Journal of Theoretical Biology 396 (2016) 25–41

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Evolutionary dynamics of a smoothed war of attrition game

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HIGHLIGHTS

- Formulation of a new game theory model to describe the War of Attrition when there are errors in the implementation of an individuals strategy and possibly non-linear costs.
- Detailed study of the evolutionary dynamics of the model, both analytically using adaptive dynamics and through individual-based simulations.
- Complex and subtle evolutionary outcomes can readily arise in this model which are quite different from those that occur in the classical War of Attrition model.

ARTICLE INFO

Article history:
Received 17 July 2014
Received in revised form
6 February 2016
Accepted 10 February 2016
Available online 20 February 2016

Keywords:
War of Attrition
Evolutionary game theory
Continuous strategy games
Adaptive dynamics
Spatial games

ABSTRACT

In evolutionary game theory the War of Attrition game is intended to model animal contests which are decided by non-aggressive behavior, such as the length of time that a participant will persist in the contest. The classical War of Attrition game assumes that no errors are made in the implementation of an animal's strategy. However, it is inevitable in reality that such errors must sometimes occur. Here we introduce an extension of the classical War of Attrition game which includes the effect of errors in the implementation of an individual's strategy. This extension of the classical game has the important feature that the payoff is continuous, and as a consequence admits evolutionary behavior that is fundamentally different from that possible in the original game. We study the evolutionary dynamics of this new game in well-mixed populations both analytically using adaptive dynamics and through individual-based simulations, and show that there are a variety of possible outcomes, including simple monomorphic or dimorphic configurations which are evolutionarily stable and cannot occur in the classical War of Attrition game. In addition, we study the evolutionary dynamics of this extended game in a variety of spatially and socially structured populations, as represented by different complex network topologies, and show that similar outcomes can also occur in these situations.

1. Introduction

Evolutionary game theory was introduced into biology over 40 years ago and in that time it has become a fundamental theoretical framework for studying the evolution of frequency dependent systems (Maynard Smith and Price, 1973; Maynard Smith, 1974, 1982; Hofbauer and Sigmund, 1998; Nowak, 2006). Evolutionary game theory has been applied in a wide variety of situations in biology, and also to an increasing extent in economics and the social sciences. The theory has shed light on many fundamental problems in biology including the evolution of cooperation (Axelrod and Hamilton, 1981; Axelrod, 1985), animal conflicts (Maynard Smith and Price, 1973; Maynard Smith, 1982), the evolution of sex ratios (Hamilton, 1967), and the origin of anisogamy (Parker et al., 1972). More recently, evolutionary game theory has been applied to understand the evolution of systems with non-transitive interactions (Sinervo and Lively, 1996; Kerr et al., 2002; Kirkup and Riley, 2004).

It is rather remarkable that three of the simplest discrete strategy games, the Prisoners Dilemma game (Axelrod and Hamilton, 1981; Axelrod, 1985), the Hawk–Dove (or Snowdrift) game (Maynard Smith and Price, 1973; Maynard Smith, 1974, 1982), and the Rock–Paper–Scissors game (Maynard Smith, 1982; Hofbauer and Sigmund, 1998; Schreiber and Killingback, 2013) have all been applied to study important biological problems, namely the evolution of cooperation (Axelrod and Hamilton, 1981; Axelrod, 1985), the evolution of animal contests (Maynard Smith

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http://dx.doi.org/10.1016/j.jtbi.2016.02.014
0022-5193/

and Price, 1973; Maynard Smith, 1982), and the evolutionary dynamics of non-transitive interactions (Sinervo and Lively, 1996; Kerr et al., 2002; Kirkup and Riley, 2004).

The Prisoners Dilemma, Hawk–Dove, and Rock–Paper–Scissor games are all examples of discrete strategy games. In contrast to these cases, the game theory framework appropriate for analyzing biological problems such as the evolution of sex ratios (Hamilton, 1967) or the evolution of anisogamy (Parker et al., 1972) naturally involves continuous strategy games. Continuous strategy versions of the Prisoners Dilemma (Killingback and Doebeli, 2002), Snowdrift (Doebeli et al., 2004), and related games (Killingback et al., 2010) have also been studied. One of the most important examples of a continuous strategy game in biology is the War of Attrition (Maynard Smith and Price, 1973; Maynard Smith, 1974; Bishop and Cannings, 1978; Bishop et al., 1978; Maynard Smith, 1982; Ydenberg et al., 1988).

