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Kleptoparasitic melees - modelling food stealing featuring contests with multiple individuals

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Abstract. Kleptoparasitism is the stealing of food by one animal from another. This has been modelled in various ways before, but all previous models have only allowed contests between two individuals. We investigate a model of kleptoparasitism where individuals are allowed to fight in groups of more than two, as often occurs in real populations. We find the equilibrium distribution of the population amongst various behavioural states, conditional upon the strategies played and environmental parameters, and then find evolutionarily stable challenging strategies. We show that there is always at least one ESS, but sometimes there are two or more, and discuss the circumstances when particular ESSs occur, and when there are likely to be multiple ESSs.

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1. Introduction

Kleptoparasitism is the stealing of items of food by one animal from another (Rothschild and Clay 1952), and is common amongst many types of animals for example insects (Jeanne 1972), fish (Grimm and Klinge 1996) and mammals (Kruuk 1972). It is perhaps most common in birds (see Brockmann and Barnard 1979 for a review), and especially seabirds (Steele and Hockey 1995, Triplet et al. 1999, Spear et al. 1999).

A significant body of literature using game theoretic models to investigate kleptoparasitic behavior in nature has been built up (e.g. Barnard and Sibly 1981; Stillmann et al. 1997; Broom and Ruxton 1998; Ruxton and Broom 1999; Broom and Ruxton 2003). The original model of Broom and Ruxton (1998) has been developed in a variety of ways in recent papers. For instance Luther and Broom (2004) showed that key dynamic assumptions of the model were correct, Broom et al. (2004) developed the game by allowing handling birds to surrender food items and varying the success probability of the contestants, Broom and Rychtář (2007) analysed the models using adaptive dynamics for the first time, and Luther et al. (2007) considered two groups of birds, kleptoparasites and those which only foraged. However in each of these papers, fights were limited to two contestants only. In all of these earlier models, the key ingredient was this contest over food between the two animals, and where the different models gave different results, it was often because the nature of these contest changed from one scenario to another.

If an individual came across a contest for food already in progress, it was not allowed to intervene. This is not always reasonable, and it has been observed (e.g. Steele and Hockey, 1995) that large numbers of birds can fight over the same piece of food. Such groups can be particularly visible compared to smaller contests, and so such multiple contests may be very common. In this paper we explore this situation by allowing challenges to groups contesting a food item, and individuals have to decide whether to challenge any given sized group.

We find the equilibrium distribution of the population conditional on the strategies employed by the population members and find conditions when it is worth challenging a group in a given situation; this is more complicated than in the previous models where only single individuals could be challenged. Every individual can choose what size groups it is prepared to challenge. We investigate how large a group is worth challenging and the distribution of contest sizes in the population. We show that the only sensible strategies are to challenge groups up to a certain maximum size, and not to challenge larger groups. In particular we look for what parameter values such strategies are Evolutionarily Stable Strategies (ESSs). We show that there is always at least one ESS in every case, but that there can be two or more ESSs, sometimes many.

2. The Model

Individuals are either searchers (S), handlers (H) or involved in fights. Such kleptoparasitic contests can involve fights in groups of size i, for general $i \geq$

2. Searchers are allowed to challenge groups already involved in a contest, thus increasing the number of contestants by one. Let F_i be the density of individuals involved in fighting in groups of size i, and G_i the density of such groups, so that $F_i = iG_i$. Note that in the original model of Broom & Ruxton (1998) individuals were only allowed to fight in groups of size two, and their density was labeled A (equivalent to F_2 here).

Transitions between the states occur according to a continuous time Markov chain, so every possible transition is associated with a single rate. Food is found at rate $\nu_f f$, and is handled at rate $1/t_h$. All fights, irrespective of the size of the groups, end at rate $1/t_c$, where t_c is the expected duration of a contest. In previous papers where all such contests contained two individuals, this average fighting time t_c was written as $t_a/2$. Searchers find groups of size i fighting over food at rate $\nu_{h_i} G_i$ (so that the rate of finding a handler is $\nu_{h_1} H$). When a searcher sees a group of size i, it challenges with probability p_i (so the probability of challenging a handler is p_1). These probabilities may be fixed properties of the population, or be potentially different for different individuals. We will consider particular fixed systems, but we will be particularly interested in the optimal values of p_i if all possibilities are allowed in the population. When contests end each group member is equally likely to be the winner, and emerge as a handler, all others becoming searchers. The parameters of the model are summarised in Table 1 and the transitions are shown in Figure 1.

