Citation: Hadjichrysanthou, C. & Broom, M. (2012). When should animals share food? Game theory applied to kleptoparasitic populations with food sharing. Behavioral Ecology, 23(5), pp. 977-991. doi: 10.1093/beheco/ars061

This is the unspecified version of the paper.

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When should animals share food? Game theory applied to kleptoparasitic populations with food sharing

Abstract

Animals adopt varied foraging tactics in order to survive. Kleptoparasitism, where animals attempt to steal food already discovered by others, is very common among animal species. In this situation, depending on the ecological conditions, challenged animals might defend, share or even, retreat and leave their food to the challenger. A key determinant of the likely behaviour is the nature of the food itself. If food is discovered in divisible clumps, it can be divided between animals in a number of ways. This is the general assumption in one type of game-theoretical models of food stealing, producer-scrounger models. Alternatively, food items may be essentially indivisible, so that sharing is impossible and either the attacker or defender must retain control of all of the food. This is the assumption of the alternative game-theoretical models of kleptoparasitism. In this paper, using a game-theoretic approach, we relax this assumption of indivisibility and introduce the possibility of limited food sharing behaviour between animals in kleptoparasitic populations. Considering the conditions under which food sharing is likely to be common, it is shown that food sharing should occur in a wide range of ecological conditions. In particular, if food availability is limited, the sharing process does not greatly reduce the short-term consumption rate of food and food defence has a high cost and/or a low probability of success, then the use of the food sharing strategy is beneficial. Thus, the assumption of the indivisibility of food items is an important component of previous models.

Key words: social foraging, food stealing, evolutionary games, strategy, ESS.

Introduction

In many biological situations, animals may decide to share their food in order to avoid any injuries or energetic and time costs of a possible conflict with an attacking foraging animal, or to obtain other immediate or delayed benefits such as mating opportunities and reciprocal altruism. Food sharing is commonly observed in animal populations in a wide range of species, including social carnivores, insects, birds, cetaceans, vampire bats and primates (see Feistner and McGrew, 1989; Stevens and Gilby, 2004, for reviews). In the literature, food sharing is defined in many different ways and various theoretical models have been developed to consider the different biological situations where food sharing among animals occurs. In the rest of this paper, we consider food sharing in kleptoparasitic populations, populations where foraging animals steal food discovered by others. We define food sharing to be the situation where the resource owner shows tolerance and allows a competitor animal to consume a part of its food although it has the ability to fight and try to keep all of its food.

Kleptoparasitism is a common foraging strategy. Different forms of kleptoparasitic behaviour are observed in many species of animals, for example species of spiders (e.g., Coyl et al., 1991), birds (e.g., Brockman and Barnard, 1979), snails (e.g., Iyengar, 2002), lizards (e.g., Cooper and Perez-Mellado, 2003), fish (e.g., Hamilton and Dill, 2003), primates (e.g., Janson, 1985), carnivores (e.g., Carbone et al., 2005) and insects (e.g., Erlandsson, 1988). This behaviour of animals has been recently well documented in a review paper (Iyengar, 2008). The biological phenomenon of kleptoparasitism has attracted the interest of many researchers from different areas. There are a number of theoretical models focused on the kleptoparasitic behaviour of animals using different mathematical methods, in particular evolutionary game theory. Two of the fundamental game-theoretical models which consider kleptoparasitic behaviour are the producer-scrounger model, originally introduced by Barnard and Sibly (1981), and the model of Broom and Ruxton (1998). In its original form, the producer-scrounger game is a frequency-dependent game where animals forage for food using two strategies. They either search for food (producer's strategy) or search for opportunities to kleptoparasitize (scrounger's strategy). The scrounger strategy does better when scroungers are rare and worse when they are common. When the frequency of the two strategies is such that the payoff obtained by each strategy is the same, there is a stable equilibrium where the two strategies coexist. Many variations of this model have followed in order to consider different factors that might affect the foraging process (e.g., Caraco and Giraldeau, 1991; Vickery et al., 1991; Dubois and Giraldeau, 2005). One key feature of this type of models is that food is usually discovered in patches and can be easily split over foraging animals. Hence, the concept of food sharing is central to these models. In addition, in these models costs from aggressive strategies are energetic, rather than time, costs. Thus, the different strategies do not directly affect the distribution of feeding and foraging animals and the main effect of population density is to reduce the "finder's share", the portion of the food eaten by a finder before other foragers discover it. The model of Broom and Ruxton (1998), based on the mechanistic model of Ruxton and Moody (1997), follows a different approach. Food comes in single indivisible items, which must be consumed completely by an individual. Thus, food can never be shared and challenging animals attempt to steal the whole item from the owner (or not). In particular, in this model it is assumed that each of the animals in the population either searches for food, has already acquired and is handling a food item prior to its consumption or fights with another animal over a food item. When foraging animals encounter an animal in the handling state, they can either decide to attack in order to steal the prey or ignore the handler animal and continue searching. Attacked animals always defend their food and a fight takes place. The population density has a direct effect in this model as fights take time, with this loss of time the cost of more aggressive strategies, and the more potential kleptoparasites there are, the more time is wasted on fighting. The model predicts the optimal strategy for a foraging animal (to attack or not to attack) under varying food availability and fight time cost. Broom et al. (2004) later reconstructed this model in a more general framework by introducing different competitive abilities between the attacker and the attacked animal and allowing the attacked animal to surrender its food to the attacker avoiding the time cost of a fight. A series of publications has appeared developing the original model of Broom and Ruxton (1998) in a number of ways (e.g., Broom and Ruxton, 2003; Broom and Rychtar, 2007;

Luther et al., 2007; Yates and Broom, 2007; Broom et al., 2008; Broom and Rychar, 2009; Broom and Rychtar, 2011). Crowe et al. (2009) provide a brief review on the main theoretical work on kleproparasitism prior to the investigation of a stochastic model of kleptoparasitism in finite populations. A comparison between some main models of kleptoparasitism following the two fundamental game-theoretic approaches is discussed in Vahl (2006) (see Chapter 6) and an alternative model is presented. There is also a series of related mechanistic, but not game-theoretic, models which investigate interference competition where foraging animals engage in aggressive interactions in order for example to defend their territory, resulting in negative effects on their foraging efficiency (e.g., Beddington, 1975; Ruxton et al., 1992; Van der Meer and Ens, 1997; Vahl, 2006; Smallegange and Van der Meer, 2009; Van der Meer and Smallegange, 2009).

There are many game-theoretical models which investigate sharing behaviour as an alternative strategy of foraging animals. The Dove strategy in the famous and widely used Hawk-Dove game (Maynard Smith and Price, 1973; Maynard Smith, 1982) can be thought of as an example of this non-aggressive behaviour. However, the Hawk-Dove game and a large number of variations of this game (see for example, Sirot, 2000; Dubois et al., 2003) are unable to show why in many biological situations animals prefer to share the acquired prey without any contest taking place. The non-aggressive behaviour of the Dove is shown to never be a pure Evolutionarily Stable Strategy (ESS), i.e. a strategy that if adopted by the population cannot be invaded by any alternative strategy, and can only exist as a mixed ESS (with Hawks) in a proportion depending on the value of the resource and the cost of a potential contest. This is mainly due to the fact that the Hawk-Dove game considers just a single contest between the two strategies. Although the reward of adopting the Hawk strategy against an animal playing Hawk might be equal or lower than the reward of adopting the Dove strategy, in a contest between a Hawk and a Dove, the Hawk is always the optimal strategy. However, in group foraging populations, animals usually have repeated interactions over food items. In iterated Hawk-Dove type games, it has been shown that if the attacked animal can adopt the strategy of its opponent (for example play a Retaliator type strategy (Maynard Smith and Price, 1973; Maynard Smith, 1982) or a tit-for-tat type strategy (Axelrod and

Hamilton, 1981)) then, under some circumstances, food sharing without any aggressive interactions might be an ESS (Dubois and Giraldeau, 2003, 2007). A different game-theoretical food sharing model is considered in Stevens and Stephens (2002) in a situation where the owner of the food might decide to share its food with a beggar due to the fitness costs of harassment or interference (e.g. screams, slapping of the ground, grabbing at the food). In this case, it is shown that food sharing might be the optimal choice for the food owner in situations where the fitness cost caused by the beggar's harassment, if the food is defended, exceeds the fitness cost of sharing.

In this paper, we extend the model of kleptoparasitism presented in Broom et al. (2004) by assuming divisible food items and allowing animals to share their prey with attacking foraging animals. A foraging animal, encountering an animal handling a food item has the possibility to either attack attempting to steal or share the food, or just ignore it and continue foraging. On the other hand, an attacked animal which owns a food item, has the possibility to defend its food, to share it or to retreat leaving all the food to the attacking animal. Through a game-theoretic approach we examine the optimal strategy for an animal under different ecological circumstances.

The model

In a population of foragers of density P, each animal might either be in a state of searching for food, or a state where it is handling a food item that it has acquired. Let S denote the density of searchers and H the density of handlers. Each handler consumes the food item and resumes searching in a time drawn from an exponential distribution with mean t_h, so equivalently following a Markov process at rate t_h^{-1}. There is a constant density of food items f available and searchers cover an area ν_f per unit time whilst searching for food, so that they find food at rate $\nu_f f$. As well as finding food themselves when foraging, searchers can acquire food by trying to steal it from a handler, and they can search an area ν_h per unit time for handlers. Once a searcher comes upon a handler, it attacks to either steal or share the food item with probability p_1 or ignores the handler with probability $1 - p_1$ and continues searching for food. If the searcher attacks, the handler might decide to resist and defend its food item. This happens with probability which we label p_3. In this case, the attacking searcher (A) and the defender (R) engage in a fight. The rate at which searchers encounter handlers and engage in a fight (become attackers, A) is equal to $p_1 p_3 \nu_h H$ while handlers are found by searchers and resist a possible attack (become defenders, R) with rate $p_1 p_3 \nu_h S$. The fight lasts for a time drawn from an exponential distribution with mean $t_a/2$. The attacker animal wins the fight and becomes a handler with probability α and thus, with the same probability, the defender loses its food and starts searching again; so this happens at rate $2\alpha/t_a$. Otherwise, the attacking searcher loses the fight and returns to the searching state with rate $2(1-\alpha)/t_a$ and thus, with the same rate, the defender wins and continues handling its food. Note that the winner of the fight might face other subsequent challenges. In general, the circumstances under which fights occur might give a high advantage to defender or attacker (the attacker might have to catch the defender in the air, but the defender may be hampered by a heavy food item) and so α may be significantly greater or less than 0.5.

