

# Laws of Adaptation

A course on biological evolution in eight lectures  
by Carlo Matessi

## Lecture 5

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

Part III – frequency dependent selection

Wednesday October 11, 16:00-17:00

## 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  $x_\kappa$ ,  $\kappa = \alpha, \dots, \omega$

- ❖ 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  $w_\alpha$

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

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

LTE condition

$$w_{00} > w_{0i} \quad \forall g_i \in \mathcal{G}_1 \quad , \quad w_{00} > 2R(i|0i)w_{0i} \quad \forall g_i \notin \mathcal{G}_1 \quad , \quad \forall \mathcal{G}$$

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

$$w_{0i} = W(X(g_0 g_i)) = v(X(g_0 g_i), X(g_0 g_0)) = v(X(g_0 g_i), x^\circ)$$

$$w_{00} = W(X(g_0 g_0)) = v(X(g_0 g_0), X(g_0 g_0)) = v(x^\circ, x^\circ)$$

- ❖ 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

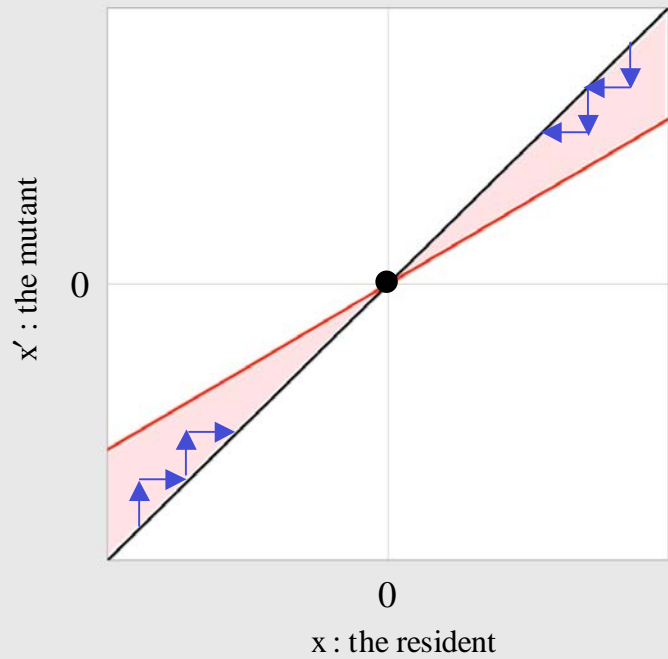
$$v(x',x) = (1 + ax'^2) [1 - (a+b)(x'-x)^2] \quad , \quad b > 0, a + b > 0$$

- ❖ The condition for ESS (and LTE) is

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

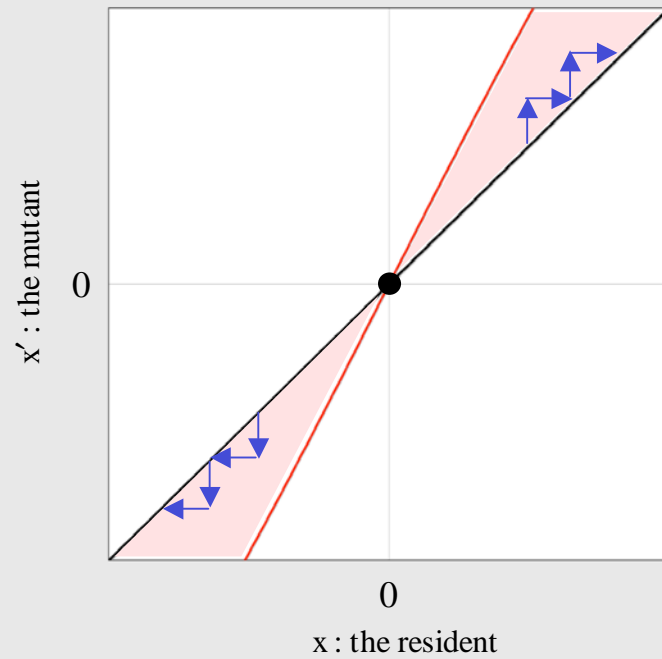
- ❖ Hence the unique LTE occurs at  $x^o=0$ ,  $\forall a \neq 0$  and  $\forall b > 0$  ; but convergence to this LTE depends on the sign of  $a$ , as shown by two the following numerical examples

$a = -0.4$  ,  $b = 2$

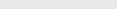
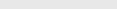



$x^0$  is “continuously stable”

$a = 1$  ,  $b = 2$



$x^0$  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  $x^\circ$ , 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  $x^\circ$ ; formally:

$$v(x',x) > v(x,x) \text{ only if } (x-x')(x-x^\circ) > 0 \quad (1)$$

- ❖ 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

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

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

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

$$v(x',x) - v(x,x) = [A(x' - x) + 2(A + B)(x - x^\circ)](x' - x) + o(\varepsilon^2) \quad \text{where} \quad A = \left. \frac{1}{2} \frac{\partial^2 v(x',x)}{\partial x'^2} \right|_{x'=x=x^\circ}, \quad B = \left. \frac{1}{2} \frac{\partial^2 v(x',x)}{\partial x' \partial x} \right|_{x'=x=x^\circ}$$