	Meaning
P	the density of individuals in the population
$\nu_f f$	the rate that food items are found
$1/t_h$	the rate that food items are handled
$1/t_c$	the rate that fights are resolved
v_{h_1}	the rate that handlers are found
v_{h_i}	the rate that groups of i fighters are found
S	the density of searchers
H	the density of handlers
G_i	the density of groups of i individuals; $G_1 = H$
F_i	the density of individuals in groups of size i, $F_i = iG_i$
p_1	the probability a handler is challenged if found
p_i	the probability a group of i fighters is challenged if found
$\mathbf{p}$	the challenging strategy, $\mathbf{p}= (p_1, p_2, p_3, \ldots)$
V_k	the strategy to challenge groups of size $< k$ only
π_i	the probability of becoming a handler when currently in G_i
ρ_i	the probability that a new individuals joins G_i
X_k	any value X if all individuals play V_k (e.g. G_i becomes $G_{i,k}$)

Table 1. A summary of model parameters (top section) and notation (bottom section).

The transitions translate into the following system of differential equations.

$$\frac{dS}{dt} = \frac{H}{t_h} - \nu_f f S + \frac{1}{t_c}\sum_{i=2}^{\infty}(i-1)G_i - \nu_{h_1} p_1 SH - S\sum_{i=2}^{\infty}\nu_{h_i} p_i G_i$$

$$\frac{dH}{dt} = \nu_f f S - \frac{H}{t_h} - \nu_{h_1} p_1 SH + \frac{1}{t_c}\sum_{i=2}^{\infty} G_i$$

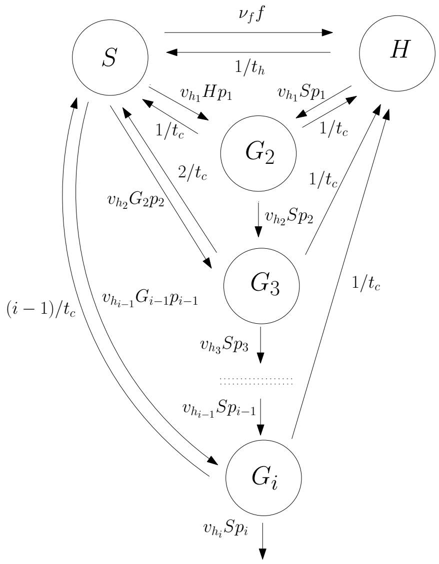

Fig. 1. Schematic description of the model.

$$\frac{dG_i}{dt} = \nu_{h_{(i-1)}} S G_{i-1} p_{i-1} - \frac{1}{t_c} G_i - G_i \nu_{h_i} S p_i \qquad i = 2, 3, \ldots$$

3. Evaluating the population state densities

We first proceed to find expressions for each of the state densities described above. The system of differential equations described above tends to equilibrium exponentially fast, following Luther & Broom (2004). Hence, the time derivatives can be considered 0 and by labeling the following summations

$$F_T = \sum_{i=2}^{\infty} i G_i$$
$$G_T = \sum_{i=2}^{\infty} G_i$$
$$G_S = \sum_{i=2}^{\infty} \nu_{h_i} p_i G_i$$

we obtain

$$
\begin{aligned}
0 &= \frac{H}{t_h} - \nu_f f S + \frac{1}{t_c}(F_T - G_T) - \nu_{h_1} p_1 S H - S G_S && (1)\\
0 &= \nu_f f S - \frac{H}{t_h} - \nu_{h_1} p_1 S H + \frac{1}{t_c} G_T && (2)\\
\frac{dG_2}{dt} &= \nu_{h_1} S H p_1 - G_2 \left(\frac{1}{t_c} + \nu_{h_2} S p_2 \right) = 0 && (3)\\
0 &= (\nu_{h_{(i-1)}} S p_{i-1}) G_{i-1} - \left(\frac{1}{t_c} + \nu_{h_i} S p_i \right) G_i \qquad i = 3, 4, \ldots && (4)
\end{aligned}
$$

