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ORIGINAL ARTICLE

Is Food Worth Fighting For? ESS's in Mixed Populations of Kleptoparasites and Foragers

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Abstract We extend the game theoretic model of kleptoparasitism discussed in Broom et al. (2004), by considering a population of foragers consisting of two groups with different behaviours—those who forage and steal from other feeders, and those who only forage. We assume that those who do not steal have a better foraging rate than those who are also looking out for opportunities to steal. We also allow either type to resist an attack or not resist. We look for Evolutionary Stable States, of either a mixture of the two behaviours, or where the whole population has just one of these behaviours. We find nine such ESS's, dependent on the environmental parameters, although in fact only five of these are distinguishable. In general, we find that if the overall population density is low, food-stealing becomes less viable, and there is an ESS consisting of only foragers. Conversely, when there are many animals looking for, and finding, food, there is an ESS consisting of just kleptoparasites (which are also foraging). In between, an ESS will contain both pure-foragers and stealers. There is some empirical evidence of such behaviours.

We find that when there is a mixture of the two types, they must both have the same resistive behaviour. We can thus have some individuals challenging for food but not resisting challenges, and others not challenging and not resisting. This shows how aggressive behaviour may be context-dependent, as seen in practice.

Keywords Kleptoparasitism · Food-stealing · Polymorphism · Game theory · Strategy

1. Introduction

Finding sufficient food to fuel maintenance, growth and reproduction is a challenge common to all biological organisms. It commonly occurs that food is scarce

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or otherwise difficult to find, and organisms must search the environment for food items. A foraging organism can often find itself in visual (or other sensory) contact with conspecifics also searching for food. If a nearby conspecific finds a food item, then there may be an advantage to be gained from attempting to steal that food item from its discoverer. However, the potential gain from stealing the food item must be weighed against costs such as the time required to wrest the food item from its current owner, or the risk of injury entailed. Hence, food-stealing (or kleptoparasitic) behaviour can usefully be thought of within the cost–benefit economic framework that has been at the heart of investigations into behavioural ecology for decades (e.g. Krebs and Davies, 1993). Further, the economics of kleptoparasitism are influenced by the extent to which the current owner will resist an attempt to steal from it, and the likelihood that others will attempt to steal the food item from our focal individual, should it successfully take ownership. That is, the best strategy for one individual to adopt is intrinsically linked to the strategies played by the other individual that it might interact with. This is the type of situation where game theory has been very successfully applied to the study of animal behaviour (e.g. Maynard Smith, 1982). Hence, there is now a substantial literature of works using game theoretic approaches to elucidate the situations where we should and should not expect to see kleptoparasitic behavior in nature (e.g. Barnard and Sibly, 1981; Stillmann et al., 1997; Broom and Ruxton, 1998; Ruxton and Broom, 1999; Broom and Ruxton, 2003).

In the latest published development of a game theoretic model of kleptoparasitism (Broom et al., 2004), we expanded the generality of the original model of Broom and Ruxton (1998) in two key ways: allowing flexibility in the likelihood that a challenger will be able to successfully steal a prey item from a handler, and allowing challenged individuals the behavioral flexibility to surrender items without a time-consuming extended aggressive encounter. This showed that (depending on the values given to ecological variables) three different types of Evolutionarily Stable Strategies were possible: one where individuals both challenged for food items and resisted challenges from others (Hawk), one where individuals challenged but did not resist (Marauder), and one where individuals did not challenge, but would resist if themselves challenged (Retaliator). Further, in some circumstances, more than one of these was possible as alternates, depending on the history of the system as well as its current parameter values. The Marauder strategy is particularly interesting ecologically, giving an economic explanation for one individual to surrender a valuable food item without a fight to another individual in the absence of dominance hierarchies or intrinsic asymmetries in competitive abilities between individuals.

In this paper we wish to relax one of the most important simplifying assumptions in Broom et al. (2004), that searching for kleptoparasitic opportunities is cost free. Specifically, the original paper assumed that an individual can search for kleptoparasitic opportunities (individuals in possession of a food item that could be stolen) at no cost to their ability to detect food items themselves. As we have previously argued (Broom and Ruxton, 1998), this is unlikely to be true, and in reality a trade-off between these two modes of obtaining food is likely. This trade-off can be brought about by the physical limitations of sensory organs. For example, in a group of estuarine birds searching an inter-tidal mud flat for food, a bird must look downwards and focus at a near distance in order to detect food itself, but must look sideways and focus at a greater distance to detect when another bird has found food. Perhaps more generally, the trade-off will stem from cognitive limitations in the "attention" that the animal's brain can give to competing tasks. There is increasing understanding that animals have limited attention span that they can devote to information processing and information gathering tasks that are occurring simultaneously (Dukas, 2002), and that increased concentration on one task can only be bought with reduced concentration on another task. The use of the concept of limited attention has recently proved very powerful in understanding aspects of prey selectivity, and the ability of a forager to detect cryptic prey items (Dukas and Ellner, 1993; Dukas and Kamil, 2001).

Here, we model this trade-off by assuming that the population of foragers is composed of one or both of two different types: one type P_1 is unable to kleptoparasitise because individuals of this type dedicate themselves to maximizing their own ability to find food; whereas the other type P_2 pays for its ability to detect kleptoparasitic opportunities with reduced ability to find food itself. We have in mind two groups, which are indistinguishable, from a single species. Such a situation can occur in some species of seabird where most birds forage only, but a group get a large proportion of their resources from kleptoparasitism (for example Shealer and Spendelow (2002) investigated such a situation in a population of Roseate Terns). Our aim is to understand how this generalization affects the predictions of our earlier model, and in particular to consider whether each of the two predator types can exist on its own (resisting invasion from the other) and whether circumstances exist where the two can co-exist. This will aid our understanding not only of when we should expect to observe kleptoparasitism in the natural world, but also help to delineate circumstances where valuable resources are surrendered without a fight, and where they are not. In particular, in mixed populations are there circumstances in which one group should resist attacks and the other should not? This may seem plausible, since the increased basic foraging rate of the P_1 individuals might at first sight give them less incentive to defend their food. In fact, we show that when there is a stable mixture of the two types within the population, this difference in resistive behaviours will not occur. This should cast light on the evolution of hierarchies and social conventions of dominance.

2. The model

In a previous paper (Broom et al., 2004), we considered a homogenous population of animals, in which each animal had the option of attempting to steal food from others. Additionally, when attacked whilst handling food, each individual had the option of resisting such an attempted theft. We now go on to consider models where members of a population of indistinguishable animals can have one of two different types of behavior. Type P_2 forage for their own food, and also may attack others (of either type) who are handling food; type P_1 only forage, and do not attack handlers. Apart from their behaviour, the two types are identical, so that each type has the same parameter values (except that the foraging rate of P_2 is lower

Table 1 The model parameters and their definitions.

Parameter	Meaning
P_1	The population label (and population size) of non-kleptoparasites
P_2	The population label (and population size) of kleptoparasites
P	The total number of birds in the population $P = P_1 + P_2$
S_i	The number of birds of type i which are searching for food
H_i	The number of birds of type i which are handling a food item
A_i	The number of birds of type i involved in a contest over food
H	The total number of birds handling a food item $H = H_1 + H_2$
h_r	The handling ratio H/P in a population of (resisting) P_2 individuals
f	The density of food items per unit area
ν_{f1}	The area that P_1 birds can search for food per unit time
ν_{f2}	The area that P_2 birds can search for food per unit time
ν_{h}	The area that P_2 birds can search for handlers per unit time
t_{h}	The expected time that it takes a handler to consume a food item
$t_a/2$	The expected duration of a contest over food when the defender fights
α	The probability that the challenger wins when the defender fights
T_1	The expected time for a P_1 searcher to acquire a food item
T_2	The expected time for a P_2 searcher to acquire a food item
T_c	The expected time for a searcher to acquire and consume a food item
C_1	The food finding—consumption ratio for P_1 individuals
C_2	The food finding—consumption ratio for P_2 individuals

since they devote some of their attention to looking for handlers). See Table 1 for a description of the model parameters, and a comparison between P_1 and P_2. Thus the aggressor P_2 treats handlers from P_1 and P_2 identically (it cannot distinguish the two). However, the two groups may differ in the manner in which they respond to challenges, with one type resisting and the other not resisting. We assume that the numbers of each type vary in proportion to the evolutionary fitness of that type, so that if, say, P_1 is doing better, then in the next generation, more P_1 will breed than P_2; however, we take the total $P_1 + P_2 = P$ to be a constant.

