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# Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits

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## Summary

We present models of adaptive change in continuous traits for the following situations: (1) adaptation of a single trait within a single population in which the fitness of a given individual depends on the population's mean trait value as well as its own trait value; (2) adaptation of two (or more) traits within a single population; (3) adaptation in two or more interacting species. We analyse a dynamic model of these adaptive scenarios in which the rate of change of the mean trait value is an increasing function of the fitness gradient (i.e. the rate of increase of individual fitness with the individual's trait value). Such models have been employed in evolutionary game theory and are often appropriate both for the evolution of quantitative genetic traits and for the behavioural adjustment of phenotypically plastic traits. The dynamics of the adaptation of several different ecologically important traits can result in characters that minimize individual fitness and can preclude evolution towards characters that maximize individual fitness. We discuss biological circumstances that are likely to produce such adaptive failures for situations involving foraging, predator avoidance, competition and coevolution. The results argue for greater attention to dynamical stability in models of the evolution of continuous traits.

**Keywords:** fitness; continuous traits; evolutionary stable strategy; frequency dependence

## Introduction

Many evolutionary problems are currently analysed by game theory models (e.g. Maynard Smith, 1982; Vincent and Brown, 1988; Parker and Maynard Smith, 1990; Krebs and Davies, 1991). In most of these analyses, adaptive evolution is assumed to result in trait values which maximize individual fitness, conditional on the traits or strategies of other individuals in the population (or in other populations). This method of thinking was foreshadowed by Fisher (1930) before the birth of evolutionary game theory (Maynard Smith and Price, 1973). By taking into account the frequency dependence inherent in many ecological and evolutionary situations, game theory has resulted in major advances (Maynard Smith, 1982).

A major criticism of game theory models has been their focus on conditions for evolutionary equilibria and lack of consideration of the dynamical stability or genetic attainability of those equilibria (e.g. Eshel and Motro, 1981; Lande, 1981; Eshel, 1983; Eshel and Akin, 1983; Thomas, 1985; Cressman *et al.*, 1986; Hofbauer and Sigmund, 1988; Taylor, 1989; Charlesworth,

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1990; Hastings and Hom, 1990; Lessard, 1990; Christiansen, 1991). Eshel and Motro (1981) were apparently the first to show that a continuous trait value which satisfies Maynard Smith's (1982) definition of an ESS could be dynamically unstable, even under the simplifying genetic assumptions (haploid population, infinite population size, mutations of small effect) that were generally used to derive ESS conditions. They (Eshel and Metro, 1981; Eshel, 1983) showed that it was possible for traits to maximize individual fitness if all members of the population possessed those traits, and thus be uninvadable, but still not be stable. This occurred in situations where, if the mean trait of the population deviated from the uninvadable value, the trait would evolve away from this value. This difference between criteria for maximizing individual fitness and criteria for dynamic stability has recently been discussed by Taylor (1989) and Christiansen (1991). Earlier treatments of the dynamics of non-continuous traits are summarized by Hofbauer and Sigmund (1988).

In this article, we point out that very general models of the adaptation of continuous traits can result in both dynamically stable fitness minima and dynamically unstable fitness maxima. We show that these phenomena can occur by similar mechanisms in three situations: (1) evolution of single traits within a population when the fitness of an individual depends on its own trait value and the mean trait value within the population (i.e. intraspecific frequency dependence); (2) evolution of two traits within a single population; (3) coevolution or behavioural coadaptation of interacting species (with or without frequency dependence). Previous work has not surveyed the ecological situations that are likely to result in the failure of the adaptive process to maximize fitness. In fact, Taylor (1989) suggests that there may be no biological examples in which stable fitness minima could arise. We give examples of ecological situations which seem most likely to result in stable fitness minima or unstable maxima and discuss previous theory regarding the evolution of continuous traits.

### The dynamics of a frequency-dependent trait

We first consider the dynamics of adaptive change within a single species, when the fitness of an individual with a particular trait depends on the group mean trait value. A feature of all types of adaptation – whether behavioural, developmental or evolutionary – is that the trait values change in a direction which increases fitness. If we denote the fitness of an individual by  $F$ , this quantity may depend on its own trait value ( $x$ ) and the mean trait value of its population ( $x^*$ ), assuming there are no interacting populations. More generally, fitness may depend on the precise distribution of trait values in the population, but we will not consider this situation here.

There are many circumstances when an individual's fitness depends only on the population mean value. If the trait is related to rate of resource exploitation, the amount of resource available depends on the mean uptake rate of the population. If the trait is related to predator escape ability, the level of predator satiation, and, thus risk, depends on the mean escape ability of the prey population. There are many other examples in which an individual's fitness is a function of a mean trait value in the population (see Maynard Smith, 1982 and below).

This analysis is based on a generalized model of adaptive change. The model assumes that the adaptive process will change the individual's trait value more rapidly, the more rapidly fitness changes with a given change in the trait. The trait therefore changes at a rate which increases with the derivative of individual fitness,  $F$  with respect to the individual's trait value,  $x$ . This derivative is the fitness gradient,  $\partial F/\partial x$ . Most of the article is based on the simplest possible assumption, i.e. the rate of change in the mean trait value is directly proportional to the fitness gradient evaluated for an individual with the mean trait value:

$$dx^*/dt = k \partial F(x, x^*) / \partial x|_* \quad (1)$$

where  $k$  is the rate constant of the adaptive process and  $|_*$  indicates that the derivative is evaluated where  $x = x^*$ . This model has been assumed in several ESS approaches to the evolution of continuous traits (Hofbauer and Sigmund, 1988; Abrams, 1992; Taper and Case, 1992). It can be derived as an approximation to simple quantitative genetic models; Iwasa *et al.* (1991) and Taper and Case (1992) showed that this approximation is valid under the assumption that the phenotypic variance of the trait is constant and relatively small.

Appendix 3 of this article provides a more detailed discussion of the conditions under which Equation 1 is a good description of quantitative genetic models and shows that it can also apply to some cases with a large phenotypic variance. If the adaptation is by genetic change in a quantitative trait, the rate constant,  $k$ , is the additive genetic variance (Lande, 1982);

$$k = \sigma_p^2 h^2 \quad (2)$$

where  $\sigma_p^2$  is the phenotypic variance of the trait and  $h^2$  is the narrow sense heritability (the ratio of additive genetic variance to total phenotypic variance). The additive genetic variance,  $k$ , is often assumed to be constant, although this assumption is usually not satisfied precisely (Turelli, 1988).

If the trait changes behaviourally, there is less justification for assuming a linear relationship between the fitness gradient and trait dynamics. Here, we could assume that the rate of change of the mean trait value is an arbitrary increasing function,  $\xi$ , of the fitness gradient,  $\partial F / \partial x$ , where  $\xi(0) = 0$ . In this case, if the phenotypic variance is again small, the rate of change of  $x^*$  is given by

$$dx^*/dt = \xi(\partial F / \partial x|_*) \quad (3)$$

Another related model of adaptation assumes that the rate of change in the character is proportional to the fitness gradient multiplied by a function of the mean trait value. This is likely to be true when the trait is close to its minimum or maximum possible value. For example, if the trait is determined by a single locus with two alleles having purely additive effects, the rate of change in the character approaches zero as either allele approaches fixation, regardless of the selection gradient. It is also plausible that behaviours begin to change less rapidly as they approach maximum or minimum values. Any of these cases may be better approximated by the following equation than by Equation 1:

$$dx^*/dt = k(x^*) \partial F / \partial x|_* \quad (4)$$

where  $k$  is a non-negative function of  $x^*$  that approaches zero when the mean trait value approaches its minimum or maximum value (e.g. when additive genetic variance is depleted).

All of the above models have the same conditions for the existence and local stability of equilibrium points at intermediate character values. At an intermediate equilibrium point of Equations 1, 3 or 4, it is necessary that

$$dx^*/dt = k(x^*) \xi(\partial F / \partial x|_*) = 0 \quad (5a)$$

For Equation 5a to be satisfied at an intermediate value of  $x^*$ , it is necessary that

$$\partial F / \partial x|_* = 0 \quad (5b)$$

An equilibrium point specified by Equations 1, 3 or 4 is locally stable if, when the mean trait value departs from the stationary point specified by Equation 5b, the dynamics return it to that point. Thus, the derivative of the right-hand side of these equations with respect to  $x^*$  must be

negative. If we combine all three models so  $dx^*/dt = k(x^*)\xi(\partial F/\partial x|_*)$ , this stability condition becomes

$$\begin{aligned} (d/dx^*)[dx^*/dt] &= (d/dx^*)[k(x^*)\xi(\partial F/\partial x|_*)] \\ &= k(x^*)\xi'(\partial F/\partial x|_*)(\partial F/\partial x|_*) + (dk/dx^*)\xi(\partial F/\partial x|_*) < 0 \end{aligned} \quad (6)$$

The function  $\xi$  is monotonically increasing ( $\xi' > 0$ ) and is zero at an equilibrium point, when  $\partial F/\partial x|_* = 0$ . Therefore, the sign of the left-hand side of Inequality 6 only depends on the quantity  $(d/dx^*)(\partial F/\partial x|_*)$ , which must be negative for stability. This means that if the mean trait value moves away from the equilibrium by a small amount, the most fit individuals will be those that are closer to the equilibrium point. Thus, the dynamics of adaptation will tend to return the trait value to the equilibrium value. The local stability condition for the equilibrium point of all three models is identical. This condition may be rewritten

$$\partial^2 F/\partial x^2|_* + \partial^2 F/\partial x \partial x^*|_* < 0 \quad (7)$$

Equivalent stability conditions have been derived for one-locus genetic models by Taylor (1989) and Christiansen (1991).