3.1. Solving for the equilibrium solutions

Equation (4) rearranges to give

$$
G_i = \frac{\nu_{h_{(i-1)}} p_{i-1} S}{\nu_{h_i} p_i S + 1/t_c} G_{i-1} = G_2 \prod_{j=3}^{i} \left(\frac{\nu_{h_{(j-1)}} p_{j-1} S}{\nu_{h_j} p_j S + 1/t_c} \right) \tag{5}
$$

This in turn gives

$$
\begin{aligned}
F_T &= G_2 \sum_{i=2}^{\infty} i \prod_{j=3}^{i} \left(\frac{\nu_{h_{(j-1)}} p_{j-1} S}{\nu_{h_j} p_j S + 1/t_c} \right)\\
G_T &= G_2 \sum_{i=2}^{\infty} \prod_{j=3}^{i} \left(\frac{\nu_{h_{(j-1)}} p_{j-1} S}{\nu_{h_j} p_j S + 1/t_c} \right)\\
G_S &= G_2 \sum_{i=2}^{\infty} \nu_{h_i} p_i \prod_{j=3}^{i} \left(\frac{\nu_{h_{(j-1)}} p_{j-1} S}{\nu_{h_j} p_j S + 1/t_c} \right)
\end{aligned}
$$

We now have the system completely expressed in terms of known parameters, assuming at this stage that the values of the p_is are known, and the three unknowns S, H and G_2. We now proceed to find expressions for each of S, H and G_2.

Equation (4) implies that

$$
\sum_{i=3}^{\infty} G_i + \sum_{i=3}^{\infty} t_c \nu_{h_i} p_i S G_i = \sum_{i=2}^{\infty} t_c \nu_{h_i} p_i S G_i
$$

and hence

$$G_T = \sum_{i=2}^{\infty} G_i = G_2 + t_c \nu_{h_2} p_2 S G_2 = (1 + t_c \nu_{h_2} p_2 S) G_2.$$

From (4) we also get, for any $k > j$,

$$t_c \nu_{h_i} p_i S G_i = (1 + t_c \nu_{h_{(i+1)}} p_{i+1} S) G_{i+1} =$$

$$\sum_{j=i+1}^{k} G_j + t_c \nu_{hk} p_k S G_k = \sum_{j=i+1}^{\infty} G_j$$

using the fact that $G_i \to 0$ as $i \to \infty$, and letting $k \to \infty$. Thus,

$$\begin{aligned} t_c S G_S &= \sum_{i=2}^{\infty} t_c \nu_{h_i} p_i S G_i = \sum_{i=2}^{\infty} \left(\sum_{j=i+1}^{\infty} G_j \right) \\ &= \sum_{i=2}^{\infty} (i-2) G_i = F_T - 2G_T \end{aligned}$$

and so

$$F_T - t_c S G_S = 2G_T = 2(1 + t_c \nu_{h_2} p_2 S) G_2 \tag{6}$$

From (6) it is clear that equations (1), (2) and (3) multiplied by two add to zero and so there are really only two equations here. The third equation for our three unknowns comes from the fact that every individual is in exactly one state, so that

$$S + H + \sum_{i=2}^{\infty} F_i = S + H + F_T = P \tag{7}$$

Equations (1), (2) and (6) yield

$$H = t_h \nu_f f S. \tag{8}$$

This now means, using (3), that

$$G_2 = \frac{t_c \nu_{h_1} p_1 t_h \nu_f f S^2}{1 + t_c \nu_{h_2} p_2 S} \tag{9}$$

