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1 **When should animals share food? Game theory**  
2 **applied to kleptoparasitic populations with food**  
3 **sharing**

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**Abstract**

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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 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.

## 27 Introduction

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

41 Kleptoparasitism is a common foraging strategy. Different forms of kleptoparasitic  
42 behaviour are observed in many species of animals, for example species of spiders (e.g.,  
43 Coyl et al., 1991), birds (e.g., Brockman and Barnard, 1979), snails (e.g., Iyengar, 2002),  
44 lizards (e.g., Cooper and Perez-Mellado, 2003), fish (e.g., Hamilton and Dill, 2003), pri-  
45 mates (e.g., Janson, 1985), carnivores (e.g., Carbone et al., 2005) and insects (e.g.,  
46 Erlandsson, 1988). This behaviour of animals has been recently well documented in a  
47 review paper (Iyengar, 2008). The biological phenomenon of kleptoparasitism has at-  
48 tracted the interest of many researchers from different areas. There are a number of  
49 theoretical models focused on the kleptoparasitic behaviour of animals using different  
50 mathematical methods, in particular evolutionary game theory. Two of the fundamen-  
51 tal game-theoretical models which consider kleptoparasitic behaviour are the producer-  
52 scrounger model, originally introduced by Barnard and Sibly (1981), and the model  
53 of Broom and Ruxton (1998). In its original form, the producer-scrounger game is a  
54 frequency-dependent game where animals forage for food using two strategies. They  
55 either search for food (producer's strategy) or search for opportunities to kleptopara-  
56 sitize (scrounger's strategy). The scrounger strategy does better when scroungers are

57 rare and worse when they are common. When the frequency of the two strategies is  
58 such that the payoff obtained by each strategy is the same, there is a stable equilibrium  
59 where the two strategies coexist. Many variations of this model have followed in order  
60 to consider different factors that might affect the foraging process (e.g., Caraco and  
61 Giraldeau, 1991; Vickery et al., 1991; Dubois and Giraldeau, 2005). One key feature  
62 of this type of models is that food is usually discovered in patches and can be easily  
63 split over foraging animals. Hence, the concept of food sharing is central to these mod-  
64 els. In addition, in these models costs from aggressive strategies are energetic, rather  
65 than time, costs. Thus, the different strategies do not directly affect the distribution of  
66 feeding and foraging animals and the main effect of population density is to reduce the  
67 “finder’s share”, the portion of the food eaten by a finder before other foragers discover  
68 it. The model of Broom and Ruxton (1998), based on the mechanistic model of Ruxton  
69 and Moody (1997), follows a different approach. Food comes in single indivisible items,  
70 which must be consumed completely by an individual. Thus, food can never be shared  
71 and challenging animals attempt to steal the whole item from the owner (or not). In  
72 particular, in this model it is assumed that each of the animals in the population ei-  
73 ther searches for food, has already acquired and is handling a food item prior to its  
74 consumption or fights with another animal over a food item. When foraging animals  
75 encounter an animal in the handling state, they can either decide to attack in order to  
76 steal the prey or ignore the handler animal and continue searching. Attacked animals  
77 always defend their food and a fight takes place. The population density has a direct  
78 effect in this model as fights take time, with this loss of time the cost of more aggressive  
79 strategies, and the more potential kleptoparasites there are, the more time is wasted on  
80 fighting. The model predicts the optimal strategy for a foraging animal (to attack or  
81 not to attack) under varying food availability and fight time cost. Broom et al. (2004)  
82 later reconstructed this model in a more general framework by introducing different  
83 competitive abilities between the attacker and the attacked animal and allowing the  
84 attacked animal to surrender its food to the attacker avoiding the time cost of a fight. A  
85 series of publications has appeared developing the original model of Broom and Ruxton  
86 (1998) in a number of ways (e.g., Broom and Ruxton, 2003; Broom and Rychtar, 2007;

87 Luther et al., 2007; Yates and Broom, 2007; Broom et al., 2008; Broom and Rychar,  
88 2009; Broom and Rychtar, 2011). Crowe et al. (2009) provide a brief review on the main  
89 theoretical work on kleptoparasitism prior to the investigation of a stochastic model of  
90 kleptoparasitism in finite populations. A comparison between some main models of  
91 kleptoparasitism following the two fundamental game-theoretic approaches is discussed  
92 in Vahl (2006) (see Chapter 6) and an alternative model is presented. There is also a  
93 series of related mechanistic, but not game-theoretic, models which investigate interfer-  
94 ence competition where foraging animals engage in aggressive interactions in order for  
95 example to defend their territory, resulting in negative effects on their foraging efficiency  
96 (e.g., Beddington, 1975; Ruxton et al., 1992; Van der Meer and Ens, 1997; Vahl, 2006;  
97 Smallegange and Van der Meer, 2009; Van der Meer and Smallegange, 2009).

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

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

125 In this paper, we extend the model of kleptoparasitism presented in Broom et al.  
126 (2004) by assuming divisible food items and allowing animals to share their prey with  
127 attacking foraging animals. A foraging animal, encountering an animal handling a food  
128 item has the possibility to either attack attempting to steal or share the food, or just  
129 ignore it and continue foraging. On the other hand, an attacked animal which owns  
130 a food item, has the possibility to defend its food, to share it or to retreat leaving all  
131 the food to the attacking animal. Through a game-theoretic approach we examine the  
132 optimal strategy for an animal under different ecological circumstances.

## 133 **The model**

134 In a population of foragers of density  $P$ , each animal might either be in a state of  
135 searching for food, or a state where it is handling a food item that it has acquired. Let  
136  $S$  denote the density of searchers and  $H$  the density of handlers. Each handler consumes  
137 the food item and resumes searching in a time drawn from an exponential distribution  
138 with mean  $t_h$ , so equivalently following a Markov process at rate  $t_h^{-1}$ . There is a constant  
139 density of food items  $f$  available and searchers cover an area  $\nu_f$  per unit time whilst  
140 searching for food, so that they find food at rate  $\nu_f f$ . As well as finding food themselves  
141 when foraging, searchers can acquire food by trying to steal it from a handler, and they  
142 can search an area  $\nu_h$  per unit time for handlers. Once a searcher comes upon a handler,  
143 it attacks to either steal or share the food item with probability  $p_1$  or ignores the handler  
144 with probability  $1 - p_1$  and continues searching for food. If the searcher attacks, the  
145 handler might decide to resist and defend its food item. This happens with probability

