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13

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Game Theory, Optimization, and Quantitative Genetics

13.1 Introduction

Game theory, optimization, and quantitative genetics are among the most frequently used theoretical approaches to study evolution by natural selection. Over the last few years, the three methods have been carefully compared and contrasted (Pease & Bull 1988, Charnov 1989, Charlesworth 1990, Iwasa et al. 1991, Mangel 1992, Taper & Case 1992, Abrams et al. 1993a,b). This chapter will summarize these comparisons, describing how the approaches are used to study and predict evolutionary dynamics and equilibria for traits that evolve by natural selection. Because all three theoretical approaches consider the evolutionary roles of adaptation and constraint, a general strategy will be proposed at the end of this chapter that an empiricist might wish to follow when assessing the relative importance of adaptation and constraint in the evolution of behavioral traits in natural populations.

Another goal of this chapter is to consider how game theory, optimization, and quantitative genetic approaches apply to the evolution of complex characters such as behavior. To this end, it will be helpful to introduce some terminology and notation that will be used throughout. A complex character can often be thought of as a collection of component traits or a set of measurements. For example, an individual's foraging behavior might consist of a number of basic elements (such as searching, handling, consuming, and resting). Measurements of foraging behavior might then consist of a set of durations of each element. Mating calls are another example of a complex behavioral character for which the component traits of interest might include a call's duration, energy, frequency, and so on. In this chapter, a column vector $z=(z_1,z_2,\ldots,z_k)^T$ will be used to denote a set of k measurements that together describe a complex character with k components. (The superscript "T" means vector transpose.) For instance, if z is a mating call, the vector components z_1, z_2, z_3, ... might be, respectively, measures of call duration, energy, frequency, and so on. The discussion below can be extended to characters with an infinite number of component

traits (such as the set of potential sprint speeds that a lizard has over a range of thermal environments), but this will not be done here [see Kirkpatrick & Heckman (1989) and Kirkpatrick et al. (1990) for background].

The central aim of this chapter is to clarify when optimization, game theory, and quantitative-genetics approaches will lead to similar or different conclusions about adaptation given the same basic information on fitness and constraints. Comparisons will therefore be limited to conditions under which the approaches are equally applicable and might be expected to give comparable results. To begin, the next section will discuss how these methods are used to study the evolutionary dynamics of behavioral characters subject to natural selection.

13.2 Evolutionary Dynamics

Optimization methods were designed expressly to analyze evolutionary equilibria and thus cannot be used to study the dynamics of adaptation. Game theory and quantitative genetics approaches, however, can be applied for just such a purpose. This section will compare the assumptions and methods of game theory and quantitative genetics that are used in the study of evolutionary dynamics of a character's mean. To clarify the comparison, only continuous characters or strategies will be considered in this chapter.

Consider a continuous character (or strategy) z that evolves by natural selection. Assume that generations are discrete and nonoverlapping and that before selection the phenotypic distribution of z is described by the probability density function $f(z)$. Let $w(z)$ be the fitness of phenotype z, which may depend on the distribution of z in the population. After selection but before reproduction, the distribution of phenotypes is

$$f^*(z)=\frac{w(z)f(z)}{\bar{w}} \tag{1}$$

where $\bar{w}$ is the population's mean fitness:

$$\bar{w}=\int w(z)f(z)\,dz \tag{2}$$

(Integration here and below is assumed to be taken over all feasible values of z.)

By combining equation (1) with an appropriate description of the inheritance of z, evolutionary (i.e., between-generation) changes in the phenotypic distribution can be computed, at least in principle. Determining the between-generation change in the complete distribution is, however, usually challenging, even when approximate methods are used. Fortunately, it is often useful for many purposes to study the simpler problem of how the mean phenotype, $\bar{z}$, evolves, where

$$\bar{z}=\int zf(z)\,dz \tag{3}$$

For this reason—and to greatly simplify the math—this chapter will focus on evolutionary questions involving a population's mean phenotype. Evolutionary forces such as genetic drift and mutation are assumed to be negligible.

13.2.1 Standard Game Theory Approach

Standard evolutionary game theory assumes that phenotypes are asexually inherited (Maynard Smith 1982) or have an autosomal one-locus haploid genetic basis (Moore & Boake 1994). These assumptions are mathematically, if not biologically, equivalent. If the resemblance between parental and offspring phenotypes is perfect, then the offspring mean in the next generation, $\bar{z}'$, will be exactly the same as the mean, $\bar{z}^*$, of the selected parents. That is, $\bar{z}'=\bar{z}^*=\int zf^*(z)\,dz$, where $f^*(z)$ is the postselection distribution defined in equation (1). With such perfect asexual inheritance, the between-generation change in the population mean phenotype, $\Delta\bar{z}\equiv\bar{z}'-\bar{z}$, is simply

$$\Delta\bar{z}=s \tag{4}$$

where the *selection differential*, $s=\bar{z}^*-\bar{z}$, measures within-generation changes in the population mean due to selection. A convenient way to rewrite equation (4) for a complex character, like behavior, is

$$\Delta\bar{z}=P\beta \tag{5}$$

where P is the phenotypic covariance matrix for the components of z and $\beta=P^{-1}s$ is the *selection gradient* (Lande 1979). If the resemblance between a parent and its asexually produced offspring is not perfect, but the regression of offspring phenotype on parental genotype is linear, then the evolutionary dynamics of the population mean phenotype can be described by

$$\Delta\bar{z}=G_T\beta \tag{6}$$

where G_T is the total genetic covariance matrix and β is the same selection gradient as in equation (5).

Each element of the selection gradient, $\beta=(\beta_1,\ldots,\beta_k)^T$, describes the force of linear selection acting directly on the mean of a particular trait component, holding other components constant (Lande & Arnold 1983, Brodie et al. 1995). By comparison, the components of the selection differential, $s=(s_1,\ldots,s_k)^T$, confound effects of direct selection on a trait and selection on correlated traits (Lande and Arnold 1983).

If fitness is frequency-independent (i.e., does not depend on the distribution of phenotypes), the selection gradient β has the biologically interesting property that it indicates the direction of evolution that would produce the steepest increase in population mean fitness (Lande and Arnold 1983). However, equations (5) and (6) show that whether parent and offspring phenotypes match perfectly or not, the evolutionary response to selection will tend to deviate from the direction of most rapid increase in

mean fitness, β (see Fig. 13.1). Such adaptive "inefficiency" could be due to insufficient genetic variance for, or strong genetic correlations between, the traits being selected (as reflected in the covariance matrix P or G_T). This interpretation of β can break down if fitness is frequency-dependent, since even the most efficient evolutionary response (i.e., evolution in the direction of β) may reduce mean fitness in the next generation. Still, $\Delta\bar{z}$ will generally differ from β.

