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ON THE RELATIONSHIP BETWEEN QUANTITATIVE GENETIC AND ESS MODELS

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Two recent articles in this journal have discussed the relationship between quantitative genetic models and evolutionarily stable strategy (ESS) models of the evolution of continuous traits. Charlesworth (1990) compared the equilibrium conditions produced by the two approaches, and concluded that these were approximately the same, provided that, “the functional relationship between fitness and (the characters) is not too strongly curvilinear, and the phenotypic variances of (the characters) are sufficiently small” (Charlesworth 1990, p. 523). More recently, Taper and Case (1992) examined quantitative genetic and ESS models of the evolution of competitors. They reached essentially the same conclusion about equilibrium conditions. However, they also pointed out that dynamics of the quantitative genetic model could be approximated by a simpler (ESS) model, provided selection was weak and the phenotypic variance was sufficiently small. A similar result was shown in the appendix of Iwasa et al. (1991). The quantitative genetic and ESS models of trait dynamics, which Taper and Case (1992) compared, both predict the change in the mean of character over one generation:

$$\Delta z^* = (V_a/V_t) \int (z - z^*) W p \, dz / W^* \quad (1a)$$

and

$$\Delta z^* = (V_a/W^*)(\partial W / \partial z|_*), \quad (1b)$$

where z is an individual's trait value; V_a and V_t are additive genetic and total phenotypic variances of the trait; p is the distribution function of the phenotypic character (generally assumed to be normal); W is fitness; asterisks denote mean values; and $|_*$ indicates that the partial derivatives are to be evaluated at the point $z = z^*$. It is important to note the mean fitness, W^* , generally differs from the fitness of an individual with the mean trait value, $W(z^*, z^*)$. Because fitness is assumed to be a function of the mean trait value, z^* , as well as the individual's z , equation (1a) cannot be represented by the gradient relationship based on population mean fitness proposed by Lande (1976):

$$\Delta z^* = (V_a/W^*)(\partial W^* / \partial z^*). \quad (1c)$$

Lande (1976), Charlesworth (1990), and Taper and Case (1992) all discussed why equation (1c) is invalid when fitnesses are frequency dependent.

The purpose of the present note is to present a more detailed discussion of the relationship between equations (1a) and (1b) than those of Taper and Case (1992) and Iwasa et al. (1991). This presentation differs from the previous analyses in (1) providing explicit formulas for the errors involved in the approximation, (2) discussing how analogous approximations can be made when equation (1b) is inadequate, and (3) showing the importance of the approximation for determining the local stability of the evolutionary system. Our results also argue against Taper and Case's (1992) suggestion that the outcome of coevolution of quantitative characters be studied by numerically solving for the equilibrium point(s) of equation (1a).

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We begin with the assumption that the discrete recursion equation, (1a), accurately describes the phenotypic evolution. This representation assumes that the ratio of additive genetic to phenotypic variance remains constant and the only parameter of the phenotypic distribution that changes over time is the mean. Lande (1976) and Turelli (1988) provided somewhat different views of the adequacy of these assumptions. The fitness function, W in the numerator of (1a), is assumed to be differentiable and is approximated by a Taylor series about the point $z = z^*$.

$$W(z, z^*) \approx W(z^*, z^*) + (z - z^*) \partial W / \partial z |^* + (1/2)(z - z^*)^2 \partial^2 W / \partial z^2 |^* + (1/6)(z - z^*)^3 \partial^3 W / \partial z^3 |^* + \dots, \quad (2)$$

where $|^*$ indicates that the partial derivatives are to be evaluated at the point $z = z^*$. Each of the terms in this series is multiplied by $(z - z^*)$ in the integral in equation (1a). Because the distribution function is symmetrical (it is generally assumed to be normal), terms proportional to odd powers of $(z - z^*)$ under the integral disappear when the integration is carried out. This means that the integral in the numerator of (1a) can be approximated by

$$\int p(z - z^*) W dz \approx V_1 (\partial W / \partial z |^*) + (1/6) M_4 (\partial^3 W / \partial z^3 |^*) + (1/120) M_6 (\partial^5 W / \partial z^5 |^*) + \dots, \quad (3)$$

where M_i denotes the i th central moment of the phenotypic distribution function. If the distribution function is assumed to be normal, these even-ordered moments will be proportional to powers of the variance: $M_4 = 3V_1^2$, $M_6 = 15V_1^3$, \dots , $M_{2n} = (2n - 1)M_{2n-2}$. This means that we can approximate the integral using only the first term in the above series, provided that

$$|\partial W / \partial z |^*| \gg |(1/2)V_1 \partial^3 W / \partial z^3 |^* + (1/8)V_1^2 \partial^5 W / \partial z^5 |^*| + \left[1 / \prod_{i=1}^n 2i \right] V_1^n \partial^{2n+1} W / \partial z^{2n+1} |^* \dots |, \quad (4)$$

where the exact meaning of " \gg " depends on the accuracy of the approximation that is desired. If inequality (4) is satisfied, the recursion relationship (1a) is immediately seen to be approximated by (1b). Inequality (4) is generally satisfied for a

small enough phenotypic variance when the system is not at an equilibrium point. It is important to note, however, that the phenotypic variance need not be small for the approximation to be arbitrarily good. If the third and higher order derivatives of W with respect to z vanish, then inequality (4) is satisfied for any phenotypic variance. Thus, Charlesworth's (1990, p. 531) claim that (1b) is exact only for linear fitness functions, is too restrictive, because it is also exact for quadratic fitness functions.