146 which we label  $p_3$ . In this case, the attacking searcher ( $A$ ) and the defender ( $R$ ) engage in  
 147 a fight. The rate at which searchers encounter handlers and engage in a fight (become  
 148 attackers,  $A$ ) is equal to  $p_1 p_3 \nu_h H$  while handlers are found by searchers and resist a  
 149 possible attack (become defenders,  $R$ ) with rate  $p_1 p_3 \nu_h S$ . The fight lasts for a time  
 150 drawn from an exponential distribution with mean  $t_a/2$ . The attacker animal wins the  
 151 fight and becomes a handler with probability  $\alpha$  and thus, with the same probability,  
 152 the defender loses its food and starts searching again; so this happens at rate  $2\alpha/t_a$ .  
 153 Otherwise, the attacking searcher loses the fight and returns to the searching state with  
 154 rate  $2(1-\alpha)/t_a$  and thus, with the same rate, the defender wins and continues handling  
 155 its food. Note that the winner of the fight might face other subsequent challenges. In  
 156 general, the circumstances under which fights occur might give a high advantage to  
 157 defender or attacker (the attacker might have to catch the defender in the air, but the  
 158 defender may be hampered by a heavy food item) and so  $\alpha$  may be significantly greater  
 159 or less than 0.5.

160 So far, the model described is the same as the model investigated in Broom et al.  
 161 (2004). In this paper, this model is extended by assuming that attacked animals can  
 162 share a food item as follows. Assume that food items are divisible. The attacked handler  
 163 might decide to share its food with an attacking searcher, with probability  $p_2$ . In this  
 164 case, searchers become sharers ( $C$ ) with rate  $p_1 p_2 \nu_h H$  and the attacked handlers with  
 165 rate  $p_1 p_2 \nu_h S$ . If the handler decides to share its food with the searcher, both take a  
 166 half of the food. It is assumed, for reasons of simplicity, that both the two sharers  
 167 hold the food item and feed simultaneously on it. This discourages other animals from  
 168 attempting to steal or share the food since this would be a difficult, risky and dangerous  
 169 venture. So, food sharing results in the mutual protection of the two sharers from other  
 170 predators. As a result, a sharer animal consumes its portion of the food item without  
 171 any interruptions. Sharers eat their food unperturbed and again become searchers in a  
 172 time drawn from an exponential distribution with mean  $t_c$  or equivalently with rate  $t_c^{-1}$ .  
 173 Once the half of the food item is consumed, the sharer starts foraging again. Throughout  
 174 the paper, it is assumed that  $2t_c \geq t_h$ , i.e. the decision of food sharing might either  
 175 have no time cost or has some cost, but is never beneficial with respect to the handling

176 time.

177 The attacked handler, in order to avoid any time cost either from a fight or the sharing  
 178 process, might decide neither to defend its food item nor to share it, but to leave it to  
 179 the attacking animal and return to the searching state. This happens with probability  
 180  $1 - p_2 - p_3$  for any challenge, and so occurs at rate  $p_1(1 - p_2 - p_3)\nu_h H$  for each searcher  
 181 and rate  $p_1(1 - p_2 - p_3)\nu_h S$  for each handler.

182 The model parameters and notations are summarised in Table 1.

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

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

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

$$\frac{dC}{dt} = 2p_1p_2\nu_h SH - \frac{1}{t_c}C, \quad (3)$$

$$\frac{dA}{dt} = p_1p_3\nu_h SH - \frac{2}{t_a}A, \quad (4)$$

$$\frac{dR}{dt} = p_1p_3\nu_h SH - \frac{2}{t_a}R. \quad (5)$$

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

$$P = S + H + C + A + R, \quad (6)$$

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

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

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

192 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  
 193 searchers discover food items and the rate at which they become sharers. Note that this



194 term is clearly positive since every food item can be shared at most once (and some are  
 195 not shared), and it must be discovered beforehand. By (6) and (7),  $H$  is given by the  
 196 biologically relevant solution of the quadratic equation

$$p_1(p_2(2t_c - t_h) + p_3t_a)\nu_h H^2 + (p_1p_2t_h\nu_h P + t_h\nu_f f + 1)H - t_h\nu_f f P = 0, \quad (8)$$

197 i.e. the positive solution,

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

198 given that  $2p_1\nu_h(p_2(2t_c - t_h) + p_3t_a) > 0$ .

## 199 Optimal strategies

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

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

### 208 Average time for a single animal to consume a food item

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

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

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

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

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

- 222 - It shares the food item with probability  $q_2$ .
- 223 - It defends its food and a fight takes place with probability  $q_3$ .
- 224 - 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

$$\begin{aligned} & \left( 1 - \left( 1 - q_1 + \frac{q_1 p_2}{2} + (1 - \alpha) q_1 p_3 \right) \frac{\nu_h H}{\nu_f f + \nu_h H} \right) T_{SA}^* = q_1 p_2 t_c + q_1 p_3 \frac{t_a}{2} + \\ & + \left( 1 - q_1 + \frac{q_1 p_2}{2} + (1 - \alpha) q_1 p_3 \right) \frac{1}{\nu_f f + \nu_h H} + \\ & + \left( \left( 1 - \frac{q_1 p_2}{2} \right) \nu_f f + q_1 (1 - p_2 - (1 - \alpha) p_3) \nu_h H \right) \frac{t_h (1 + \nu_h S T_{HA}^*)}{(1 + t_h \nu_h S) (\nu_f f + \nu_h H)}. \end{aligned} \quad (10)$$

$$\begin{aligned} & \left( 1 - \frac{\left( \left( 1 - \frac{p_1 q_2}{2} \right) \nu_f f + (1 - p_1 + (1 - \alpha) p_1 q_3) \nu_h H \right) t_h \nu_h S}{(1 + t_h \nu_h S) (\nu_f f + \nu_h H)} \right) T_{HA}^* = p_1 q_2 t_c + p_1 q_3 \frac{t_a}{2} + \\ & + \left( \left( 1 - \frac{p_1 q_2}{2} \right) \nu_f f + (1 - p_1 + (1 - \alpha) p_1 q_3) \nu_h H \right) \frac{t_h}{(1 + t_h \nu_h S) (\nu_f f + \nu_h H)} + \\ & + p_1 \left( 1 - \frac{q_2}{2} - (1 - \alpha) q_3 \right) \frac{1 + \nu_h H T_{SA}^*}{\nu_f f + \nu_h H}. \end{aligned} \quad (11)$$

