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

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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 behavior 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 model of food stealing, producer–scrounger models. Alternatively, food items may be essentially indivisible, so that sharing is impossible and either the attacker or the 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 behavior 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 defense 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:* ESS, evolutionary games, food stealing, strategy, social foraging. *[Behav Ecol]*

INTRODUCTION

In many biological situations, animals may decide to share their food in order to avoid 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 (for reviews, see Feistner and McGrew 1989; Stevens and Gilby 2004). 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 behavior 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 behavior 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 behavior of animals using different mathematical methods, in particular evolutionary game theory. Two of the fundamental game-theoretical models that consider kleptoparasitic behavior 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 2 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 2 strategies is such that the payoff obtained by each strategy is the same, there is a stable equilibrium where the 2 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 model is that food is usually discovered in patches and can be easily split between 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,

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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; this loss of time is the cost to more aggressive strategies, and thus, 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, 2009, 2011; Luther et al. 2007; Yates and Broom 2007; Broom et al. 2008). Crowe et al. (2009) provide a brief review on the main theoretical work on kleptoparasitism prior to the investigation of a stochastic model of kleptoparasitism in finite populations. A comparison between some main models of kleptoparasitism following the 2 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 that 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; van der Meer and Smallegange 2009; Smallegange and van der Meer 2009).

There are many game-theoretical models that investigate food sharing behavior as an alternative strategy of foraging animals in aggressive populations. 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 nonaggressive behavior. However, the Hawk–Dove game and a large number of variations of this game (e.g., Sirot 2000; Dubois et al. 2003) are unable to show why in many biological situations animals prefer to share the acquired prey avoiding any contests. The nonaggressive behavior of the Dove is shown to never be a pure evolutionarily stable strategy (ESS), that is, 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 2 strategies, the Hawk and the Dove strategy. Although the reward for adopting the Hawk strategy against an animal playing Hawk might be equal to or lower than the reward of adopting the Dove strategy, in a contest between a Hawk and a Dove the Hawk always receives the greater reward. 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 (e.g., 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 the state of searching for food or the 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 v_f per unit time whilst searching for food, so that they find food at rate $v_f f$. 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 v_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, p_3. In this case, the attacking searcher and the defender engage in a fight. Let A and R denote the density of attacking searchers and defenders, respectively. The rate at which searchers encounter handlers and engage in a fight (become attackers, A) is equal to $p_1\ p_3\ v_h\ H$, whereas handlers are found by searchers and resist a possible attack (become defenders, R) with rate $p_1\ p_3\ v_h\ S$. 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 with rate $p_1\ p_2\ v_h\ H$ and the attacked handlers with rate $p_1\ p_2\ v_h\ S$. Let C be the density of sharers. 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 of the 2 sharers hold the food item and feed simultaneously on it. This discourages other animals from attempting to steal or share the food because this would be a difficult, risky, and dangerous venture. So, food sharing results in the mutual protection of the 2 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 in a time drawn from an exponential distribution with mean t_c, or equivalently with rate t_c^{-1}. Once the halves of the food item have been consumed, sharers start foraging again. Throughout the paper, it is assumed that $2\ t_c \geq t_h$, that is, 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 from 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 $p_1\ (1 - p_2 - p_3)\ v_h\ H$ for each searcher and rate $p_1\ (1 - p_2 - p_3)\ v_h\ S$ for each handler.

Table 1
The model notation

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
$v_f\,f$	Rate at which foragers find undiscovered food
$v_h\ H$	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

It should be noted that in the case where all the members of the population do not challenge, the strategy used by an animal in the handling position may be thought irrelevant because none of the animals will ever be attacked and thus each searcher finds a food item for itself in an average time equal to $1/v_f\,f$ 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 might be faced by a foraging animal, which attempts to steal or share the food.

The model parameters and notation are summarized 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:

$$\frac{dS}{dt} = \frac{1}{t_h}H + \frac{1}{t_c}C + \frac{2}{t_a}(1-\alpha)A + \frac{2}{t_a}\alpha R - v_f f S - p_1(p_2+p_3)v_h SH, \tag{1}$$

$$\frac{dH}{dt} = v_f f S + \frac{2}{t_a}\alpha A + \frac{2}{t_a}(1-\alpha)R - \frac{1}{t_h}H - p_1(p_2+p_3)v_h SH, \tag{2}$$

$$\frac{dC}{dt} = 2p_1p_2v_hSH - \frac{1}{t_c}C, \tag{3}$$

$$\frac{dA}{dt} = p_1p_3v_hSH - \frac{2}{t_a}A, \tag{4}$$

$$\frac{dR}{dt} = p_1p_3v_hSH - \frac{2}{t_a}R. \tag{5}$$

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

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

and one of the Equations (1–5) is thus redundant. Note that because only 2 animals can be involved in a fight over a specific food item, the density of the attacking animals, A, is always equal to that of the attacked animals, R. Hence, mathematically, the variables A and R could be defined as one variable, for example, $F = A + R$, and therefore, the system of Equations (1–5) could be reduced to 4 equations. However, because the attacking and the attacked animals might have different competitive abilities ($\alpha \neq 0.5$), we distinguish the 2 classes. This distinction is useful in subsequent calculations when we consider the average time to the consumption of a food item, since when $\alpha \neq 0.5$, the time needed for the animals in each of the 2 classes is different (see OPTIMAL STRATEGIES and APPENDIX B).

We assume that the population rapidly converges to the equilibrium state (for a proof of this assumption for the original model of Broom and Ruxton 1998, see Luther and Broom 2004). 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)

$$(S,H,C,A,R) = \left(\frac{H}{t_h d(H,p_1,p_2)}, H, \frac{2p_1p_2t_cv_hH^2}{t_h d(H,p_1,p_2)}, \frac{1}{2}\frac{p_1p_3t_av_hH^2}{t_h d(H,p_1,p_2)}, \frac{1}{2}\frac{p_1p_3t_av_hH^2}{t_h d(H,p_1,p_2)}\right), \tag{7}$$

where $d(H, p_1, p_2) = v_f f - p_1 p_2 v_h H$, that is, 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 because every food item can be shared at most once (and some are not shared), and it must be discovered beforehand. By Equations 6 and 7, H is given by the biologically relevant solution of the quadratic equation

$$p_1(p_2(2t_c - t_h) + p_3t_a)v_hH^2 + (p_1p_2t_hv_hP + t_hv_ff + 1)H - t_hv_ffP = 0, \tag{8}$$

that is, the positive solution,

$$H = \frac{-(p_1p_2t_hv_hP + t_hv_ff + 1) + \sqrt{(p_1p_2t_hv_hP + t_hv_ff + 1)^2 + 4p_1t_hv_ffv_hP(p_2(2t_c - t_h) + p_3t_a)}}{2p_1v_h(p_2(2t_c - t_h) + p_3t_a)}, \tag{9}$$

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

OPTIMAL STRATEGIES

We are interested in finding conditions under which animals playing strategy (p_1, p_2, p_3), that is, animals that 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 optimal if it minimizes the average time needed to the consumption of a food item. This minimization results in the maximizing of the long-term food intake rate of an animal playing this strategy and thus its fitness.

