



A unified modelling approach for producer–scrounger games in complex ecological conditions



Mohammad Afshar*, Luc-Alain Giraldeau¹

Department of Biological Sciences, University of Quebec in Montreal, Montreal, QC, Canada

ARTICLE INFO

Article history:

Received 23 April 2014

Initial acceptance 10 June 2014

Final acceptance 15 July 2014

Published online 16 September 2014

MS. number: A14-00344R

Keywords:

decision making

evolutionary game theory

frequency-dependent selection

learning rule

producer–scrounger

risk sensitivity

social foraging

Animal decision making in frequency-dependent situations, where the payoff of an action depends on the actions of others, has gained prominence in behavioural ecology and in social foraging in particular. One such situation involves cases where an animal can search for a new resource (produce) or join what others have already found (scrounge). A number of game-theoretic models have been proposed to predict the equilibrium combination of producer and scrounger strategists based on the evolutionarily stable strategy. However, each game model can only handle a few environmental parameters at a time and none address the flexible use of tactics that allows individuals to respond quickly and adaptively to changes in payoffs. In this study we propose an agent-based model using a linear operator learning rule as the decision mechanism. The model provides a unified framework from which to predict the effects on the expected equilibrium of producers and scroungers of group size, metabolic requirement, finder's advantage, food intake rate, cost of searching, cost of joining, patch encounter probability and patch richness. The simulation results replicate almost every producer–scrounger prediction and experimental result published to date such that the simulation provides a more general tool than any single game-theoretic model to predict behaviour under frequency-dependent conditions. The model furthermore allows us to develop a novel prediction about foraging behaviour in a more realistic environment of variable patch richness. By modelling the operation of a plausible decision rule, we can explore the validity of the behavioural gambit, the assumption that the unspecified decision mechanisms of game-theoretic models faithfully reproduce outcomes expected of natural selection operating over generations on fixed alternatives. We suggest that this simulation model can provide a tool for others to explore and predict the effect of more complex and hence realistic foraging conditions on individual levels of producer and scrounger use.

© 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Animals of the same species sometimes use different tactics when engaged in foraging or mate choice (Davies, Krebs, & West, 2012). The choice of tactic is generally made as a function of state and or time, and the rule that governs this choice is referred to as a strategy (e.g. for the tactics of wander or defend, the strategy might be 'if young, wander; if old, defend'; Gross, 1996; Houston & McNamara, 2005; Tomkins & Hazel, 2007). Behavioural ecologists are interested in why different tactics coexist in the same population under the same ecological conditions. One possible explanation is that none of the tactics can reach fixation because their fitnesses are negatively correlated with their frequencies in the

population: a negative frequency dependence that predicts stable mixtures of tactics (Barnard & Sibly, 1981; Beauchamp, Bélisle, & Giraldeau, 1997; Coolen, Giraldeau, & Lavoie, 2001; Giraldeau & Livoreil, 2000; Giraldeau, Soos, & Beauchamp, 1994; Maynard Smith, 1982; Morand-Ferron, Giraldeau, & Lefebvre, 2007; Mottley & Giraldeau, 2000; Wu & Giraldeau, 2005).

For more than three decades, evolutionary game theory has been the main tool used in frequency-dependent situations to predict an equilibrium mixture of tactics based on evolutionarily stable strategy (ESS) theory. ESS theory assumes that strategies (and so the equilibrium mixture of tactics) are determined by natural selection acting on genetic alternatives (Maynard Smith, 1982). It can predict the equilibrium when there are either pure or mixed strategies in the population. A pure strategy is when each individual always uses either one tactic or the other, and so does not alternate between them (Gross, 1996). It can arise because of genetic differences between individuals or environmental differences (Davies et al., 2012) or when the frequency of each strategy is

* Correspondence: M. Afshar, Department of Biological Sciences, University of Quebec in Montreal, C.P. 8888, Succursale Centre-ville, Montreal, QC H3C 3P8, Canada.

E-mail address: afshar.mohammad@courrier.uqam.ca (M. Afshar).

¹ E-mail address: giraldeau.luc-alain@uqam.ca (L.-A. Giraldeau).

set over generations by frequency-dependent selection and the population then appears dimorphic (Bergstrom & Godfrey-Smith, 1998). A mixed strategy is when each individual plays a fixed combination of different tactics so that the ESS is satisfied by the overall combination of the population (Gross, 1996; Tomkins & Hazel, 2007).

ESS theory only predicts the distributions of tactics. It however remains silent about the ways in which these distributions are realized and makes no explicit prediction as to the distribution of tactics in an infinite population accommodating anything from monomorphism, everyone uses the same mixture of tactics, to extreme polymorphism, where each individual adopts a unique combination of tactics (Bergstrom & Godfrey-Smith, 1998). This leaves some important questions about how complexity and diversity are realized within individuals and across a population. These questions have been addressed in Bergstrom and Godfrey-Smith (1998), Maynard Smith (1988) and Vickery (1987, 1988). In a finite population, only pure strategies are expected from purely deterministic dynamics and no mixed strategy can be an ESS (Vickery, 1987, 1988). However, if the frequency of one pure strategist is low at ESS, stochastic environmental fluctuations may cause its extinction. In this case, mixed strategies are favoured and can invade the population (Bergstrom & Godfrey-Smith, 1998; Maynard Smith, 1988; Orzack & Hines, 2005). Deterministic and stochastic methods can thus have different opposing predictions.