It is important to note that Inequality 7 is not identical to the condition that a particular trait value that satisfies Equation 5b maximizes individual fitness; this local maximization condition is simply

$$\partial^2 F(x, x^*)/\partial x^2|_* < 0 \quad (8)$$

If Inequality 8 is reversed at a critical point (satisfying Equation 5b), then the trait represents a local fitness minimum. The difference between Inequalities 7 and 8 allows two possible maladaptive equilibria of Equation 5b: (1) an evolutionarily stable fitness minimum (i.e. Inequality 7 is satisfied and Inequality 8 is violated) or (2) an unstable fitness maximum (i.e. Inequality 7 is violated and Inequality 8 is satisfied). These two possibilities need be of little concern to biologists unless ecologically relevant models suggest that the possibilities may occur frequently. Unfortunately for those who hope to be able to ignore dynamics, there are many evolutionary scenarios under which these adaptive failures may occur, as we show below. The comparison of Inequalities 7 and 8 shows that unstable fitness maxima occur when  $\partial^2 F/\partial x^2|_*$  is negative, but  $\partial^2 F/\partial x \partial x^*|_*$  is positive and larger in magnitude; stable minima occur when these signs are reversed. These abstract conditions for stability and fitness maximization to differ can be illustrated by considering three ecologically important types of traits whose fitness is generally frequency dependent. The traits considered here are (1) traits determining resource exploitation intensity, (2) traits determining susceptibility to predation and (3) traits determining success in contest competition.

### *Resource exploitation intensity*

The fitness,  $F$ , of an individual with a particular resource-exploitation intensity, denoted  $x$ , is generally a function of resource abundance,  $R$ . Intensity is used to denote exploitation rate under some standard conditions and is determined by traits such as speed of movement and morphological features related to eating.  $R$  may be expressed as a function of the mean exploitation intensity,  $x^*$ , in the population, provided the population dynamics of the resource are sufficiently fast and  $R$  approaches a stable equilibrium. Individual fitness can then often be expressed (Abrams, 1991) as a function of two variables: resource intake rate,  $I$  and exploitation intensity,  $x$ . Fitness increases with intake rate and decreases with exploitation intensity, since

greater intensity is generally accompanied by greater energy expenditure or predation risk. If handling time can be neglected,  $I = xR(x^*)$ , if not,  $I$  is a convex increasing function of  $xR$ . Here we will assume that handling time may be neglected. The possible stationary points in the evolution of  $x$  satisfy

$$dF/dx = \partial F/\partial I(\partial I/\partial x) + \partial F/\partial x = R\partial F/\partial I + \partial F/\partial x = 0 \quad (9)$$

The  $x$  values satisfying this equation represent local fitness maxima if

$$d^2F/dx^2 = R^2\partial^2F/\partial I^2 + \partial^2F/\partial x^2 + 2R\partial^2F/\partial x\partial I < 0 \quad (10)$$

where all derivatives are evaluated at  $x = x^*$ . Because  $R$  is a function of the mean exploitation intensity of the population,  $x^*$ , the stability criteria generally differ from the fitness maximization criteria. Following the theory developed above, a consumption trait value  $x$  which satisfies Equation 9 is dynamically stable if

$$(\partial R/\partial x^*)\partial F/\partial I + (R^2 + xR\partial R/\partial x^*)\partial^2F/\partial I^2 + \partial^2F/\partial x^2 + 2R\partial^2F/\partial x\partial I + x(\partial R/\partial x^*)\partial^2F/\partial x\partial I < 0 \quad (11)$$

where all derivatives are again evaluated at  $x = x^*$ . This Inequality assumes that  $R$  may be expressed as a function of  $x^*$ . If this is not true, it is necessary to analyse the stability of a system with two dynamic equations determining the rates of change of  $R$  and  $x^*$ . Appendix 1 shows that there is a critical value for the relative rates of change of these variables; if  $R$  changes sufficiently rapidly relative to  $x^*$ , the stability of the two-variable system is determined by Inequality 11.

If the terms that are present in Inequality 11, but not Inequality 10, are negative, then stable fitness minima may exist; if these terms are positive, then unstable maxima may exist. There are likely to be biological circumstances in which each is possible. Here is a list of the terms present in Inequality 11, but not Inequality 10, with a discussion of their possible signs.

(1)  $(\partial R/\partial x^*)(\partial F/\partial I)$  is usually negative. Resource density decreases with increasing consumer exploitation intensity and fitness increases with intake.

(2)  $(xR\partial R/\partial x^*)(\partial^2F/\partial I^2)$  may be positive or negative (or zero). The first factor is generally negative, but the sign of the second term depends on whether fitness increases at an accelerating or decelerating rate with resource intake. If fitness increases linearly with intake (a common occurrence; see Abrams, 1991), this term is zero.

(3)  $(x\partial R/\partial x^*)(\partial^2F/\partial x\partial I)$  is likely to be zero or positive. Its first factor is usually negative, since greater exploitation rate generally reduces resource density. Its second factor represents the effect of a larger trait value on the slope of the intake rate vs fitness relationship. If it has any affect, a larger value of a costly trait should decrease the slope, making this second term negative. Thus, the product of the two factors will generally be non-negative.

Thus, if terms (2) and (3) are zero, the left hand side of Inequality 11 is always less than the left hand side of Inequality 10 and stable fitness minima are possible, but unstable maxima are not. On the other hand, if fitness increases at a decelerating rate with intake and the fitness effects of resource intake decrease as trait value increases, unstable maxima seem more likely. If the left hand side of Inequalities 10 and 11 have different signs at different critical points (satisfying Equation 9), then unstable maxima and stable minima may occur in the same system. Abrams (1991) discusses the simple fitness expression

$$F = b(xR) - d(x) \quad (12)$$

where  $b$  may be a birth rate or benefit function and  $d$  a death rate or cost function. The above theory shows that, in this case, a stable minimum will occur if:

$$Rb' - d' = 0 \quad (13a)$$

$$R^2b'' - d'' > 0 \quad (13b)$$

$$(\partial R/\partial x^*)(b' + xRb'') + R^2b'' - d'' < 0 \quad (13c)$$

where primes denote derivatives with respect to the argument of the function. Inequality 13b is the condition for fitness minimization and Inequality 13c is the condition for stability. These two can be satisfied simultaneously under a variety of circumstances, provided  $(b' + xRb'')$  is positive and large enough in magnitude. Example 1 later in this paper is such a case. An unstable maximum occurs when Equation 13a is satisfied, but Inequalities 13b and 13c are reversed. This may occur, for example when  $d$  is linear and  $b''$  is negative.

### *Susceptibility to predation*

If the trait in question determines the ability of a species to avoid its predator, then the fitness function generally depends on the mean avoidance ability in the population, i.e. there is again frequency dependence. Higher mean avoidance may result in fewer satiated predators and a greater risk of predation for an individual with a particular avoidance ability. Alternatively, higher mean avoidance may result in a switch by the predator to other prey, resulting in decreased individual risk. These arguments may be complicated by the long-term dependence of predator population size on the prey's mean avoidance (Abrams, 1986, 1990), but, for simplicity, we will treat the predator population size as constant. It is reasonable to assume that the greater avoidance ability reduces some other component of fitness; one simple possibility is that the death rate from other causes increases as avoidance ability increases. In this case, a plausible measure of relative individual fitness in the prey species is the negative of the total mortality rate:  $-d(x) - xPg(x^*)$ , where  $x$  is prey catchability,  $P$  is predator population size,  $d$  is the mortality rate from other causes and  $g$  is a function which measures predator foraging effort;  $g$  depends on mean prey escape ability (and possibly other variables such as prey population density). If the predator has a type 2 (Holling, 1966) functional response,  $g = 1/(1 + x^*hN)$ , where  $N$  is prey population size,  $x^*$  is the prey's mean susceptibility to predation and  $h$  is the predator's handling time for a single prey. Following the methods outlined above, the potential evolutionarily stationary points ( $\partial F/\partial x = 0$ ) of the system must satisfy  $-d' - Pg(x^*) = 0$ . The values of  $x$  satisfying this equation are individual fitness maxima if  $d'' > 0$  and fitness minima if the Inequality is reversed. However, they are dynamically stable provided

$$-d'' - Pg' < 0 \quad (14)$$

Clearly, if  $g'$  is negative (as in the type 2 response), it is possible for a fitness maximum to be dynamically unstable (Example 2, see later), but it is impossible for a fitness minimum to be stable. However, if  $g'$  is positive (e.g. if the predator exhibits switching behaviour; Murdoch, 1969), then stable minima may be possible, while unstable maxima are not. In general, because  $d''$  and  $g'$  may have different signs at different stationary points, a single system may theoretically have both stable fitness minima and unstable maxima.

It is possible that the cost of greater escape ability is something other than greater mortality; it could be reduced mating success, lower birth rate, etc. Many of these other possibilities require a fitness expression different from the one discussed above. However, as long as the mean antipredator trait of the prey population affects predator hunting behaviour, there will be a difference between the conditions for a fitness-maximizing antipredator behaviour and a

dynamically stable behaviour. It should also be noted that the dynamic stability of the entire system is usually influenced by the population dynamics of predator and prey and the interaction of those dynamics with the evolutionary dynamics; these have not been considered here.

### *Contest competition ability*

The final case to consider is one in which the trait affects the outcome of intraspecific contest competition. Body size or size of antlers in ungulates are possible examples of such traits (Maynard Smith and Brown, 1986). Depending on the number of contests an individual engages in and the variance in the trait, it may be possible to express an individual's fitness based on its trait value and the mean value of the population. One relatively general formulation is that the fitness of an individual with trait  $x$  is

$$f(x/x^*) - d(x) \quad (15)$$

Here  $f$ , the probability of winning contests multiplied by the benefit from winning contests, is an increasing function of the trait value divided by the population's mean trait value.  $d(x)$  is the cost of the trait. Models of this form have been explored by Parker and Hammerstein (1985) and Packer and Abrams (1990). The stationary values of  $x$  are specified by

$$(1/x^*)f'(1) - d' = 0 \quad (16)$$

The criteria for individual fitness maximization and dynamic stability are, respectively,

$$(1/x^*)^2 f''(1) - d'' < 0 \quad (17)$$

$$-(1/x^*)^2 f''(1) - d'' < 0 \quad (18)$$

If  $f' > 0$  or  $d'' < 0$ , then there may be cases in which a fitness minimum is dynamically stable. It seems likely that  $f''$  will be negative, since the probability of winning a contest must level off (at one) when the individual has a trait value sufficiently greater than the mean. If this is true and  $d''$  is positive, then solutions of Equation 16 will always be dynamically stable fitness maxima; this seems to be the most likely situation biologically. However, if  $d''$  is negative, then dynamically unstable maxima or stable minima are possible for some functions  $f$  having negative second derivatives.