So far, the model described is the same as the model investigated in Broom et al. (2004). In this paper, this model is extended by assuming that attacked animals can share a food item as follows. Assume that food items are divisible. The attacked handler might decide to share its food with an attacking searcher, with probability p_2. In this case, searchers become sharers (C) with rate $p_1 p_2 \nu_h H$ and the attacked handlers with rate $p_1 p_2 \nu_h S$. If the handler decides to share its food with the searcher, both take a half of the food. It is assumed, for reasons of simplicity, that both the two sharers hold the food item and feed simultaneously on it. This discourages other animals from attempting to steal or share the food since this would be a difficult, risky and dangerous venture. So, food sharing results in the mutual protection of the two sharers from other predators. As a result, a sharer animal consumes its portion of the food item without any interruptions. Sharers eat their food unperturbed and again become searchers in a time drawn from an exponential distribution with mean t_c or equivalently with rate t_c^{-1}. Once the half of the food item is consumed, the sharer starts foraging again. Throughout the paper, it is assumed that $2t_c \geq t_h$, i.e. the decision of food sharing might either have no time cost or has some cost, but is never beneficial with respect to the handling time.

The attacked handler, in order to avoid any time cost either from a fight or the sharing process, might decide neither to defend its food item nor to share it, but to leave it to the attacking animal and return to the searching state. This happens with probability $1-p_2-p_3$ for any challenge, and so occurs at rate $p_1(1-p_2-p_3)\nu_h H$ for each searcher and rate $p_1(1-p_2-p_3)\nu_h S$ for each handler.

The model parameters and notations are summarised in Table 1.

The differential equation based compartmental model that describes the dynamic of the different groups of the population in the above situation is the following

$$\begin{aligned}
\frac{dS}{dt} &= \frac{1}{t_h}H + \frac{1}{t_c}C + \frac{2}{t_a}(1-\alpha)A + \frac{2}{t_a}\alpha R - \nu_f f S - p_1\left(p_2+p_3\right)\nu_h SH, && (1)\\
\frac{dH}{dt} &= \nu_f f S + \frac{2}{t_a}\alpha A + \frac{2}{t_a}(1-\alpha)R - \frac{1}{t_h}H - p_1\left(p_2+p_3\right)\nu_h SH, && (2)\\
\frac{dC}{dt} &= 2p_1p_2\nu_h SH - \frac{1}{t_c}C, && (3)\\
\frac{dA}{dt} &= p_1p_3\nu_h SH - \frac{2}{t_a}A, && (4)\\
\frac{dR}{dt} &= p_1p_3\nu_h SH - \frac{2}{t_a}R. && (5)
\end{aligned}$$

The above system of equations is a closed system where the population density, P, remains constant, i.e.

$$P = S + H + C + A + R, \tag{6}$$

and one of the equations (1)–(5) is thus redundant.

We assume that the population rapidly converges to the equilibrium state (see Luther and Broom (2004) for a proof of this assumption for the original model of Broom and Ruxton (1998)). In the equilibrium conditions, the densities of the different groups of the population, S, H, C, A and R, are given by (see Appendix A)

$$(S,H,C,A,R) = \left(\frac{H}{t_h d(H,p_1,p_2)}, H, \frac{2p_1p_2t_c\nu_h H^2}{t_h d(H,p_1,p_2)}, \frac{1}{2}\frac{p_1p_3t_a\nu_h H^2}{t_h d(H,p_1,p_2)}, \frac{1}{2}\frac{p_1p_3t_a\nu_h H^2}{t_h d(H,p_1,p_2)}\right), \tag{7}$$

where $d(H,p_1,p_2) = \nu_f f - p_1p_2\nu_h H$, i.e. the difference between the rate at which searchers discover food items and the rate at which they become sharers. Note that this term is clearly positive since every food item can be shared at most once (and some are not shared), and it must be discovered beforehand. By (6) and (7), H is given by the biologically relevant solution of the quadratic equation

$$p_1\big(p_2(2t_c - t_h) + p_3 t_a\big)\nu_h H^2 + \big(p_1 p_2 t_h \nu_h P + t_h \nu_f f + 1\big)H - t_h \nu_f f P = 0, \tag{8}$$

i.e. the positive solution,

$$H = \frac{-\big(p_1p_2t_h\nu_hP+t_h\nu_f f+1\big)+\sqrt{\big(p_1p_2t_h\nu_hP+t_h\nu_f f+1\big)^2+4p_1t_h\nu_f f\nu_hP\Big(p_2(2t_c-t_h)+p_3t_a\Big)}}{2p_1\nu_h\Big(p_2(2t_c-t_h)+p_3t_a\Big)}, \tag{9}$$

given that $2p_1\nu_h\big(p_2(2t_c - t_h) + p_3 t_a\big) > 0$.

Optimal strategies

We are interested in finding conditions under which animals playing strategy (p_1, p_2, p_3), i.e. animals which attack handlers with probability p_1 and share or defend their food when they are attacked with probability p_2 and p_3, respectively, have greater fitness than animals playing any other strategy (q_1, q_2, q_3). We are ultimately looking for conditions when the overall strategy (p_1, p_2, p_3) is an ESS.

A strategy is considered to be the optimal strategy if it minimizes the average time needed to the consumption of a food item. This would result in the maximising of the long-term food intake rate of an animal playing this strategy and thus its fitness.

Average time for a single animal to consume a food item

Assume that a mutant animal playing strategy (q_1, q_2, q_3) invades into a population playing strategy (p_1, p_2, p_3).

If the mutant is at the searching state and encounters a handler it has two options:

- It attacks in order to share or steal the food item with probability q_1. Note that once it attacks, what will happen next depends on the handler' s strategy.
- It ignores the handler animal and continues searching for a food item for itself with probability $1 - q_1$.

The time needed for the mutant searcher, who has just come upon a handler playing the population strategy, to consume a food item, T^*_{SA}, in the different scenarios is represented schematically in the diagram shown in Figure 1. The notation of food consumption times from the different foraging states is shown in Table 2.

If the mutant is at the handling state and is attacked by a searcher animal playing the population strategy it has three options:

- It shares the food item with probability q_2.
- It defends its food and a fight takes place with probability q_3.
- It leaves the food to the attacker and resumes searching with probability $1-q_2-q_3$.

The time required for the attacked mutant handler to consume a food item, T^*_{HA}, in the different scenarios is represented schematically in the diagram shown in Figure 2.

It is shown (see Appendix B) that T^*_{SA} and T^*_{HA} are given by the solution of the following system of equations

$$\begin{aligned}&\left(1-\left(1-q_1+\frac{q_1p_2}{2}+(1-\alpha)q_1p_3\right)\frac{\nu_h H}{\nu_f f+\nu_h H}\right)T^*_{\mathrm{SA}} = q_1p_2t_c+q_1p_3\frac{t_a}{2}+\\&+\left(1-q_1+\frac{q_1p_2}{2}+(1-\alpha)q_1p_3\right)\frac{1}{\nu_f f+\nu_h H}+\\&+\left(\left(1-\frac{q_1p_2}{2}\right)\nu_f f+q_1\big(1-p_2-(1-\alpha)p_3\big)\nu_h H\right)\frac{t_h(1+\nu_h S T^*_{\mathrm{HA}})}{(1+t_h\nu_h S)(\nu_f f+\nu_h H)}.\end{aligned}\tag{10}$$

$$\begin{aligned}&\left(1-\frac{\left((1-\frac{p_1q_2}{2})\nu_f f+\big(1-p_1+(1-\alpha)p_1q_3\big)\nu_h H\right)t_h\nu_h S}{(1+t_h\nu_h S)(\nu_f f+\nu_h H)}\right)T^*_{\mathrm{HA}} = p_1q_2t_c+p_1q_3\frac{ta}{2}+\\&+\left(\left(1-\frac{p_1q_2}{2}\right)\nu_f f+\big(1-p_1+(1-\alpha)p_1q_3\big)\nu_h H\right)\frac{t_h}{(1+t_h\nu_h S)(\nu_f f+\nu_h H)}+\\&+p_1\left(1-\frac{q_2}{2}-(1-\alpha)q_3\right)\frac{1+\nu_h H T^*_{\mathrm{SA}}}{\nu_f f+\nu_h H}.\end{aligned}\tag{11}$$

The average required time to the consumption of a food item for a single searcher animal of a population playing strategy (p_1,p_2,p_3), who has just met a handler animal of this population, T_{SA}, and the respective time of a single handler of the same population who has just met a searcher, T_{HA}, can be found by solving the system of equations (10) and (11) substituting (p_1,p_2,p_3) for (q_1,q_2,q_3).

In the case where all the members of the population do not challenge, i.e. $p_1 = q_1 = 0$, the strategy used by an animal in the handling position may be thought irrelevant since none of the animals will ever be attacked and thus each searcher finds a food item for itself in an average time equal to $1/\nu_f f$ and each handler consumes a discovered food item in time t_h. However, we assume that occasionally a challenge occurs "by mistake" (this is a version of the classical trembling hand argument of Selten (1975)). Thus, a handler animal of a population where animals never challenge, at some point is faced by a foraging animal which attempts to steal or share the food. In this case, the average time needed for the attacked handler animal to consume a food item if it adopts a different from the population strategy, $(0, q_2, q_3)$, is given by (see Appendix B)

$$T^*_{\mathrm{HA}} = q_2\left(t_c - \frac{1}{2}\left(\frac{1}{\nu_f f} + t_h\right)\right) + q_3\left(\frac{t_a}{2} - (1-\alpha)\frac{1}{\nu_f f}\right) + \frac{1}{\nu_f f} + t_h. \tag{12}$$

If a mutant animal can invade a population then its strategy (q_1, q_2, q_3) is a better strategy than that of the population (p_1, p_2, p_3) at least at one of the two decision points, when a searcher and potentially making a challenge or when receiving a challenge as a handler. A mutant which follows a different strategy from that of the population at just one decision point and the strategy which is followed is better than that of the population, can obviously invade. When considering whether a particular strategy is an ESS or not, it is sufficient to investigate invasion by mutants which differ in strategy at one of the two decision points only. This is because if a mutant which differ in strategy at both of the decision points can invade, it must have a superior strategy at at least one of the decision points, and so an animal which shares the same strategy as the mutant at this decision point, and the same strategy as the population at the other, could also invade.

