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Original Research Article

A model of food stealing with asymmetric information

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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),

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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

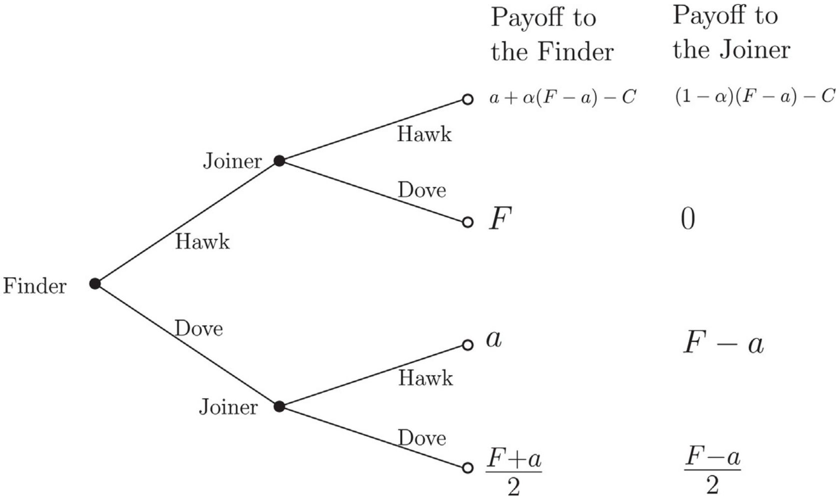

Fig. 1. The sequential Finder–Joiner game in extensive form.

a probability p_H resulting in an additional payoff of $p_H(\alpha(F-a)-C)$ for the Finder if it plays Hawk. Hence, we get

$$R(a,\, p_H) = p_H(\alpha(F-a)-C) + (1-p_H)(F-a) \tag{1}$$

Although the function $R(a, p_H)$ is formally defined only for $a \in (0, F)$, we will use the formula (1) to extend the function to $a \in [0, F]$. Note that, by (1), the function $R(a, p_H)$ is decreasing in a for any fixed value of p_H. Consequently, there is at most one critical value $a_{crit}(p_H) \in [0, F]$ such that

$$R(a,\, p_H)\begin{cases} >0, & 0<a<a_{crit}, \\ =0, & a=a_{crit}\in(0,F), \\ <0, & F>a>a_{crit}. \end{cases} \tag{2}$$

It follows that for any given strategy $(p_H, 1)$ of the Joiner, the optimal strategy of the Finder must be of the form

$$\pi_{a_{crit}}(a) = \begin{cases} 1, & a<a_{crit} \\ 0, & a\geq a_{crit}. \end{cases} \tag{3}$$

Thus it plays Hawk if and only if $a < a_{crit}$.

We will consider two types of mistakes that a Finder can make. When a Finder mistakenly follows a wrong strategy $\pi_{\tilde{a}}$ instead of the intended strategy π_{a_0} (for $\tilde{a} \neq a_0$ and typically $\tilde{a} \approx a_0$), we will call it a mistake of the first kind. When the Finder tries to follow the correct strategy π_{a_0} but still plays Hawk by mistake (with a very small frequency) for $a > a_0$ and Dove by mistake when $a < a_0$, we will call it a mistake of the second kind. The mistake of the second kind thus amounts to playing a strategy

$$\pi_{a_0,\varepsilon}(a) = \begin{cases} 1-\varepsilon_H, & a<a_0, \\ \varepsilon_D, & a\geq a_0 \end{cases} \tag{4}$$

instead of strategy π_{a_0}. When Finders make a mistake of the first kind, we get that $E[F-a] = F - \frac{\tilde{a}}{2}$. When Finders make a mistake of the second kind, we will still have that $E[F-a]$ is different from $F - \frac{a_0}{2}$. Note that for $a_0 = 0$, a mistake of a second kind is equivalent to a (big) mistake of the first kind with $\tilde{a} = F$.