The reason why a fitness minimum may be stable in all three of these ecological situations is that, under frequency dependence, the fitness function (or more generally, the adaptive landscape) changes with changes in the mean trait value. If the individual fitness function (adaptive landscape) moves faster than the mean trait value, any evolution away from the current minimum results in a large shift in the position of the fitness function, which reverses the direction of increasing fitness. This is illustrated in Fig. 1 (see also Matsuda, 1988). The situation of an unstable fitness maximum is very similar; any change in mean trait value changes the position of the maximum of the fitness function further in the same direction, making the point unstable. Curtsinger (1984) and Wilson and Turelli (1986) provide more general discussions of how the adaptive landscape can shift under frequency dependence.

If a fitness maximum is unstable, it is possible for the system to evolve to a different fitness maximum. However, it is at least theoretically possible that it will evolve to a stable minimum (if one exists). It is also possible that it will evolve to one of the extreme values of the trait. In a one-



dimensional (i.e. one dynamic variable) system governed by an ordinary differential equation with no periodic forces, sustained cycles or chaos will not occur; if there are discrete generations, however, more complex dynamics are possible in some systems with frequency dependence (Altenberg, 1991).

The stability of the extreme values of  $x$  has not yet been discussed. If, for example,  $x$  must lie between 0 and  $x_m$ , then these two values are also possible evolutionary equilibria. If  $\partial F/\partial x < 0$  when  $x = x^* = 0$ , then this point represents a local fitness maximum. The condition required for local stability of this point is also simply that  $\partial F/\partial x < 0$ . Similarly,  $x_m$  is a fitness maximum and is a locally stable point if  $\partial F/\partial x > 0$  at  $x = x^* = x_m$ . If an extreme value is a fitness maximum, it will be dynamically stable and vice versa.

The preceding theoretical treatment can be illustrated by specific examples of fitness functions; these are given after a general discussion of two other evolutionary scenarios which may also result in unstable fitness maxima or stable minima.

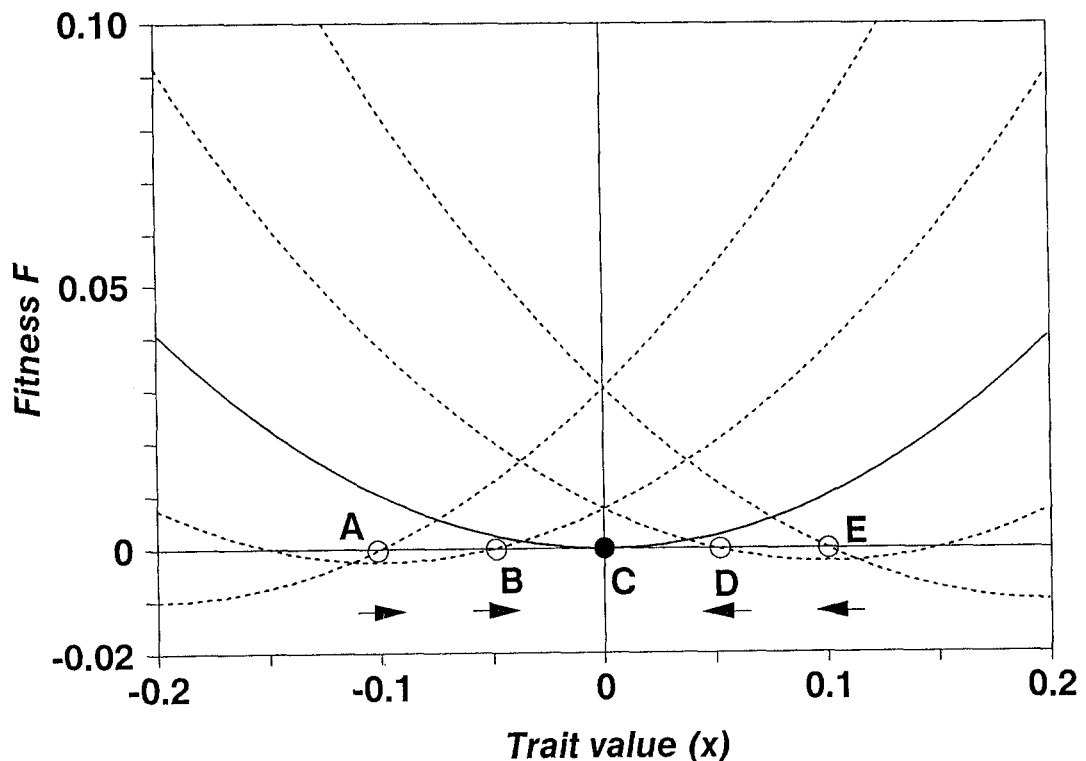


Figure 1. The individual fitness function,  $F(x, x^*)$  for variety of mean trait values,  $x^*$  (represented by the circle on each curve). In frequency-dependent selection, the adaptive landscape of  $F$  changes with the mean trait value,  $x^*$ . The closed circle at point 0 on the solid curve, C is the dynamically stable minimum and curve C represents fitness as a function of  $x$  when  $x^* = 0$ . The dotted curves A, B, D and E are fitnesses as a function of  $x$  when  $x^*$  has the values  $-0.1$ ,  $-0.05$ ,  $0.05$  and  $0.1$ , respectively. Clearly, if  $x^*$  increases, the change in the position of the fitness function will cause evolution back to  $x^* = 0$  because the position of the minimum in the fitness function shifts faster than  $x^*$ . The model used to generate these curves assumes frequency-dependent stabilizing selection with an optimum of  $x = 0$  and apostatic selection by a predator that prefers the most common prey type.

### Evolution of two traits within a species

Most ecologically important parameters such as intensity of resource consumption are influenced by a number of traits; there may be several different traits all under genetic control (which may be determined by overlapping or non-overlapping sets of loci) or various mixtures of traits under behavioural, developmental and/or genetic controls. The conditions for the stability of the dynamical system consisting of several traits determining fitness may not be the same as the conditions for maximization of fitness by those traits.

In the simplest multiple-trait situation, there are two traits with no genetic or phenotypic correlations between them. If there are genetic correlations between the two traits, these will also lead to more complex conditions for stability, which are outlined in Appendix 2. However, the basic effects of frequency dependence can be seen most clearly in the case of uncorrelated traits. A general expression for individual fitness in this case is  $F(x_1, x_2, x_1^*, x_2^*)$ . The fact that  $F$  may be a function of either or both mean trait values allows the stability and fitness-maximization conditions to differ. The condition for a pair of traits  $(x_1, x_2)$  to produce a fitness maximum are

$$\partial F/\partial x_1 = \partial F/\partial x_2 = 0 \quad (19)$$

$$\partial^2 F/\partial x_1^2 + \partial^2 F/\partial x_2^2 < 0 \quad (20)$$

$$(\partial^2 F/\partial x_1^2)(\partial^2 F/\partial x_2^2) - (\partial^2 F/\partial x_1 \partial x_2)^2 > 0 \quad (21)$$

Given our model, in which the fitness gradient determines trait dynamics, the rates of change of two uncorrelated traits may be represented by

$$dx_1^*/dt = k_1 (\partial F/\partial x_1|_*) \quad (22)$$

$$dx_2^*/dt = k_2 (\partial F/\partial x_2|_*) \quad (23)$$

where the  $k_i$  are again positive constants which scale the speed of adaptive response to the magnitude of the fitness gradient and the derivatives are evaluated assuming that individual and population trait values are identical. The conditions for a stable equilibrium in the trait dynamics system are

$$k_1 (\partial^2 F/\partial x_1^2 + \partial^2 F/\partial x_1^*) + k_2 (\partial^2 F/\partial x_2^2 + \partial^2 F/\partial x_2 \partial x_2^*) < 0 \quad (24a)$$

$$(\partial^2 F/\partial x_1^2 + \partial^2 F/\partial x_1 \partial x_1^*)(\partial^2 F/\partial x_2^2 + \partial^2 F/\partial x_2 \partial x_2^*) > (\partial^2 F/\partial x_1 \partial x_2 + \partial^2 F/\partial x_1 \partial x_2^*)(\partial^2 F/\partial x_1 \partial x_2 + \partial^2 F/\partial x_2 \partial x_1^*) \quad (24b)$$

where the derivatives are again evaluated at  $(x_1, x_2) = (x_1^*, x_2^*)$ . The differences between these two conditions and the corresponding fitness maximization conditions, inequalities 20 and 21, arise from two types of additional terms in inequalities 24a and 24b. The first type represents effects of the mean trait value on the fitness gradient for the same trait ( $\partial^2 F/\partial x_i \partial x_i^*$ ). These have been treated in the preceding discussion of a single, frequency-dependent trait. They cause Inequality 24a to differ from Inequality 20. Positive values of  $\partial^2 F/\partial x_1 \partial x_1^*$  and  $\partial^2 F/\partial x_2 \partial x_2^*$  can destabilize fitness maxima, while negative values can stabilize fitness minima. Inequality 24b for stability differs from the analogous Inequality 21 for individual fitness maximization, because of the presence of terms of the form  $\partial^2 F/\partial x_i \partial x_j^*$ . These represent the effect of the mean value of one trait on the fitness gradient with respect to the other trait. A large enough value of either or both terms ( $\partial^2 F/\partial x_2 \partial x_1^*$  and  $\partial^2 F/\partial x_1 \partial x_2^*$ ) can result in a stable fitness minimum or an unstable fitness maximum, depending on their signs. Thus, it is only necessary for fitness to depend on the mean trait value of one of several evolving traits for these maladaptive outcomes to occur.

In the simplest situation, there is no frequency dependence and a general expression for individual fitness is  $F(x_1, x_2)$ . In this case, stability Inequality 24b becomes identical to maximum Inequality 21 and Inequality 24a becomes

$$k_1 (\partial^2 F / \partial x_1^2) + k_2 (\partial^2 F / \partial x_2^2) < 0 \quad (25)$$

Inequalities 25 and 21 may only differ when  $\partial^2 F / \partial x_1^2$  and  $\partial^2 F / \partial x_2^2$  have opposite signs, however, in this case, Inequality 21 is always violated, so the point is always a dynamically unstable point which does not maximize fitness. Unstable fitness maxima and stable minima cannot occur without some form of frequency dependence.

