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# Truncation selection and payoff distributions applied to the replicator equation

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## HIGHLIGHTS

- Assumptions of mean payoffs and proportional selection are relaxed.
- Truncation selection is analyzed for replicator dynamics.
- The stable states of truncation selection and the RE coincide for constant variance.
- If all payoff variances are not equal, then cooperation can be stable.

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## ABSTRACT

The replicator equation has been frequently used in the theoretical literature to explain a diverse array of biological phenomena. However, it makes several simplifying assumptions, namely complete mixing, an infinite population, asexual reproduction, proportional selection, and mean payoffs. Here, we relax the conditions of mean payoffs and proportional selection by incorporating payoff distributions and truncation selection into extensions of the replicator equation and agent-based models. In truncation selection, replicators with fitnesses above a threshold survive. The reproduction rate is equal for all survivors and is sufficient to replace the replicators that did not survive. We distinguish between two types of truncation: independent and dependent with respect to the fitness threshold. If the payoff variances from all strategy pairing are the same, then we recover the replicator equation from the independent truncation equation. However, if all payoff variances are not equal, then any boundary fixed point can be made stable (or unstable) if only the fitness threshold is chosen appropriately. We observed transient and complex dynamics in our models, which are not observed in replicator equations incorporating the same games. We conclude that the assumptions of mean payoffs and proportional selection in the replicator equation significantly impact replicator dynamics.

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## 1. Introduction

The range of applications of evolutionary dynamics is great, and includes fields such as animal behaviour (Dugatkin and Reeve, 1998) to economics (Dopfer, 2005; Friedman, 1991, 1998). Introduced in Maynard Smith (1982), evolutionary game theory has bloomed in the last few decades as a means of explaining biological phenomena (Hammerstein et al., 1994; Hofbauer and Sigmund, 2003; Nowak and Sigmund, 2004). Examples of evolutionary dynamics include Brown–von Neumann–Nash, imitation, best response, and replicator dynamics (Hofbauer and Sigmund,

2003). In particular, replicator dynamics is immensely important, with applications that span such fields as genetics, ecology, chemistry, and sociology (Schuster and Sigmund, 1983).

Replicators are the focus of replicator dynamics. They are agents that can replicate themselves with, potentially, mutations. The evolutionary dynamics determine the change in frequencies of these agents over time. Commonly, we envisage this process as selection of replicators for survival and reproduction. ‘Fit’ replicators survive to reproduce, which determines the replicator frequencies in the next generation. The replicator equation is frequently used in this framework to model the frequency dynamics of replicators due to proportional selection, where the increase in frequencies of replicators is proportional to the difference between their fitness and the average fitness of the population (Taylor and Jonker, 1978).

The replicator equation makes several assumptions: the

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population is infinite; if the elements of the payoff matrix are stochastic, the replicators earn the mean payoffs; each replicator interacts with every other replicator non-preferentially; and selection is proportional. Much work has explored relaxations of these assumptions with other replicator dynamics, and development of further evolutionary stability concepts (Nowak and Sigmund, 2004; Ohtsuki and Nowak, 2008). Examples include finite populations (Taylor et al., 2004), heterogeneity (Bergstrom and Godfrey-Smith, 1998), networks (Roca et al., 2009; Szabó and Fath, 2007), and stochasticity (Traulsen et al., 2006).

Other selection methods have been employed in the literature (Bäck et al., 2000; Blickle and Thiele, 1995; Ficici et al., 2000). In truncation selection, after players have interacted, we rank the players from highest to lowest fitness, and a top fraction of the population survives to reproduce. The reproduction rates are equal for all survivors. The population is then normalized. The key differences between this method and proportional selection are that survival is dependent upon meeting a threshold fitness, that the reproduction rate is identical for all surviving players. In proportional selection, reproduction rates are proportional to the difference between the fitness of a player and the average fitness of the population. This selection method is important in biology where thresholds for survival exist, and because survival (and often reproduction) are binary events (they either happen or they do not). In truncation selection, selection pressure is near the threshold for survival and reproduction, and thus selection pressure is weaker at the extreme high end of the fitness distribution; the system is not selecting for excellence, but for adequacy.

Agent-based round-robin simulations have suggested that the ESS is not a useful concept in biology when truncation selection is used (Fogel et al., 1998; Fogel and Fogel, 2011). Oscillations and apparent chaos may occur in such games, where the ESS predicts no such phenomena. Further, the average population frequencies are significantly different from the ESS. The difference between these results and the ESS are due to selection at the extreme lower ends of the payoff distributions of each replicator (caused by stochastic elements of the agent-based models). Thus, the discrepancy is due to asymmetric selection pressures on either side of the ESS (Ficici et al., 2005; Ficici and Pollack, 2007).