Table 2

Notation 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 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 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 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

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 in the searching state and encounters a handler it has 2 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

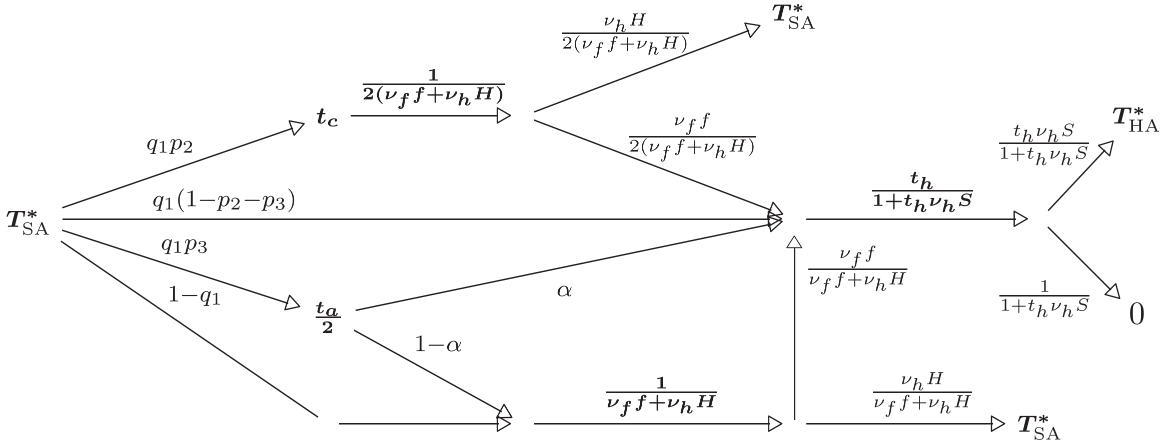

Figure 1

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.

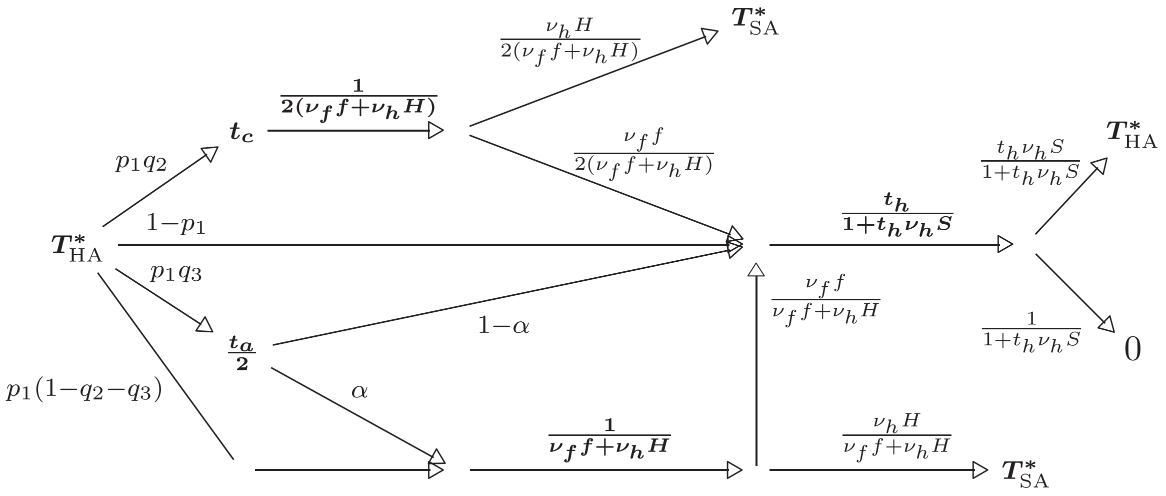

Figure 2

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.

of food consumption times from the different foraging states is shown in Table 2.

If the mutant is in the handling state and is attacked by a searcher animal playing the population strategy it has 3 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:

$$\left(1-\left(1-q_1+\frac{q_1p_2}{2}+(1-\alpha)q_1p_3\right)\frac{\nu_hH}{\nu_ff+\nu_hH}\right)T^*_{\mathrm{SA}}=q_1p_2t_c+q_1p_3\frac{t_a}{2}$$
$$+\left(1-q_1+\frac{q_1p_2}{2}+(1-\alpha)q_1p_3\right)\frac{1}{\nu_ff+\nu_hH}$$
$$+\left(\left(1-\frac{q_1p_2}{2}\right)\nu_ff+q_1(1-p_2-(1-\alpha)p_3)\nu_hH\right)\frac{t_h(1+\nu_hST^*_{\mathrm{HA}})}{(1+t_h\nu_hS)(\nu_ff+\nu_hH)}, \tag{10}$$

$$\left(1-\frac{\left(\left(1-\frac{p_1q_2}{2}\right)\nu_ff+(1-p_1+(1-\alpha)p_1q_3)\nu_hH\right)t_h\nu_hS}{(1+t_h\nu_hS)(\nu_ff+\nu_hH)}\right)T^*_{\mathrm{HA}}=p_1q_2t_c$$
$$+p_1q_3\frac{t_a}{2}+\left(\left(1-\frac{p_1q_2}{2}\right)\nu_ff+(1-p_1+(1-\alpha)p_1q_3)\nu_hH\right)$$
$$\times\frac{t_h}{(1+t_h\nu_hS)(\nu_ff+\nu_hH)}+p_1\left(1-\frac{q_2}{2}-(1-\alpha)q_3\right)\frac{1+\nu_hHT^*_{\mathrm{SA}}}{\nu_ff+\nu_hH}. \tag{11}$$

The average time required to the consumption of a food item for a single searcher animal who has just met a handler in a population where all animals play strategy (p_1, p_2, p_3), 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 none of the animals of the population challenges any other animal, that is, $p_1 = q_1 = 0$, but a challenge occasionally occurs by mistake, the average time needed for the attacked handler animal to consume a food item if it adopts a different strategy from the population, (0, q_2, q_3), is given by (see APPENDIX B)

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

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 1 of the 2 decision points, when a searcher and potentially making a challenge or when receiving a challenge as a handler. A mutant that follows a different strategy from that of the population at just one decision point and the strategy that 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 1 of the 2 decision points only. This is because if a mutant that differs 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 that 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 that uses a strategy different from that of the population at just the searching state is able to invade if $T^*_{\mathrm{SA}} \le T_{\mathrm{SA}}$, that is, if the decision that it will make at the point when it will meet a handler, when searching for food, will lead to at least as small a time until the consumption of a food item. Similarly, a mutant that 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 not lengthen the time to the consumption of a food item, that is, 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.

