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Letter to Editor

## A comment on "Towards a rigorous framework for studying 2-player continuous games" by Shade T. Shutters, Journal of Theoretical Biology 321, 40–43, 2013



Continuous evolutionary games are generalisations of games with a finite or discrete set of strategies to games with infinitely many, continuously varying strategies (e.g., Mar and St. Denis, 1994; Doebeli and Knowlton, 1998; Day and Taylor, 1998; Killingback et al., 1999; Wahl and Nowak, 1999; Ahmed and Elgazaar, 2000; Killingback and Doebeli, 2002; Doebeli et al., 2004; Cressman and Hofbauer, 2005; André and Day, 2007; McGill and Brown, 2007; Killingback et al., 2010). A recent paper, Shutters (2013), claims that earlier treatments of continuous games were "confusing" and based on "misconceptions" that led to "misclassifications". These claims seem to be based on a misunderstanding of earlier work and, in particular, of one of our papers (Doebeli et al., 2004, which was identified as DHK in Shutters (2013)).

In continuous games, the strategy of an individual is given by the cooperative investment *x*, a quantitative trait that can vary continuously in an interval of positive real numbers. In DHK, we further assumed that continuous games are defined by two functions, the benefit function *B* and the cost function *C*. For example, in analogy with widely used parameterizations of the Prisoner's Dilemma game in terms of costs and benefits, one can assume that the payoff of an individuals with trait x playing against an individual with trait y is given by B(y)-C(x). We termed this continuous analogue the "Continuous Prisoner's Dilemma game". Similarly, benefits could accrue from investments of both interacting players, such that the payoff to the x-individual in an (x-y)-interaction is P(x, y) = B(x+y) - C(x). In analogy to parameterizations of the conventional Snowdrift game, we gave the resulting continuous game the name "Continuous Snowdrift game".

Clearly, for two distinct trait values *x* and *y*, the Continuous Snowdrift game turns into a standard  $2 \times 2$ -game with a payoff matrix whose entries are determined by the cost and benefit functions, evaluated at *x*, *y*, and *x*+*y*, respectively. The nature of this standard  $2 \times 2$ -game depends on the parameter values defining the cost and benefit functions, as well as on the traits *x* and *y*. Importantly, for the Continuous Snowdrift game the resulting standard  $2 \times 2$ -game can be of *any* type and, in particular, does not necessarily result in a standard Snowdrift game. In DHK this is explained in detail in Fig. 2, where the panels are explicitly designed to illustrate the standard games that can result from substituting given values for *x* and *y* into the Continuous Snowdrift game. More specifically, the figure legend explicitly states that "Local games between strategies in the vicinity of the singular point can be of any type."

In fact, this dependence of the standard  $2 \times 2$ -game resulting from substituting particular values of *x* and *y* into the Continuous

Snowdrift game is essential for the results reported in DHK, because evolution of the trait *x* is generated by games between "residents *x*" and nearby "mutants *y*". In the case of evolutionary branching, initially such games are dominance games, which lead to directional evolution towards the branching point. However, in the vicinity of the branching point,  $x^*$ , when the resident is on one side of the branching point and the mutant is on the other side, the interactions turn into standard Snowdrift games, leading to coexistence of two traits, so that the population becomes polymorphic and consists of two branches with different trait values. Subsequently, in each trait branch evolution is again driven by dominance games, leading to evolutionary divergence of the two branches, and eventually ending in coexistence of two very distinct traits playing a standard Snowdrift game against each other. Thus, in the course of evolution of the trait *x*, various types of games are being played, and this is essential for the evolutionary dynamics.

Shutters (2013) attempts to classify continuous games by deriving the  $2 \times 2$ -game based on the payoff functions evaluated at the boundaries of the continuous trait x (i.e., by considering the payoff matrix at the traits x = "full cooperation" and y = "full defection"). Based on this. Shutters (2013) for example concludes that it is clear that in scenario D (DHK, Fig. 1) cooperation evolves to zero, because the game between full cooperation and full defection corresponds to a Prisoner's Dilemma. However, this method of classifying continuous games is invalid, as the following example shows. Consider the benefit and cost functions B(z) = $b_2z^2+b_1z$  and  $C(z)=c_2z^2+c_1z$  as in DHK, but with coefficients  $b_2=1$ ,  $b_1 = 2$ ,  $c_2 = 5$ , and  $c_1 = 1$ . The game between full cooperators (x = 1) and full defectors (y=0) is again a Prisoner's Dilemma and defection dominates (P(1, 1)=2, P(1, 0)=-3, P(0, 1)=3 and P(0, 1)=30)=0, where P(x, y) denotes the payoff of the trait x against trait y). Hence, according to the scheme proposed in Shutters (2013), it should follow that cooperation evolves to zero in this continuous game. However, it is easy to see that the selection gradient in the continuous game is positive for small x, and that the adaptive dynamics has a convergent stable and evolutionarily stable singular strategy at  $x^* = 1/6$ , and hence cooperation is maintained at intermediate levels.

In fact, any attempt to map the evolutionary dynamics of continuous games to discrete  $2 \times 2$ -games is bound to fail, because what matters for the evolution of continuous cooperative traits are the games played between residents and nearby mutants, and the nature of such games may change as a result of the evolutionary process. In particular, the game that full cooperators play against full defectors is of little importance – unless the two types emerge through evolutionary branching. It was precisely for this reason that we defined the continuous analogues of the Snowdrift game and the Prisoner's Dilemma game not through the ranking of their payoffs, but based on whether or not actors obtain (part of) the benefits they generate.

In DHK, we gave names to mathematically well-defined situations, and chose to do that in analogy with parameterizations of well-established  $2 \times 2$ -games. We extended our analysis to *N*-person games in both the Supplementary Material of Doebeli et al. (2004) and Killingback et al. (2010), where we introduced the Continuous Public Goods game and the Continuous Tragedy of the Commons in much the same spirit. Perhaps other authors would have alternative suggestions for naming these continuous games, but such naming issues are ultimately a matter of semantics.

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Michael Doebeli\* Department of Zoology, University of British Columbia, Vancouver, Canada Department of Mathematics, University of British Columbia, Vancouver, Canada E-mail address: doebeli@zoology.ubc.ca

Christoph Hauert Department of Mathematics, University of British Columbia, Vancouver, Canada

Timothy Killingback Department of Mathematics, University of Massachusetts, Boston, USA

<sup>\*</sup> Corresponding author at: Department of Zoology, University of British Columbia, Vancouver, Canada. Tel.: +1 604 822 3326; fax: +1 604 822 2416.