For given values of P_1 and P_2 we can find equilibrium states of the population, where the numbers of searchers, handlers and fighters in each population are constant. However, we then wish to go further, and to find those particular equilibrium states where the two types have equal handling ratios i.e. $H_1/P_1 = H_2/P_2$, and thus have equal fitness (where H_1, H_2 are the number of handlers from P_1, P_2 respectively). This will only happen for particular values of P_1 and P_2. When it does happen, then there will be no change in the numbers of each population from one generation to the next. If, however, we had $H_1/P_1 < H_2/P_2$, say, then, in the next generation, the number of P_1 individuals would be less than in the current generation. These states, where the values of P_1 and P_2 allow for stability from one generation to the next, are Evolutionarily Stable States (or polymorphic ESSs), which we define in the next section. The polymorphism is immune to invasion by a small number of mutants playing any strategy. It is important to realize that equilibrium states of the population are not necessarily themselves ESS's.

In addition to the numbers of animals in each population, we have to consider the individual strategies of animals in each interaction, and whether evolutionary stability (i.e. an evolutionarily stable pair of strategies) is possible for each individual interaction. Attackers may choose whether or not to challenge when they encounter a handler, and handlers can choose whether or not to resist when challenged. There are thus eight distinct scenarios for the strategic choices of the two groups, which we shall label S_{ijk} for each of $i, j, k = 1$ or 2.

$i = 1$ if P_2 individuals choose to attack, $i = 2$ if they do not.
$j = 1$ if P_1 individuals resist attacks, $j = 2$ if they do not.
$k = 1$ if P_2 individuals resist attacks, $k = 2$ if they do not.

Thus for instance S_{121} corresponds to a population where P_2's attack and resist attacks, and P_1's do not resist.

3. The states of the system

The strategic scenario defined by S_{ijk} tells us how each individual will behave in every circumstance. Combined with the sizes of the two populations given by P_1 and P_2 and the various fixed performance parameters, this completely defines the system. In particular, the values of H_1 and H_2 can be evaluated, which, in turn, directly gives us the uptake rates of the two groups. The parameters are described in detail in the following section.

3.1. *Individual decisions*

In Broom et al. (2004), we studied a pure population of P_2 (in our present terminology). Most of the definitions below, referring to our two types of forager, follow directly from that paper (with suitable alterations in terminology).

The number of individuals of P_1 (P_2) which are handling a food item is labelled H_1 (H_2). Similarly the number of individuals of type P_1 (P_2) searching for food items (and also searching for handlers in the case of P_2) is S_1 (S_2) and the number involved in an aggressive contest is A_1 (A_2). Each of these six quantities are determined by other parameters, as shown later.

The number of available food items per unit area is given by f. We assume that food items take a time to handle drawn from an exponential distribution with mean t_h (i.e. t_h is the expected time for each item of food to be consumed). At the end of handling, the handler resumes searching. When a searcher of type P_2 encounters a handler, it can choose to challenge for the food item, or not. If it does challenge, then the handler can choose to resist, or not. If it does resist, then a fight ensues (with times drawn from an exponential distribution with mean time $t_a/2$). At the end of a contest, the winner starts handling the food, and the loser resumes searching. The probability of the challenger winning the contest is given by α. Each of these parameters are common to both types of bird.

The area which individuals of type P_1 (P_2) can search for food in unit time is given by ν_{f1} (ν_{f2}). Thus the rates at which individual P_1 and P_2 searchers find food are $\nu_{f1} f$ and $\nu_{f2} f$, respectively. P_2 individuals also search for handlers; they are able to search an area of size ν_h per unit time. The rate at which a searcher finds handlers is $\nu_h H$, where H is the total number of handlers ($H = H_1 + H_2$). In general $\nu_{f1} > \nu_{f2}$, reflecting the fact that the members of P_2 are not able to devote so much attention to foraging, as they are also looking for opportunities to steal.

The mean time for the P_1 foragers to find a food item, when searching for one, is $T_1 = 1/(\nu_{f1} f)$. If there is pure P_1, or a mixture of the two types, then this P_1 search time will be the expected time for any searching individual to find food (otherwise, in the mixture, one type would do better than the other). We proceed to identify the optimal strategy for individuals of each type in the various possible scenarios that they can face (conditions 1–8). In general, we use the term T_1 (T_2) for the expected time for a $P_1(P_2)$ searcher to acquire a food item in whichever population we are discussing.

3.2. *Evolutionarily stable states*

Definition 3.1. A *state of the system* is defined by the collection of values

$$(S_{ijk}, P_1, P_2, f, \nu_{f1}, \nu_{f2}, \nu_{\mathrm{h}}, t_{\mathrm{h}}, t_a, \alpha).$$

We simplify this to (S_{ijk}, P_1), the values influenced by strategic choices and evolution, since all other parameter values are fixed natural properties (except P_2 which is given by $P_2 = P - P_1$).

Definition 3.2. A population is in an *Evolutionarily Stable State* if

(i) all members of the population have an equal uptake rate, and
(ii) any small invading group, of whatever type, playing whatever strategy, introduced into the population has an uptake rate strictly less than that of the population.

In this section, we will derive the conditions for particular populations, behaving in certain ways, to be Evolutionarily Stable States (alternatively called polymorphic ESS's). We shall simply refer to them by the term ESS for short, so that ESS means evolutionarily stable state from now onwards.

The apparent randomness of the labeling of the conditions is explained by reference to Table 2 in Section 4.1, where all the conditions are collected together.

We start by considering the best behaviour for individuals.

3.2.1. *Challenging*

From Broom and Ruxton (1998) it is advantageous for P_2 to challenge a resisting handler if $t_a/2 < \alpha T_2$. For P_2, $T_2 < 1/(\nu_{f2} f)$, because P_2 is finding handlers as well as food. Therefore, we get $\nu_{f2} f < 2\alpha/t_a$, or

$$A2 \quad C_2 < 2\alpha t_{\mathrm{h}}/t_a, \tag{1}$$

where $C_2 = \nu_{f2} f t_{\mathrm{h}}$, (analogous to $C = \nu_{f1} f t_{\mathrm{h}}$, as used in Broom and Ruxton (1998)). C_2 is the ratio of the rate of finding food items (not including stealing) and the rate of consuming these items for P_2 individuals. Similarly $C_1 = \nu_{f1} f t_{\mathrm{h}}$ is this ratio for P_1 individuals. In populations with no kleptoparasitism this ratio is

Table 2 Conditions for attacking and resisting.

Label	ESS	Condition
A1	P_1 resists	$C_1 < \frac{2t_h(1-\alpha)}{t_a}$
A2	P_2 attacks, against resistance	$C_2 < \frac{2t_h\alpha}{t_a}$
A3	P_2 resists	$C_2 < \frac{2t_h(1-\alpha)}{t_a} + H\nu_h t_h(1-2\alpha)$
A31	P_2 resists in pure resisting P_1	$C_2 < \frac{2t_h(1-\alpha)}{t_a} + \frac{(1-2\alpha)\nu_h t_h C_1 P}{C_1+1}$
A32	P_2 resists in pure resisting P_2	$C_2 < \frac{2t_h(1-\alpha)}{t_a} + (1-2\alpha)\nu_h t_h P h_r$
A33	P_2 resists in pure non-resisting P_1	$C_2 < \frac{2t_h(1-\alpha)}{t_a} - \frac{\nu_h t_h C_1 P}{C_1+1}$
A34	P_2 resists in pure non-resisting P_2	$C_2 < \frac{2t_h(1-\alpha)}{t_a} - \frac{\nu_h t_h C_2 P}{C_2+1}$
B1	A small number of P_2 succeed against non-resisting P_1 in pure P_1	$P > \frac{(C_1-C_2)(C_1+1)}{C_1\nu_h t_h}$
B2	A small number of P_2 succeed against resisting P_1 in pure P_1	$\alpha > \frac{C_1 t_a}{2t_h} + \frac{(C_1-C_2)(C_1+1)}{C_1\nu_h t_h P}$
B3	A small number of P_1 (non-resisting) succeed, in non-resisting pure-P_2	$P < \frac{(C_1-C_2)(C_2+1)}{C_2\nu_h t_h}$
B4	A small number of P_1 (resisting) succeed in resisting pure-P_2	$P < \frac{(C_1-C_2)(t_a(C_1-C_2)+(C_2+1)(\alpha t_h - C_1 t_a/2))}{C_2\nu_h(\alpha t_h - C_1 t_a/2)^2}$
B5	A small number of P_1 (resisting) succeed in non-resisting pure-P_2	$P < \frac{(C_1-C_2)(C_2+1)}{C_2\nu_h(\alpha t_h + C_1 t_a/2)}$
B6	A small number of P_1 (non-resisting) succeed in resisting pure-P_2	$P < \frac{(C_1-C_2)(t_a(C_1-C_2)+(C_2+1)(t_h - C_1 t_a))}{C_2\nu_h(t_h - C_1 t_a/2)^2}$

also the ratio of handlers to searchers and drives the uptake rate (Holling, 1959).