APPENDIX C investigates the possible existence of mixed strategy ESSs. In some cases, it is proved that at least for non-generic parameter sets, there is no mixed strategy ESS. In other cases, it is not proved but extensive numerical investigation yields results consistent with no mixed strategy ESS.

Our working assumption from these results is that there are no mixed strategy ESSs. Thus, if the population plays a nonpure 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 because this pure strategy would invade the population. Hence, we need to consider only 2 strategies for a foraging animal (always or never attempt to steal or share the prey of the other animal when the opportunities arise) and 3 strategic choices for an attacked animal (always share the food, always defend the food, or always surrender it to the attacking animal) as the components of the potential optimal strategy in any given population. Therefore, there are 6 possible pure strategies that an animal can use and need to be considered:

- Strategy (0,0,0) (Dove, D): the animal never challenges handlers and always retreats leaving the food to a challenger.
- Strategy (0,1,0) (Nonattacking Sharer, NAS): the animal never challenges handlers and always shares its food when it is challenged.
- Strategy (0,0,1) (Retaliator, R): the animal never challenges handlers but always resists when it is challenged.
- Strategy (1,0,0) (Marauder, M): the animal challenges handlers at every opportunity but always retreats leaving the food to a challenger.
- Strategy (1,1,0) (Attacking Sharer, AS): the animal challenges handlers at every opportunity and always shares the food when it is challenged.
- Strategy (1,0,1) (Hawk, H): the animal challenges handlers at every opportunity and always resists any challenges.

The optimal strategy for an animal in 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 invade 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 in the handling state is the same, that is, $p_2 = q_2$ 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 $p_2 = q_2 = 0$ 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 summarized in Table 3 (conditions (C.3), (C.6), (C.9), (C.10), (C.13), and (C.16)).

The optimal strategy for an animal in the handling state

In the handling position, an animal can use 3 strategies when it is challenged. 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 3 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, that is, $p_1 = q_1 = 1$.

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)	/	$2t_c-t_h>\frac{1}{v_f f}$ (C.1)	$v_f f>\frac{2(1-\alpha)}{t_a}$ (C.2)	The mutant always invades (C.3)	—	—
	(0,1,0)	$2t_c-t_h<\frac{1}{v_f f}$ (C.4)	/	$2t_c-t_h<t_a-\frac{1-2\alpha}{v_f f}$ (C.5)	—	$2t_c-t_h>\frac{1}{v_f f}$ (C.6)	—
	(0,0,1)	$v_f f<\frac{2(1-\alpha)}{t_a}$ (C.7)	$2t_c-t_h>t_a-\frac{1-2\alpha}{v_f f}$ (C.8)	/	—	—	$v_f f>\frac{2\alpha}{t_a}$ (C.9)
	(1,0,0)	The mutant never invades (C.10)	—	—	/	$2t_c-t_h>\frac{1}{v_f f}$ (C.11)	$v_f f>\frac{2(1-\alpha)}{t_a}-\frac{t_h v_f f v_h P}{t_h v_f f+1}$ (C.12)
	(1,1,0)	—	$2t_c-t_h<\frac{1}{v_f f-v_h H_a}$[a] (C.13)	—	$2t_c-t_h<\frac{1}{v_f f-v_h H_a}$[a] (C.14)	/	$(2t_c-t_h)\big(v_f f-\alpha v_h H_a\big)v_f f<$ $\big(t_a v_f f+\alpha\big)v_f f+(1-\alpha)\big((t_h v_h P-1)$ $v_f f-\big(v_f f+v_h P\big)t_h v_h H_a\big)$[a] (C.15)
	(1,0,1)	—	—	$v_f f<\frac{2\alpha}{t_a}$ (C.16)	$v_f f<\frac{2(1-\alpha)}{t_a}+(1-2\alpha)v_h H_b$[b] (C.17)	$(2t_c-t_h)\big(v_f f+\alpha v_h H_b\big)>t_a$ $\big(v_f f+2\alpha v_h H_b\big)+\alpha t_h v_h(P-H_b)+$ $2\alpha-1$[b] (C.18)	/

[a] H_a is given by the solution of the equation $(2t_c-t_h)v_h H_a^2+\big(t_h v_f f+t_h v_h P+1\big)H_a-t_h v_f f P=0$.

[b] H_b is given by the solution of the equation $t_a v_h H_b^2+\big(t_h v_f f+1\big)H_b-t_h v_f f P=0$.

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} because the times needed for animals which always challenge, that is, 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 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), (C.14), (C.15), (C.17), and (C.18)).

Optimal strategies in a nonaggressive population

In the case where all the members of the population do not challenge, that is, $p_1 = q_1 = 0$, 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 Equation 12 ($T_{\mathrm{HA}}$ in this case is similarly given by Equation 12 substituting p_2 and p_3 for q_2 and q_3, respectively) we obtain the condition

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

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 summarized in Table 3 (conditions (C.1), (C.2), (C.4), (C.5), (C.7), and (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 1 of the 2 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 4 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 4 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, $v_f f$, vary.

Obviously, these regions in the $t_a/2$, t_c plane in Figure 3 and P, $v_f f$ plane in Figure 4 will vary, depending on the other parameter values. However, some general conclusions can be extracted. Figures 3 and 4 suggest that between the regions where 2 strategies are unique ESSs, there can be a region where the 2 strategies are simultaneous ESSs and among the regions of 3 pairs of ESSs configured by 3 strategies, there might be a region where the 3 strategies might coexist as ESSs. This excludes the possibility of the Retaliator and the Hawk strategies being simultaneous ESSs because this can never happen due to the contradiction of the conditions (C.9) and (C.16) (see Table 3). This gives 11 distinct regions as summarized in Figures 3 and 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, that is, 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 for an argument that actual mixed strategy ESSs are not possible, see APPENDIX C), we cannot definitively rule out this possibility.