We thus have every other density term $(H, G_2, G_3, \ldots)$ expressed as a function of the density of searchers S. Finally we obtain an equation for S by substitution into (7). This yields

$$\begin{aligned} P = S + H + F_T &= S(1 + t_h\nu_f f) + G_2 \sum_{i=2}^{\infty} i \prod_{j=3}^{i} \left(\frac{t_c \nu_{h_{(j-1)}} p_{j-1} S}{t_c \nu_{h_j} p_j S + 1} \right) \\ &= S(1 + t_h\nu_f f) + t_h \nu_f f S \sum_{i=2}^{\infty} i \prod_{j=2}^{i} \left(\frac{t_c \nu_{h_{(j-1)}} p_{j-1} S}{t_c \nu_{h_j} p_j S + 1} \right) \qquad (10) \end{aligned}$$

3.2. Special cases and examples

3.2.1. Challenging handlers only. If $p_1 > 0$ and $p_i = 0$, for all $i > 1$, then (10) becomes

$$S(1 + t_h\nu_f f) + t_h \nu_f f S \times 2 t_c \nu_{h_1} p_1 S = P$$

which rearranges to

$$\left(\frac{H}{P} \right)^2 t_a \nu_{h_1} p_1 P + \frac{H}{P}(1 + t_h \nu_f f) = t_h \nu_f f$$

as in the original Broom & Ruxton (1998) model. Note that the equation for H/P was used because the rate of food consumption in the population is directly proportional to H/P.

3.2.2. Challenging handlers or groups of at most two fighters. If $p_1 > 0, p_2 > 0$, and $p_i = 0$, for all $i > 2$, then (10) becomes

$$S(1 + t_h\nu_f f) + t_h \nu_f f S \left(2 \frac{t_c \nu_{h_1} p_1 S}{t_c \nu_{h_2} p_2 S + 1} + 3 \frac{(t_c \nu_{h_1} p_1 S)(t_c \nu_{h_2} p_2 S)}{t_c \nu_{h_2} p_2 S + 1} \right) = P$$

which rearranges to

$$3 A_1 A_2 C S^3 + (A_2(1 + C) + 2 A_1 C) S^2 + (1 + C - P A_2) S - P = 0$$

where $C = t_h\nu_f f$, $A_1 = t_c\nu_{h_1}p_1$ and $A_2 = t_c\nu_{h_2}p_2$.

This in turn rearranges to

$$\begin{aligned} 0 = 3A_1A_2P^2\left(\frac{H}{P}\right)^3 + (A_2(1+C)+2A_1C)P\left(\frac{H}{P}\right)^2 \\ +C(1+C-PA_2)\frac{H}{P} - C^2. \qquad (11) \end{aligned}$$

The first two terms in (11) are positive, and the third may or may not be. If the third term is positive, it is clear that there is a unique root. If it is negative, the function of H/P on the right hand side of (11) has at most one turning point; combined with the fact that the value of the function is negative if H/P is replaced by 0, and positive if it is replaced by 1, this again means that the cubic equation gives us the handing ratio uniquely.

3.2.3. Challenging all groups with equal probability. If $\nu_{h_i} = \nu_h, p_i = p$ for all $i \geq 1$, then (10) becomes

$$S(1+t_h\nu_f f) + t_h\nu_f fS\sum_{i=2}^{\infty} i\prod_{j=2}^{i}\left(\frac{t_c\nu_h pS}{t_c\nu_h pS+1}\right) = P$$

We set

$$a = \frac{t_c\nu_h pS}{1+t_c\nu_h pS}$$

and since

$$\begin{aligned} \sum_{i=2}^{\infty} ia^{i-1} &= \frac{1}{(1-a)^2} - 1 \\ &= (t_c\nu_h pS+1)^2 - 1(t_c\nu_h pS)^2 + 2t_c\nu_h pS, \end{aligned}$$

we get

$$S(1+t_h\nu_f f) + t_h\nu_f fS^2((t_c\nu_h p)^2S + 2t_c\nu_h p) = P.$$

Using (8) where again $C = t_h \nu_f f$ and $A = t_c \nu_h p$ we obtain

$$P^2 A^2 \left(\frac{H}{P}\right)^3 + 2ACP\left(\frac{H}{P}\right)^2 + C(1+C)\frac{H}{P} = C^2 \qquad (12)$$

It should again be noted that since all right-hand terms of (12) are positive, (12) determines the handling ratio uniquely.