3.2.2. Resisting

The conditions for resistance to occur are more complicated (as shown in Broom et al. (2004)).

For P_1 to resist, we have $t_a/T_1 < 2(1-\alpha)$ i.e.

$$A1 \quad C_1 < 2(1-\alpha)t_h/t_a. \tag{2}$$

For P_2, however, the conditions depend on what others are doing. If others are resisting, then an individual should resist if

$$A3 \quad C_2 < 2(1-\alpha)t_h/t_a + (1-2\alpha)\nu_h t_h H. \tag{3}$$

If others are not resisting, then the condition for resistance becomes

$$C_2 < 2(1-\alpha)t_h/t_a - \nu_h t_h H. \tag{4}$$

We then find H for the four different background populations, giving the conditions for P_2 to resist as:

in pure resisting P_1

$$A31 \quad C_2 < 2(1-\alpha)t_h/t_a + (1-2\alpha)\nu_h t_h C_1 P/(C_1+1); \tag{5}$$

(where $H = CP/(C+1)$ is Holling's result (Holling, 1959), elaborated in Broom and Ruxton (1998)):

in pure resisting P_2

$$A32 \quad C_2 < 2(1-\alpha)t_\mathrm{h}/t_a + (1-2\alpha)\nu_\mathrm{h}t_\mathrm{h}Ph_\mathrm{r} \tag{6}$$

(where h_r is the handling ratio, from Broom and Ruxton (1998), Eq. (5)):

in pure non-resisting P_1 if

$$A33 \quad C_2 < 2(1-\alpha)t_\mathrm{h}/t_a - \nu_\mathrm{h}t_\mathrm{h}C_1P/(C_1+1). \tag{7}$$

in pure non-resisting P_2 if

$$A34 \quad C_2 < 2(1-\alpha)t_\mathrm{h}/t_a - \nu_\mathrm{h}t_\mathrm{h}C_2P/(C_2+1). \tag{8}$$

We now look for ESS's by considering a particular state of the system, and then considering what happens if it is slightly disturbed. We find conditions for the invasion of each type of population by each type of possible mutant in turn (conditions B1–B6). One of our principal interests is whether an ESS can occur in a mixed population i.e. some of P_1 and P_2, or whether ESS's can only occur in single pure populations.

3.3. *Pure-P_1*

We start by considering a population consisting of pure-P_1, and then introduce a very small number of P_2 animals. Members of P_1 on their own have an equilibrium handling rate given by Holling's formula $C_1/t_\mathrm{h}(C_1+1)$, as found in the original Broom–Ruxton analysis, and so we must compare Holling's handling rate with the handling rate of a small number of P_2.

3.3.1. Resistance

To find the handling rate of a P_2, we must consider the model where all handlers resist, with probability $1-\alpha$ of winning when challenged. For P_2, searching is a pooled Poisson process, with rate $C_2/t_\mathrm{h} + \nu_\mathrm{h}H$. If it finds a food item first, by foraging, with probability $\frac{C_2}{C_2+\nu_\mathrm{h}t_\mathrm{h}H}$, then it starts handling. Alternatively, if it finds a handler first, with probability $\frac{\nu_\mathrm{h}t_\mathrm{h}H}{C_2+\nu_\mathrm{h}t_\mathrm{h}H}$ there will be a fight, lasting $t_a/2$, at the end of which it can start handling (if it won, with probability α) or it starts searching again (if it lost). The tree for this interaction is shown in Fig. 1.

Following Fig. 1 and comparing the handling ratio for the mutant with that of the population of P_1 individuals (see Appendix A) we find that the mutant successfully invades if

$$B2 \quad P > \frac{(C_1-C_2)(C_1+1)}{C_1\nu_\mathrm{h}t_\mathrm{h}(\alpha - C_1t_a/2t_\mathrm{h})}. \tag{9}$$

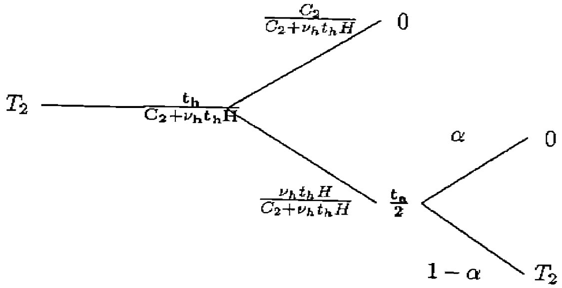

Fig. 1 Probability tree to find the expected time for a P_2 searcher who always attacks to obtain a food item (T_2). The tree shows the expected time to discover an item or a handler (in *bold* at the second node); the tree splits according to the probability (*normal text*) that this item is a free food item (acquired in 0 time), or being handled. If the item is being handled a contest ensues (time $t_a/2$ in *bold*) which is either won (with probability α), so the food item is acquired or lost, which means a return to searching (and expected acquisition time T_2).

As already seen, if there is sufficient resistance to deter attacks, then both populations are simply foraging. In this situation, the handling ratios of P_1 and P_2 are $C_1/(C_1+1)$ and $C_2/(C_2+1)$, respectively, and so P_1 alone will be an ESS if $C_1/(C_1+1) > C_2/(C_2+1)$ i.e.

$$C_1 > C_2,$$

which is intuitively obvious—the more efficient forager will win, given that there is no kleptoparasitism.

3.3.2. No resistance

If there is no resistance to attack, then in the preceding results, we may replace t_a by 0, and α by 1 in B2, to get

$$B1 \quad P > \frac{(C_1 - C_2)(C_1 + 1)}{C_1 \nu_h t_h}, \tag{10}$$

as the condition for P_2 mutants to do better than the pure P_1 population. We may interpret this as meaning that the total value of P is high enough for the members of P_2 to meet enough victims to maintain a high enough handling ratio.

This lower bound on P is lower than before, showing that if P_1 individuals resist attack, then they can exist as a pure ESS for a wider range of parameter values than if they do not. Put another way, it is easier for P_2 mutants to invade if the P_1 do not resist.

3.4. Pure-P_2

We now turn to consider the circumstances in which a population of just P_2 cannot be invaded by P_1. Again, we compare the handling ratio of a pure-P_2 population with that of some P_1 mutants, which, if successful, would lead to a mixture.

3.4.1. *Resistance*

Firstly, suppose that there is sufficient resistance to deter challenges. As in the previous section, the most efficient forager will survive, so that P_2 alone will be an ESS if $\frac{C_2}{C_2+1} > \frac{C_1}{C_1+1}$, so that

$$C_2 > C_1,$$

(as in 3.2.1, the more efficient forager will win when there is no kleptoparasitism.) However, we are assuming throughout this paper that $\nu_{f1} > \nu_{f2}$ i.e. $C_1 > C_2$, so if there is sufficient resistance to deter challenges, pure P_2 cannot be an ESS.

However, if the resistance is insufficient to deter challenges, we have the most general situation. The Broom–Ruxton result (with the introduction of our notation) for the equilibrium proportion of handlers in a pure P_2 population is given by

$$\frac{H_2}{P_2} = \frac{-(C_2+1) + \sqrt{(C_2+1)^2 + 4\nu_{\text{h}} t_a C_2 P_2}}{2\nu_{\text{h}} t_a P_2},$$

from which we then find S_2, using $S_2 = H_2/C_2$. Assuming that the population is almost entirely P_2 (because we are considering an ESS of pure-P_2), we can take $P_2 \approx P$.

If a small number of P_1 are introduced, their handling ratio can again be found from consideration of searching times, using a similar tree to above, except that there is now a fight at the end. Using this time to compare the handling ratios of the population and the mutant (Appendix B) gives the condition for the mutant to succeed as

$$B4 \quad P < \frac{(C_1 - C_2)(t_a(C_1 - C_2) + (C_2+1)(\alpha t_{\text{h}} - C_1 t_a/2))}{C_2 \nu_{\text{h}}(\alpha t_{\text{h}} - C_1 t_a/2)^2}. \tag{11}$$

3.4.2. *No resistance*

Again, we may replace t_a by 0, and α by 1, but this time in B4, to get the condition for mutant P_1 to succeed against pure P_2, when neither are resisting attacks:

$$B3 \quad P < \frac{(C_1 - C_2)(C_2+1)}{C_2 \nu_{\text{h}} t_{\text{h}}}. \tag{12}$$

This means that the total value of P is so low that the members of P_2 will not meet enough victims to maintain a high enough handling ratio.

We note, in both resisting and non-resisting cases, that, when $C_2 = 0$ there is no ESS of pure-P_2. This is because the P_2 members themselves are not foraging, and if there are no P_1 members present to attack, then the P_2 population cannot survive alone.