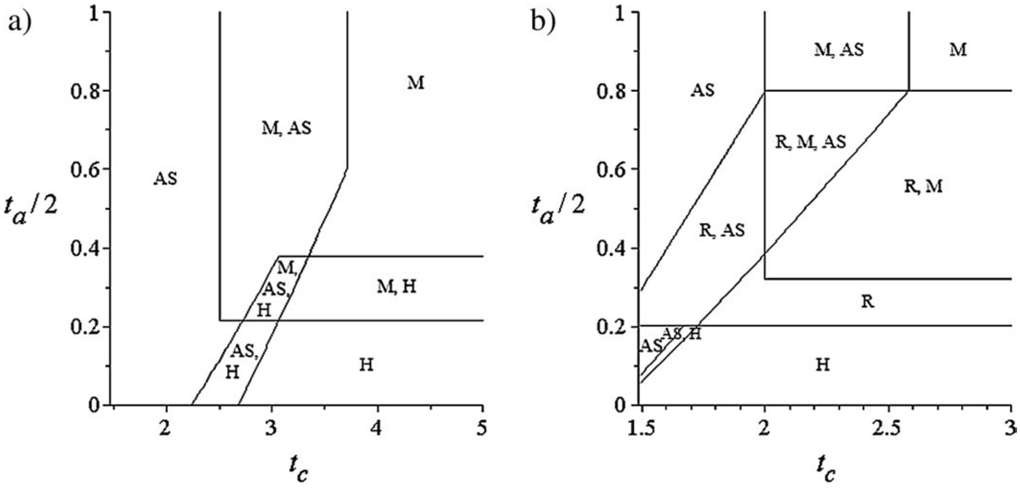

Figure 3
Graphs showing examples of the region where each of the 4 possible ESSs (Retaliator [R], Marauder [M], Attacking Sharer [AS], and Hawk [H]) is an ESS as the duration of the content, $t_a/2$, and the handling time of a sharer, t_c, vary. In each region, a single letter "X" indicates that the strategy X is the unique ESS, "X, Y" indicates that the strategies X and Y are simultaneous ESSs, and "X, Y, Z" that the 3 strategies X, Y and Z are simultaneous ESSs. (a) $t_h = 3$, $v_f f = 0.5$, $v_h = 1.5$, $\alpha = 0.7$, $P = 1$; (b) $t_h = 3$, $v_f f = 1$, $v_h = 2$, $\alpha = 0.2$, $P = 1$.

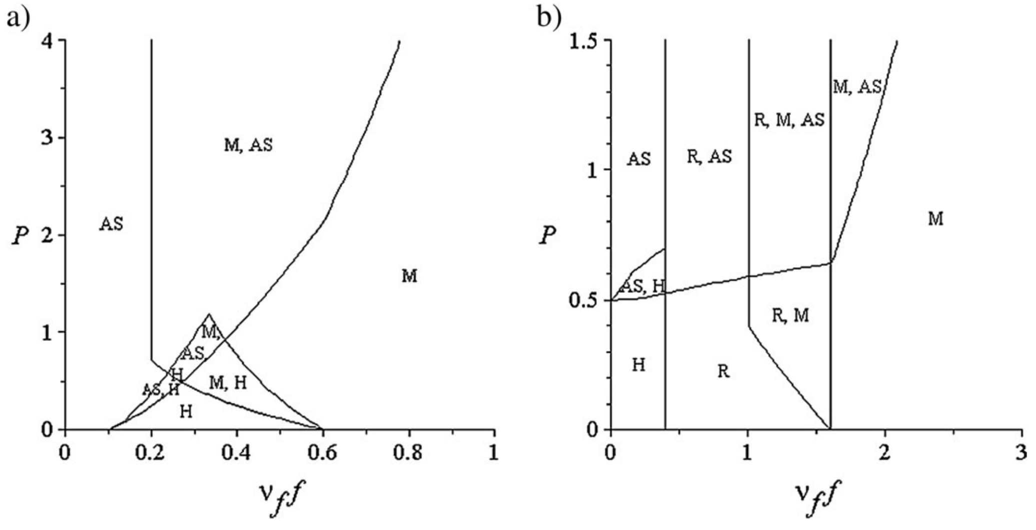

Figure 4
Graphs showing examples of the region where each of the 4 possible ESSs (Retaliator [R], Marauder [M], Attacking Sharer [AS], and Hawk [H]) is an ESS as the density of the population, *P*, and the rate at which foragers find undiscovered food, $v_f f$, vary. In each region, a single letter "X"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

PREDICTIONS OF THE MODEL

In the case where neither the members of the population nor any mutant share the food, that is, 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, that is, 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 nonattacking 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 ($t_c + ((1/v_f f) + t_h)/2$) is less than the average time needed to find an undiscovered food item ($1/v_f f$) 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 ($((1/v_f f) + t_h)/2)$). On the other hand, an Attacking Sharer mutant does better than a member of a population of Nonattacking Sharers if $t_c \leq ((1/v_f f) + t_h)/2$ as well. Hence, as we see in Table 3, condition (C.4) contradicts condition (C.6) and thus a Nonattacking 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 in the searching state. A population of Attacking Sharers can potentially be invaded by Nonattacking Sharers, Marauders, and Hawks. The conditions under which a Nonattacking 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 Nonattacking Sharer can invade if it is better not to challenge for a food item that will be shared (so again searching is better than sharing). Increasing the rate at which foragers find food, $v_f f$, increases the parameter range where Nonattacking Sharers and Marauders invade the population of Attacking Sharers. Depending on the values of the other parameters, the increase of $v_f f$ might favor the invasion of Hawks as well (usually when food is difficult to discover). Hence, increasing $v_f f$ decreases the range of the parameter values in which the Attacking Sharer strategy is an ESS (e.g., see Figure 4). A similar situation appears by decreasing the area in which foragers search for handling sharers per unit time, v_h. As it is observed in the conditions (C.13)–(C.15) and Figure 4, 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 2 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 (e.g., see Figure 3). 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 favored. 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 (e.g., see Figure 3).

A special case

As a special case, we consider the case where $2\ t_c = t_h$, that is, 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 Nonattacking Sharer

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 2 $t_c = t_h$

		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	$v_f f > \frac{2(1-\alpha)}{t_a}$	The mutant always invades	—	—
	(0,1,0)	The mutant never invades	/	$v_f f > \frac{1-2\alpha}{t_a}$	—	The mutant always invades	—
	(0,0,1)	$v_f f < \frac{2(1-\alpha)}{t_a}$	$v_f f < \frac{1-2\alpha}{t_a}$	/	—	—	$v_f f > \frac{2\alpha}{t_a}$
	(1,0,0)	The mutant never invades	—	—	/	The mutant always invades	$v_f f > \frac{2(1-\alpha)}{t_a} - \frac{t_h v_f f v_h P}{t_h v_f f + 1}$
	(1,1,0)	—	The mutant never invades	—	The mutant never invades	/	$(t_a v_f f + \alpha)(t_h v_f f + t_h v_h P + 1) - (1-\alpha)(t_h v_f f + 1) > 0$
	(1,0,1)	—	—	$v_f f < \frac{2\alpha}{t_a}$	$v_f f < \frac{2(1-\alpha)}{t_a} + (1-2\alpha) v_h H_b$[a]	$t_a\ (v_f f + 2\ \alpha\ v_h\ H_b) + \alpha\ t_h\ v_h\ (P - H_b) + 2\ \alpha - 1 < 0$[a]	/

[a] H_b is given by the solution of the equation $t_a v_h H_b^2 + (t_h v_f f + 1) H_b - t_h v_f f P = 0$.