The arguments in this section may be extended in a relatively straightforward way to the case of three traits, although the algebra becomes considerably more complex.

### Coevolution of interacting species

Several previous papers have noted that the coevolution of interacting species can result in a subset of those species having traits which actually minimize their fitness (Roughgarden, 1978; Takada and Kigami, 1991). These previous works have considered cases in which there is no intraspecific frequency dependence, i.e. the fitness of the individual depends on its own trait value and the mean trait value of the other species, but not on the mean trait value of its own species. However, these cases are very similar to the cases of intraspecific frequency dependence considered above, because the mean trait value of the other species represents a (delayed) response to the mean trait value of the first species. Because the mean trait value of the other species always affects individual fitness, coevolution is effectively a form of frequency dependence, albeit indirect. In the first section, for example, high mean resource consumption intensity in the population led to reduced resource abundances, to produce the frequency dependence. If the resource abundance is fixed, but the resource population evolves greater escape ability in response to greater consumption, then the effect is very similar; there is a delayed dependence of resource availability on the consumer's mean trait value.

However, the conditions for coevolutionary stability based on the assumption of no direct intra-specific frequency dependence (Roughgarden, 1979; Takada and Kigami, 1991) are not generally applicable. If frequency dependence is usually present in the evolution of single species, then it will also be present in the coevolution of interacting species. Because intraspecific frequency dependence alone can give rise to non-maximization of fitness, one might expect even more examples of non-maximization of fitness when there is coevolution under intraspecific frequency dependence. Below, we present general conditions for the stability of a coevolutionary equilibrium with two interacting species and explore the implications for fitness maximization.

We consider the case of two species coevolving with the first species having fitness function  $F(x, x^*, y^*)$  with individual trait value  $x$  (as before) and the second species having fitness  $G(y, x^*, y^*)$  and trait value  $y$ . The potential stationary values for the traits are those points which satisfy the conditions  $\partial F / \partial x = 0$  and  $\partial G / \partial y = 0$ . The conditions that each trait represents a fitness maximum are simply that the derivatives  $\partial^2 F / \partial x^2$  and  $\partial^2 G / \partial y^2$  are negative when evaluated where  $x = x^*$  and  $y = y^*$ . This point by definition represents a Nash equilibrium. Given the previous assumptions of a narrow phenotype distribution and an adaptive process whose rate depends on the fitness gradient, the dynamics of both mean trait values are

$$dx^*/dt = k_1 (\partial F / \partial x)|_* \quad (26a)$$

$$dy^*/dt = k_2 (\partial G / \partial y)|_* \quad (26b)$$

where the  $k_i$  are again rate constants of the adaptive process. If these equations represent evolutionary change in quantitative genetic traits, the  $k$  values are additive genetic variances. If we neglect the population dynamics of the species, the stability of the trait equilibrium is determined entirely by Equations 26a and 26b, which are locally stable when

$$k_1 (\partial^2 F / \partial x^2 + \partial^2 F / \partial x \partial x^*) + k_2 (\partial^2 G / \partial y^2 + \partial^2 G / \partial y \partial y^*) < 0 \quad (27a)$$

$$\begin{aligned} & (\partial^2 F / \partial x^2 + \partial^2 F / \partial x \partial x^*) (\partial^2 G / \partial y^2 + \partial^2 G / \partial y \partial y^*) > \\ & (\partial^2 F / \partial x \partial y + \partial^2 F / \partial x \partial y^*) (\partial^2 G / \partial y \partial x + \partial^2 G / \partial y \partial x^*) \end{aligned} \quad (27b)$$

There are again a variety of ways in which one or both species may have dynamically stable fitness minima or unstable fitness maxima.

First assume that Inequality 27b is satisfied and consider Inequality 27a. The previous discussion of intraspecific frequency dependence showed that it was possible for the derivative  $(\partial / \partial x^*)((\partial F / \partial x)|_*) = \partial^2 F / \partial x^2 + \partial^2 F / \partial x \partial x^*$  to have a different sign than the derivative  $\partial^2 F / \partial x^2$  and the same may be true for analogous derivatives involving  $G$  and  $y$ . Thus, it is possible for each trait to minimize fitness within its species, yet for Inequality 27a to be satisfied as well. Similarly, the traits may represent maxima, but both derivatives in Inequality 27a may be positive, resulting in a dynamically unstable state. If there is no frequency dependence, there will be no difference between the two derivatives  $(\partial / \partial x^*)((\partial F / \partial x)|_*)$  and  $\partial^2 F / \partial x^2$  and similarly for derivatives involving  $G$  and  $y$ . However, it is still possible for Inequality 27a to be satisfied (assuming Inequality 27b is satisfied) when one of the two partial derivatives is positive, if a large enough rate constant  $k$  is associated with the other (negative) second partial derivative; in this case the more slowly adapting species will have a trait which minimizes its fitness while the faster-adapting species has a trait which maximizes fitness.

Inequality 27b is usually affected by the interaction between the species; its right-hand side would be zero if there were no interaction. Instability due to non-satisfaction of Inequality 27b does not require intraspecific frequency dependence. It is possible for a point at which individuals of one or both species have fitness maxima to be unstable because of the effects of the trait value of each species on the fitness gradient of the other species (i.e. the right-hand side of Inequality 27b). Inequality 27b is most likely to be violated when the two factors on the right-hand side have the same sign; biologically this means that for *both* species either (1) an increase in trait value of the other species decreases the fitness gradient of the given species or (2) an increase in the trait value of the other species increases the fitness gradient of the given species.

If the stability Conditions 27a and 27b are not satisfied at a particular equilibrium point, the system may approach a different point. It is also possible that the system will exhibit sustained cycles of the trait values around the equilibrium point or a more complex attractor. Cycles and chaos in parasite–host models (e.g. Seger and Hamilton, 1988) and cycles in models of the coevolution of competitive dominance (e.g. Pease, 1984) are examples of such sustained non-equilibrium dynamics. In these systems, the trait of a given species at a given time will not be that which would maximize (or minimize) fitness if evolution in the other species could be frozen at its current value. Stenseth and Maynard Smith (1984) argue that this type of instability is quite likely in large groups of interacting species.

It is important to remember that coevolution takes place in the context of an ecological community and unstable population dynamics can result in a continually changing environment, which may cause sustained cycles in traits whose fitness is related to either population density or an ecological interaction. Alternatively, the evolutionary dynamics can themselves drive population cycles (Abrams, 1992), providing an additional feedback effect on the evolutionary variables. These types of instability will not be analysed here.

## Two simple examples

To illustrate some of the theoretical results, we present two examples of the phenomena discussed. We have chosen fitness functions that are biologically motivated, but that are chosen more for their algebraic simplicity than for biological realism. We also confine ourselves to the simplest of the three scenarios discussed above; frequency-dependent evolution of a single trait.

### *Example 1: a stable fitness minimum in a trait determining resource consumption intensity*

The resource density is a function of the mean trait value  $x^*$  which determines consumption rate by the consumer. Resource density at equilibrium will be represented by  $R = 1/(a + x^*)$ , where  $a$  is a constant, giving the inverse of the equilibrium resource density in the absence of consumption. The individual consumption rate is  $xR = x/(a + x^*)$ . As consumption rate increases from very low levels, the efficiency of converting resources into offspring increases;  $b = (xR)^2 = x^2/(a + x^*)^2$ . (Birth rate must have some upper limit, since there is a limit on resource intake rate; if  $xR$  is greater than some threshold value,  $M$ , then intake is  $M$ .) There is a cost (possibly mortality) to the individual of having a high consumption rate, given by  $Dx$ . Thus, fitness has the form of Equation 12 and is

$$\begin{aligned} F(x, x^*) &= x^2/(a + x^*)^2 - Dx & \text{if } x/(a + x^*) < M \\ F(x, x^*) &= M^2 - Dx & \text{if } x/(a + x^*) > M \end{aligned} \quad (28)$$

Because this function is negative for many possible values of  $x$ , it can be considered to be a component of fitness that combines additively with another (positive) component. This function is illustrated in Fig. 2A. It is assumed that  $x$  has a minimum value of 0 and a maximum of  $x_m$ .

The possible extrema of individual fitness are the points  $x = 0$ ,  $x = x_m$  and the pair of intermediate values determined by solving the pair of equations,  $\partial F/\partial x = 0$  and  $x = x^*$ , i.e.

$$x_1 = (1 - aD - \sqrt{1 - 2aD})/D \quad (29a)$$

$$x_h = (1 - aD + \sqrt{1 - 2aD})/D \quad (29b)$$

(Note that these are different values of a particular trait, not different traits.) We assume that  $aD < 1/2$ , so that both possible equilibria exist. Because  $\partial^2 F/\partial x^2|_* = 2/(a + x^*)^2 > 0$  for all  $x^*$ , both of these points represent minima of individual fitness for different mean trait values. In fact, the fitness function, Equation 28 is negative when individual and mean traits are both given by Equation 29a or 29b. However, the low value,  $x_1$  is unstable, while the high value  $x_h$  is locally stable. Figure 2B shows  $\partial F/\partial x|_* = 2x^*/(a + x^*)^2 - D$ ;  $x^*$  increases if this function is positive and decreases if it is negative. It is clear that the points  $x^* = 0$  and  $x^* = x_h$  represent locally stable equilibria; initial values of  $x^*$  greater than  $x_1$  will evolve to  $x_h$  while initial values less than  $x_1$  will decrease to  $x^* = 0$ . It is worth noting that  $F(x_h, x_h) < F(0, x_h)$  and  $F(x_h, 0) > F(0, 0)$ , which means that both of the locally stable points can be invaded by a type which is sufficiently larger (in the case of  $x = 0$ ) or smaller (in the case of  $x = x_h$ ). Such types will not be able to breed true, however, if the trait is determined by many loci with small effect.

The equilibrium points and stability conditions in this example are identical to those of an analogous quantitative genetic recursion, regardless of the size of the phenotypic variance. This result is explained in Appendix 3.