3.4.3. *Mixed resisting behaviour*

It is useful at this point to consider the possibility of different resistant behaviour by the two populations. Suppose, firstly, that a few P_1 are resisting in a non-resisting pure-P_2 population. Combining the results of this section and the previous one, we find that the P_1 will succeed if

$$B5 \quad P < \frac{(C_1 - C_2)(C_2 + 1)}{C_2 \nu_{\mathrm{h}}(\alpha t_{\mathrm{h}} + C_1 t_a/2)}. \tag{13}$$

Similarly, if the pure-P_2 are resisting, and some mutant non-resisting P_1 are introduced, then these P_1 will succeed (again, by a mixture of the results from this and the previous sections) if

$$B6 \quad P < \frac{(C_1 - C_2)(t_a(C_1 - C_2) + (C_2 + 1)(t_{\mathrm{h}} - C_1 t_a))}{C_2 \nu_{\mathrm{h}}(t_{\mathrm{h}} - C_1 t_a)^2}. \tag{14}$$

We will discuss the possibility of different resistant behaviours further in the next section.

3.5. *Mixed ESS's*

We now aim to find when an equilibrium mixture of the two populations exists, so that there is a stable polymorphism.

Firstly, we derive an important result for the number of handlers in an equilibrium mixture of populations. In such a mixture, the two populations must be feeding at the same rate, so we may equate T_1, T_2, to get

$$H = H_1 + H_2 = \frac{C_1 - C_2}{\nu_{\mathrm{h}}(\alpha t_{\mathrm{h}} - C_1 t_a/2)}. \tag{15}$$

This is an important result, which we will use several times.

We can easily adapt it to special cases:
when there is no resistance by the handlers, then we may replace $t_a/2$ by 0, and α by 1, so that

$$H = \frac{C_1 - C_2}{\nu_{\mathrm{h}} t_{\mathrm{h}}}; \tag{16}$$

when P_2 are not foraging, $C_2 = 0$, giving

$$H = \frac{C_1}{\nu_{\mathrm{h}}(\alpha t_{\mathrm{h}} - C_1 t_a/2)}; \tag{17}$$

when there is no foraging by P_2 and no resistance by handlers, we simply get

$$H = \frac{C_1}{\nu_{\mathrm{h}} t_{\mathrm{h}}}. \tag{18}$$

This may be written as

$$\nu_{\mathrm{h}} H = \nu_{f1} f,$$

where it becomes clear that the rate at which the P_2 predators are finding handlers is the same as the rate at which the P_1 foragers are finding food. This, of course, is exactly as expected in this case.

3.5.1. Resistance

It is clear that that the handling ratios of pure-P_1, equilibrium mixture, and pure-P_2, must satisfy

$$\frac{C_1}{(C_1+1)} > \frac{(C_1-C_2)}{P\nu_{\mathrm{h}}(\alpha t_{\mathrm{h}} - C_1 t_a/2)} > \frac{C_2(\alpha t_{\mathrm{h}} - C_1 t_a/2)}{(C_2+1)(\alpha t_{\mathrm{h}} + C_1 t_a/2) - t_a C_2(C_1+1)}.$$

The first inequality is true because the replacement of some P_1 members, not previously challenging or fighting, by some members of P_2 must inevitably reduce the payoff, both because P_2 are less efficient foragers and because of time wasted fighting. The second inequality is true again because P_2 are less efficient foragers, while replacement of P_1 by P_2 will increase the number of fights. (The right-hand expression for the handling ratio of P_2 is derived in Appendix B). We may think of the equilibrium handling rate as a weighted average of the pay-offs of P_1 and P_2 i.e

$$\mu E(P_1) + (1-\mu)E(P_2),$$

where μ is the proportion of P_1 in the population i.e. $\mu = P_1/P$.

We stress that these inequalities are valid because we are considering actual handling ratios, not giving criteria for successful invasion by mutants.

It is clear that a mixed ESS can only occur when P_2 are attacking the handlers—otherwise, P_1, as the better foragers, would, in a pure state, be the only ESS. For P_2 to successfully attack against resistance, in a mixture, we require P_2 to do better than the P_1 foraging rate when faced with a challenging situation, since they do worse elsewhere. We thus require $t_a/2 < \alpha T_1 = \alpha/(\nu_{f1} f)$, or $C_1 < 2\alpha t_{\mathrm{h}}/t_a$. We assume that this inequality is valid for the rest of this section. This guarantees that all the components in the inequality above are positive.

Figure 2 shows the regions in the graph of P against C_2 in which mixed or pure ESS's may occur. The boundary lines are those found in the previous sections, for pure ESS's.

If we consider the three regions, we have

(i) if $P < \frac{(C_1+1)(C_1-C_2)}{C_1\nu_{\mathrm{h}}(\alpha t_{\mathrm{h}} - C_1 t_a/2)}$, then the first inequality above is easily seen to be violated. This means that the value $(C_1-C_2)/P\nu_{\mathrm{h}}(\alpha t_{\mathrm{h}} - C_1 t_a/2)$ cannot correspond to an equilibrium state for that region of P. Thus, only pure-P_1 is an ESS in that region.

(ii) Similarly, if

$$P > \frac{(C_1-C_2)(t_a(C_1-C_2) + (C_2+1)(\alpha t_{\mathrm{h}} - C_1 t_a/2))}{C_2\nu_{\mathrm{h}}(\alpha t_{\mathrm{h}} - C_1 t_a/2)^2},$$

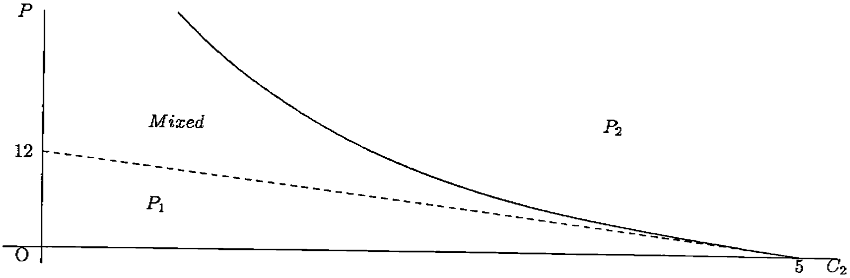

Fig. 2 Graph showing occurrence of pure and mixed population ESS's, as a function of total population size and P_2 foraging rate, when there is resistance to challenges. The *solid line* is given by $P = \frac{(C_2+1)(\alpha t_h - C_1 t_a/2)}{C_2 \nu_h (\alpha t_h - C_1 t_a/2)^2}$, the *dotted line* by $P = \frac{(C_1+1)(C_1-C_2)}{C_1 \nu_h (\alpha t_h - C_1 t_a/2)}$, ($C_1 = 5$, $\nu_h t_h = 2, \alpha = 0.75$, $\nu_h t_a = 0.4$).

then, since

$$t_a(C_1 - C_2) + (C_2 + 1)(\alpha t_h - C_1 t_a/2) > 0$$

(since $(C_1 - C_2)$ and $(\alpha t_h - C_1 t_a/2)$ are both positive)

we have

$$\frac{C_2(\alpha t_h - C_1 t_a/2)}{(t_a(C_1 - C_2) + (C_2 + 1)(\alpha t_h - C_1 t_a/2))} > \frac{C_1 - C_2}{P \nu_h (\alpha t_h - C_1 t_a/2)},$$

and so the second of the above inequalities is broken. Again, this means that only pure-P_2 is an ESS in that region.

(iii) In the intermediate region, defined by

$$\frac{(C_1 + 1)(C_1 - C_2)}{C_1 \nu_h (\alpha t_h - C_1 t_a/2)} < P < \frac{(C_1 - C_2)(t_a(C_1 - C_2) + (C_2 + 1)(\alpha t_h - C_1 t_a/2))}{C_2 \nu_h (\alpha t_h - C_1 t_a/2)^2},$$

consider the difference in pay-offs $d = E(P_1) - E(P_2)$.

When $P_1 = 0$ i.e. pure-P_2, then it can be shown that $d > 0$, while conversely, when $P_1 = P$ i.e. pure P_1, then we can show that $d < 0$.

From the comments at the beginning of this section, it is clear that the total payoff $\mu E(P_1) + (1 - \mu)E(P_2)$ is a monotonically increasing function of μ; there is, therefore, only one value of μ for which this weighted average equals the equilibrium value of the payoff, $(C_1 - C_2)/P \nu_h t_h$, and thus there is only one value of P_1 at which the pay-offs to P_1 and P_2 are equal. Thus, d behaves as in Fig. 3, crossing the $d = 0$ line at one point. It is also clear, from the shape of the graph, that this point is a stable equilibrium point—increasing P_1 means that P_1 does less well, and so will decrease back to equilibrium, and vice-versa.