A mutant which uses a strategy different from that of the population at just the searching state is considered to use a better strategy, and thus be able to invade, if $T^*_{\mathrm{SA}} \leq T_{\mathrm{SA}}$, i.e. if the decision that it will make at the point when it will meet a handler, when searching for food, will lead to a smaller time until the consumption of a food item. Similarly, a mutant which plays differently from the population just at the handling state is considered to be able to invade if the decision it will make in an encounter with a searcher, when handling a food item, will shorten the time to the consumption of a food item, i.e. if $T^*_{\mathrm{HA}} \le T_{\mathrm{HA}}$. Note that it is possible that under certain parameters T^*_{SA} is independent of q_1 and all values $0 \le q_1 \le 1$ give identical times. Similarly, T^*_{HA} might be independent of q_2 and q_3. In these circumstances, in such asymmetric games, the population can still be invaded by genetic drift.

In Appendix C, it is demonstrated through a combination of analytical and numerical investigation that the optimal strategy in either decision points is always pure (in some cases this is proved, in others it is not proved but an extensive numerical investigation has yielded consistent results with no mixed ESSs). Thus, if the population plays a non-pure strategy (p_1, p_2, p_3), for an invading animal there will be a pure strategy that will do at least as well as playing the population strategy, and so (p_1, p_2, p_3) could not be an ESS since this pure strategy would invade the population. Hence, we need to consider only two strategies for a foraging animal (always or never attempt to steal or share the prey of the other animal when the opportunities arise) and three strategic choices for the attacked animal (either always surrender the food to the attacking animal, always share the food or always defend it) as the components of the potential optimal strategy in any given population. Therefore, there are six possible pure strategies that an animal can use and need to be considered:

- Strategy (0,0,0) (Dove, D): the animal does never challenge handlers and does never resist any challenges.

- Strategy (0,1,0) (Non-Attacking Sharer, NAS): the animal does never challenge handlers and always shares its food when it is challenged.

- Strategy (0,0,1) (Retaliator, R): the animal does never challenge handlers but always resists when it is challenged.

- Strategy (1,0,0) (Marauder, M): the animal challenges handlers at every opportunity but it does never resist any challenges.

- Strategy (1,1,0) (Attacking Sharer, AS): the animal challenges handlers at every opportunity and it always shares the food when it is challenged.

- Strategy (1,0,1) (Hawk, H): the animal challenges handlers at every opportunity and it always resists any challenges.

The optimal strategy for an animal at the searching state

Consider a population playing strategy (p_1, p_2, p_3) that is potentially invaded by a mutant animal playing a different strategy (q_1, q_2, q_3). For reasons explained in the previous section, in order to study whether the mutant can evolve because it uses a better strategy at the searching state, we assume that the strategy which is used by all the animals when they are at the handling state is the same, i.e. $p_2 = q_2$ and $p_3 = q_3$. We consider the strategy used by a searcher animal of the population when coming across a handler, p_1, to be advantageous over a mutant strategy, q_1, (and thus the population cannot be invaded by the mutant) if the average time required for the searcher playing the population strategy to gain and consume a food item, T_{SA}, is less than that required for the mutant searcher, T^*_{SA}. Using the equations (10), (11) and (7)–(9) we find all the necessary conditions under which a mutant playing strategy $q_1 \in \{0, 1 : q_1 \neq p_1\}$ cannot invade a population playing strategy $p_1 \in \{0, 1 : p_1 \neq q_1\}$ for the cases where either $p_2 = q_2 = 0$ and $p_3 = q_3 = 1$, $p_2 = q_2 = 1$ and $p_3 = q_3 = 0$ or $p_2 = q_2 = 0$ and $p_3 = q_3 = 0$. These are summarised in Table 3 (conditions (C.3), (C.6), (C9), (C.10), (C.13) and (C.16)).

The optimal strategy for an animal at the handling state

In the handling position an animal can use three strategies when it is challenged. Either it shares the food with the challenger, it defends its food or it retreats leaving the food to the attacking animal, and depending on the ecological conditions it obtains the highest benefit when it always takes one of these three actions. As before, assume that a population already at equilibrium conditions is invaded by a mutant, which now uses a different strategy as a handler but the same strategy as a searcher.

Optimal strategies in an aggressive population

Assume that all the members of the population behave aggressively when encountering a handler animal, i.e. $p_1 = q_1 = 1$. We consider the strategy of an attacked handler of the population to be advantageous over the strategy used by an attacked handler mutant (and thus the mutant cannot invade) if the average time required for the first to consume a food item, T_{HA}, is less than that required for the second, T^*_{HA} (in this case, this is equivalent to the comparison of T_{SA} with T^*_{SA} since the times needed for animals which always challenge, i.e. when $p_1 = q_1 = 1$, to acquire a food item and be discovered by a foraging animal are identical, independently of the strategies they use as handlers). Using again the equations (10), (11) and (7)–(9) we find the necessary conditions under which a mutant in this scenario cannot invade a population playing a different strategy at the handling state. These conditions are presented in Table 3 (conditions (C.11), (C.12), (C14), (C.15), (C.17) and (C.18)).

Optimal strategies in a non-aggressive population

In the case where all the members of the population do not challenge, i.e. $p_1 = q_1 = 0$, an animal of the population playing $(0, p_2, p_3)$ does better than a mutant playing $(0, q_2, q_3)$, and thus the population cannot be invaded by this mutant, if $T_{\mathrm{HA}} < T^*_{\mathrm{HA}}$, where by (12) ($T_{\mathrm{HA}}$ in this case is similarly given by (12) substituting p_2 and p_3 for q_2 and q_3, respectively) we obtain the condition

$$(q_2 - p_2)\left(t_c - \frac{1}{2}\left(\frac{1}{\nu_f f} + t_h\right)\right) + (q_3 - p_3)\left(\frac{t_a}{2} - (1-\alpha)\frac{1}{\nu_f f}\right) > 0. \tag{13}$$

The conditions under which a mutant playing strategy $(0, q_2, q_3)$ is unable to invade a population playing strategy $(0, p_2, p_3)$ are summarised in Table 3 (conditions (C.1), (C.2), (C.4), (C.5), (C.7), (C.8)).

Evolutionarily Stable Strategies

Table 3 shows all the appropriate conditions under which a population playing strategy (p_1, p_2, p_3) cannot be invaded by a mutant playing a different strategy at one of the two decision points, (q_1, q_2, q_3), for all the possible cases where all animals play a pure strategy.

According to the results shown in Table 3, strategies (0,0,0) and (0,1,0) can never resist all of the possible invading strategies and there are thus four possible ESSs:

- Strategy (0,0,1) is an ESS if the conditions (C.7), (C.8) and (C.9) are satisfied.
- Strategy (1,0,0) is an ESS if the conditions (C.11) and (C.12) are satisfied.
- Strategy (1,1,0) is an ESS if the conditions (C.13), (C.14) and (C.15) are satisfied.
- Strategy (1,0,1) is an ESS if the conditions (C.16), (C.17) and (C.18) are satisfied.

Figure 3 shows the regions in parameter space in which each of the four strategies, Retaliator, Marauder, Attacking Sharer and Hawk, is an ESS, for specific parameter values as the duration of the contest, $t_a/2$, and the handling time of a sharer, t_c, vary. Figure 4 shows how these regions vary as the density of the population, P, and the rate at which foragers find undiscovered food, $\nu_f f$, vary. Obviously, these regions in the t_a, t_c plane in Figure 3 and $P, \nu_f f$ plane in Figure 4 will vary, depending on the other parameter values. However, some general conclusions can be extracted. Figure 3 and Figure 4 suggests that between the regions where two strategies are unique ESSs, there can be a region where the two strategies are simultaneous ESSs and among the regions of three pairs of ESSs configured by three strategies, there might be a region where the three strategies might coexist as ESSs. This excludes the possibility of the Retaliator and the Hawk strategies being simultaneous ESSs, since this can never happen due to the contradiction of the conditions (C.9) and (C.16) (see Table 3). This gives eleven distinct regions as summarised in Figure 3 and Figure 4. It appears that every set of parameters yields one or more pure ESSs. Numerical examples on a wide range of parameter values indicate that there is no parameter set where this is not the case i.e. that there are not any mixtures of strategies or cases where there are no ESSs. Although we do not believe that there will be any parameter set where there will be such a polymorphic mixture or no ESS (in similar models such cases do not occur, and see Appendix C for an argument that actual mixed strategy ESSs are not possible), we cannot definitively rule out this possibility.

Predictions of the model

In the case where neither the members of the population nor any mutant share the food, i.e. in the case where $p_2 = q_2 = 0$, all the above results agree with the results obtained in previous work (Broom et al., 2004). Hence, here we concentrate on the cases where the members of the population or a mutant animal or both, always share their food when they are attacked, i.e. cases where either p_2 or q_2 or both are equal to 1. This provides both new potential ESSs and also new mutant strategies to invade other strategies, so that strategies that were ESSs in Broom et al. (2004) will no longer be in some cases.

In a non-attacking population, a sharer does better than a Dove when they are attacked if the average time needed for a sharer to consume a whole food item ($t_c + ((1/\nu_f f) + t_h)/2$) is less than the average time needed to find an undiscovered food item ($1/\nu_f f$) and consume it (t_h) (equivalently in this case, if the time the sharer needs to consume the half of the food item (t_c) is on average less than half of the time needed to find and consume a whole food item($((1/\nu_f f)+t_h)/2)$). On the other hand, an Attacking Sharer mutant does better than a member of a population of Non-Attacking Sharers if $t_c \leq ((1/\nu_f f) + t_h)/2$ as well. Hence, as we see in Table 3, condition (C.4) contradicts condition (C.6) and thus a Non-Attacking Sharer is never an ESS. The food sharing strategy can be an ESS only if the sharer challenges a handler at every opportunity when it is at the searching state. A population of Attacking Sharers can potentially be invaded by Non-Attacking Sharers, Marauders and Hawks. The conditions under which a Non-Attacking Sharer and a Marauder can invade a population of Attacking Sharers are the same. This occurs because in such a population a Marauder can invade if it is better for any handler to give up a food item rather than share (so being a searcher is better than sharing a food item) and a Non-Attacking Sharer can invade if it is better not to challenge for a food item, which will be shared (so again searching is better than sharing). Increasing the rate at which foragers find food, $\nu_f f$, increases the parameter range where Non-Attacking Sharers and Marauders invade the population of Attacking Sharers. Depending on the values of the other parameters, the increase of $\nu_f f$ might favour the invasion of Hawks as well (usually when food is difficult to discover). Hence, increasing $\nu_f f$ decreases the range of the parameter values in which the Attacking

Sharer strategy is an ESS (see Figure 3 for an example). A similar situation appears by decreasing the area in which foragers search for handling sharers per unit time, ν_h. As it is observed in Figure 4 and the conditions (C.13)–(C.15), the decrease of the density of the population, P, might also create unpropitious circumstances for food sharing. For a given set of parameter values for which the Attacking Sharer strategy is an ESS, increasing the time cost of the sharing process which results in the increase of t_c, the area where the Attacking Sharer strategy is an ESS reduces, as one would expect. Depending on the other ecological conditions, this strategy might coexist as an ESS with either one of the other possible ESSs (Retaliator, Marauder or Hawk) or two of them (Retaliator and Marauder or Marauder and Hawk). At very high levels of t_c such that the time spent in sharing would be better spent in searching for another food item or in defending the food item, Attacking Sharer cannot be an ESS. In this case, the predictions of the model approach those of the model of Broom et al. (2004), where sharing was not possible.