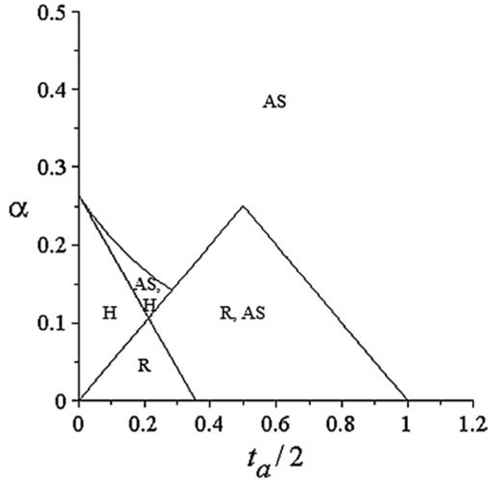

Figure 5
A graph showing an example of the region where each of the 3 possible ESSs (Retaliator [R], Attacking Sharer [AS], and Hawk [H]) can occur in the special case where 2 $t_c = t_h$, as the probability α of the challenger winning and the duration of the content, $t_a/2$, vary. In each region, a 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 3 strategies X, Y and Z are simultaneous ESSs. 2 $t_c = t_h = 3$, $v_f f = 0.5$, $v_h = 1.5$, $P = 1$.

strategies which as we have seen in the previous section are never ESSs, in this case, the Marauder strategy is also never an ESS because 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 the few cases where the chance of a successful defense is relatively high, that is, 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 the pure Hawk ESS coexists with the pure Attacking Sharer ESS. When the defender is likely to succeed, that is, α is small, defense of the food item might be the favored strategy even if the fight time is relatively long, especially in cases where available food is scarce. Hence, there is a range where either pure Retaliator is the only ESS or the pure Retaliator ESS coexists with the pure Attacking Sharer ESS. Although such ecological conditions favor a handler animal defending its food in a fight, in an Attacking Sharer population the subsequent potential attacks that a defender faces make the defending strategy less attractive. For similar reasons, in a population that is using the Attacking Sharer ESS, every searcher should attempt to share. Now, in a population using the Retaliator ESS, defending the food is a more attractive strategy than sharing it because a successful defense is likely, and animals in the population do not attack. On the other hand, attacking a handler and engaging in a fight in conditions where aggressive interactions favor the attacked handler is not a good strategy and thus attacking strategies cannot invade.

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 the model of the present paper can choose among 2 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 steal the food of other animals 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) that are hard to divide, in which case, the original modeling 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, 2005, 2007; Dubois et al. 2003) could be appropriate models.

Considering the time 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 nonaggressive strategy where animals do not challenge other animals but share their food when challenged can never be an ESS because depending on the ecological parameters, this strategy is always invaded either by the Dove or by 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 2 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 3 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 availability, the use of the Attacking Sharer strategy is enhanced, whereas at high food densities, food sharing becomes a less profitable strategy. A high time cost of food defense, a small probability of a successful food defense, a high rate at which searchers encounter handlers, a high population density, and a low time cost of food sharing are also conditions which favor 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 a few cases, where the time cost of the defense is small, but never attacking and always defending might be an ESS even if the defense will result in a high time cost. Attacking and always retreating when attacked never occurs in this case because 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. This process might result in immediate benefits for animals, for example, the creation of cooperation for the increase of foraging success or predation avoidance, or the increase of 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). In such cases, food sharing might not be immediately beneficial but result in long-term benefits such as future reciprocal sharing, that is, 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 foraging 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 behavior might occur, for example, in cases where a beggar challenges a food owner, a situation which is observed in monkey and chimpanzee populations (for examples of this behavior, see Stevens and Gilby 2004). A particular feature of our model compared with other models in the literature, is that by sharing food, the 2 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 maximizes 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, might share it in order to increase the efficiency of defending the prey from invading hyenas (e.g., see 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 fight over this (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 (e.g., see White 1994) as well as the contest duration (e.g., see 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 also 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. 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 (see also Luther and Broom 2004). In the same way, although it is assumed that the cost from the sharing process is equal for the 2 animals that share food, in reality, the 2 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 (e.g., see 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 (e.g., see 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 by introducing the choice to the loser animal to attack the winner again or not, following similar assumptions to those made in some owner–intruder types of games (e.g., Morrell and Kokko 2003).

Another interesting extension of the model that could add some realism is to assume that the attacking animal, after its first attack, has the possibility to update its strategy based on the decision of the attacked handler. For example, it could be assumed that if the attacking searcher is offered a share, it has the possibility to either give up and resume searching for another food item or attack again attempting to get the whole food item from the present handler. A handler sharer, being attacked again by the attacking searcher either defends the food and a fight takes place or it retreats and leaves the food to the attacker in order to avoid a fight. This extension would add new strategic choices for the animals. However, it would not add any new observable behavior (at any time the new strategies will look exactly the same as the strategies in the model considered in this paper). Although an analysis of such extended models is required in order to extract safe conclusions, we predict that the new strategies under some conditions might be able to invade other strategies that in the current model are ESSs. This would reduce the regions in parameter space where each of the current strategies is evolutionarily stable. For example, we can predict that under some circumstances, an animal should attack again a handler that offers a share in the first attack but will give up on a second attack. In the current model, for very large fight duration, $t_a/2$, the optimal strategy for an attacked handler might be to offer a share to an attacking searcher and the optimal strategy for the challenger to accept the share (e.g., see Figure 3). However, if the challenger has the possibility to attack again, then this would be the best strategic choice for it because the defender will retreat and leave the food item to the attacker rather than defend it and engage in a very long fight. Similarly, when $t_a/2$ is small, it might be optimal for an attacked handler to offer a share (see Figure 3). However, in the extended model, it might be better for the challenger to attack again because it will be worth fighting for the whole food item.

In natural systems, foraging animals might be faced with more than one foraging option with different variances 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 kinds of unpredictable interruptions (e.g., bad weather). The forager might be either risk averse and choose the predictable option or risk prone and choose a risky option, respectively (e.g., see Kacelnik and Bateson 1996). For example, an animal with low food reserves might choose a safe lower level of return, provided it is 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.