ESS theory also accommodates situations where the fixed combination of each tactic is acquired by learning. In this case it assumes that an evolutionary stable (ES) learning rule exists whose characteristics lead the population within a generation to the same equilibrium combination as would frequency-dependent selection over generations (Maynard Smith, 1982). It is unclear whether a learned equilibrium should generate a monomorphic, dimorphic or polymorphic population. Whatever the type of strategy expected at the ESS, be it pure, mixed or learned, the ESS theory approach in the context of animal behaviour suffers three important limitations that we consider in turn.

The first is that, if selection is acting on genetic alternatives, individual behaviour must be genetically fixed. Yet, in many frequency-dependent tasks, such as the producer–scrounger (PS) game, prisoner’s dilemma and ideal free distribution, behaviour does not appear genetically fixed but rather a learned ESS (Belmaker, Motro, Feldman, & Lotem, 2012; Lendvai, Barta, & Liker, 2004; Morand-Ferron & Giraldeau, 2010; Morand-Ferron, Varnnes, & Giraldeau, 2011; Morand-Ferron, Wu, & Giraldeau, 2011). Furthermore, many behavioural games are probably played several times and under different conditions within a generation (Stephens & Clements, 1998). The optimality of any tactic thus changes during an individual’s lifetime. Here, any genetically fixed mechanism may be handicapped to respond to the changes in the structure of the games. Therefore, it seems unlikely that the optimality of such a game would be fixed in merely a genetic mechanism during evolutionary timescale. The expectation that a learned ESS will always generate a combination of strategy use that corresponds to that expected from selection acting on genetic alternatives remains an untested assumption (Harley, 1981; Harley & Maynard Smith, 1983; Hines & Bishop, 1983; Maynard Smith, 1982; Tracy & Seaman, 1995), and its acceptance, what Giraldeau and Dubois (2008) described as accepting the ‘behavioural gambit’, may be incorrect (Fawcett, Hamblin, & Giraldeau, 2013; McNamara & Houston, 2009).

The second limitation of the ESS approach is its inability to deal effectively with complicated situations (Fawcett et al., 2014). For example, the possibility that ecological conditions (the frequency-dependent nature of many games and the specificities of the decision mechanism) may constrain the equilibrium that a population

can be expected to reach is also largely ignored (Fawcett et al., 2013; Grodzinski, Dor, & Lotem, 2011; McNamara & Houston, 2009). Because of the analytical complexity of solving ESS models in more realistic situations, most of these models consider conditions in which the organism is omniscient and the environment is oversimplified and often static. The predictions from these models then encourage experimentalists to test their predictions in equally simplistic and hence unrealistic conditions. This oversimplification of conditions in which frequency dependence is considered has been justly criticized for being too far removed from the world in which organisms have evolved (Fawcett et al., 2014).

Finally, behaviourists that wish to predict how individuals behave in a population cannot rely on ESS theory to predict it. This is because ESS theory only predicts the average stable mixtures of strategies across populations, not the tactic combination for each individual within a population. ESS theory remains silent concerning whether all individuals should adopt the same proportion of each tactic (monomorphism), or whether some individuals should use higher proportions of one tactic while others use lower proportions (dimorphism). If we are to predict individual behaviour it would be important, therefore, to develop a way of predicting it in situations of frequency dependence that rely on learning. Such an approach should allow us to predict individual behaviour and explore the effects of more realistic environmental conditions not only on individual tactic use, but on its expected variation among individuals within populations. A behavioural mechanism based on learning not only responds to a repeated game with changing conditions during an individual’s lifetime (Stephens & Clements, 1998), it can furthermore be used in multiple games affecting different equilibriums simultaneously.

To this end, in this study we address the first and the second limitations of ESS theory by proposing a simulation model that predicts the same population equilibrium as ESS does. This model incorporates a commonly used learning rule as the individual’s cognitive decision mechanism (Arbilly & Laland, 2014; Beauchamp, 2000; Beauchamp et al., 1997; Dridi & Lehmann, 2014; Dubois, Morand-Ferron, & Giraldeau, 2010; Hamblin & Giraldeau, 2009; Katsnelson, Motro, Feldman, & Lotem, 2012; Kurvers, Hamblin, & Giraldeau, 2012). We then tackle the second limitation by adding complexity to the environment beyond what has been possible with game-theoretic PS models and the experimental studies they generated. We use the model to bring a novel prediction about the expected effect of patch quality variance on the equilibrium use of search and join tactics.

In our simulation we assume that agents use their experience of payoffs to decide on the tactic they adopt: we assume learning. We acknowledge that the evolution and use of learning in the context of such frequency-dependent games is not straightforward. For instance, Dubois et al. (2010) showed that although learning individuals experience an initial advantage in a producer–scrounger game, they never evolve to fixation. The population is thus made up of a mixture of fixed and flexible (learning) players. Moreover, by explicitly modelling learning in a producer–scrounger game, Katsnelson et al. (2012) showed that learning can evolve to fixation but only when there is sufficient environmental fluctuations or when there is asymmetry in individual’s phenotype. Notwithstanding these difficulties concerning the origins of learning in groups, we choose to assume that our agents used learning rules to decide on tactic use, an assumption that is supported by a number of empirical studies. Learning rules, for instance, have been used in psychology, ethology and behavioural ecology for many years to model animal behaviour individually or in groups (Arbilly & Laland, 2014; Bush & Mosteller, 1951; Dridi & Lehmann, 2014; Estes, 1950; Hamblin & Giraldeau, 2009; Harley, 1981; Herrnstein, 1961; Krebs, Kacelnik, & Taylor, 1978; McNamara & Houston, 1985; Stephens,

Download English Version:

<https://daneshyari.com/en/article/2416364>

Download Persian Version:

<https://daneshyari.com/article/2416364>

[Daneshyari.com](https://daneshyari.com)