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Does the *G*-function deserve an *F*?

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INTRODUCTION

In his reply to a recent paper of ours (Cohen *et al*., 1999), Abrams (2001) claims errors and weaknesses in the fitness-generating (*G*-function) approach to modelling evolutionary games. Specifically, he claims that the *G*-function concept requires: (1) speciation on demand at evolutionarily stable points; (2) slow evolutionary dynamics (on the strategies u) relative to fast population dynamics (on the populations x); and (3) stable population dynamics. His claims result from a misinterpretation of our work. None of these items are requirements. Finally, Abrams (2001) states that the *G*-function approach and the individual fitness function (F) approach are not different, since they result in the same dynamics. Indeed, both approaches must result in the same dynamics for a set of given circumstances. However, one of the main advantages of the *G*-function is that one need not specify the specific circumstances *a priori*.

THE MAIN POINTS OF OUR PAPER

We incorporated the various definitions of stability (convergence, m and δ) into a single definition of evolutionarily stable strategy (ESS). The definition includes both convergence stability and resistance to invasion by rare, alternative strategies. We expanded the formal conditions for convergence stability to explicitly include population size and the coupling between x and u dynamics (term C in our equation 10). In their derivation of convergence stability, Abrams *et al*. (1993b) restricted themselves to non-explicit population dynamics that allows for term C.

Evolutionarily stable minima, a significant discovery of Abrams *et al*. (1993b), are convergent-stable yet not resistant to invasion. Stable minima invite modelling of adaptive speciation (Brown and Pavlovic, 1992; Mészena and Czibula, 1997; Dieckmann and Doebeli, 1999; Kisdi and Geritz, 1999). However, adaptive speciation at such minima is an empirical issue. We suggest that such speciation is likely. The *G*-function approach allows for speciation but does not require it. If an evolving population (coupled dynamics

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of x and u) settles to an evolutionarily stable minimum, it can stay there indefinitely only if speciation or invasion by a different species does not occur. The *G*-function becomes a fitness function only when the virtual strategy (v in our vernacular) is replaced by a specific strategy value u. In other words, if an invader perturbs a convergent-stable system, in terms of the *G*-function approach, it simultaneously creates a new system with two more state variables for its population density and strategy.

Some developments of the condition for convergence stability have incorporated explicitly or implicitly (Abrams *et al.*, 1993a; Metz *et al.*, 1996; Geritz *et al.*, 1998) an assumption of slow evolutionary dynamics. Hence, in our formulation we simply ask: 'What is the criterion for convergence stability with fast x-dynamics (compared to u)?' Generically, our approach does not require this. The original proof of the strategy dynamics requires no assumption about evolutionary speed; see equation (38) in Vincent *et al.* (1993).

Of course, G and F can boil down to the same function under certain conditions (Cohen *et al.*, 1999). When formulated correctly (which includes a clear distinction between the fitness consequences of one's own strategy and the consequences of the strategies of others in the population), most fitness formulations for evolutionary games with continuous strategies are special cases of a more general *G*-function. Lawlor and Maynard Smith (1976) and Auslander *et al.* (1978) provide early examples of continuous evolutionary games. However, in these games and others (including that of Abrams) not using a *G*-function, the modeller is forced to fix the dimensionality of the problem in terms of extant strategies and the number of independently evolving populations or species. Selecting the 'wrong' dimensionality for the model system will not reveal the ESS, or other points that vary in terms of convergence stability and resistance to invasion. The explicit formulation of a *G*-function allows for any dimensionality of the evolving system in terms of resident strategies and evolving populations. It also makes transparent the sources of frequency- and density-dependent selection, eases the task of finding the ESSs, ensures that the modeller uses the correct fitness gradient, and allows for easy definition and evaluation of the adaptive landscape.

THE *G*-FUNCTION: A SIMPLIFICATION AND A CONCEPT

The *G*-function is a concept that does not require stability of either the population or strategy dynamics. Nor does it require slow evolutionary and fast population dynamics. We have developed the *G*-function as a concept in which the definitions and formalism are all stated explicitly. It has a firm mathematical foundation and has proven to be *simple to use* when applied to a variety of evolutionary issues. These are its strengths:

- One can readily determine the number of co-existing species that emerge from the ESS solution.
- The concept of adaptive landscape and how it changes over time emerges from the evolutionary dynamics precisely because of the *G*-function approach (see fig. 5 in Cohen *et al.*, 1999).
- The *G*-function has allowed us to apply a unified approach to topics such as: co-evolution and diversity of prey and predator systems (Brown and Pavlovic, 1992), species diversity under competition (Brown and Vincent, 1987; Vincent *et al.*, 1993; Cohen and Vincent, 1997; Cohen *et al.*, 1999), matrix games (Vincent and Brown, 1988; Vincent

and Cressman, in press), the link between evolution and ecosystem processes (Cohen *et al.*, 2000), non-point equilibrium dynamics (Vincent and Brown, 1987), life-history evolution, vector-valued strategies and spatial evolutionary dynamics.

The last 10 years has seen gratifying strides in the scope and formal detail of evolutionary game theory. We owe much to the work of Peter Abrams and others cited in Cohen *et al.* (1999). We look forward to many new exciting developments, refinements and breakthroughs.

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