13.2.2 Quantitative Genetics Approach

The usual quantitative genetics approach used to study evolution assumes a sexually reproducing population in which genetic variation and covariation of traits are affected by many loci of small phenotypic effect (Bulmer 1985, Falconer 1989; other genetic models could also be used but will not be considered here). Under these assumptions, it can be shown (e.g., Lande 1979) that the evolutionary response to selection of the mean phenotype is

$$\Delta\bar{z} = G\beta \tag{7}$$

where G is the *additive-genetic* (for brevity, "genetic") covariance matrix and β is the selection gradient defined above. As with the asexual models, equation (7) shows that the evolutionary response to selection will generally differ from β (see Fig. 13.1).

Equation (7) does not require that G be constant to be valid. In fact, if G is changed by selection, equation (7) will still correctly describe evolutionary (between-generation) change in $\bar{z}$ provided the regression of offspring on parental phenotypes is linear (Bulmer 1985, p. 145; but see Hastings 1990, Nagylaki 1992). This implies that equation (7) is accurate for at least a single generation (see Grant & Grant 1995 for an empirical demonstration). Turelli and Barton (1994) have shown theoretically that G may be nearly constant over several generations for a broad range of selection strengths. Moreover, assuming that G is constant in equation (7) over several generations may give a reasonably accurate approximation to the evolution of $\bar{z}$, even if G actually changes between generations due to conventional evolutionary forces. This is because the mean often evolves much faster than the genetic variance (Barton & Turelli 1987).

It is reasonable to expect that the accuracy of such an approximation will break down after some period of time; however, it is an open question as to what the length of that period will be (Turelli 1988). Empirical results suggest that G (or its general matrix structure) may often be stable over fairly long evolutionary time scales (e.g., Lofsvold 1986, Kohn & Atchley 1988, Wilkinson et al. 1990, Arnold 1992). In any event, there is no reason why evolutionary changes in G could not be incorporated into equation (7). In fact, there are a number of ways this could be done; for example, one could update estimates of G every few generations (in an empirical application) or model the evolution of G using, say, an extension of Bulmer's infinitesimal model (Bulmer 1971, 1985). Regardless of how one handles the evolution of G, the critical point is that the constancy of genetic variances and covariances need not be an assumption underlying quantitative-genetic models of evolution by selection of mean phenotypes. Of course, the period over which individual fitnesses remain constant is an equally important consideration when using any of the above models to draw long-term evolutionary inferences.

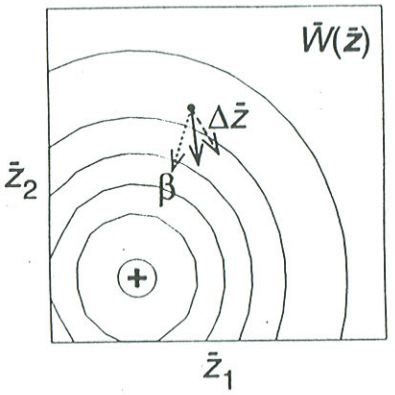

Figure 13.1. Evolutionary responses to selection in the mean of a two-component character, $\bar{z} = (\bar{z}_1, \bar{z}_2)$. Closed curves indicate mean phenotypes with the same population mean fitness, i.e., contours of $\bar{w}$. The plus sign shows the location of the mean phenotype with maximal mean fitness. The common base of the three arrows lies at a population's initial mean phenotype. Between-generation changes in the mean phenotype, $\Delta\bar{z}$, under perfect asexual inheritance and sexual inheritance are shown, respectively, by the solid and dashed arrows. The dotted arrow is the direction β favored by selection.

13.2.3 Comparing Evolutionary Dynamics

How do the above game theory and quantitative genetics models of evolution compare? The approaches are similar in that they use the selection gradient β to quantify the within-generation effects of selection on the mean phenotype. Another shared feature is that evolution generally does not proceed in the direction favored by selection (as indicated by β), even when parent and offspring resemble one another perfectly [equation (5)]. However, for a given selection regime and pattern of phenotypic/genotypic variances and covariances, evolution of the mean phenotype should proceed in a direction most similar to β with perfect asexual inheritance and least similar to β with sexual inheritance (see Fig. 13.1). This is because evolutionary constraints that are apparent at the phenotypic or total genetic level (P or G_T) must also occur at the additive-genetic level (G), but not necessarily vice versa (Pease and Bull 1988; see below).

Essentially, the only difference between game-theoretic and quantitative-genetic models for evolutionary dynamics of the mean phenotype is in how within-generation effects are assumed to be transmitted across generations. So provided that the basis of trait inheritance is understood, there is no actual distinction between game-theoretic and quantitative-genetic descriptions of the evolutionary dynamics of $\bar{z}$ under natural selection. It turns out, however, that equilibrium predictions of the approaches can differ widely, as will be discussed in the next section.

13.3 Evolutionary Equilibria

Optimization, game theory, and quantitative genetics offer different ways to predict evolutionary equilibria of continuous characters under selection. Game-theoretic approaches are appropriate when fitness is frequency-dependent (i.e., when individual fitness depends on the distribution of phenotypes), while optimization methods are appropriate when fitnesses are frequency-independent. Quantitative genetic approaches can be used to analyze equilibria for both types of fitness. The next two sections compare these approaches for frequency-independent and, then, frequency-dependent fitness. The dynamic stability of equilibria will not be considered here; see Abrams et al. (1993b) for an interesting discussion.

For simplicity, assume that the distribution of phenotypes, $f(z)$, is normal with mean $\bar{z}=(\bar{z}_1, \ldots, \bar{z}_k)^T$ and covariance matrix P. This condition is commonly satisfied in natural populations when traits are measured on appropriate scales (see, e.g., Falconer 1989). If the fitness function, $w(z)$, is differentiable with respect to the components of $\bar{z}$, then

$$\nabla_{\bar{z}}\bar{w} = \int w(z)\nabla_{\bar{z}} f(z)\, dz + \int f(z)\nabla_{\bar{z}} w(z)\, dz \doteq \bar{w}P^{-1}s + \overline{\nabla_{\bar{z}} w} \tag{8}$$

where $\nabla_{\bar{z}}=(\partial/\partial\bar{z}_1, \partial/\partial\bar{z}_2, \ldots, \partial/\partial\bar{z}_k)^T$ is the gradient operator with respect to components of $\bar{z}$, and $\overline{\nabla_{\bar{z}} w}=\int f(z)\nabla_{\bar{z}} w(z)\, dz$ is the mean gradient of individual fitness. Since $\beta=P^{-1}s$, equation (8) can be rearranged to express the selection gradient in terms of population mean fitness and individual fitness as

$$\beta = \frac{\nabla_{\bar{z}}\bar{w} - \overline{\nabla_{\bar{z}} w}}{\bar{w}} \tag{9}$$

For a simple character ($k=1$), equation (9) reduces to $\beta=(d\bar{w}/d\bar{z}-\int \partial w/\partial\bar{z} f(z)\, dz)/\bar{w}$, an expression first given by Lande (1976). If fitness is frequency-independent, the term $\overline{\nabla_{\bar{z}} w}$ vanishes because $\nabla_{\bar{z}} w(z)=0$ for every z; then equation (9) reduces to the well-known equation $\beta=(\nabla_{\bar{z}}\bar{w})/\bar{w}=\nabla_{\bar{z}}\ln\bar{w}$ (Lande 1979). If fitness is frequency-dependent, $\overline{\nabla_{\bar{z}} w}$ may or may not be zero, depending on the form of w.