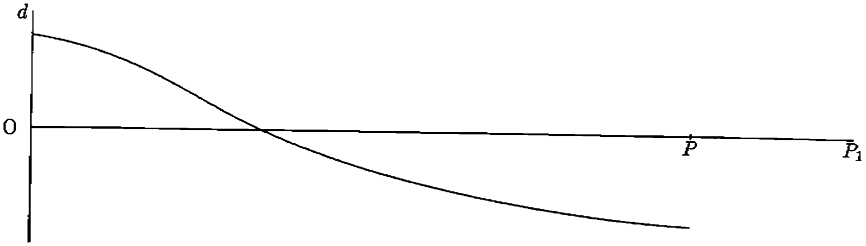

Fig. 3 The difference in pay-offs for P_1 and P_2, as a function of P_1.

We can see, therefore, that there is just one mixed ESS in this situation. In fact, the pattern shown in Fig. 3 is clear. For most values of C_2, there is only a very small range of population densities that will support a mixture as an ESS. In general, a low value of P leads to pure P_1, while a high value leads to pure P_2. Only when C_2 is much smaller than C_1 do we get a widespread occurrence of a mixture as an ESS. Another feature to notice is that when P is above a certain value—in this case, 12—then pure P_1 is not possible at all, and we either get a mixture, for low C_2, or pure P_2, for high C_2.

3.5.2. *Non-resistance*

We can easily adapt the previous results, by replacing t_a by 0, and α by 1, to find when mixed ESS's are possible, in the case where there is no resistance. We find a similar figure to Fig. 2, except that the boundary between P_1 and *Mixed* meets the P axis at 3, instead of 12. Thus, as one would expect, when there is resistance pure P_1 and mixed ESS's are possible for a wider range of parameters.

3.5.3. *Mixed resisting behaviour*

The possibility of different resisting behaviours by P_1 and P_2, when both are present in significant numbers, needs careful consideration, and, in fact, we can show that an equilibrium mixture of populations with different resistance behaviours is not possible. Suppose that P_2 resists, and P_1 does not. Then we know, from the general condition for resistance, that the search time T_2 for P_2 satisfies $T_2 > \frac{t_a}{2(1-\alpha)}$ (if it did not then it would be optimal for P_2 individuals not to resist, and such individuals would invade the population). If P_1 does not resist, then its search time satisfies $T_1 < \frac{t_a}{2(1-\alpha)}$ (again, otherwise it would be optimal for P_1 individuals to resist). Thus, P_1 will start handling food quicker than P_2. However, we must also consider what happens when either is attacked. For P_2, the time to start handling food following an attack is $\frac{t_a}{2} + \alpha T_2 > \frac{t_a}{2} + \frac{\alpha t_a}{2(1-\alpha)} = \frac{t_a}{2(1-\alpha)}$, while for P_1, the time to find food after an attack is simply its original $T_1 < \frac{t_a}{2(1-\alpha)}$. Again, therefore, the time taken by P_1 is less than that taken by P_2.

In both phases of the cycle, therefore, P_1 finds food in a time less than $\frac{t_a}{2(1-\alpha)}$, whilst P_2 in both cases takes longer than $\frac{t_a}{2(1-\alpha)}$. Thus, P_2 could improve its foraging success by switching its defensive strategy to that of P_1, and so P_2 will be eliminated in favour of P_1, and pure P_1 will be the only possible ESS.

Similarly, if P_1 does resist attack, but P_2 does not, then exactly the same argument applies in reverse, and the P_2 will find food quicker than P_1, and thus come to dominate, producing a pure P_2 population.

4. ESS conditions and parameter space

Having now derived the conditions for the various possible strategic choices that individuals can make, we now collect them together, in order to analyse how their occurrence depends on the environmental parameters.

4.1. The conditions

The conditions for whether or not to attack or resist may be taken from Table 2 in Section 3:

In this table, the A. labels represent conditions for individuals to act in a particular way, and the B. labels represent conditions for mutants to invade a pure population.

Assuming that $C_1 > C_2$, then $B1^C \Rightarrow B3$, $B3^C \Rightarrow B1$, and $B4^C \Rightarrow B2$, $B2^C \Rightarrow B4$.

We shall now investigate whether, and under what conditions, a state of the system is an ESS.

4.2. ESS's and mixed populations

From the previous section, we know that a mixture of P_1 and P_2 can only exist as an ESS when P_2 attacks and both populations show identical resistance behaviour (i.e. either both resist, or neither resists). We thus have the following two possibilities:

1. If P_2 attacks and neither resist, then we know that

$$H = \frac{C_1 - C_2}{\nu_h t_h},$$

and because H increases with the proportion of P_1 in the total population, we have

$$\frac{C_2 P}{C_2 + 1} < \frac{C_1 - C_2}{\nu_h t_h} < \frac{C_1 P}{C_1 + 1}$$

i.e.

$$\frac{(C_1 + 1)(C_1 - C_2)}{C_1 \nu_h t_h} < P < \frac{(C_2 + 1)(C_1 - C_2)}{C_2 \nu_h t_h}.$$

There is no condition for P_2 to attack, as this will always happen if the handlers are not resisting. The condition for neither to resist is equivalent to that for P_1 not to resist, which is

$$C_1 > \frac{2(1 - \alpha) t_h}{t_a}.$$

The state of the system in this case, which we shall refer to as State 1, is (S_{122}, P_1), where P_1 is such that $H_1/P_1 = H_2/P_2$ and $0 < P_1 < P$. The overall condition, then, for this ESS is $A1^C \wedge B1 \wedge B3$.

2. Alternatively, if P_2 attacks against both populations resisting, then

$$H = \frac{C_1 - C_2}{\nu_\mathrm{h}(\alpha t_\mathrm{h} - C_1 t_a/2)},$$

and the monotonicity of the proportion of handlers gives

$$h_\mathrm{r} P < \frac{C_1 - C_2}{\nu_\mathrm{h}(\alpha t_\mathrm{h} - C_1 t_a/2)} < \frac{C_1 P}{C_1 + 1}$$

i.e.

$$\frac{(C_1 + 1)(C_1 - C_2)}{C_1 \nu_\mathrm{h}(\alpha t_\mathrm{h} - C_1 t_a/2)} < P < \frac{C_1 - C_2}{h_\mathrm{r} \nu_\mathrm{h}(\alpha t_\mathrm{h} - C_1 t_a/2)},$$

where h_r is the handling ratio. P_2 will only attack if

$$C_2 < \frac{2\alpha t_\mathrm{h}}{t_a},$$

and both resist if P_1 resists, i.e.

$$C_1 < \frac{2 t_\mathrm{h}(1 - \alpha)}{t_a}.$$

The state of the system here, labelled State 2, is (S_{111}, P_1), again where $H_1/P_1 = H_2/P_2$ and $0 < P_1 < P$. Thus, this ESS will occur if $A2 \wedge A1 \wedge B2 \wedge B4$.

4.3. ESS's—pure populations

In some situations, identical resisting behaviour will result in pure populations; in addition, as we have seen above, differing resistance behaviour can only produce an ESS in a pure population; altogether there are 16 states of the system leading to pure population ESS's. Ten of these are (see Table 3):

Of the remaining six, it is clear that the four states $((S_{211}, 0), (S_{212}, 0), (S_{221}, 0), (S_{222}, 0))$ in which P_2 does not attack, with pure P_2 resulting, are impossible; when there is no attacking, a foraging competition will always be won by P_1. The other two states $((S_{221}, P), (S_{222}, P))$ not listed are those in which P_2 does not attack, P_1 does not resist, and pure P_1 results—since there is no resistance, it is clear that attacking is a superior strategy for P_2 individuals, and so these states are unstable.

We can immediately rule out some other states:

State 10 is impossible, since we need $\alpha < 1/2$ for P_1 to resist and P_2 not to attack, given that the foraging rate of P_1 is greater than that of P_2. But then we should

Table 3 Possible ESS's with pure populations.

State label	P_2 attacks	P_1 resists	P_2 resists	Population	State of system	Conditions
3	Y	Y	Y	Pure P_1	(S_{111}, P)	$A2 \wedge A1 \wedge A31 \wedge B2^C$
4	Y	Y	Y	Pure P_2	$(S_{111}, 0)$	$A2 \wedge A1 \wedge A32 \wedge B4^C$
5	Y	N	N	Pure P_1	(S_{122}, P)	$A1^C \wedge A33^C \wedge B1^C$
6	Y	N	N	Pure P_2	$(S_{122}, 0)$	$A1^C \wedge A34^C \wedge B3^C$
7	N	Y	Y	Pure P_1	(S_{211}, P)	$A2^C \wedge A1 \wedge A31$
8	Y	N	Y	Pure P_1	(S_{121}, P)	$A1^C \wedge A33 \wedge B1^C$
9	Y	Y	N	Pure P_2	$(S_{112}, 0)$	$A1 \wedge A34^C \wedge B5^C$
10	N	Y	N	Pure P_1	(S_{212}, P)	$A2^C \wedge A1 \wedge A31^C$
11	Y	N	Y	Pure P_2	$(S_{121}, 0)$	$A2 \wedge A1^C \wedge A32 \wedge B6^C$
12	Y	Y	N	Pure P_1	(S_{112}, P)	$A2 \wedge A1 \wedge A31^C \wedge B2^C$

expect P_2 to resist, as it is likely to win any defensive contest. This can be confirmed algebraically by considering $A1$ and $A2^C$.