4. Optimal challenging strategies

We now consider the various situations that an individual may face, and what the best strategy is in each case. In particular, if a group of i individuals involved in a contest is observed, should a bird challenge or not (i.e. what should its value of p_i be)? We shall assume that all other individuals in the population play the strategy $\mathbf{p} = (p_1, p_2, \ldots)$ and we consider a mutant individual playing $\mathbf{q} = (q_1, q_2, \ldots)$. We find what ESSs are possible, and then conditions for each of them to actually be ESSs.

4.1. Preliminary calculations

4.1.1. Calculation of the searching time. We define T_S as the expected time for an individual in the searching state to become a handler and let π_k denote the probability of becoming a handler at the end of the contest when presently in a group of size k. We shall first consider individuals which join a contest. The Markov property guarantees that contests end at rate $1/t_c$ irrespective of the size of the group or whether new individuals have challenged since our focal individual joined the group. Thus the expected time taken for an individual to become a handler when joining such a contest already containing k individuals is

$$t_c + 0 \times \pi_{k+1} + T_S \times (1 - \pi_{k+1})$$

Following on from this, the expected time to become a handler from the searching position is

$$\begin{aligned}T_S = {} & \frac{1}{\nu_f f + \sum_{i=1}^{\infty} \nu_{h_i} G_i q_i} + \frac{\nu_f f}{\nu_f f + \sum_{i=1}^{\infty} \nu_{h_i} G_i q_i} \times 0 \\ & + \frac{1}{\nu_f f + \sum_{i=1}^{\infty} \nu_{h_i} G_i q_i} \sum_{i=1}^{\infty} \nu_{h_i} G_i q_i \Big(t_c + \big(\pi_{i+1} \cdot 0 + (1 - \pi_{i+1}) T_S\big)\Big).\end{aligned}$$

Hence,

$$T_S = \frac{1 + t_c \sum_{i=1}^{\infty} \nu_{h_i} G_i q_i}{\nu_f f + \sum_{i=1}^{\infty} \nu_{h_i} G_i q_i \pi_{i+1}}. \tag{13}$$

4.1.2. Calculation of π_k*.* Since π_k is the probability of becoming a handler when in a group of size k, clearly $\pi_1 = 1$. For groups of size at least two, the next event that occurs is either the resolution of a contest, so that all individuals have an equal chance of gaining the food, or a new individual joining a contest. A new individual joins with probability

$$\rho_i = \frac{\nu_{h_i} p_i S}{1/t_c + \nu_{h_i} p_i S} = \frac{t_c \nu_{h_i} p_i S}{1 + t_c \nu_{h_i} p_i S} \tag{14}$$

so that, for $i \geq 2$,

$$\pi_i = \frac{1}{i}(1 - \rho_i) + \rho_i \pi_{i+1}. \tag{15}$$

Note that it follows immediately from (15) that

$$\pi_{i+1} < \pi_i$$

since, trivially, $\pi_{i+1} < \frac{1}{i}$.

From (15) we obtain

$$\begin{aligned}\pi_i &= \frac{1}{i}(1-\rho_i) + \rho_i\left(\frac{1}{i+1}(1-\rho_{i+1}) + \rho_{i+1}\pi_{i+2}\right) = \ldots \\ &= \frac{1}{i} - \sum_{l=i}^{\infty} \frac{1}{l(l+1)} \prod_{j=i}^{l} \rho_j \end{aligned} \tag{16}$$

since $\prod_{j=i}^{l} \rho_j \to 0$ as $l \to \infty$.

