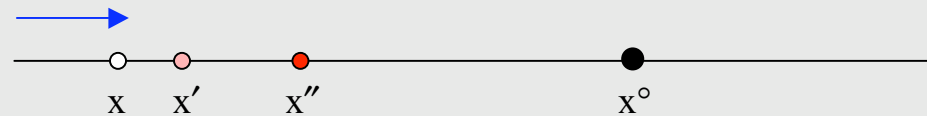
$$A = \frac{1}{2} \left. \frac{\partial^2 v(x', x)}{\partial x'^2} \right|_{x'=x=x^\circ}, \quad B = \frac{1}{2} \left. \frac{\partial^2 v(x', x)}{\partial x' \partial x} \right|_{x'=x=x^\circ}$$

Since, for any given $|x - x^\circ|$, (*) must hold for all sufficiently small $|x' - x|$, it is obvious that (*) is satisfied if and only if

$$A + B = \frac{1}{2} \left. \frac{\partial^2 v(x', x)}{\partial x'^2} \right|_{x'=x=x^\circ} + \frac{1}{2} \left. \frac{\partial^2 v(x', x)}{\partial x' \partial x} \right|_{x'=x=x^\circ} < 0$$

Convergence to “continuously stable” LTE

- ❖ *Continuous stability* guarantees convergence in the case of asexual (clonal) reproduction (e.g., Eshel, Motro & Sansone, 1997), but with sexual reproduction (mendelian genetics) this is no longer true. On the other hand, without continuous stability divergence from a LTE is almost certain
- ❖ As in the case of constant selection, assume a unique, continuously stable LTE, x° , partial dominance and mutations of small size (limited by $\delta \approx 0$), and consider a monomorphic state $X(gg)=x \notin [x^\circ - \delta, x^\circ + \delta]$, and a one-gene mutant gamete g^* such that $X(g^*g)=x'$ and $X(g^*g^*)=x''$. It is clear that if g^* invades g then x' and x'' are on the same side of x° as x , x' is closer to x° than x and x'' is closer to x° than x'



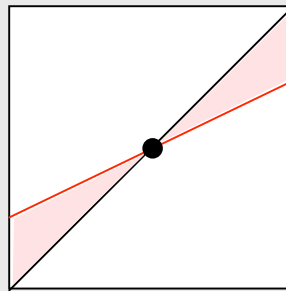
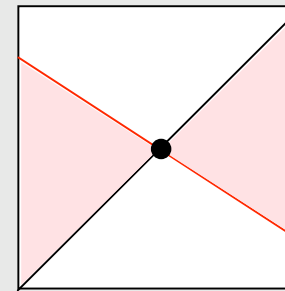
Hence, by continuous stability, g cannot invade back g^*

- ❖ This is not enough to prove that in fact invasion by g^* results in complete replacement of g (as under constant selection) but the conjecture that such is indeed the case is most plausible, particularly under the weak selection implied by mutations of small size. It seems therefore likely that, as long as the interval $(x^\circ - \delta, x^\circ + \delta)$, is not attained the population remains monomorphic and evolves toward x°

- ❖ The character of further evolution after attainment of $(x^\circ - \delta, x^\circ + \delta)$ depends on whether $v(x', x) - v(x, x) > 0$ whenever x' and x are on *opposite* sides of x° :

$$v(x', x) - v(x, x) \cong [A(x' - x) + 2(A + B)(x - x^\circ)](x' - x) \rightarrow -(A + 2B)(x - x^\circ)^2 \quad \text{as } x' \rightarrow x^\circ$$

- ❖ Hence, for x' close to x° , x' invades, when it is on the *opposite* side of x° as x , if and only if $A + 2B < 0$

Case I: $A + 2B > 0$ Case II: $A + 2B < 0$ 

- ❖ **Case I.** Once $x^\circ - \delta < x < x^\circ + \delta$ is attained, invasion of g by a mutant g^* such that $x < x' < x^\circ < x''$, or $x'' < x^\circ < x' < x$ becomes possible. In this event however g could not invade g^* , because x' and x'' are on opposite sides of x° . It is uncertain whether a polymorphism can ever be attained. Maybe evolution proceeds through a sequence of monomorphic states within $(x^\circ - \delta, x^\circ + \delta)$, jumping from one side of x° to the other
- ❖ **Case II.** In this case, within $(x^\circ - \delta, x^\circ + \delta)$, a situation similar to that examined under constant selection is most likely to arise. Namely occurrence of a mutant such that x and x'' are on opposite sides of x° , while $v(x', x) > v(x, x)$ but, at the same time, $v(x', x'') > v(x'', x'')$, so that g^* invades g , but also g could invade back g^* . One-gene polymorphism, which might easily complicate into multi-gene polymorphism, is unavoidable and further evolution cannot be predicted

$$\alpha = A, \beta = -(A + 2B) \quad ; \quad A = \frac{1}{2} \frac{\partial^2 v(x', x)}{\partial x'^2} \Big|_{x'=x=0}, \quad B = \frac{1}{2} \frac{\partial^2 v(x', x)}{\partial x' \partial x} \Big|_{x'=x=0}$$

Frequency dependence: polymorphic LTE

- ❖ Let $v(x', x) \cong 1 + \alpha x'^2 - (\alpha + \beta) x x' + \beta x^2$, $\alpha < 0, \alpha - \beta < 0$ with $x', x \approx 0$

With this payoff function, $x^\circ = 0$ is a *continuously stable* (monomorphic) LTE

- ❖ Suppose that in the vicinity of x° there exists a *polymorphic* LTE such that the phenotypic mean and variance are respectively \bar{x} and s^2
- ❖ In such a population the fitness of an individual (e.g., a mutant) of phenotype y is

$$W(y) = 1 + \alpha y^2 - (\alpha + \beta) \bar{x} y + \beta (\bar{x}^2 + s^2)$$

while the mean fitness of the population residents is

$$\bar{W} = 1 + (\alpha + \beta) s^2$$

and

$$W(y) - \bar{W} = (y - \bar{x})(\alpha y - \beta \bar{x}) - \alpha s^2$$

- ❖ Since $\alpha < 0$, the term $-\alpha s^2$ is positive. Hence the mutant certainly has a greater fitness than the average resident if

$$\bar{x} < 0 \quad \text{and} \quad \bar{x} < y < \frac{\beta}{\alpha} \bar{x} \quad \text{or}$$

$$\bar{x} > 0 \quad \text{and} \quad \frac{\beta}{\alpha} \bar{x} < y < \bar{x} \quad \text{or}$$

$$\bar{x} = 0 \quad \text{and} \quad \alpha(y^2 - s^2) > 0 \quad \Leftrightarrow \quad y^2 < s^2$$

- ❖ By the Eshel-Feldman-Lessard criterion, it follows that any mutation such that all new genotypes generated by it are assigned trait values confined within the intervals

$$\begin{aligned} & \left(\bar{x}, \frac{\beta}{\alpha} \bar{x} \right) \quad \text{if } \bar{x} < 0 \\ & \left(\frac{\beta}{\alpha} \bar{x}, \bar{x} \right) \quad \text{if } \bar{x} > 0 \\ & (-s, s) \quad \text{if } \bar{x} = 0 \end{aligned}$$

is able to invade the corresponding polymorphic population

- ❖ We conclude that **no polymorphic LTE can possibly exist under frequency dependent selection** of this type, in a neighborhood of a monomorphic LTE