Similarly, State 11 is also impossible: the generic criterion for resistance is that $(1-\alpha)t_s > t_a/2$ (where t_s is the time for an individual to acquire a food item). Thus, the search time T_1 for P_1 is $T_1 < \frac{t_a}{2(1-\alpha)}$ (because it is not resisting) while that for P_2 has $T_2 > \frac{t_a}{2(1-\alpha)}$ (because it is resisting). Therefore, P_2 takes longer to find food than P_1, so pure P_2 is unstable.

State 12 is another situation that is not possible. In contrast to 11, here the search time for P_1 has $T_1 > \frac{t_a}{2(1-\alpha)}$, whilst that for P_2 has $T_2 < \frac{t_a}{2(1-\alpha)}$. Thus, in this case, P_2 finds food faster, so pure P_1 is not an ESS.

4.4. Regions of parameter space

We now seek to relate each of the ESS's to a region of parameter space. We do this by partitioning parameter space into a set of disjoint regions, matching the ESS regions where possible, and investigating carefully those that do not obviously match.

Our partition is initially based on $A1$, $A2$:

(a) $A2^C \wedge A1$
(b) $A2 \wedge A1 \wedge B2 \wedge B4$
(c) $A2 \wedge A1 \wedge B2^C \wedge A31$
(d) $A2 \wedge A1 \wedge B2^C \wedge A31^C$
(e) $A2 \wedge A1 \wedge B4^C \wedge A32$
(f) $A2 \wedge A1 \wedge B4^C \wedge A32^C$
(b) to (f) partition $A2 \wedge A1$ completely, since $B2^C \wedge B4^C = \phi$.
(g) $A1^C \wedge B1 \wedge B3$
(h) $A1^C \wedge B1^C \wedge A33$
(i) $A1^C \wedge B1^C \wedge A33^C$
(j) $A1^C \wedge B3^C \wedge A34$
(k) $A1^C \wedge B3^C \wedge A34^C$
(g) to (k) partition $A1^C$ completely since $B1^C \wedge B3^C = \phi$.

Table 4 ESS's and regions of parameter space.

ESS	1	2	3	4	5	6	7	8
Region	g	b	c	e	i	k	a	h

Some ESS's can immediately be associated with a particular region (see Table 4):

It should be remembered that the regions are disjoint, whereas the ESS's are not necessarily so—thus, it is possible for more than one state of the system to be an ESS in a particular region.

We can see that State 9 is not immediately situated in any of the regions, and that Regions d, f and j are not immediately occupied. We now reconcile these as follows:

Region d is exactly the same set of conditions as State 12, which we have shown to be impossible. Therefore, Region d does not exist.

Region j is impossible: $A1^C$, $A34$ give

$$C_1 > C_2 + \frac{\nu_h t_h C_1 P}{C_2 + 1},$$

or

$$P < \frac{(C_1 - C_2)(C_2 + 1)}{\nu_h t_h C_2}$$

which contradicts $B3^C$.

We thus need only investigate State 9 and Region f. Let the region of validity of State 9 be labelled r. We show, firstly, that Region f is totally enclosed within r. The possible intersection of r^C with f is $(A1 \wedge A34 \wedge B5^C) \cup (A1^C \wedge A34 \wedge B5) \cup (A1 \wedge A34^C \wedge B5)$. It is clear that f does not overlap the last two subsets, since, trivially, $A1 \wedge A1^C = \phi$, and, less obviously, $B4^C \wedge B5 = \phi$; this follows because together they give

$$\frac{(C_1 - C_2)(C_2 + 1)}{C_2 \nu_h(\alpha t_h + C_1 t_a/2)} > \frac{C_1 - C_2}{h_r \nu_h(\alpha t_h - C_1 t_a/2)},$$

or

$$h_r > \frac{C_2(\alpha t_h + C_1 t_a/2)}{(C_2 + 1)(\alpha t_h - C_1 t_a/2)} > \frac{C_2}{C_2 + 1},$$

which is impossible.

Now consider $A1 \wedge A34 \wedge B5^C \wedge f = A1 \wedge A34 \wedge B5^C \wedge A2 \wedge B4^C \wedge A32^C$—we will show that this is empty. $A34$, $A32^C$ give

$$(2\alpha - 1)h_r > \frac{C_2}{C_2 + 1},$$

Table 5 Parameter values for State 9.

State/region	h_r	$P\nu_h t_a/2$	C_2	$\nu_h t_h/\nu_h t_a/2$	C_1	α
a and 9	4/5	25/32	9	32	16	1/4
a and not-9	1/2	1	2	12	10	1/10
b and 9	1/3	4.5	2	18	7	5/9
b and not-9	1/2	1	2	28	3	1/4
c and 9	1/3	4.5	2	16	7	1/2
c and not-9	1/2	1	2	16	2.5	1/6
e and 9	1/3	4.5	2	14	5	4/7
e and not-9	1/2	1	2	30	3.5	1/4

which is not possible, since $(2\alpha - 1)h_r \leq h_r \leq \frac{C_2}{C_2+1}$. Therefore, f does not overlap any other subsets of $A1$ other than that equal to State 9.

Thus, r contains Region f, and so State 9 may also be a ESS in other regions; a, b, c and e are the only possible ones. We can show (see Table 5), by finding specific parameter sets, that this does indeed occur—in each of regions a, b, c and e, there are points where State 9 is an ESS, and other points where it is not.

To summarize, then, parameter space partitions into the following Regions, with associated ESS's (see Table 6):

We can illustrate this partition by plotting graphs with two of the parameters as axes. We cannot use α against t_a, as before, because the conditions $B1$, $B3$ depend on neither. Better parameters are α against f.

It is quickly seen from the graphs, and confirmed algebraically, that several triples of lines are concurrent.

$A1$, $B4$, $A32$ all intersect at one point, as do $A1$, $B2$, $A31$. Also,
$A1$, $A33$, $B1$ all intersect at one point and so do $A1$, $A34$, $B3$.

This latter intersection is particularly interesting, as it also transpires that B5 goes through this point of intersection. Using this, we can show that, when A1 is valid, the condition $B5^C$ is automatically satisfied by the condition $A34^C$. We may thus ignore the line $B5$, when considering the occurrence of State 9.

From this, we can deduce that some of the conditions are superfluous, and we can simplify the region definitions as follows:

(a) $A2^C \wedge A1$,
(b) $A1 \wedge B2 \wedge B4$,
(c) $A1 \wedge A2 \wedge B2^C$,
(e) $A1 \wedge B4^C \wedge A32$,
(f) $A1 \wedge A32^C$,
(g) $A1^C \wedge B1 \wedge B3$,

Table 6 ESS's and regions of parameter space.

ESS	7, 9 or 7	2, 9 or 2	3, 9 or 3	4,9 or 4	9	1	8	5	6
Region	a	b	c	e	f	g	h	i	k

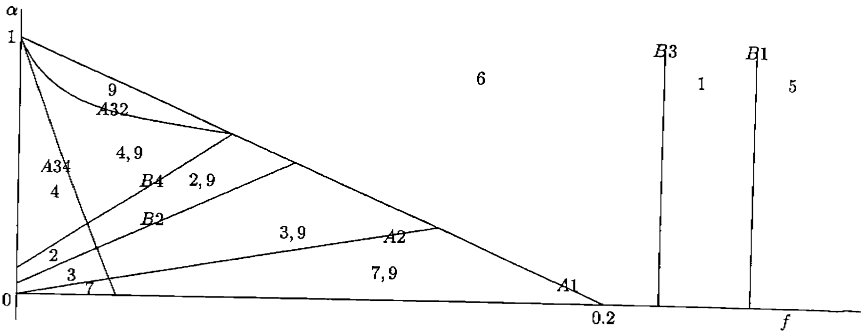

Fig. 4 Graph showing occurrence of ESS, as a function of α and f ($P = 5, \nu_{f1} = 5, \nu_{f2} = 2, \nu_h = 3, t_a = 2, t_h = 1$).

(h) $A1^C \wedge B1^C \wedge A33$,
(i) $B1^C \wedge A33^C$,
(k) $A1^C \wedge B3^C$

When P is large, the ESSs are as shown in Fig. 4.

As P decreases, the pattern of ESS's changes, as various boundaries become relevant or irrelevant. When P goes below 0.5, the B3 line is left of the y-axis, so State 6 is no longer an ESS; also B4 becomes irrelevant, as it is always above $\alpha = 1$, so State 4 goes. A32 is now above A1, so there is no occurrence of 9 there; in addition, A34 is above A1, so State 9 no longer occurs anywhere. This is shown in Fig. 5.