13.3.1 Frequency-Independent Fitness

When fitness is frequency-independent, optimization approaches assume individual fitness is maximized at an evolutionary equilibrium, possibly subject to phenotypic

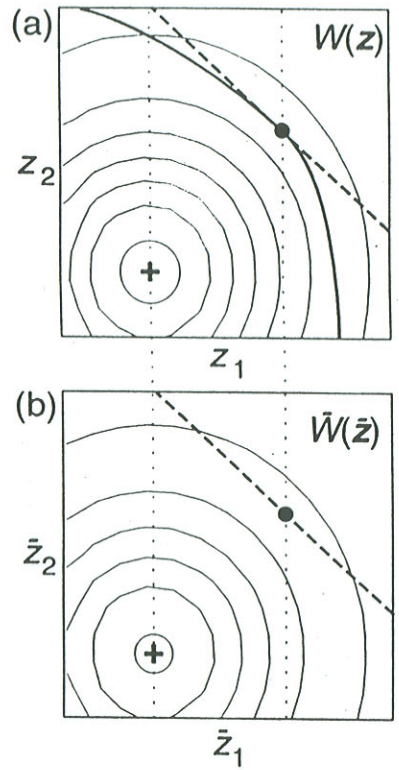

Figure 13.2. Optimization and quantitative genetics analyses of evolutionary equilibria for a two-component character. (a) Thin lines are contours for individual fitness, w, as a function of the character components z_1 and z_2. The plus sign indicates the phenotype with highest individual fitness, i.e., the global optimum. The thick curve shows a hypothetical constraint function, which determines the possible values of z_1 and z_2. The filled circle shows the location of the optimal phenotype, given these constraints. (b) Contours for mean fitness, $\bar{w}$, based on the individual fitness function shown in (a). Scales for $\bar{z}_1$ and $\bar{z}_2$ are the same as for z_1 and z_2 above. The fixed fitness difference between contours in (b) is the same as in (a), so the topography of $\bar{w}$ is less rugged than w. The plus sign indicates the mean phenotype associated with highest mean fitness, i.e., the global optimum. The dashed line represents the evolutionarily accessible directions given the constraint in (a); this line is also drawn in (a). The filled circle is the constrained optimum. The position of the constrained (unconstrained) optimum in (a) is similar to the corresponding optimum in (b).

constraints (reviewed in Parker & Maynard Smith 1990). That is, the predicted equilibrium phenotype maximizes $w(z)$, perhaps subject to satisfying a set of constraints. For example, if $w(z)$ were smooth and there were no constraints on z, then the optimal phenotype $\hat{z}$ would be a solution of the equation

$$\nabla_z w(z) = 0 \tag{10}$$

where $\nabla_z = (\partial/\partial z_1, \partial/\partial z_2, \ldots, \partial/\partial z_k)^T$ is the gradient with respect to components of z. Figure 13.2a illustrates this approach when individual fitness depends on a character with two trait components, $z = (z_1, z_2)$, such as a mating call characterized by its duration (z_1) and intensity (z_2). Without constraints, fitness is globally maximized at an evolutionary equilibrium (indicated by the plus sign), whereas with constraints, fitness is maximized at equilibrium (filled circle) to the extent possible given the constraints (heavy curve).

A quantitative genetics analysis of frequency-independent selection starts with the basic evolution equation (7). An equilibrium mean phenotype, $\hat{\bar{z}}$, must be a solution of $\Delta\bar{z} = G\beta = 0$. Because individual fitness is frequency-independent, $\overline{\nabla_z w} = 0$ in equation (9) (see above), so that $\hat{\bar{z}}$ need only satisfy the simpler

$$\Delta\bar{z}\big|_{\hat{\bar{z}}} = G\beta\big|_{\hat{\bar{z}}} = G\left.\frac{\nabla_z \bar{w}}{\bar{w}}\right|_{\hat{\bar{z}}} = 0 \tag{11}$$

where the notation "$|_{\hat{\bar{z}}}$" means evaluated at $\hat{\bar{z}}$.

Equation (11) may be satisfied in two qualitatively different ways. First, $\Delta\bar{z}|_{\hat{\bar{z}}} = 0$ if $\nabla_{\bar{z}}\bar{w}|_{\hat{\bar{z}}} = 0$. In this case, $\hat{\bar{z}}$ globally maximizes mean fitness, $\bar{w}$ (Fig. 13.2b, plus sign). This represents an "ecological optimum" in the sense that there is no net linear selection on $\hat{\bar{z}}$. Such an equilibrium will eventually be reached, even if G varies through time, provided that there are no persistent genetic barriers to evolutionary change (such as lack of heritable variation or sufficiently strong genetic correlations; see below) and may be reached even if such constraints are ever-present, but changing (Hammerstein 1996, this volume).

Alternatively, an equilibrium could occur with the population not at an ecological optimum (i.e., with $\nabla_{\bar{z}}\bar{w}|_{\hat{\bar{z}}} \neq 0$) if there is a lack of appropriate genetic variation, as reflected in G (see below). In this case, $\bar{w}$ is not globally maximized at equilibrium; rather, $\bar{w}$ is maximized over a subset of "evolutionarily accessible" directions for the mean phenotype (filled circle in Fig. 13.2b). Evolutionarily accessible directions can be thought of as the complement of the set of "evolutionarily forbidden" directions (Kirkpatrick & Lofsvold 1992), which is the set of all selection gradients that would produce no evolutionary response in the current population. The notion of "evolutionarily forbidden" directions gives a quantitatively precise and biologically useful definition of an important type of evolutionary constraint (Arnold 1992).