Let us now assume that all Finders follow a strategy π_{a_0} for some a_0. We have to find the optimal value of p_H for the Joiner. When the Finder plays Hawk, the expected payoff to a Joiner playing p_H is

$$p_H((1-\alpha)E[F-a]-C) \tag{5}$$

where $E[F-a]$ denotes the expected value of the remaining resources given the Finder played Hawk. When Finders follow the strategy π_{a_0} exactly and without mistakes, we get that

$$E[F-a] = F - E[a] = F - \frac{a_0}{2}. \tag{6}$$

The payoff to a Joiner playing Dove would be 0, and thus the optimal value of p_H is given by

$$p_{H,opt} = \begin{cases} 1, & \text{when } (1-\alpha)E[F-a]-C>0, \\ 0, & \text{when } (1-\alpha)E[F-a]-C<0. \end{cases} \tag{7}$$

The case when

$$(1-\alpha)E[F-a]-C=0 \tag{8}$$

could potentially lead to a Joiner's mixed strategy $p_H \in (0, 1)$. However, the exact equality in (8) cannot hold when Finders do make mistakes and thus the stable value of p_H will always be either 0 or 1.

We will now investigate all possible candidates for ESSs and we will look for them as pairs (a_{crit}, p_H). Here a_{crit} represents the strategy $\pi_{a_{crit}}$ of the Finder given in (3) (to play Hawk if and only if $a \in (0, a_{crit})$) and p_H represents the strategy of the Joiner (to play Hawk with probability p_H given the Finder has already played Hawk).

3.1. *Case* $a_{\mathrm{crit}} = 0$

If $a_{crit} = 0$, we have

$$R(0,\, p_H) = p_H(\alpha F - C) + (1-p_H)F \leq 0. \tag{9}$$

Since $p_H \leq 1$, and $R(0, p_H) = F - p_H((1-\alpha)F + C)$ is decreasing in p_H, we must have

$$R(0,1) = \alpha F - C \leq 0. \tag{10}$$

Let $p_0 = \min\{p_H\,;\,(9)\text{holds}\}$. Clearly $p_0 > 0$. Also, when (10) holds, all pairs $(0, p)$ for any $p \geq p_0 > 0$ are possible candidates for an ESS.

Given $a_{crit} = 0$, no Finder should ever play Hawk and thus the value of p_H does not really matter if there are no mistakes in the population. If there are mistakes, there will be an occasional Finder playing Hawk and the exact value of p_H will thus matter. Since our candidate value must satisfy $p_H \geq p_0 > 0$, we have that the only possible ESS is $(0, 1)$ and that will happen when $(1-\alpha)E[F-a] - C > 0$. When there are mistakes of the first kind and occasionally a Finder plays a strategy $\pi_{\tilde{a}}$ instead of π_0, the pair $(0, 1)$ is an ESS if and only if (10) holds and

$$(1-\alpha)\left(F - \frac{\tilde{a}}{2}\right) > C. \tag{11}$$

Here we have $\tilde{a} \approx a_{crit} = 0$, and so inequality (11) becomes

$$(1-\alpha)F > C. \tag{12}$$

When there are mistakes of the second kind, $a_{crit} = 0$ implies that Hawk is equally likely to be played by the Finder for any value of, so that $E[F-a] = F/2$. This gives the equivalent condition to (11) as

$$(1-\alpha)\frac{F}{2} > C. \tag{13}$$

3.2. *Case* $a_{\mathrm{crit}} = \mathrm{F}$

If $a_{crit} = F$, we must have

$$R(F,\, p_H) = \mathbf{x2212;C\,p_Hx2265;0} \tag{14}$$

which is possible only if $p_H = 0$. It thus remains to investigate when the pair $(F, 0)$ is stable. Clearly, the Finder's strategy is optimal against the Joiner's strategy $p_H = 0$ (regardless of any parameter values).