Finally, for very small P, below $P = 0.2$, B2 becomes irrelevant, above $\alpha = 1$, and so State 2 disappears. B1 is now to the left of O, so State 1 no longer occurs, whilst State 8 has now appeared, as shown in Fig. 6.

The ESSs are as shown, and we get a relatively simple picture. The states in each region all involve pure P_1, which is to be expected when the population is very low—any P_2 searchers are unlikely to find handlers, and so the P_1, being the better foragers, will dominate.

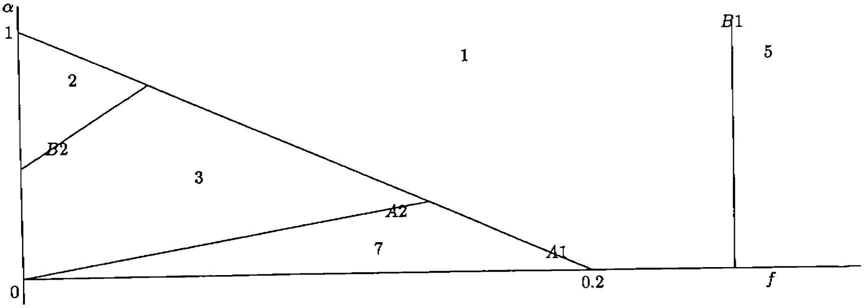

Fig. 5 Graph showing occurrence of ESS, as a function of α and f ($P = 0.45, \nu_{f1} = 5, \nu_{f2} = 2, \nu_h = 3, t_a = 2, t_h = 1$).

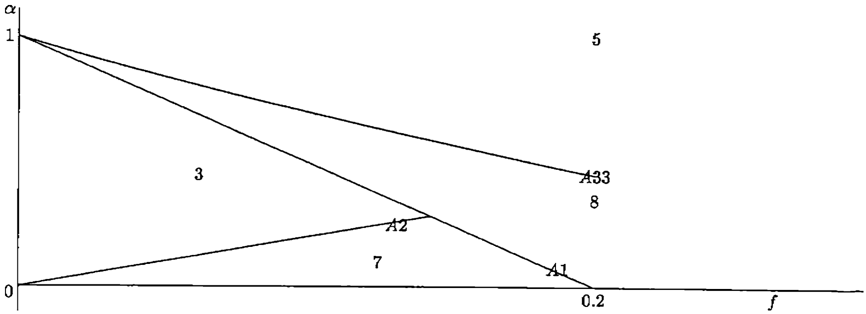

Fig. 6 Graph showing occurrence of ESS, as a function of α and f ($P = 0.1, \nu_{f1} = 5, \nu_{f2} = 2, \nu_h = 3, t_a = 2, t_h = 1$).

4.4.1. Special cases

We shall consider two special cases of our model. Firstly if $\alpha = 1/2$, several of the conditions become identical: $A2 = A31 = A32$. Thus, several of the intersections of sets simplify, or become empty: $A2 \wedge A31 = A2$, $A2 \wedge A31^C = \phi$ etc., and $C_1 > C_2 \rightarrow A2^C \wedge A1 = \phi$, $A2 \wedge A1 = A1$. This leaves the following conditions (see Table 7):

We get a restricted version of the previous breakdown of parameter space (see Table 8):

Note that every ESS is one in which P_2 attacks—when $\alpha = 1/2$, there is no ESS for which P_2 should not attack. We also note that P_1 always resists for low food, then gives up resistance when the food supply is high enough. The variable that changes most is the resistance behaviour of P_2.

If P is large, we start with strategies 4 or 9—P_2 may or may not resist (depending on past history). Ignoring 9 for the moment, P_2 resists, and pure P_2 results. Then 4 changes to 2, where a mixture is the ESS, and then to pure P_1, all with both resisting. Then, above $f = 1/\nu_{f1}t_a$, both change to non—resistance, and the sequence repeats - pure P_2, then a mixture, then pure P_1. If, for historical reasons, ESS 9 had prevailed, with P_2 not resisting, it would be likely to have continued, until P_1 also stopped resisting at $f = 1/\nu_{f1}t_a$.

Table 7 Possible ESS's with pure populations, when $\alpha = 1/2$.

State label	P_2 attacks	P_1 resists	P_2 resists	Population	State of system	Conditions
1	Y	N	N	Mixture	(S_{122}, P_1)	$A1^C \wedge B3 \wedge B1$
2	Y	Y	Y	Mixture	(S_{111}, P_1)	$A1 \wedge B4 \wedge B2$
3	Y	Y	Y	Pure P_1	(S_{111}, P)	$A1 \wedge B2^C$
4	Y	Y	Y	Pure P_2	$(S_{111}, 0)$	$A1 \wedge B4^C$
5	Y	N	N	Pure P_1	(S_{122}, P)	$A1^C \wedge B1^C \wedge A33^C$
6	Y	N	N	Pure P_2	$(S_{122}, 0)$	$A1^C \wedge B3^C$
7	N	Y	Y	Pure P_1	(S_{211}, P)	Impossible
8	Y	N	Y	Pure P_1	(S_{121}, P)	$A1^C \wedge A33 \wedge B1^C$
9	Y	Y	N	Pure P_2	$(S_{112}, 0)$	$A1 \wedge A34^C$

Table 8 ESS's and regions of parameter space, when $\alpha = 1/2$.

ESS	2,9	3,9	4,9	1	8	5	6
Region	b	c	e	g	h	i	k

The second special case is where resistance is compulsory. It is of interest to consider the case where the handlers must resist any challenge. This was the assumption of the original model in Broom and Ruxton (1998), and so consideration of this case will enable comparison with the work from this paper. It is also noteworthy that several other workers e.g. Stillmann (1997), have assumed that handlers resist, when constructing their models.

In this situation, several of the conditions become compulsory: $A1$, $A31$, $A32$, $A33$, $A34$. Thus, any condition involving the complement of any of these sets becomes impossible. This leaves the following ESS's (see Table 9): i.e. the three possible ESS's when challenging does occur, together with the possibility of not-challenging. For high food supply, and low chance of an attack succeeding, P_2 does not attack, with both resisting, and we get pure P_1. As food decreases and/or α increases, P_2 attacks, and we get a sequence of pure P_1, then a mixture, and, for lowest food and highest α, pure P_2.

5. Discussion

One general prediction of this model—that increasing the density of foragers is likely to increase the attractiveness of food-stealing—is in accord with previous theoretical and empirical work (see Broom and Ruxton (1998), and references therein). Specifically, here we predict that at low population densities the population will consist of only P_1 individuals (since P_2 individuals would encounter kleptoparasitic opportunities too infrequently to compensate for their reduced food-finding ability). Conversely, at high population densities, the population consists of only P_2 individuals (because P_2 can capitalize on the high density of kleptoparasitic opportunities afforded by a high density of conspecifics). At intermediate population densities, the model predicts that the population will be made up of a stable mix of both P_1 and P_2 populations.

The limiting case $C_2 \to 0$ represents the situation where in order to exploit kleptoparasitism an individual has to forgo any ability to find food itself. Here we find that it is theoretically possible for P_2 individuals (and so kleptoparasitism) to persist, providing the population also contains P_1 type individuals to actually find food

Table 9 Possible ESS's, when resistance is compulsory.

State label	P_2 attacks	P_1 resists	P_2 resists	Population	State of system	Conditions
2	Y	Y	Y	Mixture	(S_{111}, P_1)	$A2 \wedge B4 \wedge B2$
3	Y	Y	Y	Pure P_1	(S_{111}, P)	$A2 \wedge B2^C$
4	Y	Y	Y	Pure P_2	$(S_{111}, 0)$	$A2 \wedge B4^C$
7	N	Y	Y	Pure P_1	(S_{211}, P)	$A2^C$

in the first place. Hence, obligate kleptoparasites appear theoretically possible. Indeed the Roseate Terns of Shealer and Spendelow (2002) had a small group of individuals that behaved in this way. However, we know of no extant species where a significant fraction of individuals survive purely by kleptoparasitism, Even skuas and frigate birds, for which kleptoparasitism is an important source of food, have some ability to find food themselves (Brockman and Barnard, 1979; Furness, 1987). It may be that there is no set of ecological circumstances where the requirements of kleptoparasitism and intrinsic food finding ability are so entirely incompatible that a kleptoparasite must forgo all ability to find food itself in order to be able to exploit kleptoparasitic opportunities. In such cases, we would expect kleptoparasites to benefit from utilizing any ability they have to take advantage of undiscovered food that they encounter, and so an obligate foraging strategy would not evolve.