225 The average required time to the consumption of a food item for a single searcher animal  
 226 of a population playing strategy  $(p_1, p_2, p_3)$ , who has just met a handler animal of this  
 227 population,  $T_{SA}$ , and the respective time of a single handler of the same population who  
 228 has just met a searcher,  $T_{HA}$ , can be found by solving the system of equations (10) and  
 229 (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  $1/\nu_{ff}$  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)

$$T_{\text{HA}}^* = q_2 \left( t_c - \frac{1}{2} \left( \frac{1}{\nu_{ff}} + t_h \right) \right) + q_3 \left( \frac{t_a}{2} - (1 - \alpha) \frac{1}{\nu_{ff}} \right) + \frac{1}{\nu_{ff}} + t_h. \quad (12)$$

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

242 A mutant which uses a strategy different from that of the population at just the  
 243 searching state is considered to use a better strategy, and thus be able to invade, if  
 244  $T_{\text{SA}}^* \leq T_{\text{SA}}$ , i.e. if the decision that it will make at the point when it will meet a handler,  
 245 when searching for food, will lead to a smaller time until the consumption of a food item.  
 246 Similarly, a mutant which plays differently from the population just at the handling state  
 247 is considered to be able to invade if the decision it will make in an encounter with a

248 searcher, when handling a food item, will shorten the time to the consumption of a food  
 249 item, i.e. if  $T_{HA}^* \leq T_{HA}$ . Note that it is possible that under certain parameters  $T_{SA}^*$  is  
 250 independent of  $q_1$  and all values  $0 \leq q_1 \leq 1$  give identical times. Similarly,  $T_{HA}^*$  might  
 251 be independent of  $q_2$  and  $q_3$ . In these circumstances, in such asymmetric games, the  
 252 population can still be invaded by genetic drift.

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

- 266 - Strategy (0,0,0) (Dove, D): the animal does never challenge handlers and does  
 267 never resist any challenges.
- 268 - Strategy (0,1,0) (Non-Attacking Sharer, NAS): the animal does never challenge  
 269 handlers and always shares its food when it is challenged.
- 270 - Strategy (0,0,1) (Retaliator, R): the animal does never challenge handlers but  
 271 always resists when it is challenged.
- 272 - Strategy (1,0,0) (Marauder, M): the animal challenges handlers at every opportu-  
 273 nity but it does never resist any challenges.
- 274 - Strategy (1,1,0) (Attacking Sharer, AS): the animal challenges handlers at every  
 275 opportunity and it always shares the food when it is challenged.

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

### 278 **The optimal strategy for an animal at the searching state**

279 Consider a population playing strategy  $(p_1, p_2, p_3)$  that is potentially invaded by a mu-  
 280 tant animal playing a different strategy  $(q_1, q_2, q_3)$ . For reasons explained in the previous  
 281 section, in order to study whether the mutant can evolve because it uses a better strat-  
 282 egy at the searching state, we assume that the strategy which is used by all the animals  
 283 when they are at the handling state is the same, i.e.  $p_2 = q_2$  and  $p_3 = q_3$ . We consider  
 284 the strategy used by a searcher animal of the population when coming across a handler,  
 285  $p_1$ , to be advantageous over a mutant strategy,  $q_1$ , (and thus the population cannot  
 286 be invaded by the mutant) if the average time required for the searcher playing the  
 287 population strategy to gain and consume a food item,  $T_{SA}$ , is less than that required  
 288 for the mutant searcher,  $T_{SA}^*$ . Using the equations (10), (11) and (7)–(9) we find all  
 289 the necessary conditions under which a mutant playing strategy  $q_1 \in \{0, 1 : q_1 \neq p_1\}$   
 290 cannot invade a population playing strategy  $p_1 \in \{0, 1 : p_1 \neq q_1\}$  for the cases where  
 291 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  
 292  $p_3 = q_3 = 0$ . These are summarised in Table 3 (conditions (C.3), (C.6), (C.9), (C.10),  
 293 (C.13) and (C.16)).

### 294 **The optimal strategy for an animal at the handling state**

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

### 301 **Optimal strategies in an aggressive population**

302 Assume that all the members of the population behave aggressively when encountering  
 303 a handler animal, i.e.  $p_1 = q_1 = 1$ . We consider the strategy of an attacked handler  
 304 of the population to be advantageous over the strategy used by an attacked handler  
 305 mutant (and thus the mutant cannot invade) if the average time required for the first to  
 306 consume a food item,  $T_{HA}$ , is less than that required for the second,  $T_{HA}^*$  (in this case,  
 307 this is equivalent to the comparison of  $T_{SA}$  with  $T_{SA}^*$  since the times needed for animals  
 308 which always challenge, i.e. when  $p_1 = q_1 = 1$ , to acquire a food item and be discovered  
 309 by a foraging animal are identical, independently of the strategies they use as handlers).  
 310 Using again the equations (10), (11) and (7)–(9) we find the necessary conditions under  
 311 which a mutant in this scenario cannot invade a population playing a different strategy  
 312 at the handling state. These conditions are presented in Table 3 (conditions (C.11),  
 313 (C.12), (C.14), (C.15), (C.17) and (C.18)).

### 314 **Optimal strategies in a non-aggressive population**

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

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

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

### 323 **Evolutionarily Stable Strategies**

324 Table 3 shows all the appropriate conditions under which a population playing strategy  
 325  $(p_1, p_2, p_3)$  cannot be invaded by a mutant playing a different strategy at one of the

326 two decision points,  $(q_1, q_2, q_3)$ , for all the possible cases where all animals play a pure  
 327 strategy.