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APPENDIX A

The densities of the different groups of the population, *S*, *H*, *C*, *A*, and *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

$$\frac{dC}{dt}=2p_1p_2v_hSH-\frac{1}{t_c}C=0, \tag{15}$$

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

$$C=2p_1p_2t_cv_hSH. \tag{16}$$

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

$$A=R=\frac{p_1p_3t_av_hSH}{2}. \tag{18}$$

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 Equation 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 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:

$$T^*_\mathrm{SA} = q_1\left(p_2T^*_\mathrm{C} + p_3T^*_\mathrm{A} + (1 - p_2 - p_3)T^*_\mathrm{H}\right) + (1 - q_1)T^*_\mathrm{S}. \quad (20)$$

Recall that we assume that 2 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

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

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 1 of the 2 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 $0.5t_c+0.5\left(t_c+T^*_\mathrm{S}\right)$, which leads to Equation 21.
Substituting Equation 21 into Equation 20 we obtain

$$T^*_\mathrm{SA} = q_1\left(p_2t_c + p_3T^*_\mathrm{A} + (1 - p_2 - p_3)T^*_\mathrm{H}\right) + \left(1 - q_1 + \frac{q_1p_2}{2}\right)T^*_\mathrm{S}. \quad (22)$$

An attacker animal that 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, whereas with a complementary probability α, it beats the defender and acquires the food item. Thus, T^*_A is given by the following equation:

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

A searcher animal is looking either for a food resource or for a handler animal. At this stage, it spends an average time equal to $1/(v_f f + v_h H)$ before it finds either an unattended food item (this happens with probability $v_f f/(v_f f + v_h H)$) and becomes a handler, or a handler animal (with probability $v_h H/(v_f f + v_h H)$). Thus, T^*_S is given by the following equation:

$$T^*_\mathrm{S} = \frac{v_hH}{v_f f + v_hH}T^*_\mathrm{SA} + \frac{v_f f}{v_f f + v_hH}T^*_\mathrm{H} + \frac{1}{v_f f + v_hH}. \quad (24)$$

Once the searcher animal acquires a food item, it either consumes it without being found by any searcher animal, with probability $(1/t_h)/((1/t_h) + v_hS)$, or it is discovered by a searcher, with probability $v_h\,S/((1/t_h) + v_h\,S)$, 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 $1/((1/t_h) + v_h\,S)$. T^*_H is thus given by

$$T^*_\mathrm{H} = \frac{1}{1 + t_hv_hS}0 + \frac{t_hv_hS}{1 + t_hv_hS}T^*_\mathrm{HA} + \frac{t_h}{1 + t_hv_hS}. \quad (25)$$

Substituting Equations (23–25) into Equation 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 in the handling state is attacked by a searcher animal playing the population strategy, with a nonzero probability ($p_1 \neq 0$), then T^*_HA is given by the following equation:

$$T^*_\mathrm{HA} = p_1\left(q_2T^*_\mathrm{C} + q_3T^*_\mathrm{R} + (1 - q_2 - q_3)T^*_\mathrm{S}\right) + (1 - p_1)T^*_\mathrm{H}, \quad (26)$$

where T^*_R is the average time required until the consumption of a food item for a handler that decides to defend its food against a challenge. Substituting Equation 21 into Equation 26, we obtain

$$T^*_\mathrm{HA} = p_1\left(q_2t_c + q_3T^*_\mathrm{R} + \left(1 - \frac{q_2}{2} - q_3\right)T^*_\mathrm{S}\right) + (1 - p_1)T^*_\mathrm{H}. \quad (27)$$

In a similar way as before, T^*_R is given by

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

Substituting Equations 24, 25, and 28 into Equation 27, we obtain Equation 11.

Average time for a single handler animal to consume a food item in a nonaggressive population

In the case where all the members of the population do not challenge, that is, $p_1 = q_1 = 0$, 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

$$T^*_\mathrm{HA} = q_2\left(t_c + \frac{T^*_\mathrm{S}}{2}\right) + q_3T^*_\mathrm{R} + (1 - q_2 - q_3)T^*_\mathrm{S}, \quad (29)$$

where T^*_R is given by Equation 28. Because the population is not making challenges, $(1/v_f f) + t_h$ and $T^*_\mathrm{H} = t_h$. Substituting into Equation 29, we obtain Equation 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 summarized 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

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

Strategies denoted by * are strategies with $p_2 = 0$, strategies denoted by ** are pure strategies with $p_2 = 1$ and strategies denoted by *** are strategies with $p_1 = 0$ and $0 < p_2 < 1$.

monotonic function (except with the possible exception of a nongeneric 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 minimizes 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 2 additional to the Broom et al. (2004) model pure strategies, where $p_2 = 1$, that is, 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, that is, $p_1 = q_1 = 0$ (strategies denoted by (***) in Table 5 are such strategies where $0 < p_2 < 1$), the average time required for an attacked mutant handler that plays strategy $(0, q_2, q_3)$ 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, $v_f f$ 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 $q_3 = 0$, whereas 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 that 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 $\left(p_1^*,1,0\right)$ in (S 1), then $T_{\mathrm{SA}}\left(p_1^*,1,0\right)$ 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

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

On the other hand, if the strategy $\left(p_1^*,1,0\right)$ is an equilibrium strategy, then it cannot be invaded by the mutant strategy $\left(p_1^*,0,0\right)$, that is, the average required time for the mutant handler that has just been attacked in a population that plays strategy $\left(p_1^*,1,0\right)$, $T^*_{\mathrm{HA}}\left(p_1^*,0,0\right)$, is higher than the average time required when playing the population strategy, $T_{\mathrm{HA}}\left(p_1^*,1,0\right)$. Using Equation 27, we find that

$$T^*_{\mathrm{HA}}\left(p_1^*,0,0\right) > T_{\mathrm{HA}}\left(p_1^*,1,0\right) \tag{34}$$

$$\Rightarrow T^*_{\mathrm{S}}\left(p_1^*,0,0\right) > T_{\mathrm{C}}\left(p_1^*,1,0\right) \Rightarrow T^*_{\mathrm{S}}\left(p_1^*,0,0\right) = T_{\mathrm{S}}\left(p_1^*,1,0\right) > 2t_c. \tag{35}$$

This contradicts Equation 33. Consequently, there is not 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 (e.g., see Figure 6a).

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 $\left(0<p_1^*<1, 0<p_2^*<1, 0<p_3^*<1\right)$, $p_2^*+p_3^*<1$, then $T^*_{\mathrm{HA}}\left(p_1^*,0,0\right)$, $T^*_{\mathrm{HA}}\left(p_1^*,1,0\right)$ and $T^*_{\mathrm{HA}}\left(p_1^*,0,1\right)$ should all be identical, otherwise one of the strategies $\left(p_1^*,0,0\right)$, $\left(p_1^*,1,0\right)$, $\left(p_1^*,0,1\right)$ could invade $\left(p_1^*,p_2^*,p_3^*\right)$. In this case, using Equations 27 and 28, we find that

$$T_{\mathrm{S}}\left(p_1^*,p_2^*,p_3^*\right) - T_{\mathrm{H}}\left(p_1^*,p_2^*,p_3^*\right) = \frac{1}{1-\alpha}\frac{t_a}{2}. \tag{36}$$

