



Zebra finches scrounge more when patches vary in quality: experimental support of the linear operator learning rule



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ARTICLE INFO

Article history:

Received 10 October 2014
Initial acceptance 15 December 2014
Final acceptance 18 March 2015
Published online
MS. number: A14-00808R

Keywords:

decision making
evolutionary game theory
frequency-dependent selection
learning rule
linear operator
producer–scrounger
risk sensitivity
social foraging
Taeniopygia guttata
zebra finch

The use of evolutionary game theory and the concept of the evolutionarily stable strategy (ESS) have come under criticism lately because game-theoretic models are often constrained to overly simplistic situations. Furthermore, game-theoretic models commit the behavioural gambit, that is, they assume that individuals have some unspecified decision mechanism that duplicates the outcomes that would be expected from natural selection acting on genetic alternatives. The producer–scrounger game is an ideal illustration of the criticisms aimed at the game-theoretic approach; it has generated a number of game-theoretic models that make specific predictions for highly simplified foraging conditions. Simulation models of the producer–scrounger game that incorporate the linear operator learning rule, however, have been more successful in replicating the empirical results. In these models, groups of animals forage for patches of food using a linear operator learning rule. The linear operator model furthermore provides a new prediction about the effect of variation in patch quality within a producer–scrounger game. Current models based on evolutionarily stable strategies and empirical investigations have always assumed or used patches of uniform quality. Yet patches vary in quality and some environments are potentially more variable than others. The linear operator model predicts an increase in scrounging behaviour when patch quality varies. We tested this prediction using captive foraging flocks of male zebra finches, *Taeniopygia guttata*, in two treatments with variable and nonvariable patch quality. The results show that as individuals have more experience in the variable environment, they increase their scrounging behaviour. Linear operator models may therefore provide a general and empirically valid means of exploring the outcome of animal decisions in social foraging situations too complex to be addressed by evolutionary game models.

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Situations where the outcome of an individual's behaviour depends on the behaviour used by others commonly call for evolutionary game theory as an analytical tool (Giraldeau & Caraco, 2000; Maynard Smith, 1982). The use of evolutionary game theory and the concept of the evolutionarily stable strategy (ESS), however, have come under criticism because game-theoretic models are often constrained to overly simplistic situations that bear little resemblance to actual conditions under which the behavioural decision has evolved (Afshar & Giraldeau, 2014; Fawcett et al., 2014; Grodzinski, Dor, & Lotem, 2011). As a result, tests of these models' predictions are often conducted under equally unrealistic and oversimplified situations.

Another critique of evolutionary game theory, and of optimality in general, has been that it assumes the operation within individuals of some unspecified decision mechanism that duplicates the outcomes that would be expected from natural selection acting on genetic alternatives. It therefore commits the behavioural gambit by assuming that psychological mechanisms do not constrain the behavioural phenotypes that can evolve (Fawcett, Hamblin, & Giraldeau, 2013; Giraldeau & Dubois, 2008; McNamara & Houston, 2009). Several authors have thus argued that it would be more useful to explore the outcomes of decision mechanisms in game situations directly, rather than assume their operation and outcome (Arbilly, Motro, Feldman, & Lotem, 2011; Fawcett et al., 2013; Katsnelson, Motro, Feldman, & Lotem, 2012).

In a recent study, Afshar and Giraldeau (2014) developed a simulation model that explored the outcomes of groups of individuals using an explicit learning rule in a producer–scrounger (PS) game (Barnard & Sibly, 1981). In a PS game, individuals can obtain food by searching for a new food patch (producing) or by

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joining patches already found by others (scrounging). The game assumes that these two foraging alternatives are temporally incompatible, as is the case for animals like ground-feeding birds (Coolen, Giraldeau, & Lavoie, 2001). When the scrounger strategy is rare, it receives a higher payoff than the producer tactic. Increasing the frequency of scrounging, however, decreases everyone's payoffs. The payoff for both alternatives is therefore affected by the frequency of the scrounger strategy. ESS game-theoretic models predict a specific evolutionarily stable frequency of scrounging where the payoffs of both alternatives are equal (Giraldeau & Beauchamp, 1999). The principal question, therefore, in PS research has been to explore how environmental and individual state parameters affect this equilibrium. The PS game is an ideal illustration of the criticisms aimed at the game-theoretic approach; it has generated a number of game-theoretic models that make specific predictions for highly simplified foraging conditions (Afshar & Giraldeau, 2014). In Afshar and Giraldeau (2014), the individual chooses which tactic to express based on the matching ratio, adopting the tactics in proportion to their estimated values, at each time step. This agent-based simulation was remarkably successful in replicating almost every published prediction and experimental result concerning PS games (Afshar & Giraldeau, 2014). Given the success of their simulation, they argued that the explicit decision model was a more effective means of predicting the effect of environmental factors on PS behaviour than ESS models. They backed this claim by generating an entirely novel prediction for a situation that was too complex for the outcome to be anticipated using a conventional ESS approach. Every previous ESS model and test of PS behaviour had considered only environments of homogeneous patch quality; ignoring the effect that a mixture of patch qualities would have on PS behaviour. The Afshar and Giraldeau (2014) simulation model showed, however, that the variance in patch quality should affect the expected level of scrounging, and it predicted that increasing variance should lead to increased scrounging. Furthermore, the simulation model showed that, because individuals use learning and hence their experience to adjust their behaviour, any changes in the amount of scrounging is expected to happen gradually as individuals gain experience and the population slowly converges to a stable level of scrounging after sufficient time.