In all, nine different types of ESS's are possible, depending on the values assigned to the model parameters. However, they are not all distinguishable; ESS's 3, 5, 7 and 8 are all pure P_1, so the differing behavior of P_2 in each one is irrelevant—an observer would simply see pure P_1, just foraging. In a similar way, states 6 and 9 both involve pure P_2, so the differing behaviour of P_1 has no effect—an observer would see a population of Marauders. Thus, there are actually just five distinguishable ESS's possible in this model.

As with the previous model, we find that alternate ESS's can be possible for particular combinations of parameter values: strategies can exist where food items are surrendered without a fight, and they can also exist where challenges for food lead to escalated conflicts. One generality we predict is that, where both forager types are present, then both types should have the same response to a challenge at ESS: both should always surrender the food without a struggle, or both should always seek to repel a challenger. (This does not apply to states 8 and 9, because they each have a pure population only, not a mixture). This leads to a novel and empirically testable prediction from our model, that, in the absence of dominance hierarchies or intrinsic differences between individuals, economic considerations can lead to heterogeneity between individuals in their propensity to challenge for food, but cannot lead to between-individual differences in how they deal with challenges. Birds feeding on inter-tidal mudflats may provide particularly suitable systems for study, since kleptoparasitism has often been recorded, and flocks are often sufficiently big and dynamic enough to impede development of dominance hierarchies. We stress again, that though we sometimes expect heterogeneity between individuals, we expect no variation within an individual, as strategies for interactions between individuals are pure, in the sense that an individual should always adopt the the same behaviour in different incidences of the same situation. Notice that an ESS can evolve where an individual appears to be aggressive in some situations but not in others: that is where P_2 individuals will take any opportunity to challenge for a food item, but those same individuals will never resist a challenge, surrendering food to challengers without a fight. This suggests that the economic arguments used here may be a powerful weapon in developing our understanding of mounting empirical evidence that use of aggressive behaviours by an individual can be highly context-dependent.

Appendix A

From Fig. 1 we obtain

$$T_2 = t_{\mathrm{h}}/(C_2 + \nu_{\mathrm{h}} t_{\mathrm{h}} H) + \nu_{\mathrm{h}} t_{\mathrm{h}} H/(C_2 + \nu_{\mathrm{h}} t_{\mathrm{h}} H)(t_a/2 + (1-\alpha)T_2),$$

i.e.

$$T_2 = \frac{t_{\mathrm{h}} + \nu_{\mathrm{h}} t_{\mathrm{h}} H t_a/2}{C_2 + \alpha \nu_{\mathrm{h}} t_{\mathrm{h}} H}.$$

Then, the handling ratio for the mutant P_2 is

$$\frac{H_2}{P_2} = \frac{t_{\mathrm{h}}}{t_{\mathrm{h}} + T_2} = \frac{C_2 + \alpha \nu_{\mathrm{h}} t_{\mathrm{h}} H_1}{C_2 + \alpha \nu_{\mathrm{h}} t_{\mathrm{h}} H_1 + 1 + \nu_{\mathrm{h}} t_a H_1/2}.$$

Using $H_1 = C_1 P/(C_1 + 1)$ (i.e. assuming that $P_1 = P$), we require, in order that the mutants should successfully invade,

$$\frac{C_1}{C_1 + 1} < \frac{C_2(C_1 + 1) + \alpha \nu_{\mathrm{h}} t_{\mathrm{h}} C_1 P}{(C_2 + 1)(C_1 + 1) + C_1 \nu_{\mathrm{h}}(\alpha t_{\mathrm{h}} + t_a/2)P}.$$

This can be written as

$$C_2 > C_1 - \frac{C_1 P \nu_{\mathrm{h}}(\alpha t_{\mathrm{h}} - C_1 t_a/2)}{C_1 + 1}$$

or

$$P > \frac{(C_1 - C_2)(C_1 + 1)}{C_1 \nu_{\mathrm{h}} t_{\mathrm{h}}(\alpha - C_1 t_a/2t_{\mathrm{h}})}.$$

Appendix B

The tree for the time a searcher of type P_1 takes to successfully handle a food item (T_1) in a population of resisting P_2 is shown in Fig. B.1.

The forager has to find an item, taking time t_{h}/C_1. It then either completes the handling or has the food stolen; this is a pooled Poisson process, with rate $1/t_{\mathrm{h}} + \nu_{\mathrm{h}} S_2 = (1 + \nu_{\mathrm{h}} t_{\mathrm{h}} S_2)/t_{\mathrm{h}}$. If it completes its handling first, no more time is required, but if it loses its prey before completion of handling, then it starts the whole sequence again. Then the expected time for a complete cycle of handling is given by

$$T_{\mathrm{c}} = \frac{t_{\mathrm{h}}}{C_1} + \frac{t_{\mathrm{h}}}{1 + \nu_{\mathrm{h}} t_{\mathrm{h}} S_2} + \frac{\nu_{\mathrm{h}} t_{\mathrm{h}} S_2}{1 + \nu_{\mathrm{h}} t_{\mathrm{h}} S_2}(t_a/2 + (1-\alpha)(T_{\mathrm{c}} - t_{\mathrm{h}}/C_1) + \alpha T_{\mathrm{c}}).$$

(The term $T_{\mathrm{c}} - t_{\mathrm{h}}/C_1$ occurs when the defender wins the fight and resumes handling without having to find prey again). We readily find that $T_{\mathrm{c}} = t_{\mathrm{h}}(1 + C_1 + \nu_{\mathrm{h}} t_{\mathrm{h}} S_2)/C_1 + \nu_{\mathrm{h}} t_{\mathrm{h}} S_2 t_a/2$.

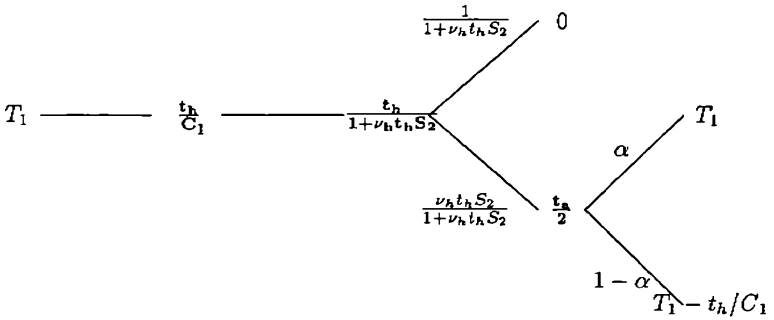

Fig. B.1 Probability tree for the time a searcher of type P_1 takes to successfully handle a food item (T_1). The forager takes time t_h/C_1 (shown in *bold*) to find the food, and a further time (again shown in *bold*) to either handle the food successfully or be challenged by a P_2. The tree splits into two branches; if the food is handled (with probability shown on the upper branch) the food is acquired with 0 further time, otherwise a contest ensues (taking further time $t_a/2$). If the contest is lost (probability α) the individual returns to searching, if it is won then it returns to handling (with expected time for a new handler $T_1 - t_h/C_1$).

Therefore, the handling ratio for P_1 is

$$\frac{t_h}{T_c} = \frac{H_1}{P_1} = \frac{C_1}{C_1 + 1 + \nu_h(\alpha t_h + C_1 t_a/2)S_2}.$$

Comparing the two ratios, a mutant success requires

$$\frac{H_2}{P} < \frac{C_1}{C_1 + 1 + \nu_h(\alpha t_h + C_1 t_a/2)S_2},$$

which we may write as

$$\nu_h H_2^2(\alpha t_h + C_1 t_a/2) + H_2(C_1+1)C_2 > C_1 P C_2.$$

We then use the above quadratic equation for H_2,

$$\nu_h t_a H_2^2 + H_2(C_2+1) - C_2 P = 0$$

to substitute for H_2^2, giving

$$H_2 > \frac{C_2 P(\alpha t_h - C_1 t_a/2)}{(C_2+1)(\alpha t_h + C_1 t_a/2) - t_a C_2(C_1+1)}.$$

Comparing this with the solution to the quadratic itself gives

$$\frac{-(C_2+1) + \sqrt{(C_2+1)^2 + 4\nu_h t_a C_2 P}}{2\nu_h t_a P} > \frac{C_2 P(\alpha t_h - C_1 t_a/2)}{(C_2+1)(\alpha t_h + C_1 t_a/2) - t_a C_2(C_1+1)},$$

which reduces, after squaring both sides of the equation, to

$$P < \frac{(C_1 - C_2)(t_a(C_1 - C_2) + (C_2 + 1)(\alpha t_{\mathrm{h}} - C_1 t_a/2))}{C_2 v_{\mathrm{h}}(\alpha t_{\mathrm{h}} - C_1 t_a/2)^2}.$$

(It should be noted, however, that the squaring has introduced an extra root into this equation. Thus, when solving for α, we only take the appropriate root of the quadratic equation.)

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