### *Example 2: an unstable fitness maximum in a trait determining predator escape ability*

The prey's susceptibility to predation is again measured by  $x$  and the predator is assumed to have a type 2 functional response. The death rate due to causes other than predation has a maximum value of  $D$  when predator susceptibility is at a minimum ( $x = 0$ ) and decreases with increasing

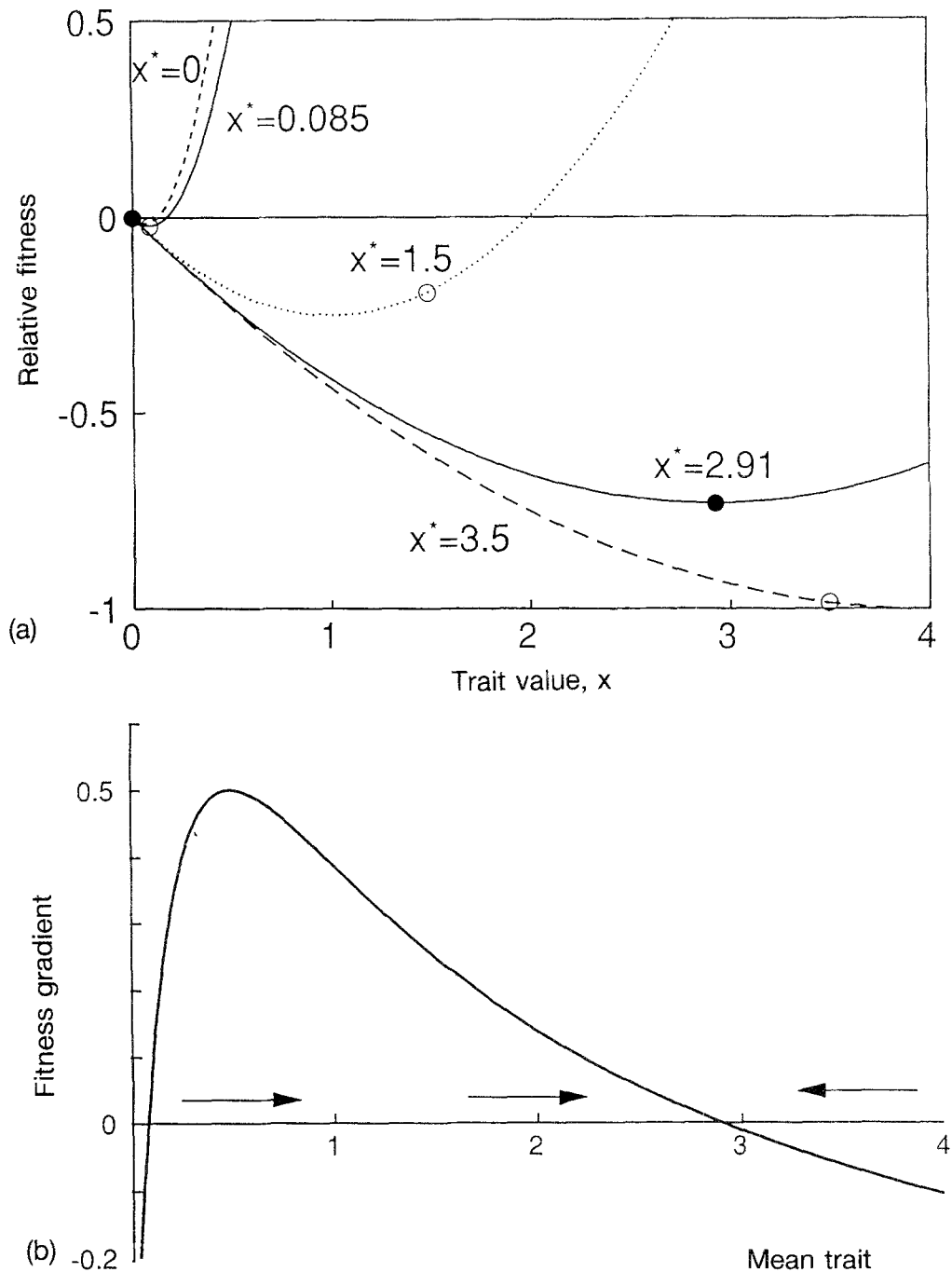


Figure 2. Fitness function (a) and fitness gradient (b) for Example 1. Parameter values are  $a = 0.5$ ,  $D = 0.5$  and  $M = 2.4$ . Individual fitnesses for five different mean trait values are plotted in (a), while (b) is a plot of the fitness gradient. The mean trait increases for character values where the gradient is positive and decreases where it is negative; thus  $x^* = 0$  and the larger of the two values where the fitness gradient is zero are both locally stable.

predator susceptibility according to  $D/(1 + x)$ . The type 2 functional response means that a prey individual's risk of being eaten decreases as prey population increases or as prey susceptibility increases. If  $N$  is prey population density scaled so handling time is unity and  $P$  is predator population density, an individual's risk per unit time is  $xP/(1 + Nx^*)$ . Thus, if fitness is measured by the negative of the total death rate,

$$F(x, x^*) = -D/(1 + x) - xP/(1 + Nx^*) \quad (30)$$

This function is illustrated in Fig. 3A. Clearly, there is a single local fitness maximum for each  $x^*$  under the parameter values chosen here. The derivative,  $\partial F/\partial x|_* = D/(1 + x^*)^2 - P/(1 + Nx^*)$ , is plotted as a function of the mean trait value in Fig. 3B. Under the conditions that  $DN > 2P$ ,  $P > D$  and  $P < DN^2/4(N - 1)$ , there are two points where  $\partial F/\partial x|_* = 0$ :

$$x_1 = \{DN - 2P - \sqrt{[(DN - 2P)^2 - 4P(P - D)]}\}/2P \quad (31a)$$

$$x_h = \{DN - 2P + \sqrt{[(DN - 2P)^2 - 4P(P - D)]}\}/2P \quad (31b)$$

As Fig. 3B illustrates, the points  $x^* = 0$  and  $x^* = x_h$  are locally stable points of the dynamic system, while  $x^* = x_1$  is unstable even though it represents a maximum individual fitness for that mean trait value. It is also interesting to note that the fitness of an individual with the mean trait value is greater when the population has the unstable value (Equation 31a), than when it has the dynamically stable value of Equation 31b. Given that  $P > D$ , the mean trait value  $x^* = 0$  maximizes group fitness.

Appendix 3 sketches the analysis of a quantitative genetic recursion relationship based on this fitness function. The results show again that a relatively large phenotypic variance has very little effect on the above analysis; stationary values are changed slightly, but their stability is not altered.

## Discussion

### *When is the model of adaptation appropriate?*

The model of adaptation we have used assumes that the population is characterized by a distribution of phenotypes with a fixed distribution function relative to the mean, as is often assumed in quantitative genetic models (e.g. Taper and Case, 1992). This enables the dynamics of the entire distribution to be characterized by changes in the mean. However, in general, the mean trait value is insufficient to determine trait dynamics if the shape of the trait distribution can change significantly. This is always true of a population that can consist of a mixture of two (or several) extreme types. There are a number of adaptive mechanisms under which mixtures of extreme types may occur. These include (1) most types of behavioural plasticity, (2) populations consisting of a wide array of asexual phenotypes and (3) traits determined by one or few loci having some alleles with large effects on the trait value. In all three of these situations, the fitness of an individual with the mean trait value may be very different from the mean fitness. If individual fitness for a given mean trait value,  $F(x; x^*)$ , has a single intermediate minimum, then under any of the above three schemes, the population will eventually consist of a mixture of the minimum and maximum trait values (plus some intermediates in case (3), depending on the degree of dominance and other genetic details). The mean trait value produced by adaptation in such cases is often very different from that predicted by the above analysis and mean fitness may be very different from the fitness of an individual with the mean trait value. Maynard Smith and Brown (1986) discuss the frequency-dependent evolution of body size. They show that models in which the trait is determined by many additive loci show a different behaviour (escalation of size)