By (7) and (6), $p_H = 0$ is an optimal response to the Finder's strategy π_F (and the pair $(F, 0)$ is stable) if and only if

$$(1-\alpha)E[F-a] - C = \frac{(1-\alpha)F}{2} - C < 0. \tag{15}$$

3.3. *Case* $a_{\mathrm{crit}} \in (0,\, \mathrm{F})$

Since $R(a_{crit}, p_H) = 0$, we must have $p_H > 0$. It follows from above that the Finder's strategy is optimal when the Joiner plays p_H and we only have to check when $p_H = 1$ is optimal for the Joiner.

Table 1
Summary of the ESSs. An ESS pair (a_{crit}, p_H) means that the Finder will follow a strategy $\pi_{a_{crit}}$ as in (3) and the Joiner will play Hawk with probability p_H if the Finder played Hawk or with probability 1 if the Finder played Dove.

ESS	Condition
$(0, 1)$	$(1-\alpha)F > C > \alpha F$ (for mistakes of the first kind) or $(1-\alpha)\frac{F}{2} > C > \alpha F$ (for mistakes of the second kind),
$(F - \frac{C}{\alpha}, 1)$	$C < \alpha F$ and $C(3\alpha - 1) < \alpha(1-\alpha)F$
$(F, 0)$	$C > \frac{1-\alpha}{2} F$

If $p_H = 1$, we get that $R(a, 1) = \alpha(F - a) - C$ and thus

$$a_{crit} = F - \frac{C}{\alpha}. \tag{16}$$

Hence, $a_{crit} > 0$ only if

$$C < \alpha F \tag{17}$$

which complements the condition (10) for (0, 1) being an ESS. By (7), the value $p_H = 1$ is optimal for the Joiner only if

$$\begin{aligned} 0 < (1-\alpha)E[F-a] - C &= (1-\alpha)\left(F - \frac{a_{crit}}{2}\right) - C \\ &= (1-\alpha)\frac{\alpha F + C}{2\alpha} - C \\ &= \frac{(1-\alpha)F}{2} + C\frac{1-3\alpha}{2\alpha} \end{aligned} \tag{18}$$

which is equivalent to

$$C(3\alpha - 1) < \alpha(1-\alpha)F. \tag{19}$$

The inequality (19) always holds for $\alpha < 1/2$ since we already must have $C < \alpha F$ and for $\alpha < 1/2$ we also have $(3\alpha - 1) < (1 - \alpha)$.

Hence, $(F - \frac{C}{\alpha}, 1)$ is an ESS if $C < \alpha F$ and $\alpha < 1/2$ or when $C < \alpha F$, $\alpha > 1/2$ and $C(3\alpha - 1) < \alpha(1-\alpha)F$.

Table 1 shows the summary of the conditions on various ESSs and the situation is also shown in Fig. 2.

4. Comparisons between the symmetric and asymmetric information cases

In Dubois et al. (2003) (see also Broom and Rychtář, 2013, p. 364), the authors investigated the Finder–Joiner game for the symmetric information case (when a Joiner also knows the exact value of a) and determined conditions on a, F, C, α for when the Finder (and the Joiner) should play Hawk. Table 2 shows an overview of the ESS actions for all possible values and available information.

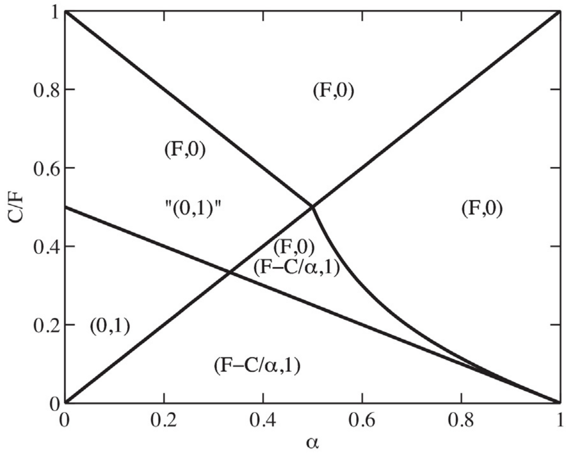

Fig. 2. ESSs of the game for the asymmetric information case, where all terms are as defined in Table 1. The label "(0, 1)" denotes a region where there is an ESS of (0, 1) for the case of mistakes of the first kind (Finder plays Hawk for small values of a). The label (0, 1) denotes a region where there is an ESS of (0, 1) for either kind of mistakes.