In conditions where the duration of aggressive interactions is high, the defending strategy is less profitable and thus the avoidance of any aggressive interaction is favoured. Hence, under these circumstances, it is observed that animals should decide either to surrender their food (use the Marauder strategy) or to share it (use the Attacking Sharer strategy) when they are challenged, even if they have a high probability of defending their food successfully. Therefore, at high fight durations each of Marauder and Attacking Sharer strategies might be the unique ESS or both might be ESSs simultaneously.

A special case

As a special case, we consider the case where $2t_c = t_h$, i.e. where sharing does not reduce the speed of food consumption. The results obtained in this case are shown in Table 4. It is observed that, as well as the Dove and Non-Attacking Sharer strategies which as we have seen in the previous section are never ESSs, in this case the Marauder strategy is also never an ESS since it can always be invaded by an Attacking Sharer animal. The Attacking Sharer strategy can only be invaded by the Hawk strategy. Moreover, this can happen just in few cases where the chance of a successful defence is relatively high, i.e. the probability α is relatively small, and the time spent in a contest, $t_a/2$, is small. For

$\alpha \geq 0.5$, the conditions (C.7) and (C.9) indicate that the Retaliator strategy can never be an ESS. In this case, the condition (C.18) also indicates that an Attacking Sharer can always invade a population playing Hawk and thus the Hawk strategy can never be an ESS as well. Hence, at least for $\alpha \geq 0.5$, Attacking Sharer is the only ESS no matter what the other parameter values are. The Hawk strategy is an ESS mainly when $t_a/2$ and α are small. As $t_a/2$ and/or α increase, depending on the other parameter values, there might be a range where Hawks and Attacking Sharers coexist as ESSs. When the defender is likely to succeed, i.e. α is small, defence of the food item might be the favoured strategy even if the fight time is relatively long, especially in cases where available food is scarce. Hence, there is a range where the Retaliator strategy is either the only ESS or coexists with the Attacking Sharer strategy. Figure 5 shows a region with all the possible ESSs in this specific case, as the probability α of the challenger winning and the duration of the content, $t_a/2$, vary.

Discussion

Food sharing is a very common tactic adopted by a broad group of animal species for their survival. Using a game theoretic approach, the present model investigates the ecological circumstances under which animals should share their food when they are challenged by other foraging animals. We have extended the game-theoretical model of Broom et al. (2004) by allowing animals to share their food. Hence, animals in this model can choose among two additional strategies: either to attempt to share or steal the food from a handler when foraging and share their food when they are challenged by a forager, or to ignore any opportunities to share or to steal food when foraging but share when another animal attacks. This model is likely to be an improvement if caught food items are at least partly divisible, for instance fruit species (e.g., White, 1994), as opposed to for example a nut or a fish (e.g., Iyengar, 2008) which are hard to divide, in which case the original modelling system will be more appropriate. At the opposite extreme, in situations where food items come in patches, for instance seed patches (e.g., Barnard and Sibly, 1981), which are easily divisible, then the producer-scrounger type models (e.g., Dubois and Giraldeau, 2003; Dubois et al., 2003; Dubois and Giraldeau, 2005, 2007) could be appropriate models.

Considering the time cost needed for a food item to be acquired and consumed, the model predicts that there is a wide range of ecological conditions in which attempting to share or steal the food at every opportunity and sharing the food when attacked is the optimal strategy that should be used by animals. The non-aggressive strategy where animals do not challenge other animals but share their food when challenged can never be an ESS since depending on the ecological parameters this strategy is always invaded either by the Dove or the Attacking Sharer strategy. This adds one possible ESS to the model of Broom et al. (2004). Investigation of the model suggests that under any ecological parameters, there is always at least one ESS that an animal can use. Every two ESSs can occur as ESSs simultaneously, apart from the Retaliator and the Hawk strategy where it is shown that they can never be ESSs simultaneously. It is also possible that under some conditions there are three simultaneous ESSs (Retaliator, Marauder and Attacking Sharer or Marauder, Attacking Sharer and Hawk).

Different ecological factors might influence the strategic choice of food sharing. Food availability is one of the crucial factors. In conditions of limited food, the use of the Attacking Sharer strategy is enhanced while at high food densities, food sharing becomes a less profitable strategy. A high time cost of food defence, a small probability of a successful food defence, a high rate at which searchers encounter handlers, a high population density and a low time cost of food sharing are also conditions which favour animals sharing their food. In the special case where food sharing has no additional time cost, foraging animals should almost always attempt to share food with a handler and handlers should almost always share their food. Defending the food might be the optimal strategy for the owner, especially when food is difficult to be discovered, and the success of this is likely. Moreover, attacking at every opportunity and defending when attacked is an ESS in just very few cases, where the time cost of the defence is small, but never attack and always defend might be an ESS even if the defence will result in a high time cost. Attack and always retreat when attacked never occurs in this case since sharing is always a better strategy.

Food sharing is a complicated mechanism. Different animal species share their food for different reasons and under different ecological and biological conditions. In many situations, food sharing is a voluntary process where animals choose to share their food without any kind of menace from other foraging animals coming before. This process might result to immediate benefits for animals, for example the creation of cooperation for the increase of foraging success or predation avoidance, or to increase mating opportunities (see Stevens and Gilby, 2004). It is also often the case that sharing occurs between relatives or between animals with a social interaction, even if those animals are not relatives e.g. between roost mates (Wilkinson, 1990). As a result, food sharing might not be immediately beneficial but result in long term benefits such as future reciprocal sharing, i.e. altruism (see Stevens and Gilby, 2004). In the present model, food sharing is considered to be the process where a food owner shows tolerance to an attacking animal and shares its food with it, although it would be better for the owner not to be discovered by any other animal. This animal behaviour might occur in cases where a beggar challenges a food owner, a situation which is observed in monkeys and chimpanzees populations (see Stevens and Gilby (2004) for examples of this behaviour). The particularity of this model compared to other models in the literature, is that by sharing food, the two animals protect each other from potential subsequent costly challenges that might extend the time until the consumption of a food item. Hence, on average a half of the food item is consumed without the risk of other delays apart from the time required for sharing. This, under certain conditions, might be the least costly process with respect to the expected time needed for the consumption of food and thus a process which maximises the food intake rate. Although there is no empirical data to support precisely the above assumptions, there is evidence that in nature, animals in many cases prefer to share food with other animals to reduce the risk of losing the entire prey. For example, a lion instead of defending its prey against an approaching member of the pride, it might share it in order to increase the efficiency of defending the prey from invading hyenas (see for example, Cooper, 1991; Stevens and Gilby, 2004).

In addition, our model assumes that the members of the population are of the same type. However, real populations consist of individuals with biological and physiological differences and the optimal strategic choices depend on the characteristics of the individuals and those of their opponent. For example, recent observational and experimental studies on the dung roller beetle *Canthon cyanellus cyanellus* have shown that males of similar size are more likely to share the resource rather than to defend it (Chamorro-Florescano et al., 2010). Fight duration may be correlated with the differences between the opponents as well (e.g., Rovero et al., 2000). The size and the quality of the food items or the estimation of the value of the resource might also affect significantly the frequency of food sharing (see for example, White, 1994) as well as a contest duration (see for example, Enquist and Leimar, 1987).

In our model all costs are expressed in terms of time used and we ignore other costs which can be important, such as energy costs and possible injuries resulting from fights (for a model which incorporates energy costs see Vahl, 2006). For simplicity we do not impose extra time penalties on animals in contests. A resulting limitation is that the winner and the loser of a contest face the same cost. Although this can be the case in nature (e.g., Smith and Taylor, 1993), experimental studies have shown that either the loser (e.g., Chellapa and Hungtingford, 1989; Neat et al., 1998) or the winner (e.g., Hack, 1997) might suffer higher energetic or other cost, such as a high recovery time cost (see also, Luther and Broom, 2004). For instance, if the handler uses more energy (e.g. because it is carrying a food item during the contest) then it might need a higher recovery time. This would decrease the food intake rate making the defending strategy less attractive and the choice of alternative strategies more likely. In the same way, although it is assumed that the cost from the sharing process is equal for the two animals that share food, in reality the two animals might suffer a different cost. Furthermore, it is assumed that once an animal loses a contest with another animal, it does not initiate a new fight with the same animal but starts searching for alternative food resources. This is generally reasonable, as often contests between animals can have strong (at least short-term) effects on their relationship (winner and loser effects) which reinforce the dominance of the winner (see for example, Dugatkin, 1997). Similarly, in related contests between animals for territory acquisition animals that lose an agonistic interaction often leave the areas in which they were defeated (see for example, Stamps and Krishnan, 1994). However, we should note that in some cases an animal may attack repeatedly the owner after iterated losing tries (e.g., Stamps, 1994). One way that the model could be extended and relax this assumption, is to allow the loser animal to attack repeatedly the winner. This could be done, for example, by introducing the choice to the loser to attack again or not, following similar assumptions to those in some owner-intruder type of games (e.g., Morrell and Kokko, 2003).

In natural systems, foraging animals might be faced with more than one foraging option with different variance in food intake. For example, they might be faced with a constant food resource versus a variable food resource, a food resource with fixed delay versus the same food resource with variable delay, or an immediate gain of food versus a delayed gain. There is strong empirical evidence that a forager's choice may depend on many ecological factors, such as the energetic status of the animal, the type of food variance, the energy requirements of the animal within a certain time interval and the probability of delays due to different kind of unpredictable interruptions (for example bad weather). The forager might be either risk-averse and choose the predictable option, or risk-prone and choose a risky option, respectively (see for example, Kacelnik and Bateson, 1996). For example, an animal with low food reserves might choose a safe lower level of return, provided it was sufficient for survival. Food sharing might be a way for animals to reduce such variances in food intake (e.g., Wenzel and Pickering, 1991). Although the present model does not consider any risk associated with alternative food sources, it would be interesting to incorporate in future work such parameters that might influence the foraging decisions.

Further research taking into consideration all these different factors will help us to better understand the reasons why and the conditions under which animals prefer to share their food.