4.1.3. To challenge or not to challenge a group of size k. When faced with the opportunity to challenge a group of size k the best option is the one which has the least expected time to become a handler, so that (neglecting the extremely unlikely possibility of equality) it should challenge if and only if

$$t_c + T_S(1-\pi_{k+1}) < T_S$$

which is equivalent to

$$\frac{\pi_{k+1}}{t_c} > \frac{1}{T_S}. \tag{17}$$

Thus, $q_k = 1$ is optimal if

$$\pi_{k+1} - t_c\nu_f f + t_c \sum_{i=1}^{\infty} \nu_{h_i} G_i q_i (\pi_{k+1} - \pi_{i+1}) > 0. \tag{18}$$

Otherwise, $q_k = 0$ is optimal.

4.1.4. Candidate strategies. The left-hand term of (18) is clearly decreasing with k, so that for any internally consistent set of q_is (i.e. each q_j is optimal in conjunction with $\mathbf{q}= (q_1, q_2, q_3, \ldots)$), optimal invading strategies must be of the form $q_i = 1$, for $i < K$ and $q_i = 0$, for $i \geq K$, for some constant K; i.e. groups up to a certain size only should be challenged.

$\nu_f f$	0.01	0.11	0.21	0.31	0.41	0.51	0.61	0.71	1.21	2.51
S_7	963	749	640	568	515	474	441	414	321	213
H_7	9.63	82	134	176	211	242	269	294	389	535
$G_{2,7}$	4.73	35	52	64	72	78	82	86	95	94
$G_{3,7}$	2.32	15	20	23	24	25	25	25	23	16
$G_{4,7}$	1.14	6.47	7.97	8.36	8.31	8.06	7.72	7.35	5.59	2.90
$G_{5,7}$	0.56	2.77	3.11	3.03	2.82	2.59	2.36	2.15	1.36	0.509
$G_{6,7}$	0.27	1.19	1.21	1.10	0.960	0.83	0.72	0.63	0.03	0.01
$G_{7,7}$	0.26	0.89	0.78	0.62	0.5	0.4	0.32	0.26	0.11	0.02

Table 2. Group densities (times 10^3) for strategy V_7 as $\nu_f f$ varies. Other parameter values are $t_h = 1, t_c = 1, \nu_h = 1, P = 1$.

Let V_k be the strategy to challenge all groups of size less than k. For a population all playing V_k, the maximum group size is k, occurring when a group of size $k-1$ is challenged. We can use (10) to find the value of S, and then (8), (9) and (5) to give the values of H and G_i, which in turn give the values of ρ_i and π_i. Each of these will depend upon the value of k and we thus label the values of S, H, G_i, ρ_i and π_i for a population playing strategy V_k as $S_k, H_k, G_{i,k}, \rho_{i,k}$ and $\pi_{i,k}$ respectively.

For illustration we give a numerical example; the densities of the various group sizes for the example population V_7 are shown in Table 2. As the rate of finding food increases, the densities of searchers declines, the density of handlers increases, and the density of groups of each size first increases and then declines.

4.2. Evolutionarily Stable Strategies

We have shown that if any strategy can invade residents playing $\mathbf{p}$, a strategy V_k, for some k, can invade. What is the "best" of such potentially invading strategies will depend upon the values of the p_is, while although they do not appear in (18) explicitly, they do implicitly since the G_is are functions of them. Note also that any strategy $\mathbf{p}$ which is not of the form V_k must be invadable, since we can consider a 'mutant' which plays $\mathbf{p}$ exactly. It clearly performs equally well to the resident population, but above we have shown that there is a better mutant, which hence must invade. We can thus confine our attentions to the strategies V_k.

4.2.1. Comparison of expressions for V_k populations for different k. From (10) - since for V_k, p_i takes value 1 for $i < k$ and 0 otherwise - it is clear that S_k decreases with k. This in turn means that H_k, by (8), $G_{2,k}$, by (9), $G_{i,k}$, by (5), and $\rho_{i,k}$, by (14) all decrease with k.

Rearranging (15) we obtain

$$\rho_i = \left(\frac{1}{i} - \pi_{i+1}\right) / \left(\frac{1}{i} - \pi_i\right)$$

Since $\rho_{i,k}$ decreases with k then this implies that if $\pi_{i,k} > \pi_{i,k+1}$ then $\pi_{i+1,k} > \pi_{i+1,k+1}$. In particular, if $\pi_{2,k} > \pi_{2,k+1}$ then $\pi_{i,k} > \pi_{i,k+1}$, for all $i \geq 2$.