Comparing the symmetric information case with the asymmetric information case when the ESS is $(F, 0)$, it follows that the asymmetric information case is never worse for the Finder and never better for the Joiner (with the cases being same only when $C > (1-\alpha)F$). Indeed, in the symmetric information case there may be fights (when $a < \min\{\alpha F, (1-\alpha)F\}$) with positive expected reward for both parties yet with a cost C associated with it, and the Finder may give up for some values of a (when $\alpha < 1/2$), whereas in the asymmetric information case and $(F, 0)$ ESS, the Finder always gets F while the Joiner gets 0, i.e. the best outcome for the Finder and the worst possible ESS outcome for the Joiner.

On the other hand, the asymmetric information case is better for the Joiner (and worse for the Finder) when the ESS is (0, 1) or similarly when it is $(F - \frac{C}{\alpha}, 1)$ and $\alpha < 1/2$. This is because for large a, in the symmetric information case the Finder plays Hawk while the Joiner gives up, i.e. the Finder gets F and Joiner 0, whereas in the asymmetric information case, the Finder has to play Dove for large a, thus getting only a and the Joiner getting $F - a$. Moreover, in the case of $\alpha \le 1/2$ and $a < F - \frac{C}{\alpha}$ and the symmetric information case, the Finder and the Joiner both play Hawk to get a positive expected reward while in the asymmetric information case and (0, 1) ESS, the Finder gives up, gets only a and the Joiner gets $F - a$ (without paying the cost of the fight).

Also, when $\alpha > 1/2$ and $F - \frac{C}{1-\alpha} < a < F - \frac{C}{\alpha}$, then in the symmetric information case the Finder gets F while the Joiner

Table 2
Comparison of actions taken during the game in the symmetric and asymmetric information cases and various ESSs.

ESS	$0 < a < F - \frac{C}{\alpha}$		$F - \frac{C}{\alpha} < a < F - \frac{C}{1-\alpha}$		$F - \frac{C}{1-\alpha} < a$	
$\alpha \le 1/2$						
	Finder	Joiner	Finder	Joiner	Finder	Joiner
Symmetric	Hawk	Hawk	Dove	Hawk	Hawk	Dove
$(0, 1)$	Dove	Hawk	Dove	Hawk	Dove	Hawk
$(F - \frac{C}{\alpha}, 1)$	Hawk	Hawk	Dove	Hawk	Dove	Hawk
$(F, 0)$	Hawk	Dove	Hawk	Dove	Hawk	Dove
$\alpha > 1/2$						
ESS	$0 < a < F - \frac{C}{1-\alpha}$		$F - \frac{C}{1-\alpha} < a < F - \frac{C}{\alpha}$		$F - \frac{C}{\alpha} < a$	
	Finder	Joiner	Finder	Joiner	Finder	Joiner
Symmetric	Hawk	Hawk	Hawk	Dove	Hawk	Dove
$(F - \frac{C}{\alpha}, 1)$	Hawk	Hawk	Hawk	Hawk	Dove	Hawk
$(F, 0)$	Hawk	Dove	Hawk	Dove	Hawk	Dove

gets 0, yet in the asymmetric information case and $(F-\frac{C}{\alpha},1)$ ESS, the Finder and Joiner fight, resulting in a negative payoff for the Joiner and a worse outcome for the Finder. Overall, if $\alpha > 1/2$ and for the $(F-\frac{C}{\alpha},1)$ ESS, then the Finder does worse in the asymmetric information case than in the full information case and the Joiner may do better or worse depending on the exact parameter values.