The primary objective of our paper is to explore how relaxing simplifying assumptions of the classic replicator equation — namely, relaxing mean payoffs and proportional selection in favour of payoff distributions and truncation selection, respectively — influence replicator dynamics and the corresponding evolutionary stable states (ESSes). The assumptions made in the replicator equation are for mathematical tractability. However, in modelling biological systems, we should be wary of an axiomatic approach that rests on such assumptions (Gintis, 2009; Mailath, 1998). To explore the relaxations to the mean payoff and proportional selection assumptions, we develop and analyse truncation equations and agent-based simulations.

## 2. Methods

Here we examine two assumptions of the replicator equation, namely mean payoffs and proportional selection. We will show that there are significant differences between models when both of these assumptions are altered. Focussing on the Hawk–Dove game, we will begin with a discussion of fitness distributions followed by truncation selection methods.

### 2.1. Fitness distributions

The Hawk–Dove, Prisoner's Dilemma, Stag Hunt, and harmony games (Axelrod and Hamilton, 1981; Skyrms, 2004; Sugden, 1986)

are important two player models of biological systems with a rich body of literature. In contrast to the other games, the Hawk–Dove game yields a stable interior equilibrium. We will primarily focus on the Hawk–Dove game for our examples. It is set up as follows.

The Hawk–Dove game has two strategies: hawk,  $S_h$ , and dove,  $S_d$ . Let there be a resource worth a payoff of 50 that may be gained when any two players meet. If a hawk meets a dove, the hawk receives the resource and the dove receives nothing. If, however, a hawk meets another hawk, they fight. Each having an equal chance of winning, the winner receives the resource, and the loser is wounded, receiving a negative payoff,  $-100$ . If two doves meet, they posture, attempting to intimidate each other, which has a payoff cost of  $-10$ . With probability 0.5, a dove intimidates its opponent thus receiving the resource as its opponent flees. Therefore, the average payoff is 15. The following payoff matrix represents these averages of the game:

$$A = \begin{pmatrix} a_{hh} & a_{hd} \\ a_{dh} & a_{dd} \end{pmatrix} = \begin{pmatrix} -25 & 50 \\ 0 & 15 \end{pmatrix}. \quad (1)$$

This payoff matrix is used in the Hawk–Dove replicator equation. However, notice that in same strategy pairings, no player receives these averages (e.g. between two doves, one will earn  $-10$  and the other 40). As more pairings occur, the fitness (which is the average of all the payoffs earned from the pairings) will approach this average for most players. However, there will be players that will receive much higher and much lower fitnesses.

To factor in the range of possible fitnesses that can be earned in the Hawk–Dove game, we begin with observing the fitness distributions of each strategy pair. For simplicity, we will assume that the fitnesses are normally distributed. Thus, for hawks, the mean fitness of a hawk playing a hawk is  $\mu_{hh} = -25$ , and the standard deviation is:

$$\sigma_{hh} = \sqrt{(50 - (-25))^2/2 + (-100 - (-25))^2/2} = 75. \quad (2)$$

So that we may have a normal distribution for hawks vs. doves, let us assume that doves are quicker than hawks and thus may take the resource before hawks arrive with probability 0.1. Otherwise, the hawk receives the resource as usual. Table 1 summarizes these parameter values.

Now, we may derive the fitness distribution for  $S_i$ , which is dependent upon the frequencies of hawks ( $x_h$ ) and doves ( $x_d$ ). Since we have normal distributions for all strategy pairings, we have that  $\mu_i = \mu_{ii}x_i + \mu_{ij}x_j$ , and  $\sigma_i^2 = \sigma_{ii}^2x_i^2 + \sigma_{ij}^2x_j^2$ . The fitness probability density function for  $x_i$  is thus:

$$\rho_i(\phi') = \frac{1}{\sigma_i\sqrt{2\pi}} \exp\left(-\frac{(\phi' - \mu_i)^2}{2\sigma_i^2}\right). \quad (3)$$

In Section 2.4, we introduce independent and dependent truncation, which model selection upon the fitness distribution defined by Eq. (3).

### 2.2. The replicator equation

The replicator equation is a mean field model that incorporates concepts from game theory. Replicators each have a strategy,  $S_i$ ,

**Table 1**  
Parameter values for the Hawk–Dove game.

$i, j$	$\mu_{ij}$	$\sigma_{ij}$
$h, h$	$-25$	$75$
$h, d$	$45$	$15$
$d, h$	$5$	$15$
$d, d$	$15$	$25$

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