Mathematically, evolutionary constraints are present whenever the additive-genetic covariance matrix G is "singular" (i.e., at least one of its rows is a linear combination of the other rows). The corresponding evolutionarily accessible and forbidden directions are described by the eigenvectors associated with, respectively, non-zero and zero eigenvalues of G. (G must have at least one zero eigenvalue if it is singular.) These constraints will limit evolutionary responses to accessible directions (the dashed line in Fig. 13.2b). Note that some authors have assumed that genetic correlations merely slow evolution but do not prevent ultimate optimization. Not only is this incorrect (e.g., see Fig. 13.2b), but even small genetic correlations may be consistent with equilibrium populations that are far from their ecological optima (Dickerson 1955, Via 1987, Gomulkiewicz & Kirkpatrick 1992, Kirkpatrick and Lofsvold 1992).

For a given set of fitnesses and constraints, how similar are the equilibria predicted by optimization and quantitative genetics approaches? The two approaches give quite similar results, at least under some circumstances (Charnov 1989, Charlesworth 1990, Iwasa et al. 1991, Taper & Case 1992, Abrams et al. 1993a). Specifically, the function that describes individual fitness, $w(z)$, must be *analytic*, which is to say it can be represented by a Taylor series that converges to $w(z)$ for every z (see, e.g., Marsden & Tromba 1988). If, in addition, terms above a certain order in the Taylor series are small, then an equilibrium predicted by one approach will be close to that predicted by the other. The rationale in the case of a two-component character, $z = (z_1, z_2)$, goes as follows. By assumption, $w(z)$ can be expanded in a Taylor series around the current population mean $\bar{z} = (\bar{z}_1, \bar{z}_2)$:

$$\begin{aligned} w(z) = w(\bar{z}) &+ \left.\frac{\partial w}{\partial z_1}\right|_{\bar{z}} (z_1 - \bar{z}_1) + \left.\frac{\partial w}{\partial z_2}\right|_{\bar{z}} (z_2 - \bar{z}_2) \\ &+ \frac{1}{2}\left[\left.\frac{\partial^2 w}{\partial z_1^2}\right|_{\bar{z}} (z_1 - \bar{z}_1)^2 + 2\left.\frac{\partial^2 w}{\partial z_1 \partial z_2}\right|_{\bar{z}} (z_1 - \bar{z}_1)(z_2 - \bar{z}_2) + \left.\frac{\partial^2 w}{\partial z_2^2}\right|_{\bar{z}} (z_2 - \bar{z}_2)^2\right] + \ldots \end{aligned} \tag{12}$$

Substituting (12) into equation (2) leads to the following expansion for $\bar{w}$:

$$\bar{w} = w(\bar{z}) + \frac{1}{2}\left[\left.\frac{\partial^2 w}{\partial z_1^2}\right|_{\bar{z}} P_{11} + 2\left.\frac{\partial^2 w}{\partial z_1 \partial z_2}\right|_{\bar{z}} P_{12} + \left.\frac{\partial^2 w}{\partial z_2^2}\right|_{\bar{z}} P_{22}\right] + \ldots \tag{13}$$

where P_{ii} is the phenotypic variance of component z_i ($i = 1, 2$) and P_{12} is the phenotypic covariance between z_1 and z_2. The derivation of (13) relies on the facts $\int (z_i - \bar{z}_i) f(z)\, dz = 0$, $\int (z_i - \bar{z}_i)^2 f(z)\, dz = P_{ii}$, and $\int (z_1 - \bar{z}_1)(z_2 - \bar{z}_2) f(z)\, dz = P_{12}$. From (13) it follows that $\bar{w} \approx w(\bar{z})$ if all terms involving products with second and higher derivatives of $w(z)$ are small. Thus, under these conditions, a mean phenotype that maximizes population mean fitness $\bar{w}$ will also approximately maximize individual fitness $w(z)$, and vice versa. This correspondence is shown by the similar positions of the global optima in the upper and lower panels of Fig. 13.2.

The preceding argument can be extended to analyses involving evolutionary constraints. Continuing with the above example, suppose that $z_2 = h(z_1)$. For example, this might describe tradeoffs between call duration and intensity imposed by an organism's energetic capacities. If $h(z_1)$ is differentiable, the optimal phenotype satisfying this phenotypic constraint can be determined by solving the equation

$$\frac{dh(z_1)}{dz_1} = -\frac{\partial w/\partial z_1}{\partial w/\partial z_2} \tag{14}$$

for z_1 (Charnov 1989). Adapting the methods of Charlesworth (1990), it can be shown that given the constraint $z_2 = h(z_1)$, an equilibrium mean phenotype for the quantitative genetics model must satisfy

$$\left.\frac{dh(z_1)}{dz_1}\right|_{\bar{z}} = -\left.\frac{\partial \bar{w}/\partial \bar{z}_1}{\partial \bar{w}/\partial \bar{z}_2}\right|_{\bar{z}} \tag{15}$$

If higher-order terms in the expansion (13) of $\bar{w}$ are small, then $\partial\bar{w}/\partial\bar{z}_i \approx \partial w/\partial z_i|_{\bar{z}}$ for $i = 1, 2$. Thus, any $\hat{z}$ that satisfies (15) will also approximately satisfy (14) and vice versa. This shows that, with or without constraints, optimization and quantitative genetics methods will predict roughly the same equilibrium phenotype when appropriate mathematical conditions are met.

13.3.2 Frequency-Dependent Fitness

When individual fitness depends on the distribution of phenotypes—in particular, on the mean $\bar{z}$—an equilibrium phenotype can be predicted on the basis of being an "evolutionarily stable strategy" (ESS) or a stationary point of the quantitative-genetics model (7). These two approaches will be discussed in turn. Individual fitness will be denoted $w(z, \bar{z})$ to emphasize its dependence on $\bar{z}$.

The concept of an ESS was developed as an extension of game theory to evolutionary biology (Maynard Smith 1982, Parker and Maynard Smith 1990). Briefly, a mean phenotype $\hat{z}$ is an ESS if it is its own "best response" (Bulmer 1994). (For simplicity, assume this best response is unique.) The best response to a mean phenotype $\bar{z}$ is the phenotype z that maximizes individual fitness, $w(z, \bar{z})$, holding $\bar{z}$ constant. If $w(z, \bar{z})$ is differentiable with respect to its first argument, then a best response to $\bar{z}$ can be found by solving $\nabla_z w(z, \bar{z}) = 0$ for z. In this symbolism, a phenotype that is its own best response (i.e., is an ESS) must be a solution $\hat{z}$ of

$$\nabla_z w(z, \bar{z})|_{z=\bar{z}=\hat{z}} = 0 \tag{16}$$

A graphical illustration of ESS analysis for a two-component trait $z = (z_1, z_2)$ is shown in Fig. 13.3. Note that an ESS defined by (16) may not be an equilibrium for the "standard" game-theoretic model discussed above [equation (5)] if $\beta \neq 0$ when $\bar{z} = \hat{z}$.