This discussion suggests that it is generally possible to approximate the evolutionary dynamics of a trait in a population with discrete generations as being proportional to the gradient of a function that can easily be derived from the fitness function. Specifically, the function, $F(z, z^*)$, defined as follows, will have the properties that $\partial F / \partial z = 0$ at the evolutionary equilibrium, and that the rate of change in trait value is proportional to its gradient:

$$F(z, z^*) = W(z, z^*) + [M_4 / (6V_1)] (\partial^2 W / \partial z^2) + [M_6 / (120V_1)] (\partial^4 W / \partial z^4) + \dots + [M_{2(n+1)} / [V_1(2n + 1)!]] (\partial^{2n} W / \partial z^{2n}). \quad (5)$$

This function helps highlight the differences between ESS models and quantitative genetics models. In general, ESS and quantitative genetic analyses of a given problem have used the same fitness function. However, ESS models implicitly assume that types or strategies breed true, which is not the case with quantitative genetic inheritance of traits with a broad variance. Thus, an ESS analysis of such a situation should use a different fitness function that incorporates the altered trait values of descendants. Expression (5) does this in such a way that at equilibrium, $\partial F / \partial z |^* = 0$, and the dynamic of the trait is described by $\Delta z^* = (V_a / F^*) (\partial F / \partial z |^*)$. If the trait is not frequency dependent, then natural selection should result in traits that maximize F .

A continuous analogue to equation (1a) has been proposed by Lande (1982) for the case of weak selection, frequency dependence, and overlapping generations:

$$dz^* / dt = (V_a / V_1) \text{Cov}(r, z) = (V_a / V_1) (\int (z - z^*) r p dz), \quad (6)$$

where r is the intrinsic growth rate, which provides a measure of fitness when there are overlapping generations. Similar equations have been derived for other genetic assumptions by Price (1970), Crow and Nagylaki (1976), and Nagylaki

(1989). Equation (6) is otherwise identical to (1a) except for the omission of mean fitness in the denominator. The same Taylor series expansion discussed above leads to the approximation,

$$dz^*/dt = V_a \partial r / \partial z |^* \quad (7)$$

Because equation (6) is derived under the assumption of frequency independence, it is unclear, however, whether equation (7) is adequate for frequency-dependent evolution (Charlesworth 1993).

When it is justified, one of the chief advantages of the approximations over the original recursion relationships is that, by getting rid of the integral, it makes it much easier to evaluate the stability of the dynamical system. Standard techniques for local stability analysis are based on Jacobian matrices, whose entries are the derivatives of the right-hand sides of the difference or differential equations. It is often impossible to obtain an analytic expression for the integral in equation (1a) or its derivatives. This is never a problem with equations (1b) or analogous equations based on more terms in the expansion of W . If we take the simplest type of system in which there is a single evolving trait [i.e., eq. (1a)], the necessary and sufficient conditions for the local stability of an equilibrium are that

$$(\partial/\partial z^*)[(V_a/V_i) \int (z - z^*) W p \, dz / W^*] < 0 \quad (8a)$$

$$(\partial/\partial z^*)[(V_a/V_i) \int (z - z^*) W p \, dz / W^*] > -1, \quad (8b)$$

where the derivative is evaluated at the equilibrium point obtained by setting equation (1a) to zero. Condition (8b) is likely to be violated only if selection is extremely strong, and heritability (additive genetic variance divided by total variance) is high. Thus, stability is more likely to depend on condition (8a), which is equivalent to

$$(\partial/\partial z^*)\{\partial W/\partial z|^* + (1/6)(\partial^3 W/\partial z^3|^*)(M_4/V_i) + (1/120)(\partial^5 W/\partial z^5|^*)(M_6/V_i) + \dots\} < 0. \quad (9)$$

The term in brackets is $\partial F/\partial z|^*$, where F is given by equation (5).

Condition (9) is a very satisfying result, because it is similar to the continuously stable strategy (CSS) requirement derived by Eshel (1983) for a game theory model of a continuous trait. If fitness is measured by the function F [eq. (5)], condition (9) is exactly equivalent to the CSS

criterion. If fitness is measured by W , the conditions are approximately equivalent when phenotypic variance is sufficiently small. Eshel's condition has been confirmed by Taylor (1989) and Christiansen (1991) for single-locus diploid models assuming mutant alleles with small effects.

Coevolution frequently leads to limit cycles or more complex dynamics (Van Valen 1973; Hamilton 1982; Stenseth and Maynard Smith 1984; Seger and Hamilton 1988; Takada and Kigami 1991; Abrams 1992). We showed (Abrams et al. 1993) that there are many ecological scenarios, involving frequency-dependent evolution of one species or frequency dependent or independent evolution of several species, in which the evolutionary equilibria defined by equation (1b) are unstable. Thus, it is important to have a method of assessing the local stability of equilibria in models of the evolution of continuous frequency dependent traits. When there is both frequency and density dependence within a single species, or when there are coevolving species, it is necessary to analyze simultaneous dynamic equations for trait values and population densities; equations of the form of (1b) are then embedded in a larger dynamical system. Even in the single species case, it is often not adequate to assume equilibrium population sizes when analyzing evolutionary dynamics (Nagylaki 1979).

Because small errors can accumulate, the approximations suggested here may give significantly inaccurate predictions about global dynamics, or long term behavior. However, because the quantitative genetic recursion (1a) itself is an approximation, and fitness functions are seldom known precisely, accurate prediction of long-term global dynamics is not a goal of this sort of model.

The alternative to stability formula (9) is numerical analysis of the quantitative genetic recursion, equation (1a). The numerical integrations required are often prohibitively time consuming (Taper and Case 1985), and numerical analysis may obscure generalizations that could be seen from an analytical stability analysis of the approximation. This argues against Taper and Case's (1992) suggestion that coevolutionary studies rely primarily on solving numerically for the equilibrium points of equation (1a).

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