On the other hand, if $\left(p_1^*,p_2^*,p_3^*\right)$ is an equilibrium strategy, then $T^*_{\mathrm{SA}}\left(p_1^*,p_2^*,p_3^*\right) = T^*_{\mathrm{SA}}\left(1,p_2^*,p_3^*\right) = T^*_{\mathrm{SA}}\left(0,p_2^*,p_3^*\right)$ which yields that $T^*_{\mathrm{SA}}\left(1,p_2^*,p_3^*\right) = T^*_{\mathrm{S}}\left(0,p_2^*,p_3^*\right) = T^*_{\mathrm{S}}\left(1,p_2^*,p_3^*\right) = T^*_{\mathrm{S}}\left(p_1^*,p_2^*,p_3^*\right)$. Substituting into Equation 24, we obtain that

$$T^*_{\mathrm{S}}\left(p_1^*,p_2^*,p_3^*\right) - T^*_{\mathrm{H}}\left(p_1^*,p_2^*,p_3^*\right) = \frac{1}{v_f f}. \tag{37}$$

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

$$1 - \alpha = v_f f \frac{t_a}{2}, \tag{38}$$

that is, 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 nongeneric). Thus, for example, such a case would correspond to a region of

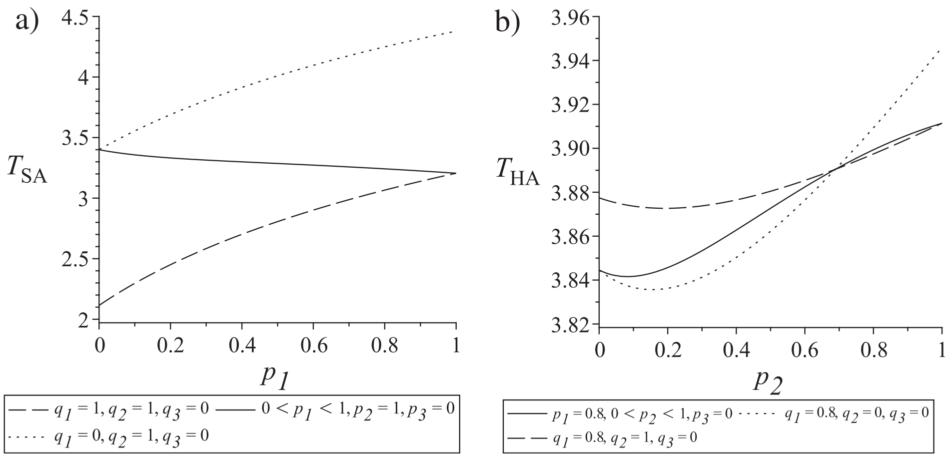

Figure 6
(a) The expected time until the consumption of a food item of mutant searcher animals playing strategies (0,1,0), (1,1,0), and $(0 < p_1 < 1,1,0)$ in a population playing strategy $(0 < p_1 < 1,1,0)$ for the example considered in Figure 3b for $t_c = 2$. Numerical examples indicate that in every population, which adopts a strategy $(0 < p_1 < 1,1,0)$, a mutant animal that plays either strategy (0,1,0) or 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 $t_h = 3$, $t_c = 2$, $v_f f = 1$, $v_h = 1.5$, $P = 1$. An equilibrium strategy $(0 < p_1 \leq 1,0 < p_2 < 1,0)$ cannot be evolutionarily stable.

zero area in a figure such as Figure 3, equivalent to the boundary lines.

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

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 $\left(p_1^*, 0 \leq q_2 \leq 1, 0\right)$ do equally well in a population playing $\left(p_1^*, p_2^*, 0\right)$, that is, $T_{\text{HA}}\left(p_1^*, p_2^*, 0\right) = T_{\text{HA}}^*\left(p_1^*, 0 \leq q_2 \leq 1, 0\right)$, whereas any other strategy does worse. Any other population playing a different strategy $\left(p_1^*, 0 < p_2 < 1, 0\right)$, $p_2 \neq p_2^*$, can be invaded either by the strategy $\left(p_1^*, 0, 0\right)$ or by the strategy $\left(p_1^*, 1, 0\right)$ (e.g., see Figure 6b). However, in a population that plays a strategy $(p_1, 0 \leq q_2 \leq 1,0)$, the required time for an attacked handler playing the population strategy, T_{HA} $(p_1, 0 \leq q_2 \leq 1,0)$, is less than that required by an attacked handler playing $\left(p_1^*, p_2^*, 0\right)$. In other words, if an infinitesimal portion of the population deviates from the equilibrium strategy, evolution will drive the population away from that equilibrium. Thus, according to the second condition of Maynard Smith and Price (1973) for a strategy to be an ESS, the strategies $\left(p_1^*, p_2^*, 0\right)$ cannot be ESS. Hence, none of the strategies (S 2) and (S 3) can be evolutionarily stable.

REFERENCES

Axelrod R, Hamilton WD. 1981. The evolution of cooperation. Science. 211:1390–1396.

Barnard CJ, Sibly RM. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. Anim Behav. 29:543–550.

Beddington JR. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. J Anim Ecol. 44: 331–340.

Brockman HJ, Barnard CJ. 1979. Kleptoparasitism in birds. Anim Behav. 27:487–514.

Broom M, Luther RM, Ruxton GD. 2004. Resistance is useless? Extensions to the game theory of kleptoparasitism. Bull Math Biol. 66:1645–1658.

Broom M, Luther RM, Ruxton GD, Rychtar J. 2008. A game-theoretic model of kleptoparasitic behavior in polymorphic populations. J Theor Biol. 255:81–91.

Broom M, Ruxton GD. 1998. Evolutionarily stable stealing: game theory applied to kleptoparasitism. Behav Ecol. 9:397–403.

Broom M, Ruxton GD. 2003. Evolutionarily stable kleptoparasitism: consequences of different prey types. Behav Ecol. 14:23–33.

Broom M, Rychtar J. 2007. The evolution of a kleptoparasitic system under adaptive dynamics. J Math Biol. 54:151–177.

Broom M, Rychtar J. 2009. A game theoretical model of kleptoparasitism with incomplete information. J Math Biol. 59:631–649.

Broom M, Rychtar J. 2011. Kleptoparasitic melees—modelling food stealing featuring contests with multiple individuals. Bull Math Biol. 73:683–699.

Caraco T, Giraldeau L-A. 1991. Social foraging: producing and scrounging in a stochastic environment. J Theor Biol. 153:559–583.

Carbone C, Frame L, Frame G, Malcolm J, Fanshawe J, FitzGibbon C, Schaller G, Gordon IJ, Rowcliffe JM, Du Toit JT. 2005. Feeding success of African wild dogs (Lycaon pictus) in the Serengeti: the effects of group size and kleptoparasitism. J Zool. 266:153–161.

Chamorro-Florescano IA, Favila ME, Macias-Ordonez R. 2010. Ownership, size and reproductive status affect the outcome of food ball contests in a dung roller beetle: when do enemies share? Evol Ecol. 25:277–289.