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

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

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

## 355 Predictions of the model

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

363 In a non-attacking population, a sharer does better than a Dove when they are  
 364 attacked if the average time needed for a sharer to consume a whole food item ( $t_c +$   
 365  $((1/\nu_f f) + t_h)/2$ ) is less than the average time needed to find an undiscovered food item  
 366  $(1/\nu_f f)$  and consume it ( $t_h$ ) (equivalently in this case, if the time the sharer needs to  
 367 consume the half of the food item ( $t_c$ ) is on average less than half of the time needed to  
 368 find and consume a whole food item  $((1/\nu_f f) + t_h)/2$ ). On the other hand, an Attacking  
 369 Sharer mutant does better than a member of a population of Non-Attacking Sharers if  
 370  $t_c \leq ((1/\nu_f f) + t_h)/2$  as well. Hence, as we see in Table 3, condition (C.4) contradicts  
 371 condition (C.6) and thus a Non-Attacking Sharer is never an ESS. The food sharing  
 372 strategy can be an ESS only if the sharer challenges a handler at every opportunity  
 373 when it is at the searching state. A population of Attacking Sharers can potentially  
 374 be invaded by Non-Attacking Sharers, Marauders and Hawks. The conditions under  
 375 which a Non-Attacking Sharer and a Marauder can invade a population of Attacking  
 376 Sharers are the same. This occurs because in such a population a Marauder can invade  
 377 if it is better for any handler to give up a food item rather than share (so being a  
 378 searcher is better than sharing a food item) and a Non-Attacking Sharer can invade if  
 379 it is better not to challenge for a food item, which will be shared (so again searching is  
 380 better than sharing). Increasing the rate at which foragers find food,  $\nu_f f$ , increases the  
 381 parameter range where Non-Attacking Sharers and Marauders invade the population of  
 382 Attacking Sharers. Depending on the values of the other parameters, the increase of  $\nu_f f$   
 383 might favour the invasion of Hawks as well (usually when food is difficult to discover).  
 384 Hence, increasing  $\nu_f f$  decreases the range of the parameter values in which the Attacking



385 Sharer strategy is an ESS (see Figure 3 for an example). A similar situation appears by  
 386 decreasing the area in which foragers search for handling sharers per unit time,  $\nu_h$ . As  
 387 it is observed in Figure 4 and the conditions (C.13)–(C.15), the decrease of the density  
 388 of the population,  $P$ , might also create unpropitious circumstances for food sharing.  
 389 For a given set of parameter values for which the Attacking Sharer strategy is an ESS,  
 390 increasing the time cost of the sharing process which results in the increase of  $t_c$ , the area  
 391 where the Attacking Sharer strategy is an ESS reduces, as one would expect. Depending  
 392 on the other ecological conditions, this strategy might coexist as an ESS with either one  
 393 of the other possible ESSs (Retaliator, Marauder or Hawk) or two of them (Retaliator  
 394 and Marauder or Marauder and Hawk). At very high levels of  $t_c$  such that the time spent  
 395 in sharing would be better spent in searching for another food item or in defending the  
 396 food item, Attacking Sharer cannot be an ESS. In this case, the predictions of the model  
 397 approach those of the model of Broom et al. (2004), where sharing was not possible.  
 398 In conditions where the duration of aggressive interactions is high, the defending strategy  
 399 is less profitable and thus the avoidance of any aggressive interaction is favoured. Hence,  
 400 under these circumstances, it is observed that animals should decide either to surrender  
 401 their food (use the Marauder strategy) or to share it (use the Attacking Sharer strategy)  
 402 when they are challenged, even if they have a high probability of defending their food  
 403 successfully. Therefore, at high fight durations each of Marauder and Attacking Sharer  
 404 strategies might be the unique ESS or both might be ESSs simultaneously.

#### 405 **A special case**

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

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

## 427 Discussion

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

443 2005, 2007) could be appropriate models.

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

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

472       Food sharing is a complicated mechanism. Different animal species share their food

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

501 In addition, our model assumes that the members of the population are of the same  
502 type. However, real populations consist of individuals with biological and physiological

503 differences and the optimal strategic choices depend on the characteristics of the individ-  
504 uals and those of their opponent. For example, recent observational and experimental  
505 studies on the dung roller beetle *Canthon cyanellus cyanellus* have shown that males of  
506 similar size are more likely to share the resource rather than to defend it (Chamorro-  
507 Florescano et al., 2010). Fight duration may be correlated with the differences between  
508 the opponents as well (e.g., Rovero et al., 2000). The size and the quality of the food  
509 items or the estimation of the value of the resource might also affect significantly the  
510 frequency of food sharing (see for example, White, 1994) as well as a contest duration  
511 (see for example, Enquist and Leimar, 1987).

512 In our model all costs are expressed in terms of time used and we ignore other costs  
513 which can be important, such as energy costs and possible injuries resulting from fights  
514 (for a model which incorporates energy costs see Vahl, 2006). For simplicity we do  
515 not impose extra time penalties on animals in contests. A resulting limitation is that  
516 the winner and the loser of a contest face the same cost. Although this can be the  
517 case in nature (e.g., Smith and Taylor, 1993), experimental studies have shown that  
518 either the loser (e.g., Chellapa and Hungtingford, 1989; Neat et al., 1998) or the winner  
519 (e.g., Hack, 1997) might suffer higher energetic or other cost, such as a high recovery  
520 time cost (see also, Luther and Broom, 2004). For instance, if the handler uses more  
521 energy (e.g. because it is carrying a food item during the contest) then it might need  
522 a higher recovery time. This would decrease the food intake rate making the defending  
523 strategy less attractive and the choice of alternative strategies more likely. In the same  
524 way, although it is assumed that the cost from the sharing process is equal for the  
525 two animals that share food, in reality the two animals might suffer a different cost.  
526 Furthermore, it is assumed that once an animal loses a contest with another animal, it  
527 does not initiate a new fight with the same animal but starts searching for alternative  
528 food resources. This is generally reasonable, as often contests between animals can have  
529 strong (at least short-term) effects on their relationship (winner and loser effects) which  
530 reinforce the dominance of the winner (see for example, Dugatkin, 1997). Similarly, in  
531 related contests between animals for territory acquisition animals that lose an agonistic  
532 interaction often leave the areas in which they were defeated (see for example, Stamps

533 and Krishnan, 1994). However, we should note that in some cases an animal may attack  
534 repeatedly the owner after iterated losing tries (e.g., Stamps, 1994). One way that  
535 the model could be extended and relax this assumption, is to allow the loser animal  
536 to attack repeatedly the winner. This could be done, for example, by introducing the  
537 choice to the loser to attack again or not, following similar assumptions to those in some  
538 owner-intruder type of games (e.g., Morrell and Kokko, 2003).