5. Discussion

Food stealing behaviour has been modelled in a number of ways, depending upon the exact scenario being modelled, and the specific features of interest from that scenario. A common factor of many of these models is that animals are faced with a choice between a small range of options, often two. This could be to steal or not to steal/to resist a stealing attempt or not to resist (Broom and Ruxton, 2003; Broom et al., 2004, 2008; Broom and Rychtář, 2007; Broom and Rychtář, 2011) or to play aggressively or passively within a contest (Barnard and Sibly, 1981; Barnard, 1984; Caraco and Giraldeau, 1991; Vickery et al., 1991; Broom et al., 2009; Grundman et al., 2009; Dubois et al., 2003). This kind of choice is of course common to a variety of ecological scenarios, such as patch foraging, where the choice may be to forage on a particular patch or to leave and go to another (Fretwell and Lucas, 1970; Křivan et al., 2008).

It is generally assumed that the value of the resources competed for in these contests are known to both players, namely that they have perfect information (van Damme, 1991). In fact it seems reasonable that an animal that has possessed a food item for longer may have more information than a challenging individual, so that the first individual knows its value but the second does not; this is a game of imperfect information, and that is the scenario that we have considered. The key parameters in our model are three general ones known to both animals, C the cost of a violent contest, α the probability that the Finder will win the contest, F the value of a complete food patch, and a single value known only to the Finder, a, how much food has been consumed by the Finder before the Joiner arrives. Thus the Finder's strategy takes a into account, but the Joiner's cannot.

The Joiner either always plays the aggressive Hawk strategy or always concedes if and only if the Finder plays Hawk (if the Finder is not aggressive it clearly benefits the Joiner to be, as this secures the resource). The Finder's optimal strategy is to play Hawk for a small enough i.e. when there is a sufficiently large amount of food left to be worth fighting for (yet this may be to play Hawk always, or never). There are three qualitatively different types of ESSs: (1) (0, 1) when the Finder always plays Dove and the Joiner always plays Hawk, (2) $(F-C/\alpha,1)$ when the Finder plays Hawk only when enough resource is still left and the Joiner always plays Hawk, (3) $(F,0)$ when the Finder always plays Hawk and the Joiner always plays Dove. There is always an ESS, and in some circumstances there are two simultaneous ESSs.

When $C > F(1-\alpha)$, corresponding to the situation where it is not beneficial for the Joiner to fight even for a maximal reward F (this type of condition is common to such models, for example Broom et al., 2004), there is no difference between the symmetric or asymmetric information case. In both situations the Finder always plays Hawk and the Joiner always plays Dove, so that aggressive defence of the resource is sufficient to deter the Joiner, and the Finder keeps the resource without any contest. Such a situation will occur where costs are high, for example if the animals have powerful weapons like horns or tusks, or if the Joiner has only a small chance of winning the contest, for example if the food patch is easy to defend.

When $F(1-\alpha) > C > F(1-\alpha)/2$, corresponding to the situation that it is not beneficial for a Joiner to fight for a reward of average value $F/2$, then $(F,0)$ is an ESS. There may, however, be other ESSs. One such ESS is (0, 1) for $\alpha < 1/2$, when the Finder gives up the resource without a fight. This corresponds to the paradoxical strategy X (Maynard Smith, 1982). We note, however, that in our scenario, this ESS is possible only if the Finder makes mistakes of the first kind, i.e. if it plays Hawk for very small a. Another possible ESS is $(F-C/\alpha,1)$ which can happen for $\alpha > 1/3$ (and $C/F < 1/2$). Here, the Finder fights when the value of the remaining resource is large enough. Thus, the fact that the Finder is prepared to fight is a good enough indication for the Joiner to fight as well.

When $C < F\frac{1-\alpha}{2}$, it is beneficial for a Joiner to fight for an average reward of $F/2$. This will happen if the potential cost is small compared to the value of the food, or if the Joiner's chance of winning is high; this means that the Joiner will always fight. Thus in the asymmetric information case that we consider here, the Finder never challenges for large a as this fight would be for a small amount of food left. Also, in this case, the Finder does worse in the asymmetric information case than it would do in the symmetric information case. If, moreover $\alpha < 1/2$, then the Joiner does better in the asymmetric information case than in the symmetric information case (although it knows less in the asymmetric information case). This is caused by the fact that in the symmetric information case, the Finder can play Hawk when a is large enough, knowing that the Joiner knows $F-a$ is small and thus it is not worth fighting for. However, in the asymmetric information case, the Joiner has no information about the exact value of a and since the Joiner knows that it is not beneficial for the Finder to play Hawk for small enough items, the Joiner plays Hawk whenever the Finder plays Hawk. Such a strategy may or may not be harmful to the Joiner (compared to the symmetric information case) when $\alpha > 1/2$, as then the Joiner fights even for items that are not worth fighting for.