In this study we provide the first experimental test of the new expected level of scrounging to test whether this linear operator learning model represents an empirically valid way to predict the outcomes of individual decisions in complex frequency-dependent foraging conditions. We test this novel prediction using captive flocks of zebra finches, *Taeniopygia guttata*. Specifically, we ask whether increasing the degree of variance in patch quality, while keeping its mean constant, will affect the frequency of scrounging in flocks of foraging captive zebra finches.

METHODS

Study Subjects

We used zebra finches purchased from a local supplier, L'oisellerie de l'Estrie, QC, Canada. These social granivorous birds have been widely used to test predictions of PS games (Beauchamp, 2000, 2001, 2006; Biondolillo, Stamp, Woods, & Smith, 1997; David, Cézilly, & Giraldeau, 2011; David & Giraldeau, 2012; Giraldeau, Hogan, & Clinchy, 1990; Mathot & Giraldeau, 2008, 2010; Mathot, Godde, Careau, Thomas, & Giraldeau, 2009). We randomly selected 20 males from our colony of 32 males.

Before the experiments, the birds were kept in groups of three to four individuals in small home cages (29 × 5 × 38 cm) with ad libitum access to water, a mixture of vitamin-supplemented seeds, and regular access to vegetables and egg mixture. Room

temperature was maintained at 24 ± 1 °C on a 12:12 h light:dark cycle. For identification, each individual had a coloured leg ring. All the birds had previous experience with the PS game, but none had been used in an experiment for at least 1 year. We randomly assigned the birds to four flocks of five birds.

During the experiments, each bird was temporarily marked with a dab of nontoxic acrylic paint on top of the head. The colour was randomly chosen from orange, yellow, green, blue and purple with the constraint that no two birds in the same flock had the same colour. The experiment lasted 15 days for each flock, and two flocks were tested concurrently in neighbouring aviaries. The experiments were conducted from 9 July to 4 August 2013 within the animal care facility at the University du Québec à Montréal. All experimental procedures complied with the guidelines from Canadian Council for Animal Care and were approved under protocol 0313-C1-712-0314 by the UQAM committee for animal care.

During the experiment, each flock was kept in a large indoor aviary (1.5 × 3.8 × 2.3 m high) with a 12:12 h light:dark cycle (0700–1900 hours). Birds had ad libitum access to water at all times and access to a bath 1 day per week. A 1.1 × 1.15 m piece of plywood grid in which 100 wells (1.3 cm diameter and 1 cm depth) had been drilled in a grid pattern (10 × 10 cm with 10 cm central distance) was placed on the floor of each aviary. A video camera hung from the ceiling 1.9 m from floor, directly above the centre of the grid so that the image captured the whole grid surface.

Experimental Procedure

The flock was allowed two consecutive days within the aviary to familiarize themselves with their surroundings. During this time, two feeders filled with millet seeds were placed on the grid. All food was removed from the aviaries at 1800 hours on day 2. The next morning five trials were conducted for one flock at 30 min intervals starting at 0800 hours and ending at 1000 hours. Trials for the second flock were started with a 15 min delay at 0815 hours, using the same procedure.

At the beginning of a trial, the experimenter (M.A.) entered the aviary, turned on the camera, and filled six randomly chosen patches with white millet seeds. To prevent the birds from recognizing or remembering the location of the full patches on the grid, the experimenter filled six experimental patches and mimed the addition of seeds at six empty patches, visiting the 12 patches in random order. He then covered the grid with a sheet of opaque white corrugated plastic (Coroplast) before exiting the aviary. From outside the aviary, the experimenter pulled a string to slide the opaque covering off the grid. The birds then landed and searched for food on the grid. Each trial continued for 9 min, after which the experimenter entered the aviary, cleaned the grid of all food and turned off the camera.

After the last trial of the day the birds were provided with ad libitum access to food until 1800 hours, when all food was removed. This procedure was repeated from day 3 to day 8 and then again from day 10 to day 15. During day 9, the birds had no trials and were provided with ad libitum food, water and bath. Days 3 and 10, the first day of each treatment, were considered training days and no data were collected. At the end of the 15th day we returned the birds to their holding colony.

Each flock was tested in two treatments, variable and non-variable patch richness. In the nonvariable treatment, all six patches in each trial contained exactly 10 seeds. In the variable treatment, there were two patches for each of three richness values: 5, 10 and 15 seeds. This changed the patch richness variance from zero (in the nonvariable treatment) to 20 (standard deviation of 4.47). Two flocks were randomly selected to experience the

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