539 In natural systems, foraging animals might be faced with more than one foraging  
540 option with different variance in food intake. For example, they might be faced with a  
541 constant food resource versus a variable food resource, a food resource with fixed delay  
542 versus the same food resource with variable delay, or an immediate gain of food versus  
543 a delayed gain. There is strong empirical evidence that a forager's choice may depend  
544 on many ecological factors, such as the energetic status of the animal, the type of food  
545 variance, the energy requirements of the animal within a certain time interval and the  
546 probability of delays due to different kind of unpredictable interruptions (for example  
547 bad weather). The forager might be either risk-averse and choose the predictable option,  
548 or risk-prone and choose a risky option, respectively (see for example, Kacelnik and  
549 Bateson, 1996). For example, an animal with low food reserves might choose a safe  
550 lower level of return, provided it was sufficient for survival. Food sharing might be  
551 a way for animals to reduce such variances in food intake (e.g., Wenzel and Pickering,  
552 1991). Although the present model does not consider any risk associated with alternative  
553 food sources, it would be interesting to incorporate in future work such parameters that  
554 might influence the foraging decisions.

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

558 **Appendix A**

559 **The densities of the different groups of the population,**  
 560  **$S, H, C, A$  and  $R$ , in the equilibrium conditions**

561 In the equilibrium conditions

$$\frac{dS}{dt} = \frac{dH}{dt} = \frac{dC}{dt} = \frac{dA}{dt} = \frac{dR}{dt} = 0. \quad (14)$$

562 From the equation

$$\frac{dC}{dt} = 2p_1p_2\nu_hSH - \frac{1}{t_c}C = 0, \quad (15)$$

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

$$C = 2p_1p_2t_c\nu_hSH. \quad (16)$$

564 Similarly, from the equations

$$\frac{dA}{dt} = \frac{dR}{dt} = 0, \quad (17)$$

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

$$A = R = \frac{p_1p_3t_a\nu_hSH}{2}. \quad (18)$$

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

$$\frac{dS}{dt} = \frac{dH}{dt} = 0, \quad (19)$$

567 and solving the system for  $S$  using equation (6), it is obtained that in the equilibrium,  
 568 the densities of the different groups of the population,  $S, H, C, A$  and  $R$ , are given by  
 569 (7).

## 570 Appendix B

### 571 Average time for a single animal to consume a food item

#### 572 Average time for a single searcher animal to consume a food item when en- 573 countering a handler animal

574

575 Assume that a mutant searcher playing  $(q_1, q_2, q_3)$  has just come upon a handler  
576 playing the population strategy,  $(p_1, p_2, p_3)$ . If the mutant searcher ignores the handler,  
577 with probability  $1 - q_1$ , then it will need an average time  $T_S^*$  until the consumption of  
578 a food item. Otherwise, if the mutant attacks, with probability  $q_1$ , the average time  
579 needed for the consumption of a food item depends on the action that the handler  
580 animal will take. If the handler decides to share the food, with probability  $p_2$ , then the  
581 further expected time required to the consumption of a whole food item by the mutant  
582 is  $T_C^*$ . If the attacked handler decides to defend its food, with probability  $p_3$ , then a  
583 fight takes place and the attacking mutant will need an average time  $T_A^*$  to acquire and  
584 consume a food item. Finally, if the attacked animal decides to leave its food to the  
585 attacking animal without taking any action, with probability  $1 - p_2 - p_3$ , the attacking  
586 searcher animal becomes a handler and it then requires an average time  $T_H^*$  until the  
587 consumption of a food item.  $T_{SA}^*$  is given by the following equation

$$T_{SA}^* = q_1(p_2T_C^* + p_3T_A^* + (1 - p_2 - p_3)T_H^*) + (1 - q_1)T_S^*. \quad (20)$$

588 Recall that we assume that two animals that share a food item do so equally. Each of the  
589 sharers needs a time  $t_c$  until consumption of the half of the food and once it consumes  
590 it, it returns to the searching state. From the searching state, the mutant needs a time  
591 on average equal to  $T_S^*$  in order to consume a whole food item. The average time needed  
592 for a mutant sharer to consume a whole food item,  $T_C^*$ , is given by

$$T_C^* = t_c + \frac{T_S^*}{2}. \quad (21)$$

593 The sharing process described above is, in terms of expected reward, entirely equivalent



594 to a process where if a searcher and a handler decide to share the food, at the end of the  
 595 sharing period, with probability 0.5 one of the two animals obtains the food item while  
 596 the other takes nothing. The loser then has to resume searching for a new food resource  
 597 and thus spend an average time  $T_S^*$  until the consumption of a food item. Both animals  
 598 suffer a time cost from the sharing process equal to  $t_c$ . Hence, the time that a sharer  
 599 needs for the consumption of a food item is on average equal to  $0.5t_c + 0.5(t_c + T_S^*)$ ,  
 600 which leads to (21).

601 Substituting (21) into (20) we obtain

$$T_{SA}^* = q_1(p_2t_c + p_3T_A^* + (1 - p_2 - p_3)T_H^*) + \left(1 - q_1 + \frac{q_1p_2}{2}\right)T_S^*. \quad (22)$$

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

$$T_A^* = \frac{t_a}{2} + (1 - \alpha)T_S^* + \alpha T_H^*. \quad (23)$$

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

$$T_S^* = \frac{\nu_h H}{\nu_f f + \nu_h H} T_{SA}^* + \frac{\nu_f f}{\nu_f f + \nu_h H} T_H^* + \frac{1}{\nu_f f + \nu_h H}. \quad (24)$$

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

616 animal is equal to  $1/((1/t_h) + \nu_h S)$ .  $T_H^*$  is thus given by

$$T_H^* = \frac{1}{1 + t_h \nu_h S} 0 + \frac{t_h \nu_h S}{1 + t_h \nu_h S} T_{HA}^* + \frac{t_h}{1 + t_h \nu_h S}. \quad (25)$$

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

619

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

622

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

$$T_{HA}^* = p_1 (q_2 T_C^* + q_3 T_R^* + (1 - q_2 - q_3) T_S^*) + (1 - p_1) T_H^*, \quad (26)$$

626 where  $T_R^*$  is the average time cost of the decision of a mutant handler to defend its food  
627 against a challenge. Substituting (21) into (26) we obtain

$$T_{HA}^* = p_1 \left( q_2 t_c + q_3 T_R^* + \left( 1 - \frac{q_2}{2} - q_3 \right) T_S^* \right) + (1 - p_1) T_H^*. \quad (27)$$

628 In a similar way as before,  $T_R^*$  is given by

$$T_R^* = \frac{t_a}{2} + \alpha T_S^* + (1 - \alpha) T_H^*. \quad (28)$$

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

630

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

633

634 In the case where all the members of the population do not challenge, i.e.  $p_1 = q_1 =$   
635  $0$ , but occasionally a challenge might occur, the average time needed for an attacked

636 handler mutant playing  $(0, q_2, q_3)$  to consume a food item,  $T_{\text{HA}}^*$ , is given by

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

637 where  $T_{\text{R}}^*$  is given by equation (28). Since the population is not making challenges,

638  $T_{\text{S}}^* = \frac{1}{\nu_{ff}} + t_h$  and  $T_{\text{H}}^* = t_h$ . Substituting into equation (29), we obtain (12).