In the quantitative genetics approach, determining evolutionary equilibria when fitness is frequency-dependent again begins with equation (7). Assuming phenotypes are normally distributed, an equilibrium mean phenotype is a solution $\hat{\bar{z}}$ of

$$\Delta\bar{z}|_{\hat{\bar{z}}} = G\beta|_{\hat{\bar{z}}} = G\left.\frac{\nabla_z \bar{w} - \overline{\nabla_z w(z, \bar{z})}}{\bar{w}}\right|_{\hat{\bar{z}}} = 0 \tag{17}$$

[see equations (7) and (9)]. As for frequency-independent fitnesses, there are two qualitatively different ways equation (17) may be satisfied. First, $\Delta\bar{z}|_{\hat{\bar{z}}} = 0$ if $\nabla_z \bar{w} = \overline{\nabla_z w(z, \bar{z})}$ when $\bar{z} = \hat{\bar{z}}$. Such a solution represents an equilibrium that would be reached in the absence of genetic constraints. Although $\hat{\bar{z}}$ will not maximize mean fitness if $\nabla_z \bar{w}(\hat{\bar{z}}) \neq 0$, it is an "ecological optimum" in the sense that there is no net force of linear selection acting to change the mean when $\bar{z} = \hat{\bar{z}}$. In contrast, $\hat{\bar{z}}$ may be

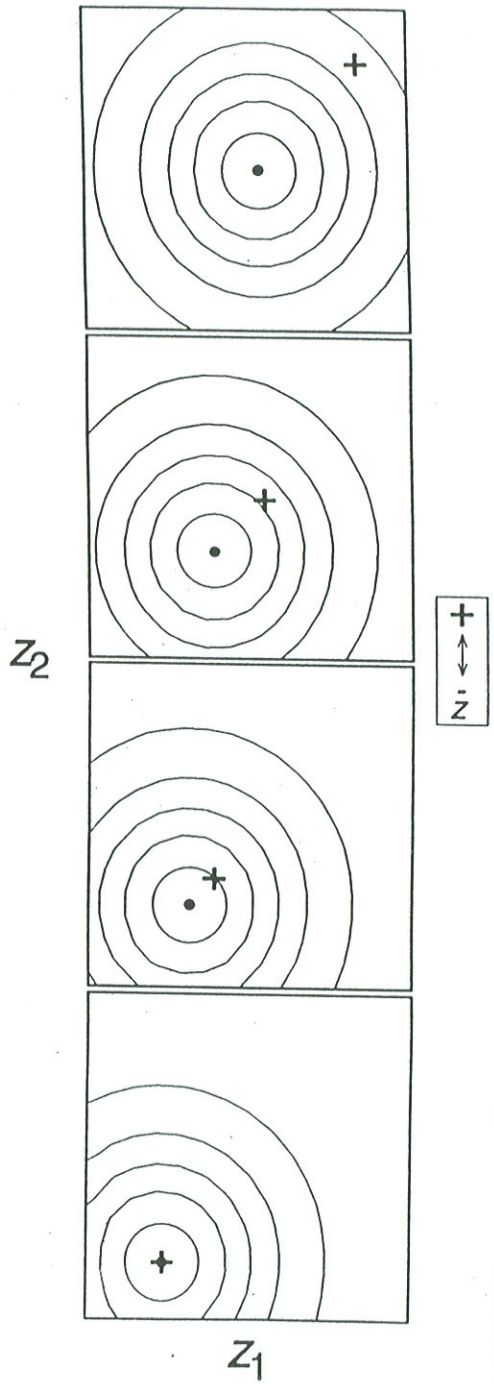

Figure 13.3. ESS analysis for a two-component character $z = (z_1, z_2)$. Individual fitness surfaces, $w(z, \bar{z})$, for four mean phenotypes (plus signs) are shown. On each surface, the filled circle represents the "best response" to $\bar{z}$. In the bottom panel, $\bar{z}$ is its own best response, i.e., it is an ESS.

a solution of (17) even though $\nabla_z \bar{w} \neq \overline{\nabla_z w(z, \bar{z})}$ at equilibrium because of genetic constraints indicated by the singularity of G. The net force of linear selection on the mean is not zero (i.e., $\bar{z}$ is not at an ecological optimum). At such an equilibrium, selection will favor changes in evolutionarily forbidden directions but have no net effect in evolutionarily accessible directions.

ESS and quantitative genetic analyses have been compared in several theoretical studies (Charlesworth 1990, Iwasa et al. 1991, Mangel 1992, Taper & Case 1992). The following generalizes the approach used by Abrams et al. (1993a,b) to multivariate characters. Assuming that the individual fitness function $w(z, \bar{z})$ is analytic in the argument z, then

$$\beta = \frac{\nabla_z \bar{w} - \overline{\nabla_z w(z, \bar{z})}}{\bar{w}} = \frac{\nabla_z F(z, \bar{z})|_{z=\bar{z}}}{\bar{w}} \tag{18}$$

where $F(z, \bar{z})$ is defined as

$$F(z, \bar{z}) = w(z, \bar{z}) + \tfrac{1}{2}\left(\sum_i P_{ii} \frac{\partial^2 w(z, \bar{z})}{\partial z_i^2} + 2\sum_{i<j} P_{ij} \frac{\partial^2 w(z, \bar{z})}{\partial z_i \partial z_j}\right) + \cdots \tag{19}$$

F has the property $F(\bar{z}, \bar{z}) = \bar{w}|_{\bar{z}}$. If the terms of expansion (19) involving second and higher derivatives of $w(z, \bar{z})$ are small, then $F(z, \bar{z}) \approx w(z, \bar{z})$ so that $\nabla_z F(z, \bar{z}) \approx \nabla_z w(z, \bar{z})$. This implies that, at least under these conditions, a phenotype satisfying the ESS condition (16) will approximately satisfy the equilibrium equation (17). (In addition, this shows that an ESS defined by (17) will only be an approximate equilibrium for the "standard" game theory model described above [equation (5)] because it is generally only approximately zero at an ESS.) The above arguments can be extended to cases in which phenotypic constraints are present (see Charlesworth 1990). Once again, ESS and quantitative genetic equilibria will be close under the appropriate mathematical conditions.

Taken together, the results of this section demonstrate that, at least under certain mathematical conditions, an optimization or ESS analysis will predict roughly the same equilibrium as the comparable quantitative genetics analysis, with or without phenotypic constraints. The next section will consider the extent to which these conditions might or might not hold in practice.

