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Adaptive dynamics: Neither *F* nor *G*

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ABSTRACT

Most recent models of phenotypic evolution make similar assumptions about the dynamics of traits and of populations. Traits in these models change at a rate proportional to the slope of the individual's fitness function. However, several different assumptions have been made about other aspects of the evolutionary process, including ecological stability and sympatric speciation. This article argues that a method (the '*G*-function approach' of Cohen *et al*., 1999) that assumes ecological stability and unlimited invasion or sympatric speciation may often not apply to biological communities. For sexual populations, evolutionarily stable trait values that minimize fitness are often a potential result of adaptive evolution.

Keywords: adaptive dynamics, evolutionarily stable strategy, fitness minimum, *G*-function, phenotypic models of evolution, stability.

INTRODUCTION

In a recent article in this journal, Cohen *et al*. (1999) have argued that a simplified method of modelling phenotypic evolution espoused by Vincent and co-authors (Brown and Vincent, 1987a,b; Vincent *et al*., 1993, 1996) is preferable to other related methods. They label their approach the '*G*-function approach' and argue that some of the related methods for simplified modelling of phenotypic evolution have predicted phenomena that could not be brought about by evolution. This article corrects some of the errors made by Cohen *et al*. (1999) in their description of previous work, and disputes their conclusions regarding the impossibility of evolutionarily stable points where fitness is minimized. Some of the disadvantages of the *G*-function approach are outlined.

INCORRECT CLAIMS BY COHEN AND CO-WORKERS (1999) ABOUT PREVIOUS WORK

1. Methods other than the *G*-function method assume that there is no genetic variation. On p. 924: *Abrams et al. (1993b), among others, assume that 'there is no phenotypic* (*or genotypic*) *variation on the strategy'.* The models in Abrams *et al*. (1993b), as well as those in all of the other papers referred to preceding this quotation, incorporate genetic variation,

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without which evolution would not occur. What is assumed by Abrams *et al*. (1993b) is that the additive genetic variance of the trait is small relative to the variance of the fitness function; this justifies the Taylor series approximation that underlies Abrams and co-workers' (1993b) equation for the dynamics of traits. Abrams *et al*. (1993a,b) show that the approximation is often good even when this assumption of small variance is violated. The same assumption of a small variance underlies the gradient dynamics equation that is used by Cohen *et al*. (1999), that is, their equation (3).

2. Fitness minima will not be observed in populations with genetic variation. On pp. 924–925: '*Because an evolutionarily stable minimum is . . . not invasion-resistant, the tiniest amount of heritable variation within the population will lead to an escape from the convergent-stable minimum point on the adaptive landscape*'. As noted above, analyses that have described stable fitness minima when fitnesses are frequency-dependent (e.g. Abrams *et al*., 1993b; Abrams and Matsuda, 1996, 1997; Taylor and Day, 1997) have all had genetic variation, just like any other model of evolution. What allows invasion of evolutionarily stable minima in the models of Cohen *et al*. (1999) has nothing to do with genetic variation. Instead, whenever such an equilibrium occurs, they introduce a new species with the same fitness function as the original species, but with independent evolution. This can only occur if there are an unlimited number of distinct potential invading species or if such an equilibrium automatically leads to sympatric speciation. In the models of Geritz *et al*. (1997), reproduction is explicitly assumed to be asexual, so new mutant types are automatically independently evolving lineages, and fitness minima often do not persist. However, if the species is sexual, if the trait is polygenic and if mating is not strongly assortative, then fitness-minimizing traits are often dynamically stable and persistent (Abrams *et al*., 1993b; Abrams and Matsuda, 1996, 1997; Taylor and Day, 1997). A sexual population may evolve to become dimorphic after arriving at such a fitness-minimizing equilibrium under some circumstances. Kisdi and Geritz (1999) have shown that this can happen with single locus diploid determination of habitat use under some conditions. Dieckmann and Doebeli (1999) have shown that dimorphism can arise in a sexual population with continuous trait variation if cost-free assortative mating can evolve. However, we do not currently know the range of conditions under which such outcomes will occur in natural systems, where assortative mating is likely to have costs and ecologically important traits are frequently polygenic. Abrams and Matsuda (1996) show that a fitness-minimizing equilibrium in one of two species may be maintained by adaptive evolution of an interacting species. Such points may be stable even when reproduction in the focal species is asexual.

3. Other methods for modelling adaptive dynamics on a phenotypic level assume that evolutionary change is much slower than population dynamics. On p. 924: *Abrams et al. (1993b) and others assume 'the dynamics of evolution is much slower than the dynamics of population sizes'*. This is simply incorrect. Abrams (1997, 1999) and Abrams and Matsuda (1996, 1997) explicitly argue against methods that make this assumption, and show how the relative evolutionary rates of different species can have a huge effect on the phenotypic results of the co-evolutionary process. On the other hand, Cohen *et al*. (1999) explicitly assume that evolution is always very slow relative to population dynamics.