Chellapa S, Hungtingford FA. 1989. Depletion of energy reserves during reproductive aggression in male three-spined stickleback, *Gasterosteus aculeatus* L. J Fish Biol. 35:315–316.

Cooper SM. 1991. Optimal hunting groups size: the need for lions to defend their kills against loss to spotted hyaenas. Afr J Ecol. 29:130–136.

Cooper WE, Perez-Mellado V. 2003. Kleptoparasitism in the Balearic lizard, Podarcis lilfordi. Amphib-Rep. 24:219–224.

Coyl FA, O'Shields TC, Perlmutter DG. 1991. Observations on the behaviour of the kleptoparasitic spider, Mysmenopsis furtiva (Araneae, Mysmenidae). J Arachnol. 19:62–66.

Crowe M, Fitzgerald D, Remington D, Rychtar J. 2009. On deterministic and stochastic models of kleptoparasitism. J Interdiscip Math. 12:161–180.

Dubois F, Giraldeau L-A. 2003. The forager's dilemma: food-sharing and food-defense as risk-sensitive foraging options. Am Nat. 162:768–779.

Dubois F, Giraldeau L-A. 2005. Fighting for resources: the economics of defense and appropriation. Ecology. 86:3–11.

Dubois F, Giraldeau L-A. 2007. Food sharing among retaliators: sequential arrivals and information asymmetries. Behav Ecol Sociobiol. 62:263–271.

Dubois F, Giraldeau L-A, Grant JWA. 2003. Resource defense in a group foraging context. Behav Ecol. 14:2–9.

Dugatkin LA. 1997. Winner and loser effects and the structure of dominance hierarchies. Behav Ecol. 8:583–587.

Enquist M, Leimar O. 1987. Evolution of fighting behaviour: the effect of variation in resource value. J Theor Biol. 127:187–205.

Erlandsson A. 1988. Food sharing vs. monopolising prey: a form of kleptoparasitism in Velia caprai (Heteroptera). Oikos. 53:203–206.

Feistner ATC, McGrew WC. 1989. Food-sharing in primates: a critical review. In: Seth PK, Seth S, editors. Perspectives in primate biology. Vol. 3. New Delhi (India): Today and Tomorrow's Printers and Publishers. p. 21–36.

Hack MA. 1997. The energetic costs of fighting in the house cricket, *Acheta domesticus* L. Behav Ecol. 8:28–36.

Hamilton IM, Dill LM. 2003. The use of territorial gardening versus kleptoparasitism by a subtropical reef fish (*Kyphosus cornelii*) is influenced by territory dependability. Behav Ecol. 14:561–568.

Iyengar EV. 2002. Sneaky snails and wasted worms: kleptoparasitism by Trichotropis cancellata (Mollusca, Gastropoda) on Serpula columbiana (*Annelida, Polychaeta*). Mar Ecol Prog Ser. 244:153–162.

Iyengar EV. 2008. Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. Biol J Linn Soc. 93:745–762.

Janson CH. 1985. Aggressive competition and animal food consumption in wild brown capuchin monkeys (Cebus apella). Behav Ecol Sociobiol. 18:125–138.

Kacelnik A, Bateson M. 1996. Risky theories—the effects of variance on foraging decisions. Am Zool. 36:402–434.

Luther RM, Broom M. 2004. Rapid convergence to an equilibrium state in kleptoparasitic populations. J Math Biol. 48:325–339.

Luther RM, Broom M, Ruxton GD. 2007. Is food worth fighting for? ESS's in mixed populations of kleptoparasites and foragers. Bull Math Biol. 69:1121–1146.

Maynard Smith J. 1982. Evolution and the theory of games. Cambridge (UK): Cambridge University Press.

Maynard Smith J, Price GR. 1973. The logic of animal conflict. Nature. 246:15–18.

van der Meer J, Ens BJ. 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. J Anim Ecol. 66:846–858.

van der Meer J, Smallegange IM. 2009. A stochastic version of the Beddington-DeAngelis functional response: modelling interference for a finite number of predators. J Anim Ecol. 78:134–142.

Morrell LJ, Kokko H. 2003. Adaptive strategies of territory formation. Behav Ecol Sociobiol. 54:385–395.

Neat FC, Taylor AC, Huntingford FA. 1998. Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. Anim Behav. 55:875–882.

Rovero F, Hughes RN, Whiteley NM, Chelazzi G. 2000. Estimating the energetic cost of fighting in shore crabs by noninvasive monitoring of heartbeat rate. Anim Behav. 59:705–713.

Ruxton GD, Gurney WSC, De Roos AM. 1992. Interference and generation cycles. Theor Popul Biol. 42:235–253.

Ruxton GD, Moody AL. 1997. The ideal free distribution with kleptoparasitism. J Theor Biol. 186:449–458.

Selten R. 1975. Reexamination of the perfectness concept for equilibrium points in extensive games. Int J Game Theory. 4:25–55.

Sirot E. 2000. An evolutionarily stable strategy for aggressiveness in feeding groups. Behav Ecol. 11:351–356.

Smallegange IM, van der Meer J. 2009. The distribution of unequal predators across food patches is not necessarily (semi)truncated. Behav Ecol. 20:525–534.

Smith IP, Taylor AC. 1993. The energetic cost of agnostic behaviour in the velvet swimming crab, *Necora* (=*Liocarcinus*) *puber* (L.). Anim Behav. 45:375–391.

Stamps J. 1994. Territorial behavior: testing the assumptions. Adv Study Behav. 23:173–232.

Stamps JA, Krishnan VV. 1994. Territory acquisition in lizards: II. Establishing social and spatial relationships. Anim Behav. 47: 1387–1400.

Stevens JR, Gilby IC. 2004. A conceptual framework for nonkin food sharing: timing and currency of benefits. Anim Behav. 67:603–614.

Stevens JR, Stephens DW. 2002. Food sharing: a model of manipulation by harassment. Behav Ecol. 13:393–400.

Vahl WK. 2006. Interference competition among foraging waders [PhD thesis]. [Groningen (the Netherlands)]: University of Groningen.

Vickery WL, Giraldeau L-A, Templeton JJ, Kramer DL, Chapman CA. 1991. Producers, scroungers and group foraging. Am Nat. 137:847–863.

Wenzel JW, Pickering J. 1991. Cooperative foraging, productivity, and the central limit theorem. Proc Natl Acad Sci U S A. 88:36–38.

White FJ. 1994. Food sharing in wild pygmy chimpanzees, Pan paniscus. In: Roeder JJ, Thierry B, Anderson JR, Herrenschmidt N, editors. Current primatology: social development, learning and behavior. Vol. 2. Strasbourg (France): Universite Louis Pasteur. p. 1–10.

Wilkinson GS. 1990. Food sharing in vampire bats. Sci Am. 262:76–82.

Yates GE, Broom M. 2007. Stochastic models of kleptoparasitism. J Theor Biol. 248:480–489.