13.4 Dissimilarities

The last section showed that optimization or ESS methods will predict equilibria similar to those using quantitative genetics methods provided that three conditions hold: (1) The function describing individual fitness, w, must be analytic, (2) terms in the expansion of $\bar{w}$ or $F(z, \bar{z})$ involving higher-order derivatives of w and their coefficients must be small, and (3) constraints that occur at the additive-genetic level must also appear at the phenotypic level. The extent to which an evolutionary equilibrium can be considered a common prediction to quantitative genetic and optimization (or ESS) analyses depends on how often the above three conditions hold in situations

of biological interest. (Technically, the previous section only showed that the three conditions are sufficient since the methods may predict similar equilibria under other circumstances.) In this section I argue that there are many biologically realistic situations in which at least one of these conditions fail and that, in those situations, the different methods generally give widely different results. This suggests that the extent to which optimization/ESS and quantitative genetics results agree may be substantially limited. For simplicity, only one-component characters will be considered in this section, although the situations described below can easily arise for more complex characters.

The outwardly most innocuous of the above three requirements is that the individual fitness function must be analytic. Mathematically, this means that the Taylor series of the fitness function must converge to $w(z)$, or $w(z, \bar{z})$, for every value z (e.g., Marsden & Tromba 1988). Although analytic functions enjoy widespread use in the theoretical and statistical literature, this requirement is not met in a number of biologically important circumstances, of which just three examples will be considered.

The first example is a "threshold character" model for the evolution of strategies in a two-person, two-strategy game, such as the Hawk–Dove game (Maynard Smith 1982). A threshold character is a character with discrete states that are not inherited in a simple way (Falconer 1989). If the inheritance of strategies is not simple, then it is reasonable to model the set of strategies as a threshold character. In such a model, the expression of each character state (strategy) is assumed to depend on an underlying continuous "liability." Consider, for example, a two-strategy game with pure strategies A and B. Let z denote the liability. Assume that an individual with $z \leq T$ plays strategy A and plays strategy B otherwise.

If the distribution of z is normal with a fixed variance P, then the proportion of individuals playing strategy A or B is a function of the mean liability, $\bar{z}$ (Charlesworth 1990). In particular, the proportion playing A is $\Theta[(T-\bar{z})/\sqrt{P}]$, where $\Theta(\cdot)$ is the cumulative distribution function of the standard normal distribution. Now suppose E_{IJ} is the fitness payoff to strategy I in a contest with an opponent playing strategy J. Then the expected fitnesses for strategies A and B in a population with mean $\bar{z}$ are, respectively,

$$w_A(\bar{z}) = E_{AA}\Theta\left(\frac{T-\bar{z}}{\sqrt{P}}\right) + E_{AB}\left[1 - \Theta\left(\frac{T-\bar{z}}{\sqrt{P}}\right)\right] \tag{20a}$$

$$w_B(\bar{z}) = E_{BA}\Theta\left(\frac{T-\bar{z}}{\sqrt{P}}\right) + E_{BB}\left[1 - \Theta\left(\frac{T-\bar{z}}{\sqrt{P}}\right)\right]$$

The (frequency-dependent) individual fitness function for the liability z is thus

$$w(z, \bar{z}) = \begin{cases} w_A(\bar{z}) & \text{if } z \leq T \\ w_B(\bar{z}) & \text{if } z > T \end{cases} \tag{20b}$$

(see Fig. 13.4a). Provided that $w_A(\bar{z}) \neq w_B(\bar{z})$, $w(z, \bar{z})$, is discontinuous at the threshold point $z = T$ and cannot be analytic. Moreover, the ESS analysis for the continuous

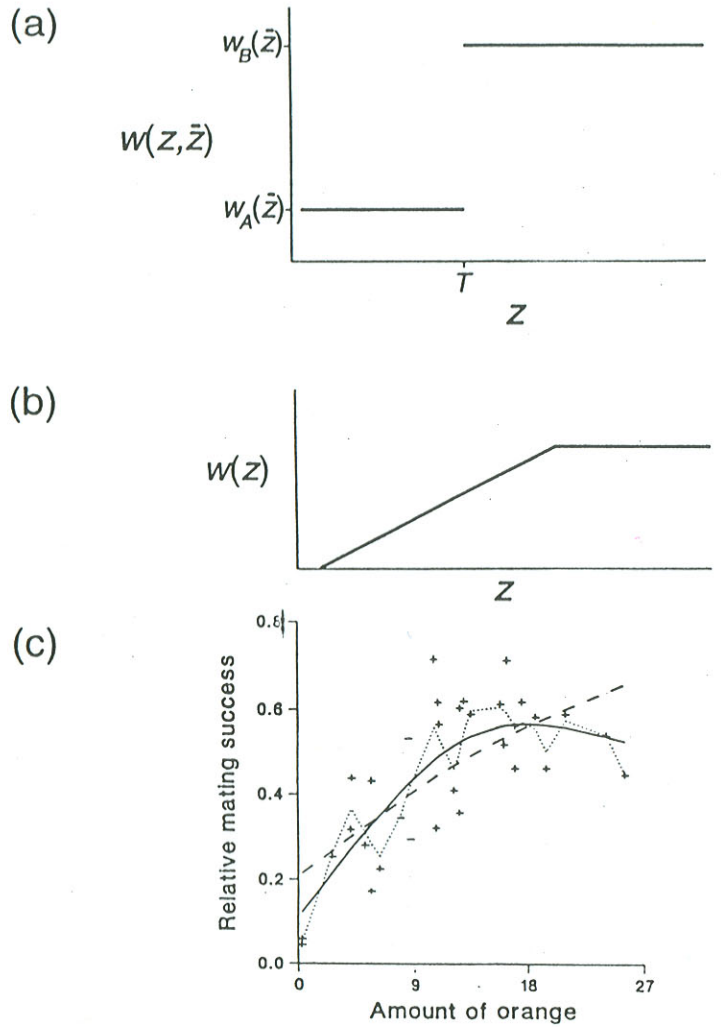

Figure 13.4. Individual fitness functions, $w(z)$ or $w(z, \tilde{z})$, that are not analytic. (a) Fitnesses for a two-person, two-strategy game with pure strategies A and B as described in the text (eq. 20). (b) A continuous fitness function with a discontinuous first derivative. (c) Fitness functions estimated using nonparametric regression. Taken from Figure 2 of Schluter (1988), which is based on data from Houde (1987). Shown is mating success of male guppies, *Poecilia reticulata*, as a function of the percentage of body area that is colored orange. Curves correspond to fitness function estimates obtained using different levels of a smoothing parameter. See Schluter (1988) for details. Figure (c) used by permission of The Society for the Study of Evolution.

