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Original Research Article

A model of food stealing with asymmetric information

Mark Broom [a,*], Jan Rychtář [b]

[a] Department of Mathematics, City University London, Northampton Square, London EC1V 0HB, UK
[b] Department of Mathematics and Statistics, The University of North Carolina at Greensboro, Greensboro, NC 27402, USA

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ABSTRACT

Many animals acquire food by stealing it from others. There are species of specialist thieves, but more commonly animals will search for both food items and items already found by others, often conspecifics, that can be stolen. This type of behaviour has previously been modelled using a range of approaches. One of these is the Finder–Joiner model, where one animal, the "Finder", discovers a food patch that takes some time to be consumed. Before consumption of the patch can be completed, another individual, the "Joiner", discovers the Finder and its food patch, and has the opportunity to attempt to steal it. Depending upon how large the patch was, and how long the Finder has been alone on the patch, there may be much or little food remaining. In this paper, building on previous work, we consider a version of this game where the Finder knows the value of the remaining food patch, but the Joiner does not. We see that depending upon the model parameters, the extra information possessed by the Finder can be beneficial or detrimental in comparison to the case where both individuals have full information.

1. Introduction

To survive and reproduce animals need a variety of resources, including food. Often these resources have been acquired in competition with other animals, often conspecifics, but sometimes also those of other species. The nature of the competition will depend upon the animals and resources involved. For example territories may be of value for a long period of time, whereas food resources might be available for a relatively short period of time (Kruuk, 1972; Hamilton and Dill, 2003; Iyengar, 2008; Kokko, 2013).

In this paper it is competition over food in particular that we are interested in. Many animals acquire food by stealing it from others (see Iyengar, 2008 for a good review). Whilst there are species of specialist thieves, a more common situation is where animals search for both food items and items already found by (usually) conspecifics, that can be stolen. If a food item can be consumed immediately by the individual that discovered it, then there is no chance for another to steal it. Often, however, food items need some preparation time prior to consumption, "handling time", which allows a potential thief a chance. This can be because the food item needs to be transported to a nest for offspring, or it might take a while to consume because it has a tough exterior that needs to be penetrated, like a shell, or needs to be consumed in pieces which requires a bird to land to eat it (Spear et al., 1999; Steele and Hockey, 1995; Triplet et al., 1999). This type of scenario has been modelled by Broom and Ruxton (2003), Broom et al. (2004, 2008), Broom and Rychtář (2007), Broom and Rychtář (2011).

Alternatively the resource might be a food patch containing a large number of small items which takes time to consume, which is the focus of producer-scrounger/finder–joiner models (Barnard and Sibly, 1981; Barnard, 1984; Caraco and Giraldeau, 1991; Vickery et al., 1991), see Giraldeau and Livoreil (1998), Kokko (2013), Broom and Rychtář (2013) for more general reviews. In this type of model one animal, the "Finder", discovers such a food patch. Whilst the animal is still feeding on the patch, a second individual, the "Joiner", discovers the Finder at the patch, and has the opportunity to attempt to steal the patch, or at least to steal some of the food within it. In most such models, in particular that of Dubois et al. (2003), the competitors play a classical Hawk Dove game (Maynard Smith and Price, 1973; Maynard Smith, 1982), where they have the choice of a passive strategy (Dove) or an aggressive strategy (Hawk).

Depending upon how large the patch was initially, and how long the Finder has been feeding on the patch prior to the arrival of the Joiner, the amount of food remaining can take a variety of values, from very small to very large. In previous models, and in particular Dubois et al. (2003), it was assumed that both animals knew the value of the resource. In this paper, building on previous work of Broom and Rychtář (2013), see also Broom et al. (2013a,b),

* Corresponding author. Tel.: +44 2070403672.
E-mail addresses: mark.broom@city.ac.uk (M. Broom), rychtar@uncg.edu (J. Rychtář).

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we consider a version of this game where the Finder knows the value of the food patch at the start of the contest, but the Joiner does not. This is reasonable in any case where the value of the patch is not immediately apparent from a distance, but can be ascertained (or at least estimated) by close observation, for example a nest of eggs. In the following sections, we detail the mathematical assumptions of the model, perform a general analysis for our model, and then investigate the results. In particular we compare our results to the alternative case where both individuals know the value of the food patch. Finally we discuss the implications of our results both biologically, and for future models.

2. The model

In this paper we will follow the work of Dubois et al. (2003) and model an interaction of two individuals by a sequential Hawk–Dove game. A Finder discovers a food patch and a Joiner arrives subsequently and tries to take some of the food. We assume that the Finder utilizes the resource before the Joiner arrives and that the Joiner does not know the true value of the resource at the time of its arrival.

We let the total value of the patch be F (either a number of distinct items, or a single easily divisible item), of which value a, the *Finder's share*, has already been consumed by the Finder before the Joiner arrives. The sequential Hawk-Dove contest is modelled as a game in extensive form as in Fig. 1. In this game the Finder makes an initial choice of strategy Hawk or Dove. This is observed by the Joiner which then responds with a choice of Hawk or Dove itself. Given this sequence of choices the payoffs are then given as shown in Fig. 1.