Appendix A

The densities of the different groups of the population, $\boldsymbol{S}, \boldsymbol{H}, \boldsymbol{C}, \boldsymbol{A}$ and $\boldsymbol{R}$, in the equilibrium conditions

In the equilibrium conditions

$$\frac{dS}{dt} = \frac{dH}{dt} = \frac{dC}{dt} = \frac{dA}{dt} = \frac{dR}{dt} = 0. \tag{14}$$

From the equation

$$\frac{dC}{dt} = 2p_1p_2\nu_h SH - \frac{1}{t_c}C = 0, \tag{15}$$

it follows that in the equilibrium, the number of sharers is given by

$$C = 2p_1p_2t_c\nu_h SH. \tag{16}$$

Similarly, from the equations

$$\frac{dA}{dt} = \frac{dR}{dt} = 0, \tag{17}$$

it is derived that the number of attackers and defenders in the equilibrium is given by

$$A = R = \frac{p_1p_3t_a\nu_h SH}{2}. \tag{18}$$

Substituting equations (16) and (18) into the system of equations

$$\frac{dS}{dt} = \frac{dH}{dt} = 0, \tag{19}$$

and solving the system for S using equation (6), it is obtained that in the equilibrium, the densities of the different groups of the population, S, H, C, A and R, are given by (7).

Appendix B

Average time for a single animal to consume a food item

Average time for a single searcher animal to consume a food item when encountering a handler animal

Assume that a mutant searcher playing (q_1, q_2, q_3) has just come upon a handler playing the population strategy, (p_1, p_2, p_3). If the mutant searcher ignores the handler, with probability $1 - q_1$, then it will need an average time T^*_{S} until the consumption of a food item. Otherwise, if the mutant attacks, with probability q_1, the average time needed for the consumption of a food item depends on the action that the handler animal will take. If the handler decides to share the food, with probability p_2, then the further expected time required to the consumption of a whole food item by the mutant is T^*_{C}. If the attacked handler decides to defend its food, with probability p_3, then a fight takes place and the attacking mutant will need an average time T^*_{A} to acquire and consume a food item. Finally, if the attacked animal decides to leave its food to the attacking animal without taking any action, with probability $1 - p_2 - p_3$, the attacking searcher animal becomes a handler and it then requires an average time T^*_{H} until the consumption of a food item. T^*_{SA} is given by the following equation

$$T^*_{\mathrm{SA}} = q_1\big(p_2 T^*_{\mathrm{C}} + p_3 T^*_{\mathrm{A}} + (1 - p_2 - p_3) T^*_{\mathrm{H}}\big) + (1 - q_1) T^*_{\mathrm{S}}. \tag{20}$$

Recall that we assume that two animals that share a food item do so equally. Each of the sharers needs a time t_c until consumption of the half of the food and once it consumes it, it returns to the searching state. From the searching state, the mutant needs a time on average equal to T^*_{S} in order to consume a whole food item. The average time needed for a mutant sharer to consume a whole food item, T^*_{C}, is given by

$$T^*_{\mathrm{C}} = t_c + \frac{T^*_{\mathrm{S}}}{2}. \tag{21}$$

The sharing process described above is, in terms of expected reward, entirely equivalent to a process where if a searcher and a handler decide to share the food, at the end of the sharing period, with probability 0.5 one of the two animals obtains the food item while the other takes nothing. The loser then has to resume searching for a new food resource and thus spend an average time T_{S}^{*} until the consumption of a food item. Both animals suffer a time cost from the sharing process equal to t_c. Hence, the time that a sharer needs for the consumption of a food item is on average equal to $0.5t_c + 0.5(t_c + T_{\mathrm{S}}^{*})$, which leads to (21).

Substituting (21) into (20) we obtain

$$T_{\mathrm{SA}}^{*} = q_1\big(p_2 t_c + p_3 T_{\mathrm{A}}^{*} + (1 - p_2 - p_3)T_{\mathrm{H}}^{*}\big) + \Big(1 - q_1 + \frac{q_1 p_2}{2}\Big) T_{\mathrm{S}}^{*}. \tag{22}$$

An attacker animal which has just been involved in a fight will have a cost of an average time $t_a/2$ spent in the contest. With probability $1-\alpha$ the attacker loses the fight and starts searching again for food while with a complementary probability α, it beats the defender and acquires the food item. Thus, T_{A}^{*} is given by the following equation

$$T_{\mathrm{A}}^{*} = \frac{t_a}{2} + (1-\alpha)T_{\mathrm{S}}^{*} + \alpha T_{\mathrm{H}}^{*}. \tag{23}$$

A searcher animal is looking either for a food resource or a handler animal. At this stage, it spends an average time equal to $1\big/(\nu_f f + \nu_h H)$ before it finds either an unattended food item (this happens with probability $\nu_f f\big/(\nu_f f + \nu_h H)$) and becomes a handler or a handler animal (with probability $\nu_h H\big/(\nu_f f + \nu_h H)$). Thus, T_{S}^{*} is given by the following equation

$$T_{\mathrm{S}}^{*} = \frac{\nu_h H}{\nu_f f + \nu_h H} T_{\mathrm{SA}}^{*} + \frac{\nu_f f}{\nu_f f + \nu_h H} T_{\mathrm{H}}^{*} + \frac{1}{\nu_f f + \nu_h H}. \tag{24}$$

Once the searcher animal acquires a food item, it either consumes it without being found by any searcher animal, with probability $(1/t_h)\big/((1/t_h) + \nu_h S)$, or it is discovered by a searcher, with probability $\nu_h S\big/((1/t_h) + \nu_h S)$, resulting in an additional expected time cost T_{HA}^{*} until the consumption of a food item. The average time that the animal is at the handling state before it either consumes its food item or is discovered by a searcher animal is equal to $1/((1/t_h) + \nu_h S)$. T^*_{H} is thus given by

$$T^*_{\mathrm{H}} = \frac{1}{1 + t_h \nu_h S} 0 + \frac{t_h \nu_h S}{1 + t_h \nu_h S} T^*_{\mathrm{HA}} + \frac{t_h}{1 + t_h \nu_h S}. \tag{25}$$

Substituting equations (23), (24) and (25) into (22), after some calculations we obtain equation (10).

Average time for a single handler animal to consume a food item when encountering a searcher animal in an aggressive population

If a mutant animal at the handling state is attacked by a searcher animal playing the population strategy, with a non-zero probability ($p_1 \neq 0$), then T^*_{HA} is given by the following equation

$$T^*_{\mathrm{HA}} = p_1 \big(q_2 T^*_{\mathrm{C}} + q_3 T^*_{\mathrm{R}} + (1 - q_2 - q_3) T^*_{\mathrm{S}} \big) + (1 - p_1) T^*_{\mathrm{H}}, \tag{26}$$

where T^*_{R} is the average time cost of the decision of a mutant handler to defend its food against a challenge. Substituting (21) into (26) we obtain

$$T^*_{\mathrm{HA}} = p_1 \left(q_2 t_c + q_3 T^*_{\mathrm{R}} + \left(1 - \frac{q_2}{2} - q_3 \right) T^*_{\mathrm{S}} \right) + (1 - p_1) T^*_{\mathrm{H}}. \tag{27}$$

In a similar way as before, T^*_{R} is given by

$$T^*_{\mathrm{R}} = \frac{t_a}{2} + \alpha T^*_{\mathrm{S}} + (1 - \alpha) T^*_{\mathrm{H}}. \tag{28}$$

Substituting equations (24), (25) and (28) into (27), we obtain (11).

Average time for a single handler animal to consume a food item in a non-aggressive population

In the case where all the members of the population do not challenge, i.e. $p_1 = q_1 = 0$, but occasionally a challenge might occur, the average time needed for an attacked handler mutant playing $(0, q_2, q_3)$ to consume a food item, T^*_{HA}, is given by

$$T^*_{\mathrm{HA}} = q_2\left(t_c + \frac{T^*_{\mathrm{S}}}{2}\right) + q_3 T^*_{\mathrm{R}} + (1 - q_2 - q_3)T^*_{\mathrm{S}}, \tag{29}$$

where T^*_{R} is given by equation (28). Since the population is not making challenges, $T^*_{\mathrm{S}} = \frac{1}{\nu_f f} + t_h$ and $T^*_{\mathrm{H}} = t_h$. Substituting into equation (29), we obtain (12).

Appendix C

The optimal strategy is always pure

In the present model, there are 21 possible groups of strategies that an animal can play, 6 of which consist of pure strategies and 15 of mixed strategies. These are summarised in Table 5.

Strategies denoted by (*) in Table 5, are strategies with $p_2 = 0$, that is, strategies where animals never share their food. In this case, the model reduces to the model considered in Broom et al. (2004). In this paper, the authors have shown that the mean time required for a searcher animal that has just encountered a handler to consume a food item is a strictly monotonic function (except with the possible exception of a non-generic parameter set, see below) of the probability with which the searcher attacks the handler, p_1. Therefore, depending on the parameter values, the searcher animal minimises the time it needs for the consumption of a food item by playing either $p_1 = 0$ or $p_1 = 1$. Any other strategy $0 < p_1 < 1$ results in a higher expected time and thus cannot be evolutionarily stable. Similarly, it has been shown that the average time needed for a handler to consume a food item after being attacked by a searcher is either a strictly increasing or a strictly decreasing function of p_3 and therefore the optimal strategy is always either $p_3 = 0$ or $p_3 = 1$, depending on the parameter values.

Strategies denoted by (**) are the two additional to the Broom et al. (2004) model pure strategies where $p_2 = 1$, i.e. the strategies where animals always share their food when other animals attack. It has been shown in the present paper that under certain conditions one of these can be an ESS, the other not.

In the case where none of the animals of the population behave aggressively, i.e.

$p_1 = q_1 = 0$ (strategies denoted by (***) in Table 5), the average time required for an attacked mutant handler that plays strategy (q_1, q_2, q_3) to consume a food item, T^*_{HA}, is a function of the form (see equation (12))

$$T^*_{\mathrm{HA}} = c_1 q_2 + c_2 q_3 + c_3, \tag{30}$$

where c_1, c_2 and c_3 depend only on the parameters of the model $t_a, t_h, t_c, \nu_f f$ and α. Hence, if the values of the parameters are such that c_1 and c_2 are both greater than zero, then the optimal strategy for the mutant is $q_2 = q_3 = 0$. In any other case, if $c_1 < c_2$, the optimal strategy is $q_2 = 1$ and $q_3 = 0$ while if $c_1 > c_2$ the optimal strategy is $q_2 = 0$ and $q_3 = 1$.