## 639 Appendix C

### 640 The optimal strategy is always pure

641 In the present model, there are 21 possible groups of strategies that an animal can play,  
642 6 of which consist of pure strategies and 15 of mixed strategies. These are summarised  
643 in Table 5.

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

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

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

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

$$T_{\text{HA}}^* = c_1 q_2 + c_2 q_3 + c_3, \quad (30)$$

665 where  $c_1$ ,  $c_2$  and  $c_3$  depend only on the parameters of the model  $t_a, t_h, t_c, \nu_{ff}$  and  $\alpha$ .  
 666 Hence, if the values of the parameters are such that  $c_1$  and  $c_2$  are both greater than zero,  
 667 then the optimal strategy for the mutant is  $q_2 = q_3 = 0$ . In any other case, if  $c_1 < c_2$ ,  
 668 the optimal strategy is  $q_2 = 1$  and  $q_3 = 0$  while if  $c_1 > c_2$  the optimal strategy is  $q_2 = 0$   
 669 and  $q_3 = 1$ .

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

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

$$T_{\text{SA}}^*(0, 1, 0) = T_{\text{S}}^*(0, 1, 0), \quad (31)$$

676 while

$$T_{\text{SA}}^*(1, 1, 0) = T_{\text{C}}^*(1, 1, 0) = t_c + \frac{T_{\text{S}}^*(1, 1, 0)}{2}. \quad (32)$$

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

$$T_{\text{S}}^*(0, 1, 0) = T_{\text{S}}^*(1, 1, 0) = T_{\text{S}}(p_1^*, 1, 0) = 2t_c. \quad (33)$$

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  $(p_1^*, 1, 0)$ ,

$T_{\text{HA}}^*(p_1^*, 0, 0)$ , is higher than the average time required when playing the population strategy,  $T_{\text{HA}}(p_1^*, 1, 0)$ . Using equation (27) we find that

$$T_{\text{HA}}^*(p_1^*, 0, 0) > T_{\text{HA}}(p_1^*, 1, 0) \quad (34)$$

$$\Rightarrow T_{\text{S}}^*(p_1^*, 0, 0) > T_{\text{C}}(p_1^*, 1, 0) \Rightarrow T_{\text{S}}^*(p_1^*, 0, 0) = T_{\text{S}}(p_1^*, 1, 0) > 2t_c. \quad (35)$$

680 This contradicts (33). Consequently, there is no any equilibrium strategy ( $0 < p_1 <$   
681  $1, 1, 0$ ). This is also verified from the results of numerical examples for a wide range of  
682 parameter values (see Figure 6a for an example).

683 In a similar way it is proved that there is no equilibrium strategy in the class of  
684 strategies (S 6). If there was an equilibrium strategy ( $0 < p_1^* < 1, 0 < p_2^* < 1, 0 < p_3^* <$   
685  $1, p_2^* + p_3^* < 1$ ), then  $T_{\text{HA}}^*(p_1^*, 0, 0)$ ,  $T_{\text{HA}}^*(p_1^*, 1, 0)$  and  $T_{\text{HA}}^*(p_1^*, 0, 1)$  should all be identical,  
686 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  
687 this case, using equations (27) and (28) we find that

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

688 On the other hand, if  $(p_1^*, p_2^*, p_3^*)$  is an equilibrium strategy, then  $T_{\text{SA}}^*(p_1^*, p_2^*, p_3^*) =$   
689  $T_{\text{SA}}^*(1, p_2^*, p_3^*) = T_{\text{SA}}^*(0, p_2^*, p_3^*)$  which yields that  $T_{\text{SA}}^*(1, p_2^*, p_3^*) = T_{\text{S}}^*(0, p_2^*, p_3^*) = T_{\text{S}}^*(1, p_2^*, p_3^*) =$   
690  $T_{\text{S}}^*(p_1^*, p_2^*, p_3^*)$ . Substituting into equation (24) we obtain that

$$T_{\text{S}}^*(p_1^*, p_2^*, p_3^*) - T_{\text{H}}(p_1^*, p_2^*, p_3^*) = \frac{1}{\nu_f f}. \quad (37)$$

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

$$1 - \alpha = \nu_f f \frac{t_a}{2}. \quad (38)$$

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

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

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

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**Table 1**  
**The model notations**

<b>Population's densities</b>	<b>Meaning</b>
$P$	Density of the population
$S, H, C, A, R$	Density of searchers, handlers, sharers, attackers and defenders
<b>Model Parameters</b>	<b>Meaning</b>
$\nu_f f$	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
$\alpha$	The probability that the attacker wins the fight
<b>Strategies</b>	<b>Meaning</b>
$p_1$	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**

<b>Notation</b>	<b>Meaning</b>
$T_{SA}$	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

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**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)	/	$2t_c - t_h > \frac{1}{\nu_{ff}}$ (C.1)	$\nu_{ff} > \frac{2(1-\alpha)}{t_a}$ (C.2)	The mutant always invades (C.3)	—	—
	(0,1,0)	$2t_c - t_h < \frac{1}{\nu_{ff}}$ (C.4)	/	$2t_c - t_h < t_a - \frac{1-2\alpha}{\nu_{ff}}$ (C.5)	—	$2t_c - t_h > \frac{1}{\nu_{ff}}$ (C.6)	—
	(0,0,1)	$\nu_{ff} < \frac{2(1-\alpha)}{t_a}$ (C.7)	$2t_c - t_h > t_a - \frac{1-2\alpha}{\nu_{ff}}$ (C.8)	/	—	—	$\nu_{ff} > \frac{2\alpha}{t_a}$ (C.9)
	(1,0,0)	The mutant never invades (C.10)	—	—	/	$2t_c - t_h > \frac{1}{\nu_{ff}}$ (C.11)	$\nu_{ff} > \frac{2(1-\alpha)}{t_a} - \frac{t_h \nu_{ff} \nu_h P}{t_h \nu_{ff} + 1}$ (C.12)
	(1,1,0)	—	$2t_c - t_h < \frac{1}{\nu_{ff} - \nu_h H_a}$ * (C.13)	—	$2t_c - t_h < \frac{1}{\nu_{ff} - \nu_h H_a}$ * (C.14)	/	$(2t_c - t_h)(\nu_{ff} - \alpha \nu_h H_a) \nu_{ff} < (t_a \nu_{ff} + \alpha) \nu_{ff} + (1-\alpha)((t_h \nu_h P - 1) \nu_{ff} - (\nu_{ff} + \nu_h P) t_h \nu_h H_a)$ * (C.15)
	(1,0,1)	—	—	$\nu_{ff} < \frac{2\alpha}{t_a}$ (C.16)	$\nu_{ff} < \frac{2(1-\alpha)}{t_a} + (1-2\alpha) \nu_h H_b$ ** (C.17)	$(2t_c - t_h)(\nu_{ff} + \alpha \nu_h H_b) > t_a(\nu_{ff} + 2\alpha \nu_h H_b) + \alpha t_h(\nu_h P - \nu_h H_b) + 2\alpha - 1$ ** (C.18)	/