Since, for any given  $|x-x^\circ|$ , (1) must hold for all  $|x'-x|$ , no matter how small, it is obvious that it is satisfied if and only if

$$A + B = \left. \frac{1}{2} \frac{\partial^2 v(x',x)}{\partial x'^2} \right|_{x'=x=x^\circ} + \left. \frac{1}{2} \frac{\partial^2 v(x',x)}{\partial x' \partial x} \right|_{x'=x=x^\circ} < 0 \quad (3)$$

### Convergence to “continuously stable” LTE

- ❖ Indications of convergence in this case are even more uncertain than for constant selection LTE, for the reason that, due to frequency dependence, even in one-gene selection dynamics there is no maximization of mean fitness to rely on
- ❖ As in the case of constant selection, assume a unique, continuously stable LTE,  $x^\circ$ , 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  $x^\circ$  as  $x$ , but

$$|x'' - x^\circ| < |x' - x^\circ| < |x - x^\circ|$$

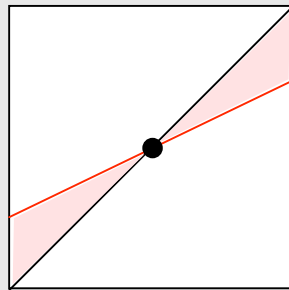
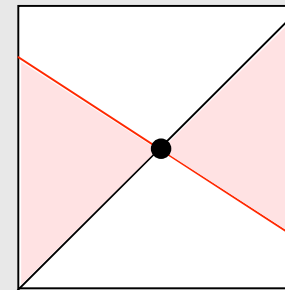
and therefore, by continuous stability,  $g$  cannot invade back  $g^*$

- ❖ 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 quite plausible that, as long as the interval  $(x^\circ - \delta, x^\circ + \delta)$ , is not attained the population remains monomorphic and evolves toward  $x^\circ$

- ❖ 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  $x^\circ$ :

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

- ❖ Hence, for all  $x'$  sufficiently close to  $x^\circ$ ,  $v(x', x) - v(x, x) > 0$  whenever  $(x' - x^\circ)(x - x^\circ) < 0$  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  $x^\circ$ . We expect therefore that a polymorphism of  $g$  and  $g^*$  is never attained, and that evolution proceeds through a sequence of monomorphic states within  $(x^\circ - \delta, x^\circ + \delta)$ , jumping from one side to the other of  $x^\circ$
- ❖ **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 the case where a mutant appears such that  $x$  and  $x''$  are on opposite sides of  $x^\circ$ , 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  $g^*$ . Now, one-gene polymorphism, which might easily complicate into multi-gene polymorphism, is unavoidable and further evolution cannot be predicted



$$v(x', x) - v(x, x) = [A(x' - x) + 2(A + B)(x - x^\circ)](x' - x) + o(\varepsilon^2) \quad \text{where} \quad A = \frac{1}{2} \frac{\partial^2 v(x', x)}{\partial x'^2} \Big|_{x'=x=x^\circ}, \quad B = \frac{1}{2} \frac{\partial^2 v(x', x)}{\partial x' \partial x} \Big|_{x'=x=x^\circ}$$

## Frequency dependence: polymorphic LTE

- ❖ It seems that, with frequency dependent selection, polymorphic states can arise in the neighborhood of a monomorphic LTE,  $x^\circ$ , only in the case  $A+2B < 0$ . Precisely in this case we now prove that *polymorphic LTE cannot exist near  $x^\circ$*
- ❖ Suppose that there exists a polymorphism with trait values  $\{x_1, \dots, x_n\}$  of frequencies  $\{P_1, \dots, P_n\}$ , in the vicinity of a monomorphic LTE with a trait value,  $x^\circ$ , that without loss of generality, we can assume to be  $x^\circ=0$ , so that  $|x_i| \leq \varepsilon$  for some small enough  $\varepsilon$
- ❖ Introduce a mutation such that all new genotypes generated by it are assigned trait values of absolute value not greater than  $\delta \ll \varepsilon$ , and apply the Eshel-Feldman-Lieberman test to it. Considering that  $w_{\text{mut}} = W(0) + O(\delta)$  we have

$$w_{\text{mut}} - \bar{w} \cong \sum_i P_i [W(0) - W(x_i)] = \sum_i \sum_j P_i P_j [v(0, x_j) - v(x_i, x_j)] = \\ \sum_i \sum_j P_i P_j \{ [v(0, x_j) - v(x_j, x_j)] - [v(x_i, x_j) - v(x_j, x_j)] \}$$

- ❖ Applying to each term  $v(x', x) - v(x, x)$  the Taylor expansion about  $x^\circ$  defined above, which is accurate up to  $O(\varepsilon^3)$ , we find

$$w_{\text{mut}} - \bar{w} \cong -A \text{Var}\{x_i\} - (A + 2B) E\{x_i\}^2$$

which is positive whenever  $A+2B < 0$ , because necessarily  $A < 0$  given that  $x^\circ$  is a monomorphic LTE

- ❖ The mutation therefore invades and the polymorphism cannot be a LTE