It remains to consider whether any of the strategies (S 1)–(S 7) is an ESS. Due to the complexity of the mathematical formulae, an analytic investigation is very difficult. Hence, we consider whether each of the remaining strategies is an ESS mainly through extensive numerical investigation.

Regarding strategies (S 1), from equation (22) we get that in a population which plays strategy $(0 < p_1 < 1, 1, 0)$,

$$T^*_{\mathrm{SA}}(0,1,0) = T^*_{\mathrm{S}}(0,1,0), \tag{31}$$

while

$$T^*_{\mathrm{SA}}(1,1,0) = T^*_{\mathrm{C}}(1,1,0) = t_c + \frac{T^*_{\mathrm{S}}(1,1,0)}{2}. \tag{32}$$

If there is any equilibrium strategy $(p_1^*, 1, 0)$ in (S 1), then $T_{\mathrm{SA}}(p_1^*, 1, 0)$ should be equal to $T^*_{\mathrm{SA}}(0,1,0)$ and $T^*_{\mathrm{SA}}(1,1,0)$. But when $T^*_{\mathrm{SA}}(0,1,0) = T^*_{\mathrm{SA}}(1,1,0)$ then $T^*_{\mathrm{S}}(0,1,0) = T^*_{\mathrm{S}}(1,1,0)$. Hence, equating equations (31) and (32) we get

$$T^*_{\mathrm{S}}(0,1,0) = T^*_{\mathrm{S}}(1,1,0) = T_{\mathrm{S}}(p_1^*, 1, 0) = 2t_c. \tag{33}$$

On the other hand, if the strategy $(p_1^*, 1, 0)$ is an equilibrium strategy, then it cannot be invaded by the mutant strategy $(p_1^*, 0, 0)$, i.e. the average required time for the mutant handler that has just been attacked in a population which plays strategy $(p_1^*, 1, 0)$,

$T^*_{\mathrm{HA}}(p^*_1, 0, 0)$, is higher than the average time required when playing the population strategy, $T_{\mathrm{HA}}(p^*_1, 1, 0)$. Using equation (27) we find that

$$T^*_{\mathrm{HA}}(p^*_1, 0, 0) > T_{\mathrm{HA}}(p^*_1, 1, 0) \tag{34}$$

$$\Rightarrow T^*_{\mathrm{S}}(p^*_1, 0, 0) > T_{\mathrm{C}}(p^*_1, 1, 0) \Rightarrow T^*_{\mathrm{S}}(p^*_1, 0, 0) = T_{\mathrm{S}}(p^*_1, 1, 0) > 2t_c. \tag{35}$$

This contradicts (33). Consequently, there is no any equilibrium strategy $(0 < p_1 < 1, 1, 0)$. This is also verified from the results of numerical examples for a wide range of parameter values (see Figure 6a for an example).

In a similar way it is proved that there is no equilibrium strategy in the class of strategies (S 6). If there was an equilibrium strategy $(0 < p^*_1 < 1, 0 < p^*_2 < 1, 0 < p^*_3 < 1)$, $p^*_2 + p^*_3 < 1$, then $T^*_{\mathrm{HA}}(p^*_1, 0, 0)$, $T^*_{\mathrm{HA}}(p^*_1, 1, 0)$ and $T^*_{\mathrm{HA}}(p^*_1, 0, 1)$ should all be identical, otherwise one of the strategies $(p^*_1, 0, 0)$, $(p^*_1, 1, 0)$, $(p^*_1, 0, 1)$ could invade (p^*_1, p^*_2, p^*_3). In this case, using equations (27) and (28) we find that

$$T_{\mathrm{S}}(p^*_1, p^*_2, p^*_3) - T_{\mathrm{H}}(p^*_1, p^*_2, p^*_3) = \frac{1}{1-\alpha}\frac{t_a}{2}. \tag{36}$$

On the other hand, if (p^*_1, p^*_2, p^*_3) is an equilibrium strategy, then $T^*_{\mathrm{SA}}(p^*_1, p^*_2, p^*_3) = T^*_{\mathrm{SA}}(1, p^*_2, p^*_3) = T^*_{\mathrm{SA}}(0, p^*_2, p^*_3)$ which yields that $T^*_{\mathrm{SA}}(1, p^*_2, p^*_3) = T^*_{\mathrm{S}}(0, p^*_2, p^*_3) = T^*_{\mathrm{S}}(1, p^*_2, p^*_3) = T^*_{\mathrm{S}}(p^*_1, p^*_2, p^*_3)$. Substituting into equation (24) we obtain that

$$T^*_{\mathrm{S}}(p^*_1, p^*_2, p^*_3) - T^*_{\mathrm{H}}(p^*_1, p^*_2, p^*_3) = \frac{1}{\nu_f f}. \tag{37}$$

Hence, if a strategy of the (S 6) class is an equilibrium strategy, then (36) and (37) must hold. This leads to

$$1 - \alpha = \nu_f f \frac{t_a}{2}. \tag{38}$$

i.e. that the probability of a challenger losing a fight is equal to the ratio of the expected duration of the fight and the mean time searching for food. These are all biologically-determined parameters, and we assume that the chance of their precise coincidence in this way is negligible (i.e. the case is non-generic). Thus, for example, such a case would correspond to a region of zero area in Figure 4, equivalent to the boundary lines.

Numerical investigation also indicates that mixed strategies are always invaded and so there are no mixed ESSs in the classes (S 4), (S 5) and (S 7).

Concerning strategies (S 2) and (S 3), numerical examples on a wide range of parameter values also imply that for every value of p_2, $0 < p_2 < 1$, strategies $(0 < p_1 < 1, p_2, 0)$ can always be invaded either by strategy $(0, p_2, 0)$ or by strategy $(1, p_2, 0)$. On the other hand, numerical examples indicate that for given p_1^*, $0 < p_1^* \leq 1$, there is a strategy p_2^*, $0 < p_2^* < 1$, such that for specific values of parameters all the invading strategies $(p_1^*, 0 \leq q_2 \leq 1, 0)$ do equally well in a population playing $(p_1^*, p_2^*, 0)$, i.e. $T_{\mathrm{HA}}(p_1^*, p_2^*, 0) = T_{\mathrm{HA}}^*(p_1^*, 0 \leq q_2 \leq 1, 0)$, while any other strategy does worse. Any other population playing a different strategy $(p_1^*, 0 < p_2 < 1, 0)$, $p_2 \neq p_2^*$, can be invaded either by the strategy $(p_1^*, 0, 0)$ or the strategy $(p_1^*, 1, 0)$ (see Figure 6b for an example). However, in a population which plays a strategy $(p_1, 0 \leq q_2 \leq 1, 0)$, the required time for an attacked handler playing the population strategy, $T_{\mathrm{HA}}(p_1, 0 \leq q_2 \leq 1, 0)$, is less than that required by an attacked handler playing $(p_1^*, p_2^*, 0)$. In other words, if an infinitesimal portion of the population deviates from the equilibrium strategy, the evolution will drive away the population from that equilibrium. Thus, according to the second condition of Maynard Smith and Price (Maynard Smith and Price, 1973) for a strategy to be an ESS, the strategies $(p_1^*, p_2^*, 0)$ cannot be ESS. Hence, none of the strategies (S 2) and (S 3) can be evolutionarily stable.

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Table 1
The model notations

Population's densities	**Meaning**
P	Density of the population
S, H, C, A, R	Density of searchers, handlers, sharers, attackers and defenders
Model Parameters	**Meaning**
$\nu_f f$	Rate at which foragers find undiscovered food
$\nu_h H$	Rate at which foragers encounter handlers
t_h	Expected time for a handler to consume a food item if it is not attacked
t_c	Expected time for a sharer to consume the half of a food item
$t_a/2$	Expected duration of a fight
α	The probability that the attacker wins the fight
Strategies	**Meaning**
p_1	The probability that a searcher attacks a handler when they meet
p_2	The probability that an attacked handler shares its food item
p_3	The probability that an attacked handler defends its food item

Table 2
Notations of the required times to the consumption of a food item from the different foraging states

Notation	Meaning
T_{SA}	The average time needed for a searcher animal who has just encountered a handler to acquire and consume a food item
T_{HA}	The average time needed for a handler animal who has just encountered a searcher to consume a food item
T_{S}	The average time needed for an animal who has just become a searcher to acquire and consume a food item
T_{H}	The average time needed for an animal who has just become a handler to consume a food item
T_{A}	The average time needed for an attacker who has just engaged in a fight to acquire and consume a food item
T_{R}	The average time needed for a defender who has just engaged in a fight to consume a food item
T_{C}	The average time needed for a sharer to consume a food item

Table 3
Conditions under which a mutant playing strategy (q_1, q_2, q_3) cannot invade a population playing strategy (p_1, p_2, p_3)

		Mutant's strategy, (q_1, q_2, q_3)					
		(0,0,0)	(0,1,0)	(0,0,1)	(1,0,0)	(1,1,0)	(1,0,1)
Population's strategy, (p_1, p_2, p_3)	(0,0,0)	/	$2t_c - t_h > \frac{1}{\nu_f f}$ (**C.1**)	$\nu_f f > \frac{2(1-\alpha)}{t_a}$ (**C.2**)	The mutant always invades (**C.3**)	—	—
	(0,1,0)	$2t_c - t_h < \frac{1}{\nu_f f}$ (**C.4**)	/	$2t_c - t_h < t_a - \frac{1-2\alpha}{\nu_f f}$ (**C.5**)	—	$2t_c - t_h > \frac{1}{\nu_f f}$ (**C.6**)	—
	(0,0,1)	$\nu_f f < \frac{2(1-\alpha)}{t_a}$ (**C.7**)	$2t_c - t_h > t_a - \frac{1-2\alpha}{\nu_f f}$ (**C.8**)	/	—	—	$\nu_f f > \frac{2\alpha}{t_a}$ (**C.9**)
	(1,0,0)	The mutant never invades (**C.10**)	—	—	/	$2t_c - t_h > \frac{1}{\nu_f f}$ (**C.11**)	$\nu_f f > \frac{2(1-\alpha)}{t_a} - \frac{t_h \nu_f f \nu_h P}{t_h \nu_f f + 1}$ (**C.12**)
	(1,1,0)	—	$2t_c - t_h < \frac{1}{\nu_f f - \nu_h H_a}$ * (**C.13**)	—	$2t_c - t_h < \frac{1}{\nu_f f - \nu_h H_a}$ * (**C.14**)	/	$(2t_c - t_h)(\nu_f f - \alpha \nu_h H_a)\nu_f f <$ $(t_a \nu_f f + \alpha)\nu_f f + (1-\alpha)\big((t_h \nu_h P -$ $1)\nu_f f - (\nu_f f + \nu_h P) t_h \nu_h H_a\big)$ * (**C.15**)
	(1,0,1)	—	—	$\nu_f f < \frac{2\alpha}{t_a}$ (**C.16**)	$\nu_f f < \frac{2(1-\alpha)}{t_a} + (1-2\alpha)\nu_h H_b$ ** (**C.17**)	$(2t_c - t_h)(\nu_f f + \alpha \nu_h H_b) >$ $t_a(\nu_f f + 2\alpha \nu_h H_b) +$ $\alpha t_h(\nu_h P - \nu_h H_b) + 2\alpha - 1$ ** (**C.18**)	/

*H_a is given by the solution of the equation $(2t_c - t_h)\nu_h H_a^2 + (t_h \nu_f f + t_h \nu_h P + 1)H_a - t_h \nu_f f P = 0$.