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

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

**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	$\nu_{ff} > \frac{2(1-\alpha)}{t_a}$	The mutant always invades	—	—
	(0,1,0)	The mutant never invades	/	$\nu_{ff} > \frac{1-2\alpha}{t_a}$	—	The mutant always invades	—
	(0,0,1)	$\nu_{ff} < \frac{2(1-\alpha)}{t_a}$	$\nu_{ff} < \frac{1-2\alpha}{t_a}$	/	—	—	$\nu_{ff} > \frac{2\alpha}{t_a}$
	(1,0,0)	The mutant never invades	—	—	/	The mutant always invades	$\nu_{ff} > \frac{2(1-\alpha)}{t_a} - \frac{t_h \nu_{ff} \nu_h P}{t_h \nu_{ff} + 1}$
	(1,1,0)	—	The mutant never invades	—	The mutant never invades	/	$(t_a \nu_{ff} + \alpha)(t_h \nu_{ff} + t_h \nu_h P + 1) - (1-\alpha)(t_h \nu_{ff} + 1) > 0$
	(1,0,1)	—	—	$\nu_{ff} < \frac{2\alpha}{t_a}$	$\nu_{ff} < \frac{2(1-\alpha)}{t_a} + (1-2\alpha)\nu_h H_b$ *	$t_a(\nu_{ff} + 2\alpha\nu_h H_b) + \alpha t_h(\nu_h P - \nu_h H_b) + 2\alpha - 1 < 0$ *	/

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

**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



848 **Figure legends**

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

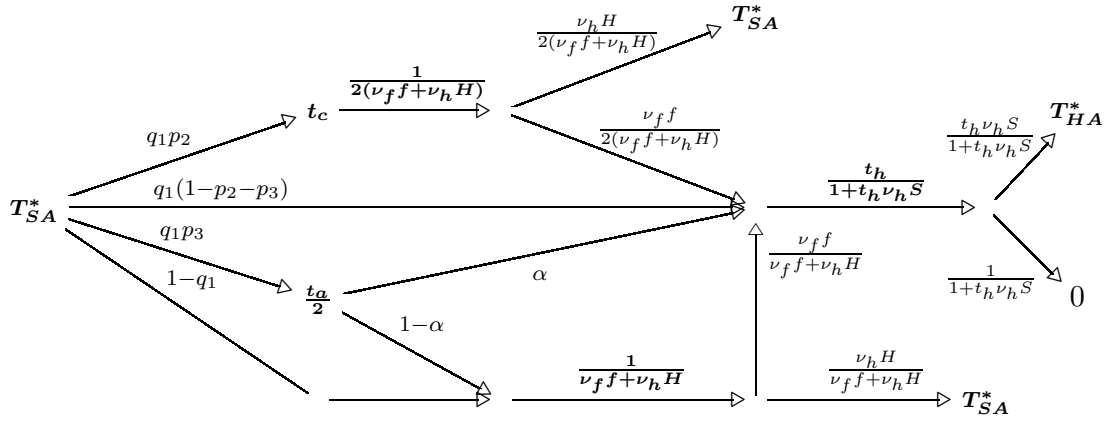
853 **Figure 2:** Schematic representation of all the possible events that might happen until  
 854 the consumption of a food item by a mutant handler playing strategy  $(q_1, q_2, q_3)$  who  
 855 encounters a searcher of a population playing strategy  $(p_1, p_2, p_3)$ . The transition prob-  
 856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

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

864 **Figure 4:** Graphs showing examples of the region where each of the four possible ESSs  
 865 (Retaliator (R), Marauder (M), Attacking Sharer (AS) and Hawk (H)) is an ESS as  
 866 the density of the population,  $P$ , and the rate at which foragers find undiscovered food,  
 867  $\nu_{ff}$ , vary. In each region, a single letter 'X' indicates that the strategy X is the unique  
 868 ESS, 'X,Y' indicates that the strategies X and Y are simultaneous ESSs and 'X, Y, Z'  
 869 that the three strategies X, Y and Z are simultaneous ESSs. (a)  $t_a/2 = 0.5, t_h = 3, t_c =$   
 870  $4, \nu_h = 1.5, \alpha = 0.7$ ; (b)  $t_a/2 = 0.5, t_h = 3, t_c = 2, \nu_h = 2, \alpha = 0.2$ .

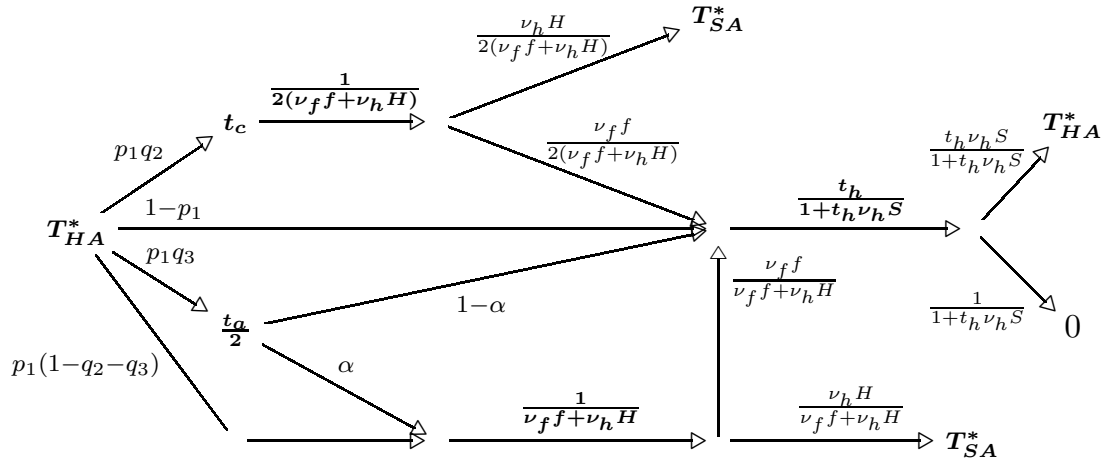
871 **Figure 5:** A graph showing an example of the region where each of the three possi-  
 872 ble ESSs (Retaliator (R), Attacking Sharer (AS) and Hawk (H)) can occur in the  
 873 special case where  $2t_c = t_h$ , as the probability  $\alpha$  of the challenger winning and the  
 874 duration of the content,  $t_a/2$ , vary. In each region, a single letter 'X' indicates that the  
 875 strategy X is the unique ESS, 'X,Y' indicates that the strategies X and Y are simulta-  
 876 neous ESSs and 'X, Y, Z' that the three strategies X, Y and Z are simultaneous ESSs.  
 877  $2t_c = t_h = 3, \nu_{ff} = 0.5, \nu_h = 1.5, P = 1$ .