4. Other methods do not take into account the effects of population dynamics on adaptive evolution. On p. 928: *Abrams et al. (1993b), among others, use an 'individual fitness approach' to studying co-evolution, which Cohen et al. (1999) label an 'F-function approach'. Their definition of this approach is that it 'considers only strategy dynamics in terms of*

fitness functions'. The remainder of p. 928 and the following page explain this definition. According to that explanation, the approach of Abrams et al. assumes either that population sizes are constant or have no effects on fitness, or that population dynamics have no effect on evolutionary dynamics. Independence of population and evolutionary dynamics is neither claimed nor assumed by Abrams *et al*. (1993b). That paper does present some examples where some populations are assumed to be constant, only as a means of simplifying the explanation of methods. However, Abrams *et al*. (1993b) do not recommend assuming that all populations are constant, or that evolutionary dynamics are independent of population dynamics, and no such assumptions are made in applications of those methods in subsequent papers (e.g. Matsuda and Abrams, 1994a,b; Matsuda *et al*., 1994; Abrams, 1995, 1997, 1999; Abrams and Matsuda, 1996, 1997; Abrams and Kawecki, 1999). The same is true of many other models of adaptive change (e.g. Dieckmann and Law, 1996; Geritz *et al*., 1997; Taylor and Day, 1997). Contrary to what Cohen *et al*. (1999, p. 931) claim, Abrams *et al*. (1993b) do not recommend ignoring population dynamics in determining evolutionary stability. In many subsequent models (e.g. Abrams, 1997; Abrams and Matsuda, 1997), the interaction of population and evolutionary dynamics leads to instability. On the other hand, it is important to note that population size and fitness can be de-coupled in some biological scenarios (Abrams, 1987), so examples in which evolution occurs in spite of a constant population size are not internally contradictory.

5. Other methods have incorrectly predicted evolutionarily unstable fitness maxima. On p. 939: *Re-analysis of the examples given by Abrams et al.* (*1993b*) *'indicated that they do not yield evolutionarily stable minima or evolutionarily unstable maxima'.* The minima have been discussed above. Cohen's argument against the unstable maxima is that evolution will proceed away from such points, so populations will not be observed occupying such points. This is in fact the same point made in Abrams *et al*. (1993b).

DISADVANTAGES OF THE *G*-FUNCTION APPROACH

Cohen *et al*. (1999) invent a method called the '*F*-function' approach, or 'individual fitness approach'. They then attribute a set of assumptions to this approach, and claim that others have made these assumptions. This is not the case; their *F*-function approach is a straw man. The basic population and trait dynamics and fitness functions assumed in recent versions of the *G*-function approach are no different from those used by the authors they criticize. The difference lies in assumptions about stability of equilibria, time scales of population and evolutionary dynamics, and ease of sympatric speciation. All of these differences are empirical questions for which no simple assumption will describe all biological communities. The goal of models is not to identify an evolutionary endpoint that will occur in some idealized and unlikely circumstances, but rather to understand what does happen in real biological communities. Three specific assumptions of the *G*-function approach are likely to make it inappropriate for understanding many biological communities:

1. The approach assumes that sympatric speciation or invasion by a similar, but independently reproducing, species occurs whenever there is disruptive selection at an equilibrium of their trait dynamics equation (3) (Cohen *et al*., 1999, p. 928). Although some scenarios for sympatric speciation have been proposed, and some potential examples have been identified, there is no evidence that this assumption is justified. Major differences in species number in similar ecological circumstances argue against such an assumption,

or the assumption of an unlimited pool of potential invading species (Abrams, 1981; many articles cited in Ricklefs and Schluter, 1993).

2. The approach assumes that population dynamics is always much faster than evolutionary dynamics, in spite of evidence to the contrary (Thompson, 1998). Evolution is probably considerably slower than population dynamics in most cases, but a universal assumption is not justified. Cohen *et al*. (1999) require a huge difference in time scales because they assume that population densities are always at the equilibrium value determined by trait values.

3. The approach assumes that the ecological interaction reaches a stable equilibrium point, in spite of abundant evidence of persistent fluctuations in biological systems (Ellner and Turchin, 1995). The assumption of Cohen *et al*. (1999) that population dynamics are always stable, while evolutionary dynamics need not be, is inconsistent. Evolutionary cycles (which are possible in a difference equation model with one species or a differential equation model with two or more species) usually drive cycles in population dynamics (Abrams and Matsuda, 1996). Moreover, there can be alternative attractors in the dynamic system of traits and populations (Abrams, 1999).

It may be useful to know what biological communities would look like if unlimited sympatric speciation occurred, if population densities were always close to an equilibrium determined by current trait values, or if ecological interactions were always stable. However, these limiting cases can be addressed by simply adding species or choosing appropriate parameter values in methods that are grounded in population genetics and that do not make specific assumptions about invasions or parameter values (e.g. Abrams *et al*., 1993b). There does not seem to be any value in combining many independent limiting assumptions and suggesting that the resulting combination of assumptions should be regarded as universal. In addition, there is at least one other important disadvantage of the *G*-function approach; because it is not derived from genetic principles, it is not straightforward to determine when particular genetic mechanisms are consistent or inconsistent with this approach.

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