**H_b is given by the solution of the equation $t_a \nu_h H_b^2 + (t_h \nu_f f + 1)H_b - t_h \nu_f f P = 0$.

Table 4
Conditions under which a mutant playing strategy (q_1, q_2, q_3) cannot invade a population playing strategy (p_1, p_2, p_3) in the special case where $2t_c = t_h$

		Mutant's strategy, (q_1, q_2, q_3)					
		(0,0,0)	(0,1,0)	(0,0,1)	(1,0,0)	(1,1,0)	(1,0,1)
Population's strategy, (p_1, p_2, p_3)	(0,0,0)	/	The mutant always invades	$\nu_f f > \frac{2(1-\alpha)}{t_a}$	The mutant always invades	—	—
	(0,1,0)	The mutant never invades	/	$\nu_f f > \frac{1-2\alpha}{t_a}$	—	The mutant always invades	—
	(0,0,1)	$\nu_f f < \frac{2(1-\alpha)}{t_a}$	$\nu_f f < \frac{1-2\alpha}{t_a}$	/	—	—	$\nu_f f > \frac{2\alpha}{t_a}$
	(1,0,0)	The mutant never invades	—	—	/	The mutant always invades	$\nu_f f > \frac{2(1-\alpha)}{t_a} - \frac{t_h \nu_f f \nu_h P}{t_h \nu_f f + 1}$
	(1,1,0)	—	The mutant never invades	—	The mutant never invades	/	$(t_a \nu_f f + \alpha)(t_h \nu_f f + t_h \nu_h P + 1) - (1-\alpha)(t_h \nu_f f + 1) > 0$
	(1,0,1)	—	—	$\nu_f f < \frac{2\alpha}{t_a}$	$\nu_f f < \frac{2(1-\alpha)}{t_a} + (1-2\alpha)\nu_h H_b$ *	$t_a(\nu_f f + 2\alpha \nu_h H_b) + \alpha t_h(\nu_h P - \nu_h H_b) + 2\alpha - 1 < 0$ *	/

*H_b is given by the solution of the equation $t_a \nu_h H_b^2 + (t_h \nu_f f + 1)H_b - t_h \nu_f f P = 0$.

Table 5
Possible ESSs

		Strategy at the handling state, p_2, p_3						
		$p_2 = 1$ $p_3 = 0$	$p_2 = 0$ $p_3 = 1$	$p_2 = p_3 = 0$	$p_2 = 0$ $0 < p_3 < 1$	$0 < p_2 < 1$ $p_3 = 0$	$0 < p_2 < 1$ $0 < p_3 < 1$ $p_2 + p_3 = 1$	$0 < p_2 < 1$ $0 < p_3 < 1$ $p_2 + p_3 < 1$
Strategy at the searching state, p_1	$p_1 = 0$	**	*	*	*	***	***	***
	$0 < p_1 < 1$	S 1	*	*	*	S 2	S 4	S 6
	$p_1 = 1$	**	*	*	*	S 3	S 5	S 7

Figure legends

Figure 1: Schematic representation of all the possible events that might happen until the consumption of a food item by a mutant searcher playing strategy (q_1, q_2, q_3) who encounters a handler of a population playing strategy (p_1, p_2, p_3). The transition probabilities and the expected times (in bold) to move from one state to another are shown.

Figure 2: Schematic representation of all the possible events that might happen until the consumption of a food item by a mutant handler playing strategy (q_1, q_2, q_3) who encounters a searcher of a population playing strategy (p_1, p_2, p_3). The transition probabilities and the expected times (in bold) to move from one state to another are shown.

Figure 3: Graphs showing examples of the region where each of the four possible ESSs (Retaliator (R), Marauder (M), Attacking Sharer (AS) and Hawk (H)) is an ESS as the duration of the content, $t_a/2$, and the handling time of a sharer, t_c, vary. In each region, a single letter 'X' indicates that the strategy X is the unique ESS, 'X,Y' indicates that the strategies X and Y are simultaneous ESSs and 'X, Y, Z' that the three strategies X, Y and Z are simultaneous ESSs. (a) $t_h = 3, \nu_f f = 0.5, \nu_h = 1.5, \alpha = 0.7, P = 1$; (b) $t_h = 3, \nu_f f = 1, \nu_h = 2, \alpha = 0.2, P = 1$.

Figure 4: Graphs showing examples of the region where each of the four possible ESSs (Retaliator (R), Marauder (M), Attacking Sharer (AS) and Hawk (H)) is an ESS as the density of the population, P, and the rate at which foragers find undiscovered food, $\nu_f f$, vary. In each region, a single letter 'X' indicates that the strategy X is the unique ESS, 'X,Y' indicates that the strategies X and Y are simultaneous ESSs and 'X, Y, Z' that the three strategies X, Y and Z are simultaneous ESSs. (a) $t_a/2 = 0.5, t_h = 3, t_c = 4, \nu_h = 1.5, \alpha = 0.7$; (b) $t_a/2 = 0.5, t_h = 3, t_c = 2, \nu_h = 2, \alpha = 0.2$.

Figure 5: A graph showing an example of the region where each of the three possible ESSs (Retaliator (R), Attacking Sharer (AS) and Hawk (H)) can occur in the special case where $2t_c = t_h$, as the probability α of the challenger winning and the duration of the content, $t_a/2$, vary. In each region, a single letter 'X' indicates that the strategy X is the unique ESS, 'X,Y' indicates that the strategies X and Y are simultaneous ESSs and 'X, Y, Z' that the three strategies X, Y and Z are simultaneous ESSs. $2t_c = t_h = 3, \nu_f f = 0.5, \nu_h = 1.5, P = 1$.

Figure 6: (a) The expected time until the consumption of a food item of mutant searcher animals playing strategies (0,1,0), (1,1,0) and $(0 < p_1 < 1, 1, 0)$ in a population playing strategy $(0 < p_1 < 1, 1, 0)$ for the example considered in Figure 3b for $t_c = 2$. Numerical examples indicate that in every population which adopts a strategy $(0 < p_1 < 1, 1, 0)$, either a mutant animal that plays strategy $(0, 1, 0)$ or a mutant animal that plays strategy $(1, 1, 0)$ always does better than any other animal that uses the population strategy. Thus, such populations can be invaded by those mutant strategies and as a result, strategies $(0 < p_1 < 1, 1, 0)$ cannot be ESSs. (b) The expected time until the consumption of a food item of mutant handler animals playing strategies (0.8,1,0), (0.8,0,0) and $(0.8, 0 < p_2 < 1, 0)$ in a population playing strategy $(0.8, 0 < p_2 < 1, 0)$ for $t_h = 3, t_c = 2, \nu_f f = 1, \nu_h = 1.5, P = 1$. An equilibrium strategy $(0 < p_1 \leq 1, 0 < p_2 < 1, 0)$ cannot be evolutionarily stable.

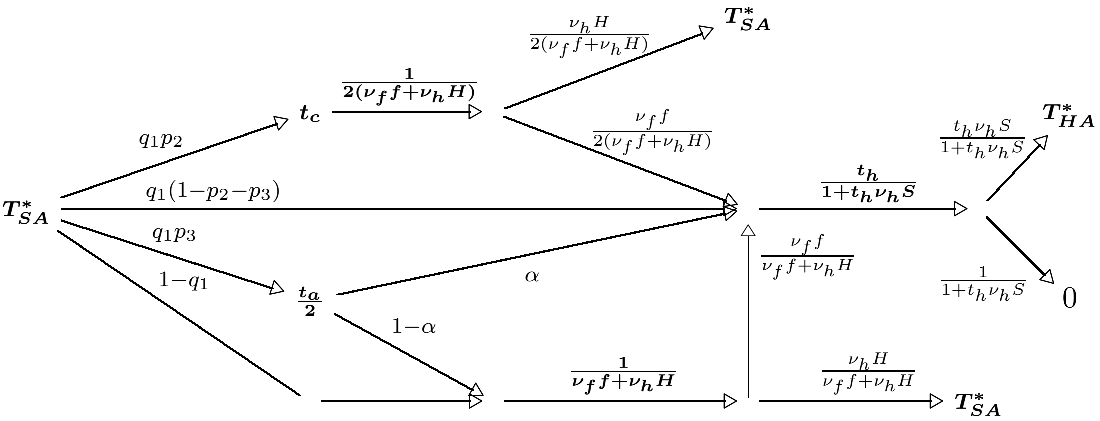


Figure 1
Schematic representation of all the possible events that might happen until the consumption of a food item by a mutant searcher playing strategy (q_1, q_2, q_3) who encounters a handler of a population playing strategy (p_1, p_2, p_3). The transition probabilities and the expected times (in bold) to move from one state to another are shown.

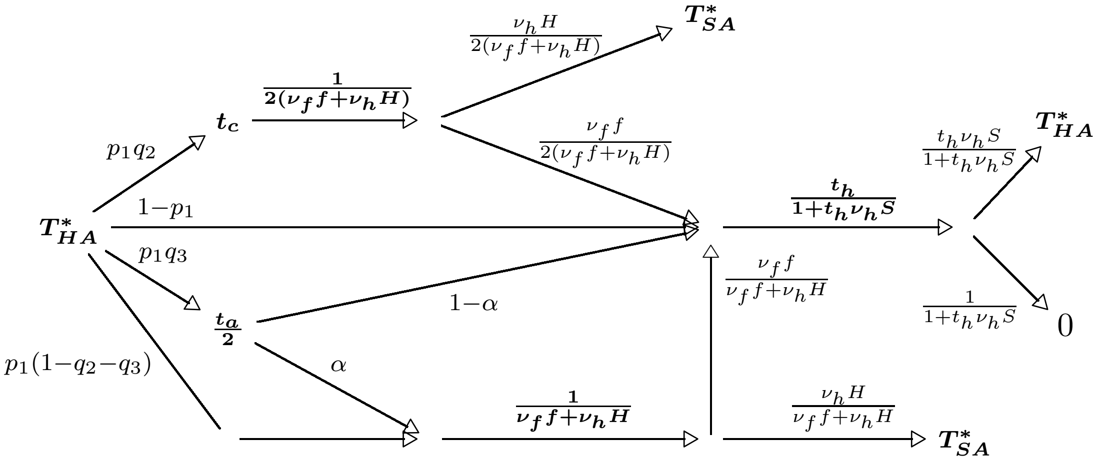


Figure 2
Schematic representation of all the possible events that might happen until the consumption of a food item by a mutant handler playing strategy (q_1, q_2, q_3) who encounters a searcher of a population playing strategy (p_1, p_2, p_3). The transition probabilities and the expected times (in bold) to move from one state to another are shown.