878 **Figure 6:** (a) The expected time until the consumption of a food item of mutant  
879 searcher animals playing strategies  $(0,1,0)$ ,  $(1,1,0)$  and  $(0 < p_1 < 1, 1, 0)$  in a popu-  
880 lation playing strategy  $(0 < p_1 < 1, 1, 0)$  for the example considered in Figure 3b for  
881  $t_c = 2$ . Numerical examples indicate that in every population which adopts a strat-  
882 egy  $(0 < p_1 < 1, 1, 0)$ , either a mutant animal that plays strategy  $(0, 1, 0)$  or a mu-  
883 tant animal that plays strategy  $(1, 1, 0)$  always does better than any other animal that  
884 uses the population strategy. Thus, such populations can be invaded by those mutant  
885 strategies and as a result, strategies  $(0 < p_1 < 1, 1, 0)$  cannot be ESSs. (b) The ex-  
886 pected time until the consumption of a food item of mutant handler animals playing  
887 strategies  $(0.8,1,0)$ ,  $(0.8,0,0)$  and  $(0.8, 0 < p_2 < 1, 0)$  in a population playing strategy  
888  $(0.8, 0 < p_2 < 1, 0)$  for  $t_h = 3, t_c = 2, \nu_{ff} = 1, \nu_h = 1.5, P = 1$ . An equilibrium strategy  
889  $(0 < p_1 \leq 1, 0 < p_2 < 1, 0)$  cannot be evolutionarily stable.



**Figure 1**

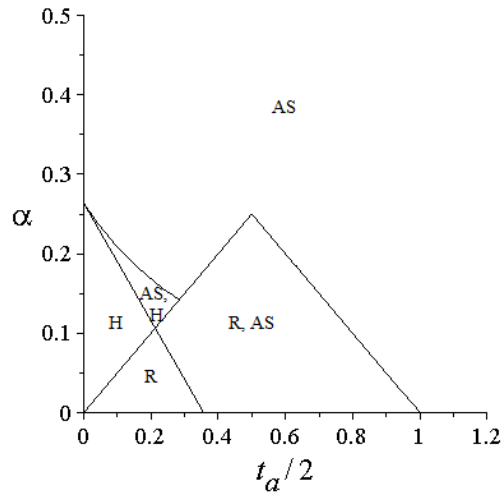
Schematic representation of all the possible events that might happen until the consumption of a food item by a mutant searcher playing strategy  $(q_1, q_2, q_3)$  who encounters a handler of a population playing strategy  $(p_1, p_2, p_3)$ . The transition probabilities and the expected times (in bold)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



**Figure 2**

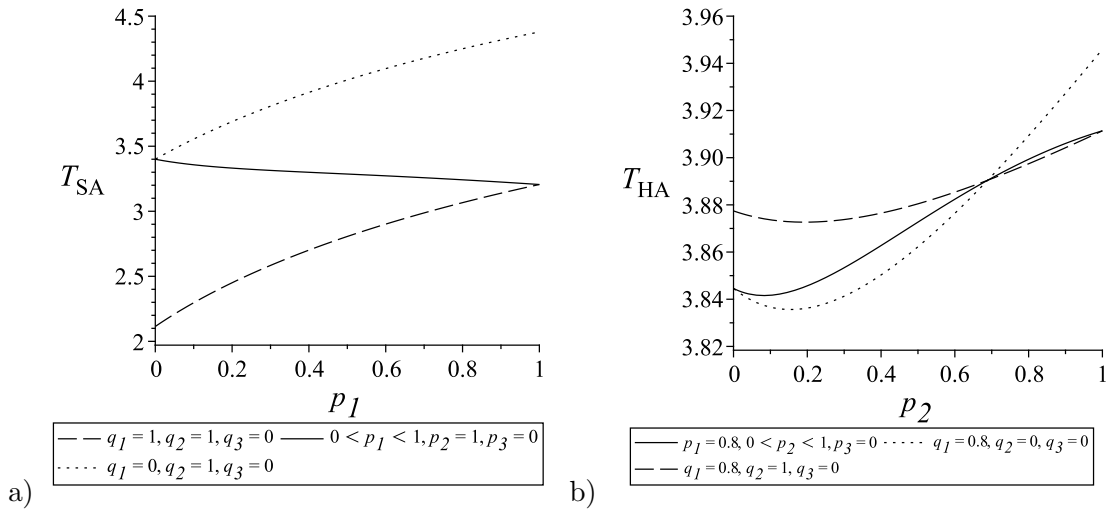
Schematic representation of all the possible events that might happen until the consumption of a food item by a mutant handler playing strategy  $(q_1, q_2, q_3)$  who encounters a searcher of a population playing strategy  $(p_1, p_2, p_3)$ . The transition probabilities and the expected times (in bold)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





**Figure 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  $\alpha$  of the challenger winning and the duration of the content,  $t_\alpha/2$ , 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.  $2t_c = t_h = 3, \nu_{ff} = 0.5, \nu_h = 1.5, P = 1$ .



**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  $t_h = 3, t_c = 2, \nu_{ff} = 1, \nu_h = 1.5, P = 1$ . An equilibrium strategy  $(0 < p_1 \leq 1, 0 < p_2 < 1, 0)$  cannot be evolutionarily stable.