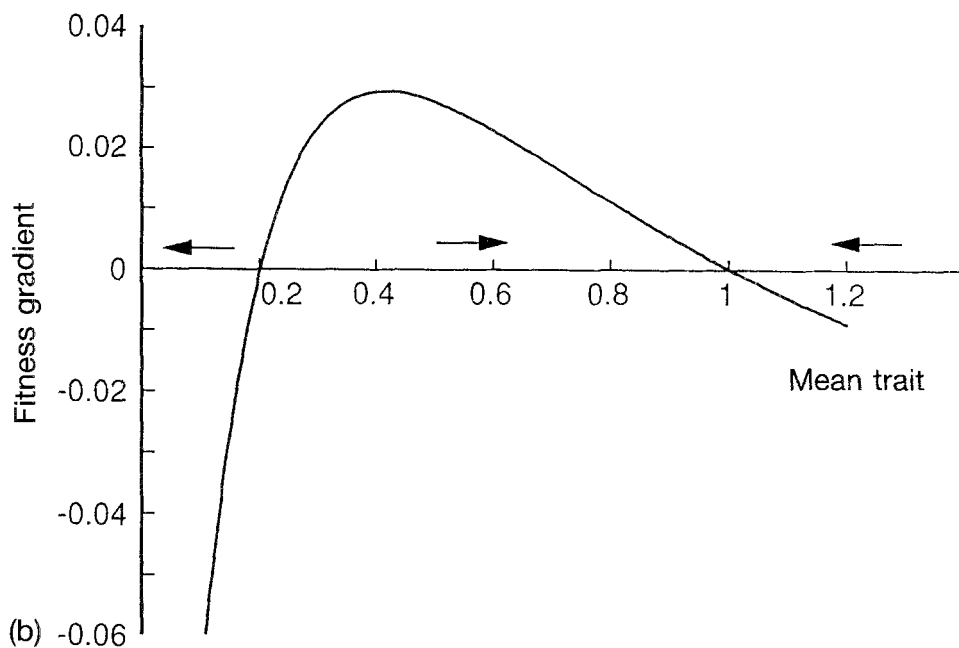
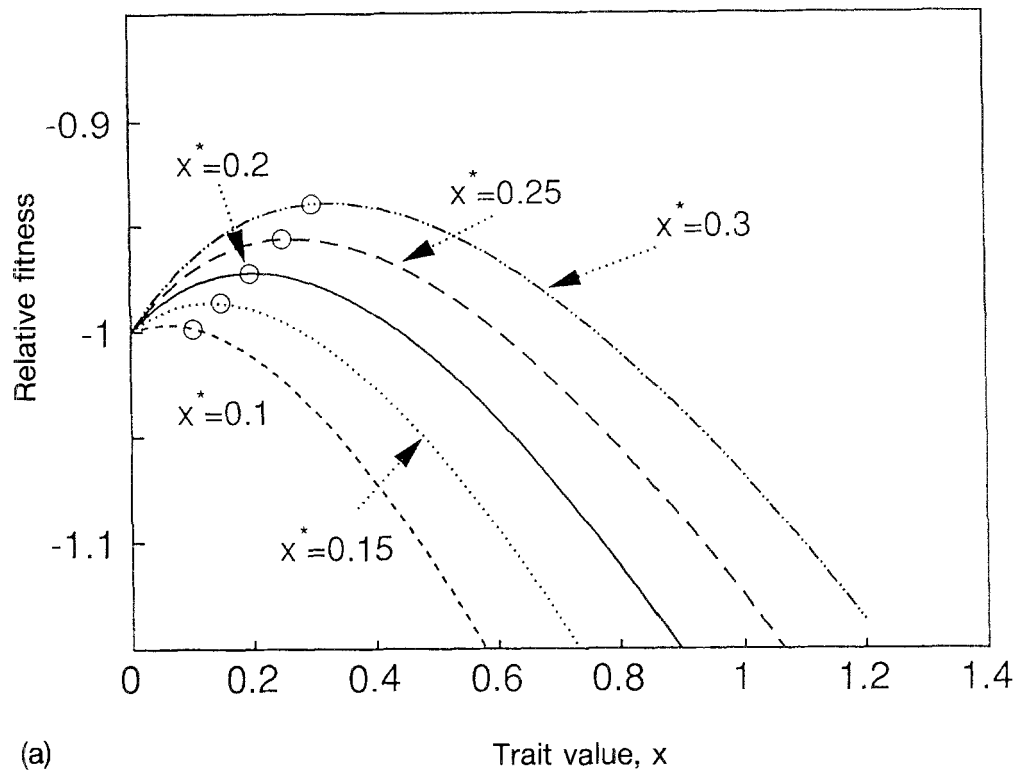


Figure 3. Fitness function (a) and fitness gradient (b) for Example 2. Parameter values are  $D = 1$ ,  $P = 1.25$  and  $N = 4$ . Individual fitnesses for three different mean trait values are plotted in (a), while (b) plots the fitness gradient. The mean trait increases for character values where the gradient is positive and decreases where it is negative, as in Fig. 2b.



than do models with a more flexible phenotypic distribution (cyclical changes in body size). Stable fitness minima are not likely to be observed in an evolutionary (adaptive) system unless the trait is determined by many independent factors, each with (relatively) small effects. Felsenstein's (1979) simulations of disruptive selection with four-locus two-allele models suggest that, unless linkage is very tight, dimorphism will not occur. It is not clear if or when continued disruptive selection will change such a system to allow dimorphism (bimodal-trait distributions).

The models with unstable fitness maxima are much less sensitive to the type of adaptive system. Here there is no disruptive selection. Simulations of a variety of systems having an unstable maximum were carried out, assuming a genetic system with an array of asexual types. These never resulted in the mean phenotype remaining close to the unstable maximum.

### *Frequency dependence and fitness maximization*

It has long been known that mean population fitness is often not maximized and may be minimized, under frequency-dependent selection (Haldane, 1932; Huxley, 1938). However, the discussion here has not dealt with mean population fitness. Mean population fitness would be maximized at a point where  $F(x^*, x^*) > F(x, x)$ , for all  $x$ . The necessary and sufficient conditions for this are  $\partial F/\partial x + \partial F/\partial x^* = 0$  and  $\partial^2 F/\partial x^2 + \partial^2 F/\partial x^{*2} + 2\partial^2 F/\partial x\partial x^* < 0$ , where these conditions are evaluated where  $x = x^*$ . Such a strategy would only be expected if group selection greatly predominated over individual level selection or if the social structure had a method of forcing individuals to adopt cooperative behaviour. These 'group optimum' strategies generally differ from both strategies which maximize individual fitness and dynamically stable strategies (Matsuda, 1988; Abrams, 1989; Taper and Case, 1992). If there is no frequency dependence and there is only one trait and no coevolving species, then all three conditions (group fitness maximization, individual fitness maximization and stability) are identical. However, this seems like an unlikely coincidence.

Most population genetics textbooks (e.g. Hartl and Clark, 1988) discuss particular genetic mechanisms (e.g. two loci with epistatic interactions) under which individual fitness may not be maximized. However, there has been little evidence that such genetic mechanisms frequently determine ecologically important traits. The quantitative genetic trait determination which underlies the present analysis has been assumed to be applicable to many ecologically important traits (Lande, 1981, 1982; Grant, 1986). This argues for greater questioning of adaptationist assumptions.

There are many treatments of the evolution of frequency-dependent continuous traits that assume evolution will produce traits that maximize individual fitness. They include Maynard Smith (1982), Brown and Vincent (1987) and Vincent and Brown (1988); however, see Christiansen (1991) for a discussion of dynamic stability in similar models. It is clear that the 'individual fitness maximization' condition will not always correctly describe the result of evolution when there are constraints on the phenotypic distribution of the population (as there will be for most quantitative traits). This is true under frequency-dependent evolution of a single trait, evolution of multiple interacting traits and coevolution of interacting species. Many of the game theory models investigated to date assume an array of discrete strategies. Here, the frequency of use of different strategies may itself represent a continuous trait. However, as Taylor (1989) has noted, because fitness is a linear function of the frequency of use of different strategies, fitness maximization and dynamic stability conditions are identical. It is possible that many other ESS analyses which have ignored dynamics are qualitatively unchanged by the addition of trait dynamics, since the necessary condition for a stable point (i.e.  $\partial F/\partial x|_* = 0$ ) is the same in both dynamic and non-dynamic models.

It is possible, however, that evolutionary stable strategies as defined by Maynard Smith (1982)

may not actually be evolutionarily stable because of the dynamics of the evolutionary process, since his definition corresponds to individual fitness maximization. This possibility is actually noted in the appendices of Maynard Smith's book and has been discussed by Eshel (1983), Taylor (1989) and Christiansen (1991). The latter two authors suggest new names for ESSs which are also dynamically stable. They refer to the dynamic stability criterion as *m*-stability, while the fitness maximization criterion is called  $\delta$ -stability. It would seem preferable to simply redefine the concept of an ESS to require dynamic stability. Dynamically unstable fitness maxima will not be observed.

There are many previous treatments of coevolution that assume there is no intraspecific frequency dependence (Roughgarden, 1978, 1979, 1987; Case, 1982; Pacala and Roughgarden, 1983; Rummel and Roughgarden, 1985). While the earliest of these analyses have pointed out the possibility that some interacting species do not attain fitness maxima at evolutionary equilibria, later works have not emphasized that possibility. In fact, Roughgarden (1983, p. 41) asserts that individual fitness will be maximized in a coevolutionarily stable community. When there is no intraspecific frequency dependence, this means that group fitness is maximized, conditional on the properties of other species. Unfortunately, some of the models analysed by Roughgarden are inherently frequency dependent (Brown and Vincent, 1987; Taper, 1988), while his method of analysis assumes no frequency dependence. This can greatly affect the predictions of the models (Taper and Case, 1992). Because of the abundant opportunities for frequency dependence generated by consumer–resource and predator–prey interactions (Abrams, 1989), the assumption of group fitness maximization seems inappropriate. Takada and Kigami (1991) have recently generalized Roughgarden's (1978) earlier stability result and shown that, even with no frequency dependence, the evolutionarily stable state of a group of coevolving species is often not identical to the state that maximizes the conditional fitness of each species.

Other treatments of coevolution (e.g. Lawlor and Maynard Smith, 1976) have included frequency dependence, but have argued that, if population dynamics are stable, the coevolutionarily stable state is a Nash equilibrium. At such an equilibrium individual fitness of each species is maximized conditional on the trait value of the other species. In the present case of continuous traits, a Nash equilibrium satisfies,  $\partial F/\partial x = 0$ ;  $\partial G/\partial y = 0$ ,  $\partial^2 F/\partial x^2 < 0$  and  $\partial^2 G/\partial y^2 < 0$ . However, Inequality 27b shows that these conditions do not ensure evolutionary stability. There are additional examples of unstable Nash equilibria for the interaction of different strategies within a single species; these include local mate competition with strong inbreeding depression and sex ratio evolution with disassortative mating (Harada, unpublished).

The possibility of unstable fitness maxima may not represent a major challenge to previous adaptationist theory, since most adaptationist theory has avoided situations in which there are multiple maxima. The fact that a fitness maximum is unstable does not lead to maladaptation at the individual level unless the system comes to rest at a stable fitness minimum. As discussed above, the likelihood of stable minima depends on the nature of the adaptive system; multilocus traits with alleles of small effect are implicit assumptions of the dynamic model used here. It is possible that evolution has modified the genetic basis of traits over time so that the present model no longer applies to traits in danger of fitness minimization. If this is so, we would expect to see a few cases where a trait that potentially possesses a dynamically stable fitness minimum is determined by many loci with alleles of small effect. Competitive exclusion by other species is also more likely if an ecologically important trait of a given species occupies a fitness minimum and this could make such minima rare in nature.

However, we cannot presently exclude the possibility that stable fitness minima are common. If this is true, we should expect to see evidence of disruptive selection on the quantitative traits involved. Endler's (1986) survey of field studies of natural selection revealed a significant number

of cases of disruptive selection; in fact his index of selection on the variance,  $j'$ , indicated disruptive rather than stabilizing selection in exactly one half of all studies (Endler, 1986, p. 211), although most of these were not statistically significant. Endler noted that the ecological reasons for the disruptive selection were not known or studied in most of these works. Since 1986, there have been additional unexplained examples of disruptive selection on quantitative traits (e.g. Wiggins, 1991), but it is still unclear whether they are common or whether they reflect the scenario described here.