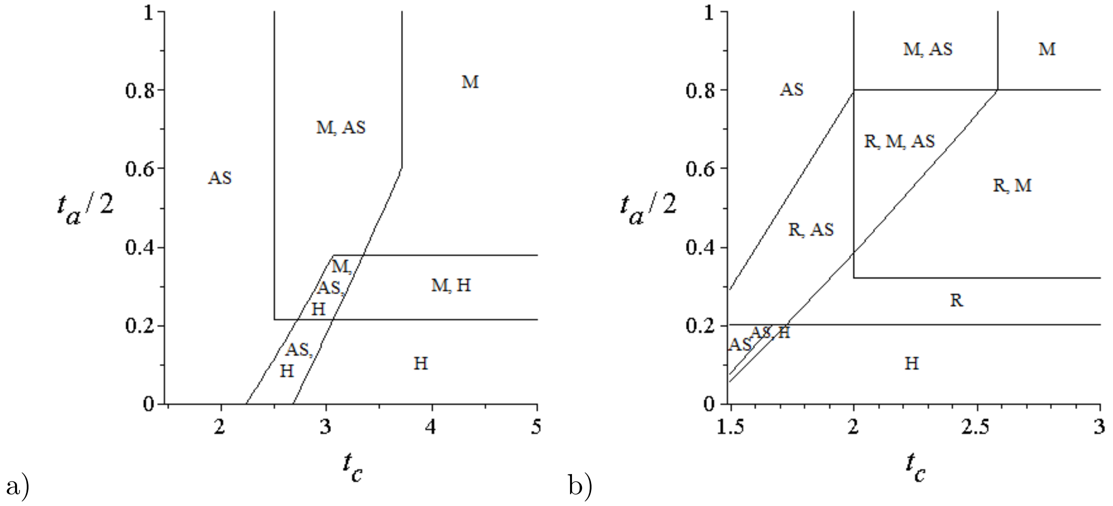


Figure 3
Graphs showing examples of the region where each of the four possible ESSs (Retaliator (R), Marauder (M), Attacking Sharer (AS) and Hawk (H)) is an ESS as the duration of the content, $t_a/2$, and the handling time of a sharer, t_c, vary. In each region, a single letter 'X' indicates that the strategy X is the unique ESS, 'X,Y' indicates that the strategies X and Y are simultaneous ESSs and 'X, Y, Z' that the three strategies X, Y and Z are simultaneous ESSs. (a) $t_h = 3, \nu_f f = 0.5, \nu_h = 1.5, \alpha = 0.7, P = 1$; (b) $t_h = 3, \nu_f f = 1, \nu_h = 2, \alpha = 0.2, P = 1$.

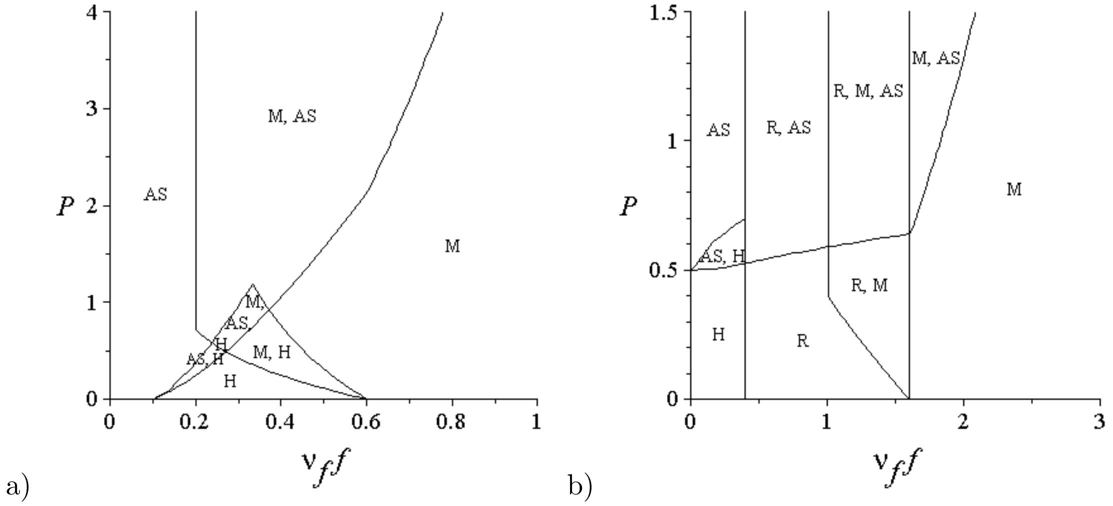


Figure 4
Graphs showing examples of the region where each of the four possible ESSs (Retaliator (R), Marauder (M), Attacking Sharer (AS) and Hawk (H)) is an ESS as the density of the population, P, and the rate at which foragers find undiscovered food, $\nu_f f$, vary. In each region, a single letter 'X' indicates that the strategy X is the unique ESS, 'X,Y' indicates that the strategies X and Y are simultaneous ESSs and 'X, Y, Z' that the three strategies X, Y and Z are simultaneous ESSs. (a) $t_a/2 = 0.5, t_h = 3, t_c = 4, \nu_h = 1.5, \alpha = 0.7$; (b) $t_a/2 = 0.5, t_h = 3, t_c = 2, \nu_h = 2, \alpha = 0.2$.

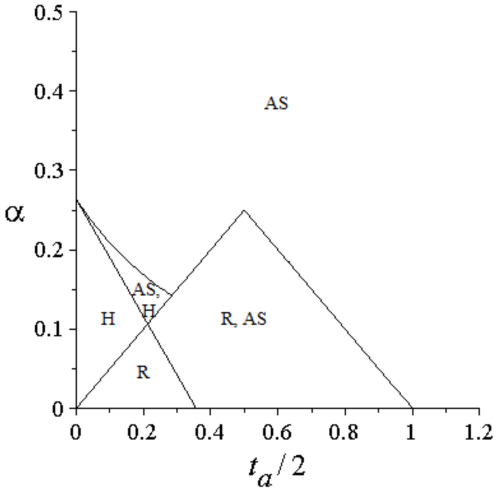
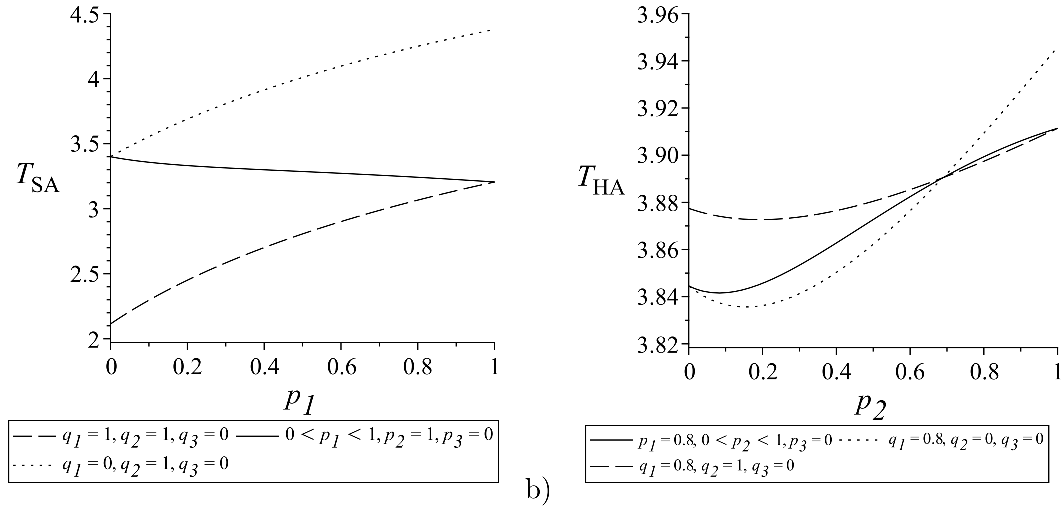


Figure 5
A graph showing an example of the region where each of the three possible ESSs (Retaliator (R), Attacking Sharer (AS) and Hawk (H)) can occur in the special case where $2t_c = t_h$, as the probability α of the challenger winning and the duration of the content, $t_a/2$, vary. In each region, a single letter 'X' indicates that the strategy X is the unique ESS, 'X,Y' indicates that the strategies X and Y are simultaneous ESSs and 'X, Y, Z' that the three strategies X, Y and Z are simultaneous ESSs. $2t_c = t_h = 3, \nu_f f = 0.5, \nu_h = 1.5, P = 1$.



a) b)

Figure 6
(a) The expected time until the consumption of a food item of mutant searcher animals playing strategies (0,1,0), (1,1,0) and $(0 < p_1 < 1, 1, 0)$ in a population playing strategy $(0 < p_1 < 1, 1, 0)$ for the example considered in Figure 3b for $t_c = 2$. Numerical examples indicate that in every population which adopts a strategy $(0 < p_1 < 1, 1, 0)$, either a mutant animal that plays strategy $(0, 1, 0)$ or a mutant animal that plays strategy $(1, 1, 0)$ always does better than any other animal that uses the population strategy. Thus, such populations can be invaded by those mutant strategies and as a result, strategies $(0 < p_1 < 1, 1, 0)$ cannot be ESSs. (b) The expected time until the consumption of a food item of mutant handler animals playing strategies (0.8,1,0), (0.8,0,0) and $(0.8, 0 < p_2 < 1, 0)$ in a population playing strategy $(0.8, 0 < p_2 < 1, 0)$ for $t_h = 3, t_c = 2, \nu_f f = 1, \nu_h = 1.5, P = 1$. An equilibrium strategy $(0 < p_1 \leq 1, 0 < p_2 < 1, 0)$ cannot be evolutionarily stable.