In evolutionary game theory, the War of Attrition (WoA) game, as originally formulated by Maynard Smith and Price (1973) and Maynard Smith (1974, 1982) is used to model animal contests in which the outcome is decided by conventional behavior (such as displaying) and there is no asymmetry between the participants that can be used to rapidly settle the contest. It is assumed that the two contestants in the game compete for a resource of value V, by which we mean that the Darwinian fitness of the individual who wins the contest and secures the resource is increased by V. The strategy available to an individual in such a contest is a non-negative real number that specifies the length of time for which the contestant will display, given that the one that persists the longest wins the resource (and thus terminates the contest) and that each contestant bears a cost proportional to the length of the contest. It is clear that under these assumptions there can be no pure evolutionarily stable strategy (ESS). It is simple to show that the mixed strategy in which the probability that an individual displays for time x is determined by the probability density function

$$p(x) = \frac{1}{V}e^{-\frac{x}{V}} \tag{1}$$

is stable against invasion by any pure strategy (Maynard Smith and Price, 1973; Maynard Smith, 1974, 1982). Furthermore, it may be shown that the mixed strategy defined by (1) is stable against invasion by any mixed strategy and that this strategy is the unique ESS in this game (Bishop and Cannings, 1978). It follows from (1) that the distribution of contest lengths in the game is $P(x) = \frac{2}{V}e^{-\frac{2x}{V}}$ (Parker and Thompson, 1980; Maynard Smith, 1982). Thus, the duration of contests in the WoA game are exponentially distributed, with mean equal to $\frac{V}{2}$.

The WoA game has been studied as a model of empirical contests for a number of organisms, including: dung flies (*Scathophaga stercoraria*) (Parker 1970a,b; Parker and Thompson, 1980) and damselflies (Odonata: Zygoptera) (Crowley et al., 1988; Marden and Waage, 1990; Marden and Rollins, 1994). The use of the WoA game to model empirical animal contests has been reviewed in Riechert et al. (1998).

It is the purpose of this paper to introduce a variant of the classical WoA game, which extends the original model in two realistic and important ways. The first is to include the effect of errors in the strategies that are implemented by the participants in a contest. It is inevitable that errors will sometimes occur when strategies are implemented in any realistic process, and it is important to understand the effect that such errors will have on the evolutionary outcome of contests. The second extension is to allow for the cost associated with a particular strategy to be a possibly non-linear function of the strategy (Norman et al., 1977; Bishop and Cannings, 1978).

The classical WoA game is based on the fundamentally unrealistic assumption that the payoff is a discontinuous function of the investments made by the two contestants. This assumption violates the key principle that in an evolutionary system a small change in the individuals' traits should only result in a small change in their fitnesses – that is, the assumption of a discontinuous payoff function in the classical WoA violates the "Continuity Tenet" (Meszéna, 2005). We show here that the result of including the effect of errors is to replace the classical WoA game, with its discontinuous payoff function, with a new game having a continuous payoff function – that is, the inclusion of errors results in a new variant of the WoA game which satisfies the Continuity Tenet. It follows as a consequence of this new model having a continuous payoff function that it admits evolutionary outcomes that are quite different from, and in many respects simpler to, those that occur in the classical WoA game. In particular, it is possible for this new game to have simple monomorphic or dimorphic configurations which are evolutionarily stable. Here we formulate this new model and study its evolutionary dynamics in some detail using the technology of deterministic adaptive dynamics. We also investigate the evolutionary dynamics of this model in both well-mixed and structured populations (with the latter represented by complex networks) using individual-based simulations.

It is also interesting to note a possible non-biological application of this work. The classical WoA game can be viewed as an *auction* – it is an example of an all-pay, second-price auction (Rose, 1978; Haigh and Rose, 1980; Krishna and Morgan, 1997; Chatterjee et al., 2012). Thus, the extension of the WoA that we consider here can be considered as modeling an auction of this type when errors may occur in the bid levels and there are possibly non-linear costs. The evolutionary dynamics of such auctions may possibly have interesting applications in economics.

2. The smoothed war of attrition game

Consider first the classical WoA game in which two individuals are competing for a resource of value V (Maynard Smith and Price, 1973; Maynard Smith, 1974; Bishop and Cannings, 1978; Maynard Smith, 1982). The strategies of the two individuals, x and y, respectively, are the investments they make to obtain the resource (e.g., their persistence times). The payoff structure of the game is determined as follows. If $x > y$, then the x-strategist obtains the resource and incurs a cost cy (where c is a constant of proportionality determining the cost of a given level of investment), while the y-strategist does not get the resource but incurs the same cost. If $x < y$, then the y-strategist obtains the resource and incurs a cost cx, while the x-strategist incurs the same cost but does not get the resource. Finally, if $x = y$, then each contestant has an equal probability of obtaining the resource, and both incur a cost cx.

The payoff in the WoA game to an x-strategist interacting with a y-strategist is therefore given by

$$P(x, y) = V\Theta(x - y) - c \cdot \min(x, y), \tag{2}$$

where $\Theta(u)$ is the Heaviside step function

$$\Theta(u) = \begin{cases} 0 & \text{if } u < 0 \\ \frac{1}{2} & \text{if } u = 0 \\ 1 & \text{if } u > 0. \end{cases} \tag{3}$$

As mentioned above, the classical WoA game defined by (2) has no pure ESS and the unique ESS is the continuous mixed strategy defined by the probability distribution (1).

In general, there is no reason for the cost to be a linear function of the investment (Sibly and McFarland, 1976), and an immediate generalization of the WoA game is obtained by allowing the payoff