When two Doves meet, they share the remaining resource, each trying to eat as much as they can (scramble competition), but it is assumed that it is eventually divided equally. When a Hawk meets a Dove, the Dove retreats and the Hawk consumes the entire remaining resource. When two Hawks meet, they fight and both pay an energetic cost of value C. The loser retreats and the winner keeps the entire resource, the probability of the Finder winning the contest being denoted by α.

Unlike as in Dubois et al. (2003) where the authors investigated the full information case (both the Finder and Joiner know the value of a and of F, C, α), here we will consider a asymmetric information case when only the Finder has the information about the amount of food already eaten $a \in (0, F)$. The Finder's strategy will thus depend on F, C, α, a, while the Joiner's strategy will depend only on F, C, α and the choice of the Finder. For a fixed F, C, α we are interested for which values of a the Finder will play Hawk, and for the corresponding response of the Joiner.

In full generality, the strategy for the Finder will be a function $\pi(a) = \pi(a, F, C, \alpha)$ where $\pi(a) \in [0, 1]$ for $a \in (0, F)$ represents the probability of the Finder playing Hawk given the amount of food already eaten is a. The strategy for the Joiner will be a pair (p_H, p_D) where p_H (p_D) is the Joiner's probability to play Hawk given the Finder played Hawk (Dove).

We will look for evolutionarily stable strategies (ESSs) of the game. For an asymmetric game with two players, an ESS is a strategy pair, i.e. a strategy for each player, where either individual would obtain a strictly worse payoff if it unilaterally changed its strategy.

To help us distinguish the ESSs, we will assume that Finders make rare mistakes. This is the principle of the "trembling hand" (Selten, 1975; van Damme, 1991; Broom and Rychtář, 2013), which suggests that individuals should make optimal choices even in situations which, formally, do not occur when all others also play optimally. This discriminates among a large set of apparently equivalent strategies, which differ only in their responses to situations which do not occur in the ESS. We specify the nature of these mistakes in Section 3.

We assume that a has either a uniform continuous distribution with the density function $d(a) = 1/F$ on $(0, F)$ or that a takes values in $\{iF/n\,;\, i = 1, 2, \ldots, n-1\}$ each with a probability $1/(n-1)$. In both cases, the expected value of a is $F/2$ and the probability of having $a = 0$ or $a = F$ is 0.

3. Analysis

It follows from Fig. 1 that regardless of the value of a, the optimal value of p_D is 1. Indeed, for any given a, the Joiner should play Hawk when $F - a > \frac{F-a}{2}$, which is always satisfied since $a < F$. Consequently, if the Finder plays Dove, it receives a payoff of a and the Joiner receives a payoff $F - a$.

Next, consider the population where Joiners play $(p_H, 1)$ and assume the Finder has already eaten a by the time that the Joiner has arrived. We will evaluate $R(a, p_H)$, the difference in payoff for the Finder between playing Hawk and Dove. The Joiner will not fight with probability $(1 - p_H)$. If the Joiner does not fight and a Finder plays Hawk, the Finder receives an additional payoff of $F - a$ (on top of the already secured payoff of a which is also the payoff the Finder would receive if playing Dove). The Joiner will fight with

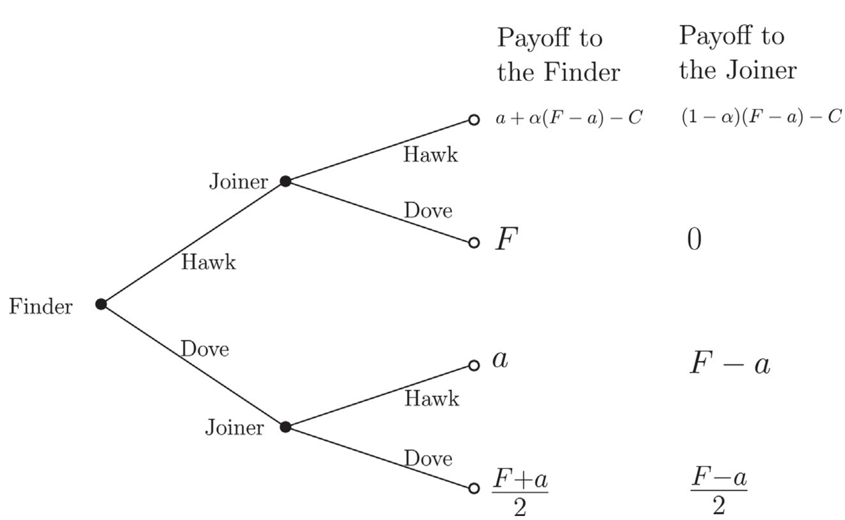

Fig. 1. The sequential Finder–Joiner game in extensive form.