trait z [see equation (16)] is inconclusive because $\partial w(z, \tilde{z})/\partial z = 0$ for all $z \neq T$. By comparison, the associated quantitative genetics equilibrium analysis [equation (17)] requires that an equilibrium $\hat{z}$ must be a solution of the equation $d\bar{w}/d\bar{z} = \overline{\partial w/\partial z}$, where

$$\bar{w}(\bar{z}) = w_A(\bar{z})\Theta\left(\frac{T-\bar{z}}{\sqrt{P}}\right) + w_B(\bar{z})\left[1-\Theta\left(\frac{T-\bar{z}}{\sqrt{P}}\right)\right]$$

and

$$\overline{\frac{\partial w}{\partial z}} = \frac{dw_A(\bar{z})}{d\bar{z}}\Theta\left(\frac{T-\bar{z}}{\sqrt{P}}\right) + \frac{dw_B(\bar{z})}{d\bar{z}}\left[1-\Theta\left(\frac{T-\bar{z}}{\sqrt{P}}\right)\right]$$

The equilibrium condition for $\hat{\bar{z}}$ reduces to $E_{AA}\hat{q} + E_{AB}(1-\hat{q}) = E_{BA}\hat{q} + E_{BB}(1-\hat{q})$, where $\hat{q} = \Theta[(T-\hat{\bar{z}})/\sqrt{P}]$ is the proportion playing strategy A at equilibrium. This is exactly the proportion predicted by the more familiar "discrete" analysis of this game [Maynard Smith 1982, equation (2.5)].

The above threshold model was, of course, chosen to illustrate how widely different ESS and quantitative genetics analyses can be when a fitness function is not analytic. It may be possible to overcome problems, like an inconclusive ESS analysis, if it were based on a different phenotypic model or scale (Charlesworth 1990). For instance, an alternative continuous trait model might let z be the probability of playing strategy A and $1-z$ the probability of playing B. Then individual fitness takes the form $w(z, \tilde{z}) = zw_A(\tilde{z}) + (1-z)w_B(\tilde{z})$, which would produce similar results whether using an ESS or quantitative-genetics analysis. In any case, the main point is simply that one should not assume by default that ESS and quantitative-genetics analyses of a given model will yield similar predictions.

The discontinuous relationship between fitness and phenotype in the last example may seem like an exceptional case with the awkward property that the fitness function is not analytic. In fact, there is an extremely large class of continuous—and even smooth—fitness functions that are not analytic. Figure 13.4 shows two examples. In Fig. 13.4b, fitness increases monotonically over lower values of z and is constant for larger z. This might describe, for example, how reproductive success depends on some measure of courtship display intensity. The function in Fig. 13.4b is continuous, but not smooth. It is not analytic because it has a discontinuous first derivative. Schmid et al. (1994) present methods for estimating nonsmooth functions like Fig. 13.4b, and they describe several empirical examples of such functions. They suggest that nonsmooth relationships are common in biology. The fitness functions in Fig. 13.4c were estimated from data using nonparametric regression methods (Schluter 1988, Schluter & Nychka 1994). Such estimates, while smooth, are not analytic because they are cubic splines. (Cubic splines are smooth but have discontinuous second derivatives.) Consequently, equilibria predicted using quantitative genetics or optimization/ESS methods based on these fitnesses may differ substantially. Other biological situations might conceivably involve even smoother fitness functions that have discontinuities in their higher-order derivatives and, thus, are not analytic. The difference between quantitative-genetics and optimization/ESS methods need not decline with increasing degrees of discontinuity. So, even for cases of very smooth

fitness functions in which only a high-order derivative is discontinuous, large differences may exist between equilibrium analyses.

Optimization/ESS and quantitative-genetics approaches may predict very different equilibria even if a fitness function is analytic. This will occur if the terms involving derivatives of second and higher order in the expansion of $\bar{w}$ or $F(z, \bar{z})$ [see equations (13) and (19)] are not small. For example, $w(z)$ will not be a good approximation of $\bar{w}$ if the higher-order terms, such as $\frac{1}{2}[P_{11}\partial^2 w/\partial z_1^2 + 2\partial^2 w/\partial z_1 \partial z_2 + P_{22}\partial^2 w/\partial z_2^2]|_{\bar{z}}$, are not negligible [see equation (13)]. For such terms to be small, not only must the higher-order derivatives of $w(z)$ not be too large, but the magnitudes of the phenotypic variances and covariances cannot be large. It is not difficult to construct hypothetical, but biologically plausible, fitness functions and phenotypic distributions in which these terms are large—as are the resulting differences between optimization (ESS) and quantitative-genetics analyses (Kirkpatrick & Gomulkiewicz, unpublished results). The "corridor model" of adaptation analyzed by Bürger (1986) is an example involving frequency-independent selection on more complex characters in which higher-order terms are not negligible. In that model, phenotypes that maximize $\bar{w}$ do not even approximately maximize in the absence of constraints.

Finally, optimization and quantitative genetics methods may predict widely different equilibria for fitness functions and phenotypic distributions that do not suffer from either of the above "problems." This can occur whenever evolutionary constraints (as reflected in G) are not apparent at the phenotypic level (as reflected in P). Charlesworth (1990) showed that if characters have more than two components, there is no simple relationship between genetic and phenotypic correlations. In fact, these correlations may have opposite signs for a particular pair of traits. This implies that the correlations underlying phenotypic constraints may often not correspond to correlations that are responsible for evolutionary constraints.

In addition to this lack of correspondence between the form of genetic and phenotypic constraints, it is possible (and even likely with a more complex character) that certain genetic constraints will be completely masked at the phenotypic level. (This is the extension to complex characters of the situation in which a phenotypically variable trait is not heritable.) Conversely, every phenotypic constraint must also appear as a genetic constraint. These properties follow from Pease & Bull (1988), who proved that if P is singular, then so is G, but not vice versa. (Technically, the "null space" of G contains that of P.) Taking their results a step further, it can be shown that G can actually be "more singular" (has a larger null space) than P, for traits with more than two components. That is, there may be fewer evolutionarily accessible dimensions associated with G than with P, even if both matrices indicate at least one evolutionarily forbidden direction. In this situation, equilibrium predictions made using optimization/ESS methods that rely on phenotypic constraints could be greatly different from those made using quantitative-genetics methods that use additive-genetic constraints. The magnitude of such a discrepancy could be quite large under biologically realistic conditions. Because the potential for constraints increases with the dimensionality of a trait (Dickerson 1955, Gomulkiewicz & Kirkpatrick 1992), this source of dissimilarity should be increasingly important for a more complex character, like behavior.

To summarize, there appear to be many biologically plausible and important circumstances in which equilibria predicted by an optimization or ESS analysis on the one hand and a quantitative genetics approach on the other can differ greatly. This argues strongly against assuming by default that the approaches will provide similar equilibrium predictions. Establishing the conditions under which the analyses are assured to give similar results would involve verifying that the fitness function is analytic, that higher-order terms are negligible, and that genetic and phenotypic constraints are the same.