The Finder's strategy is rather complex and can be prone to mistakes. Consideration of possible mistakes was needed to resolve which strategies are ESSs out of a potentially large number of apparently identical strategies (these are only identical under always perfect decision-making, which is of course not realistic). We saw an interesting phenomenon, than the regions of ESSs obtained in our solution differed depending upon the type of mistakes the Finder can make. If the Finders are prone to making only small mistakes in assessing a_{crit}, then the ESS region of (0, 1) is larger than in the case when Finders are prone to a mistake in the execution of the strategy (such as playing Hawk when they should play Dove).

Thus we have seen that depending upon the values of the parameters, the extra information possessed by the Finder can be beneficial, but it can also be harmful, when compared to the case where both individuals have full information. It is thus reasonable to ask under what circumstances will the asymmetric information situation that we have described actually occur in real populations? This is more likely to happen when resources are either not immediately visible to the animals, as in a large nest concealed within a hedgerow or if the contest between the animals progresses quickly so that the Joiner does not have chance to assess the value of the reward. In contrast in situations where contests progress more slowly and are of a clearly visible resource, for example a dead animal on an open plain, we might expect the full information case to hold.

An assumption made in our model is that the Finder chooses its strategy before the Joiner. This might be reasonable for instance if the Finder sees the Joiner approaching from a distance and has to choose a defensive position which is associated with its strategy choice. However there will be circumstances, for example if the Joiner discovers the Finder and can challenge before the Finder is aware of its presence, where it would be reasonable to assume that the Joiner chose its strategy first. As we have seen here, but is generally well known, the order of players in a sequential game is important. We have modelled the contest as a sequence of single choices, but contests may be more protracted, with a number of choices for each animal. This would also perhaps give the Joiner the opportunity to gain more information about the resource, so that it may potentially adjust its strategy as it learns more about the food patch, for instance deciding to concede if the patch is shown to be of low value. In general we see that the assumptions made in such models, relating to different real scenarios, have a crucial effect on the outcome both of the idealised model, but also, we would contend, of real contests.

In our model we have also assumed that the value of the Finder's share "a" is uniformly distributed. This is reasonable for circumstances where the food is consumed at a uniform rate, so for example a carcass approached by a scavenger. In other circumstances this would not be the case, for example when the food patch comprises a number of small prey items, e.g. ants, that need to be captured. As the number diminishes, the rate of consumption likewise goes down. In this case, it would be more likely that the Finder's share would be a large value rather than a low one. What are the consequences of the distribution not being uniform? Clearly, a large patch is still worth more than a smaller patch, so that following the same working there will still be a critical threshold a_{crit} for when the Finder should play Hawk, leading to the same results qualitatively, so that a similar figure to Fig. 2 would be obtained. The calculation could be much more complex however, and the nice clean solution for a_{crit} displayed in the figure would no longer hold.

A further assumption of our model is that F is a fixed value and known, in particular by the Finder. This may not be true, particularly in the multiple prey scenario discussed in the paragraph above. In such circumstances the Finder can use the level of the food that it has consumed a as an indication of the richness of the patch, i.e. to estimate F. Here we would have a more complex version of the game but still within our basic premise that the Finder knows more than the Joiner. In this scenario a large a acquired in a short time may indicate that there is a lot of food remaining. To consider such a situation would need a more complex model which takes into account the time that the Finder has been at the food patch as well as the distribution of F values in the environment. This would be a valuable development of the model, and is a topic for future research.

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