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## References

- Abrams, P. A. (1986) Adaptive responses of predators to prey and prey to predators: the failure of the arms race analogy. *Evolution* **40**, 1229–47.
- Abrams, P. A. (1989) The importance of intraspecific frequency dependent selection in modelling competitive coevolution. *Evol. Ecol.* **3**, 215–20.
- Abrams, P. A. (1990) The evolution of antipredator traits in prey in response to evolutionary change in predators. *Oikos* **59**, 147–56.
- Abrams, P. A. (1991) The relationship between food availability and foraging effort: effects of life history and time-scale. *Ecology* **72**, 1242–52.
- Abrams, P. A. (1992) Adaptive foraging by predators as a cause of predator–prey cycles. *Evol. Ecol.* **6**, 56–72.
- Altnerberg, L. (1991) Chaos from linear frequency-dependent selection. *Am. Nat.* **138**, 51–68.
- Brown, J. S. and Vincent, T. L. (1987) Coevolution as an evolutionary game. *Evolution* **41**, 66–79.
- Case, T. J. (1982) Coevolution in resource-limited competition communities. *Theor. Pop. Biol.* **21**, 69–91.
- Charlesworth, B. (1990) Optimization models, quantitative genetics, and mutation. *Evolution* **44**, 520–38.
- Christiansen, F. B. (1991) On conditions for evolutionary stability for a continuous varying character. *Am. Nat.* **138**, 37–50.
- Cressman, R., Dash, A. T. and Akin, E. A. (1986) Evolutionary games and two species population dynamics. *J. Math. Biol.* **23**, 221–30.
- Curtsinger, J. W. (1984) Evolutionary principles for polynomial models of frequency dependent selection. *Proc. Natl Acad. Sci. USA* **81**, 2840–2.
- Endler, J. A. (1986) *Natural Selection in the Wild*. Princeton University Press, Princeton, NJ, USA.
- Eshel, I. (1983) Evolutionary and continuous stability. *J. Theor. Biol.* **103**, 99–111.
- Eshel, I. and Akin, E. (1983) Coevolutionary instability of mixed Nash solutions. *J. Math. Biol.* **18**, 123–34.
- Eshel, I. and Motro, U. (1981) Kin selection and strong evolutionary stability of mutual help. *Theor. Pop. Biol.* **19**, 420–33.
- Felsenstein, J. (1979) Excursions along the interface between disruptive and stabilizing selection. *Genetics* **93**, 773–95.
- Fisher, R. A. (1930) *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford, UK (reprinted 1958, Dover, New York).
- Grant, P. (1986) *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton, NJ, USA.

- Haldane, J. B. S. (1932) *The Causes of Evolution*. Harper and Brothers, London, UK.
- Hartl, D. and Clark, A. (1988) *Principles of Population Genetics*, 2nd edn. Sinauer, Sunderland, MA, USA.
- Hastings, A. and Hom, C. (1990) Multiple equilibria and maintenance of additive genetic variance in a model of pleiotropy. *Evolution* **44**, 1153–63.
- Hofbauer, J. and Sigmund, K. (1988) *The theory of evolution and dynamical systems*. Cambridge University Press, Cambridge, UK.
- Holling, C. S. (1966) The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* **48**, 1–86.
- Huxley, J. S. (1938) The present standing of the theory of sexual selection. In *Evolution* (G. R. de Beer, ed.), pp. 11–42. Clarendon Press, Oxford.
- Iwasa, Y., Pomiankowski, A. and Nee, S. (1991) The evolution of costly mate preferences. II. The 'handicap' principle. *Evolution* **45**, 1431–42.
- Krebs, J. R. and Davies, N. B. (1991) *Behavioural Ecology*, 3rd edn. Blackwell Scientific, London, UK.
- Lande, R. (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30**, 314–34.
- Lande, R. (1981) Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78**, 3721–5.
- Lande, R. (1982) A quantitative genetic theory of life history evolution. *Ecology* **63**, 607–15.
- Lawlor, L. R. and Maynard Smith, J. (1976) The coevolution and stability of competing species. *Am. Nat.* **110**, 79–99.
- Lessard, S. (1990) Evolutionary stability: one concept, several meanings. *Theor. Pop. Biol.* **37**, 159–70.
- Matsuda, H. (1988) Interaction in a prey predator system and the theory of coevolution. *Bull. Pop. Ecol. Soc.* **45**, 3–10 (in Japanese).
- Maynard Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge University Press, Cambridge, UK.
- Maynard Smith, J. and Brown, R. L. W. (1986) Competition and body size. *Theor. Pop. Biol.* **30**, 166–79.
- Maynard Smith, J. and Price, G. R. (1973) The logic of animal conflict. *Nature* **246**, 15–18.
- Murdoch, W. W. (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monog.* **39**, 335–54.
- Pacala, S. W. and Roughgarden, J. (1983) The evolution of resource partitioning in a multidimensional resource space. *Theor. Pop. Biol.* **22**, 127–45.
- Packer, C. and Abrams, P. A. (1990) Are cooperative groups more vigilant than selfish groups? *J. Theor. Biol.* **142**, 341–57.
- Parker, G. A. and Hammerstein, P. (1985) Game theory and animal behaviour. In *Evolution: Essays in Honour of John Maynard Smith* (P. J. Greenwood, P. H. Harvey and M. Slatkin, eds), pp. 73–94. Cambridge University Press, Cambridge, UK.
- Parker, G. A. and Maynard Smith, J. (1990) Optimality theory in evolutionary biology. *Nature* **348**, 27–33.
- Pease, C. (1984) On the evolutionary reversal of competitive dominance. *Evolution* **38**, 109–15.
- Roughgarden, J. (1978) Coevolution in ecological systems III. Co-adaptation and equilibrium population size. In *Ecological Genetics* (P. F. Brussard, ed.). Springer-Verlag, Berlin.
- Roughgarden, J. (1979) *The Theory of Population Genetics and Evolutionary Ecology: An Introduction*. MacMillan, NY, USA.
- Roughgarden, J. (1983) The theory of coevolution. In *Coevolution* (D. J. Futuyma and M. Slatkin, eds), pp. 33–64. Sinauer, Sunderland, MA, USA.
- Roughgarden, J. (1987) Community coevolution: a comment. *Evolution* **41**, 1130–4.
- Rummel, J. D. and Roughgarden, J. (1985) The theory of faunal build-up for competition communities. *Evolution* **39**, 1009–33.
- Seger, J. and Hamilton, W. D. (1988) Parasites and sex. In *The Evolution of Sex* (R. E. Michod and B. R. Levin, eds), pp. 176–93. Sinauer Associates, Sunderland, MA, USA.
- Stenseth, N. Chr. and Maynard Smith, J. (1984) Coevolution in ecosystems: Red Queen evolution or stasis? *Evolution* **38**, 870–80.
- Takada, T. and Kigami, J. (1991) The dynamical attainability of ESS in evolutionary games. *J. Math. Biol.* **29**, 513–30.

- Taper, M. (1988) The coevolution of resource competition: appropriate and inappropriate models of character displacement. *Bull. Pop. Ecol. Soc. (Japan)* **44**, 45–54.
- Taper, M. and Case, T. J. (1992) Models of character displacement and the theoretical robustness of taxon cycles. *Evolution* **46**, 317–33.
- Taylor, P. D. (1989) Evolutionary stability in one-parameter models under weak selection. *Theor. Pop. Biol.* **36**, 125–43.
- Thomas, B. (1985) On evolutionary stable sets. *J. Math. Biol.* **22**, 105–15.
- Turelli, M. (1988) Population genetic models for polygenic variation and evolution. *Proc. Second Int. Conf. Quantitative Genetics* (B. S. Weir, E. J. Eisen, M. M. Goodman and G. Nankoong, eds), pp. 601–18. Sinauer Associates, Sunderland, MA, USA.
- Vincent, T. L. and Brown, J. S. (1988) The evolution of ESS theory. *Ann. Rev. Ecol. Syst.* **19** 423–44.
- Wiggins, D. A. (1991) Natural selection on body size and laying date in the tree swallow. *Evolution* **45**, 1169–74.
- Wilson, D. S. and Turelli, M. (1986) Stable underdominance and the evolutionary invasion of empty niches. *Am. Nat.* **127**, 835–61.

### Appendix 1: stability of resource–consumer trait system

The dynamics of a resource and the resource-exploitation trait in the consumer population can be described by the following set of differential equations:

$$dR/dt = Rf(R) - x^*RN \quad (\text{A1.1})$$

$$dx^*/dt = k(\partial F/\partial x | * + R\partial F/\partial I | *) \quad (\text{A1.2})$$

where  $f$  is a decreasing function of  $R$  giving the per capita growth rate of the resource,  $N$  is consumer population size (assumed constant here) and the dynamics of the mean consumption rate,  $x^*$ , are as described in the text. Equation A1.2 states that the rate of change of the trait is proportional to the fitness gradient. Fitness,  $F$ , is a function of  $x$  and intake rate  $I$  ( $I = Rx$ ). Standard local stability analysis of this system yields the following conditions for stability of an interior equilibrium:

$$Rf' + k\{\partial^2 F/\partial x^2 + R[2\partial^2 F/\partial I\partial x + R\partial^2 F/\partial I^2]\} < 0 \quad (\text{A1.3})$$

$$Rf'\{\partial^2 F/\partial x^2 + 2R\partial^2 F/\partial I\partial x + R^2\partial^2 F/\partial I^2\} > -RN\{\partial F/\partial I + x\partial^2 F/\partial I\partial x + xR\partial^2 F/\partial I^2\} \quad (\text{A1.4})$$

The requirement that  $dR/dt = 0$  may be differentiated with respect to  $x^*$  to yield  $N = f'(\partial R/\partial x^*)$ . When this is substituted into Inequality A1.4, this inequality becomes identical to Inequality 11 in the text. If  $k$  is small enough relative to the magnitude of  $Rf'$  (i.e. adaptation slow relative to resource dynamics), Inequality A1.3 is satisfied regardless of the fitness derivatives, since  $f' < 0$ .