13.5 An Empirical Strategy for Detecting Adaptation and Constraint

Given the potential for disparity between distinct theoretical approaches, empiricists may wonder if there are methods available that would help them to independently assess the influences of adaptation and constraint in natural populations. In fact there are. Most of the methods discussed here were developed (originally by Lande & Arnold 1983) with quantitative genetics analyses in mind; however, many of them do not require genetic data. The volume by Boake (1994) contains an excellent introduction to, and survey of, these methods as applied to behavioral characters. See Brodie et al. (1995) for a succinct review.

This section will outline an empirical strategy for resolving the roles of adaptation and constraint in an equilibrium population, similar to one proposed by Gomulkiewicz and Kirkpatrick (1992). The strategy's main advantage is that it is structured so that the least data-intensive steps are completed first; if a satisfactory explanation is attained with the relatively simpler tests, the subsequent more laborious steps can be avoided. It is crucial to bear in mind that this scheme applies only to populations that are known to be, or can reasonably be assumed to be, at equilibrium. The procedure shares many similarities with the more general proposals of Reeve and Sherman (1993).

Step 1: Test for adaptation. At a minimum, this step requires data on the relationship between phenotype and fitness. It may also require information about the phenotypic distribution. To assess adaptation and constraint in a equilibrium population, it is simplest (though not usually simple!) to begin by testing whether or not the population's mean phenotype is experiencing directional selection. One way this can be done is to determine the selection gradient, β, which can be estimated as the vector of partial regression coefficients of relative fitness on phenotype (reviewed in Arnold 1994, Brodie et al. 1995). One could also estimate β using equation (9) if an estimate of the fitness function, based on naturally occurring or artificially created variants, is available (e.g., Schluter 1988, Schluter & Nychka 1994, Brodie et al. 1995) and if phenotypes in the population are normally distributed. If $\beta = 0$, the mean is under no selection to change, which suggests that it is at an ecological optimum. Alternatively, one could determine if the distribution of phenotypes is consistent with the predicted ecological optimum. For example, Reeve and Sherman (1993) suggest that the most adapted phenotype should be predominant. If either alternative is satisfied, a reasonable conclusion is that the population occupies an ecological optimum. That is, constraints are probably playing a minor role, compared to adaptation, in maintaining the current population distribution. If β is significantly different from zero or the popula-

tion deviates from the expected distribution, then constraints are probably having an important effect.

Step 2: Detect phenotypic constraints. This step requires an estimate of the population's phenotypic covariance matrix, P, which can be estimated directly or inferred from a known constraint function (see, e.g., Charnov 1989). Phenotypic constraints are implied if P is singular. Note that determining whether or not the true P matrix is singular is a mathematically nontrivial task since *estimates* of P may fail to be non-negative definite. This problem can be partly circumvented using a procedure developed by Shaw and Geyer (1993) that constrains estimated covariance matrices to be non-negative definite.

If P is singular, then genetic (evolutionary) constraints must be present (Pease & Bull 1988). However, the phenotypic correlations may not correspond to the constraining genetic correlations (Charlesworth 1990). Despite this limitation, detecting the presence of evolutionary constraints may be of great value, even if the exact causes are obscure.

If phenotypic constraints are detected, constraints revealed by P may not provide a sufficient explanation for equilibrium, since G may be "more singular" than P (see above). Given reasonable estimates of P and β, one could test this question for the quantitative genetics approach by computing the product $P\beta$. If $P\beta \approx 0$, then the population is probably at an ecological optimum given the constraints indicated by P. If, however, $P\beta$ is significantly different from zero, then important genetic constraints may be hidden at the phenotypic level.

Step 3: Determine genetic constraints. This level of analysis requires knowing additive-genetic variances and covariances, which can be estimated using individuals of known relationship (such as parents and their offspring or sibling groups). For overviews of estimation techniques, as well as references to more specialized sources, consult Falconer (1989), Simms and Rausher (1992), and Arnold (1994). The result will be an estimate of the additive-genetic covariance matrix, G, for components of the character z. As in Step 2, genetic constraints are detected if G is singular. In the quantitative genetics framework, these constraints would provide a reasonably sufficient explanation of the equilibrium if the matrix–vector product $G\beta$ were indistinguishable from zero.

Step 4: Explore other explanations. If the roles of adaptation and constraint are not sufficiently resolved in Steps 1–3, then a number of other factors (apart from sampling error) merit consideration. First, the population may in fact not be at equilibrium. Second, the characters under consideration may be constrained by traits that have not been measured. Third, other evolutionary forces, such as migration, mutation, or parental care, may be strongly opposing selection.

At worst, a statistically powerful study that follows some or all of the above steps can rigorously establish that certain *a priori* reasonable explanations for equilibrium do not apply. (Moreover, it may be possible to use the parameter estimates to predict future evolutionary changes. See Grant & Grant 1995.) However, if all goes well, such a study would provide a clear quantitative assessment of the importance of adaptation and constraint in maintaining a population's equilibrium.

13.6 Conclusion

This chapter has attempted to compare and contrast three methods for analyzing adaptive evolution of behavioral traits: optimization, game theory, and quantitative genetics. First, it was pointed out that only game-theory and quantitative-genetics approaches are appropriate for studying evolutionary dynamics. Provided that the genetic basis is understood, these two approaches are basically identical (except for the terminology). All three approaches can be used to predict evolutionary equilibria that result from natural selection given information about fitness and constraints. Optimization and quantitative-genetics methods are used when fitness is frequency-independent, while ESS and quantitative genetics approaches apply when fitness is frequency-dependent. Given that certain mathematical conditions are satisfied, equilibria predicted by an optimization or ESS analysis versus a quantitative genetics analysis will be similar. However, if these mathematical prerequisites are not met (as probably occurs in many biologically plausible situations), then their respective equilibrium predictions may be substantially different. Finally, an empirical strategy is proposed for detecting and quantifying the roles of adaptation and constraint in maintaining equilibrium populations.

There is another distinction between game-theory/optimization and quantitative-genetics approaches that needs mentioning. Game theory and optimization thinking may be especially useful for understanding the ecological and behavioral bases of individual fitness. In contrast, individual fitness is always input to (rather than output from) quantitative-genetics analyses (Mangel & Ludwig 1992). That is, quantitative genetics does not provide a framework for predicting individual fitness functions or selection gradients from ecological and behavioral first principles (although it provides methods for measuring such fitness inputs). Quantitative-genetics methods do, however, provide powerful means for deducing evolutionary constraints and for examining the evolutionary consequences of natural selection. Still, the time horizon over which quantitative-genetics estimates remain accurate is not certain (Turelli 1988), whereas there is some evidence that optimization approaches provide reasonably good predictions of evolutionary patterns over very long time scales (e.g., Charnov 1993). This suggests that optimization, game-theory, and quantitative-genetics approaches all have important roles to play in the development of a more complete understanding of evolution by natural selection.

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