### Appendix 2: evolutionary dynamics of two correlated traits

In the text, we considered the evolutionary dynamics of two independent traits within a species. In general, however, if the traits are genetically determined there will be non-zero covariance of the two traits. If trait values can be adjusted behaviourally, there are more opportunities for the traits to be adjusted independently of each other, but there may still be correlations. If we assume an overlapping generation, a quantitative genetics model of two traits whose values are  $x_1$  and  $x_2$ , the fitness (intrinsic rate of increase) of an individual with trait value  $(x_1, x_2)$  and population mean

trait values  $(x_1^*, x_2^*)$ , is described by  $F(x_1, x_2, x_1^*, x_2^*)$ . The rate of evolutionary change in the population mean trait values is described by:

$$dx_1^*/dt = g_{11}\partial F/\partial x_1 + g_{12}\partial F/\partial x_2 \quad (\text{A2.1})$$

$$dx_2^*/dt = g_{21}\partial F/\partial x_1 + g_{22}\partial F/\partial x_2 \quad (\text{A2.2})$$

where the derivatives are again evaluated at which  $x_1 = x_1^*$  and  $x_2 = x_2^*$ , and the  $g_{ij}$  are additive genetic variances and covariances, which play the same role as the rate constants,  $k$ , used in the text. The two covariances are generally equal ( $g_{12} = g_{21}$ ) and may be positive, zero or negative.

If the determinant of the additive genetic variance–covariance matrix is not zero, the equilibrium satisfies

$$\partial F/\partial x_1 = 0 \text{ and } \partial F/\partial x_2 = 0 \quad (\text{A2.3})$$

The conditions for local stability of this equilibrium are

$$g_{11} F_{11} + g_{12}(F_{21} + F_{12}) + g_{22} F_{22} < 0 \quad (\text{A2.4})$$

and

$$(g_{11} g_{22} - g_{12}^2) [F_{11} F_{22} - F_{12} F_{21}] > 0 \quad (\text{A2.5})$$

where  $F_{ij} = \partial^2 F/\partial x_i \partial x_j + \partial^2 F/\partial x_i \partial x_j^*$ . Note that  $F_{12}$  and  $F_{21}$  are not, in general identical. Both inequalities above depend on values of the additive genetic variance and covariance. If the product of the variances is larger than the covariance squared, Inequality A2.5 is identical to the corresponding condition in the text when traits are independent (Inequality 24b). Inequality A2.4 may be easier or more difficult to satisfy than the corresponding Inequality 24a for non-correlated traits; if  $g_{12}$  and  $F_{12}$  have the same sign, the genetic correlations exert a destabilizing influence on the system, making Inequality A2.4 less likely to be satisfied.

### Appendix 3: the relationship between Equation 1 and quantitative genetic models

The simple recursion relationship used in many discrete-generation quantitative genetic models is

$$\Delta x^* = (V_a/V_t) [(\int x p(x) F(x, x^*) dx / \int p(x) F(x, x^*) dx) - x^*] \quad (\text{A3.1})$$

where  $F$  is the fitness function and the integrals are taken over the range of the phenotypic distribution function,  $p(x)$  (Lande, 1976; Taper and Case, 1992). The distribution function is usually assumed to be approximately normal. The constant,  $(V_a/V_t)$ , is the ratio of additive genetic variance to total phenotypic variance. Lande (1982) has derived an analogous expression for overlapping generations and continuous change in  $x$  under the assumption of weak selection; this has the form,

$$dx^*/dt = (V_a/V_t) [\int (x - x^*) p(x) F(x, x^*) dx] \quad (\text{A3.2})$$

We show that Equation A3.2 can often be approximated by Equation 1 in the text and that the stability conditions for equilibria of both Equations A3.1 and A3.2 can often be approximated by Inequality 7 in the text.

We begin by expanding  $F$  in Equation A3.2 as a Taylor series about  $x = x^*$ .

$$F(x, x^*) \approx F(x^*, x^*) + \partial F/\partial x|_*(x - x^*) + (1/2)\partial^2 F/\partial x^2|_*(x - x^*)^2 + (1/6)\partial^3 F/\partial x^3|_*(x - x^*)^3 + \dots \quad (\text{A3.3})$$

When this is substituted for  $F$  in the integral in Equation A3.2, the first, third, etc., terms

disappear, because the integral of  $(x - x^*)^{2n+1}$  times a distribution function that is symmetric about  $x^*$  must be zero. Thus, Equation A3.2 becomes

$$dx^*/dt \approx (V_a/V_t) [V_t \partial F/\partial x|_* + (M_4/6) \partial^3 F/\partial x^3|_* + (M_6/120) \partial^5 F/\partial x^5|_* + \dots] \quad (\text{A3.4})$$

where  $M_i$  is the  $i$ th order central moment of the distribution. This is valid for any symmetric phenotypic distribution. The higher order moments approach zero faster than the variance, as the variance becomes small. (For example, in the normal distribution, the even, higher order moments,  $M_{2n}$ , are proportional to powers of the variance,  $V_t$ , i.e.  $M_4 = 3V_t^2$ ,  $M_6 = 15V_t^3$ , . . . , if the distribution is uniform,  $M_4 = (9/5)V_t^2$ ;  $M_6 = (27/7)V_t^3$ . . . .) Thus, for a small enough variance, we can ignore the second and subsequent terms in the sum in Equation A3.4, which immediately yields Equation 1 in the text. The approximation is also valid for large phenotypic variances if the third and higher order derivatives of the fitness function are sufficiently small. The same necessary condition for stability applies to the discrete generation equation, (Equation A3.1 and the continuous equation (Equation A3.2),

$$(\partial/\partial x^*) (\int (x - x^*) p(x) F(x, x^*) dx) < 0 \quad (\text{A3.5})$$

When the integral is approximated as described above, this leads to stability Condition 7 in the text. If the phenotypic variance is too large for this approximation, a condition very similar to Inequality 7 can be derived by including more terms in the expansion given by Equation A3.4.

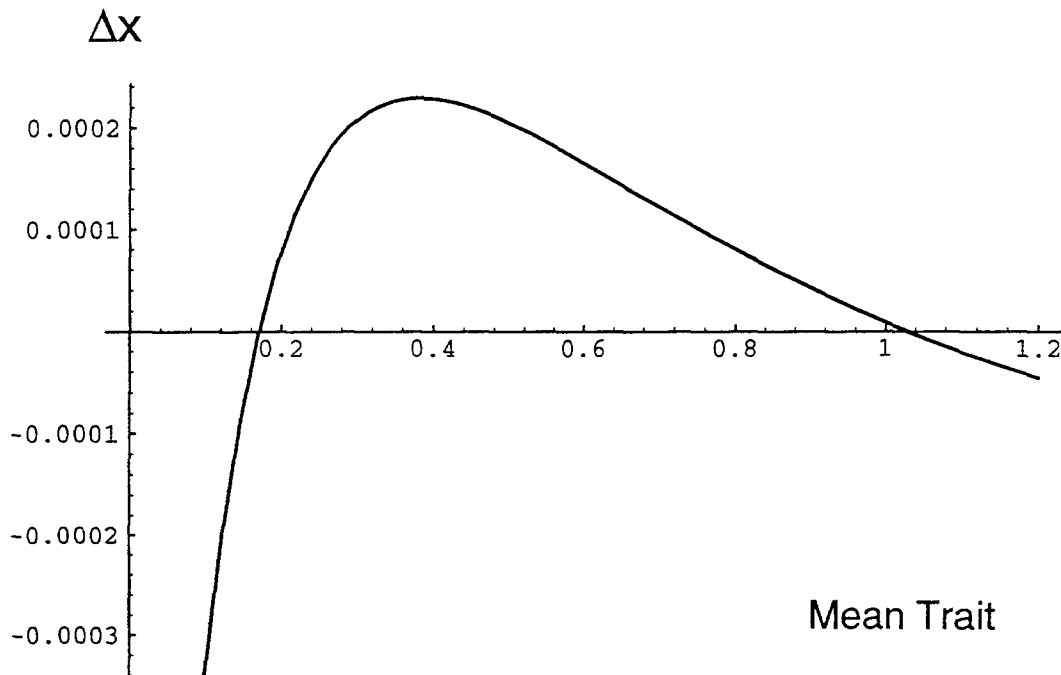


Figure 4. The right-hand side of the recursion relationship (Equation A3.1), plotted as a function of the mean trait value,  $x^*$  for Example 2. The figure is based on fitness formula (Equation 30) modified by the addition of a positive constant ( $=3$ ). Other parameter values are the same as in Fig. 3;  $D = 1$ ,  $P = 1.25$  and  $N = 4$ . The phenotypic values in the population have a uniform distribution with a range from  $x^* - 0.2$  to  $x^* + 0.2$ . The stationary values predicted by Equations 31a and 31b are 0.2 and 1.0.

Example 1 in the text has a fitness function whose third and higher order derivatives are zero, thus, Equation 1 should provide an exact description of evolutionary dynamics. This has been confirmed by iteration of Equation A3.1 after adding a constant to the function  $F$ , to ensure that  $F$  is positive (this does not affect the value of  $x^*$  for which Equation A3.1 is equal to zero). The equilibrium points and stability conditions are identical to those predicted by Equation 1.

In Example 2, the accuracy of the approximation provided by Equation 1 depends on the size of the phenotypic variance and the parameter values of the fitness function. If we take the example used in Fig. 3, the equilibria given by the approximate dynamic Equation 31 are 0.2 and 1.0. If the phenotypic distribution is assumed to be uniform, we can investigate large variances without the need to truncate the distribution to avoid negative trait values (as would be necessary with a normal distribution). The widest uniform distribution that does not produce negative trait values around either equilibrium, has a range from  $x^* - 0.2$  to  $x^* + 0.2$ . Applying the quantitative genetic recursion, Equation A3.1, to this case yields the results shown in Fig. 4; these are practically identical to Fig. 3B, which is based on Equation 1. If the  $\partial^3 F / \partial x^3|_*$  term in the Taylor series expansion is included, the approximation predicts the equilibrium values to an accuracy of greater than  $10^{-6}$ .