4.2.2. Conditions for strategy V_k to be an ESS. Consider a population of individuals playing V_k. When can an individual playing V_l invade?

If $l > k$ then groups of resident individuals form only up to size k, so that our individual may challenge such a group, but will never get the opportunity to challenge larger groups. Thus the strategy indicated for encounters with such groups is irrelevant, and the payoff to any strategy V_l, $l > k$ is identical, and so equal to the payoff of V_{k+1}.

Now suppose that $l < k$. V_l invades V_k when T_S is smaller for the invader than for the resident. By (13), this happens if

$$\frac{1 + t_c \sum_{i=1}^{l-1} \nu_{h_i} G_{i,k}}{\nu_f f + \sum_{i=1}^{l-1} \nu_{h_i} G_{i,k} \pi_{i+1,k}} < \frac{1 + t_c \sum_{i=1}^{k-1} \nu_{h_i} G_{i,k}}{\nu_f f + \sum_{i=1}^{k-1} \nu_{h_i} G_{i,k} \pi_{i+1,k}} \Rightarrow$$

$$\sum_{i=l}^{k-1} \nu_{h_i} G_{i,k} \left(\nu_f f t_c - \pi_{i+1,k} + t_c \sum_{j=1}^{l-1} \nu_{h_j} G_{j,k} (\pi_{j+1,k} - \pi_{i+1,k}) \right) > 0 \quad (19)$$

The term in brackets in (19) increases with both l and i. For $l = k - 1$ there is just a single term, and if this is negative then invasion does not occur. If $l < k - 1$, then the expression consists of the sum of several of these terms, all smaller than the $i = l = k - 1$ term, so that invasion of V_l cannot occur for $l < k - 1$ if it does not occur for V_{k-1}.

A strategy V_k is thus an ESS if and only if it can resist invasion by both V_{k-1} and V_{k+1} for $k \geq 2$ (V_1 must resist invasion only from V_2). This is equivalent to saying that in a population of V_k individuals the optimal strategy when encountering a group of size $k - 1$ is to challenge ($q_{k-1} = 1$) and the optimal strategy against a group of size k is not to challenge ($q_k = 0$). By (18), this is equivalent to

$$t_c \nu_f f > \frac{1}{k+1} + t_c \sum_{i=1}^{k-1} \nu_{h_i} G_{i,k} \left(\frac{1}{k+1} - \pi_{i+1,k} \right) \quad (20)$$

$$t_c\nu_f f < \frac{1}{k} + t_c\sum_{i=1}^{k-2}\nu_{h_i}G_{i,k}\left(\frac{1}{k} - \pi_{i+1,k}\right), \qquad (21)$$

since, in a population of V_k individuals, $\pi_{k,k} = 1/k$ and $\pi_{k+1,k} = 1/(k+1)$ for any mutant that challenged a group of size k; note that $\pi_{i,k} < \frac{1}{i}$ for $i < k$.

Notice that the right hand side of (20) is always smaller then the right hand side of (21). Thus since (20) is satisfied for sufficiently large $t_c\nu_f f$, there is an interval of values of $t_c\nu_f f$ for which V_k is an ESS.

We now proceed to express (20) and (21) in lower level terms. We will simplify the expression $\sum_{i=1}^{k-1}\nu_{h_i}G_{i,k}\pi_{i+1,k}$ that essentially appears in both (20) and (21) for $k > 1$. Firstly using (5) and (9) we obtain

$$G_{i,k} = t_h\nu_f f S_k\prod_{j=2}^{i}\left(\frac{t_c\nu_{h_{(j-1)}}p_{j-1}S_k}{1+t_c\nu_{h_j}p_jS_k}\right), \qquad i = 2,3,\ldots,k-1. \qquad (22)$$

Next, using (22) and (16),

$$\begin{aligned}
\sum_{i=1}^{k-1}\nu_{h_i}G_{i,k}\pi_{i+1,k} &= \left(\sum_{i=1}^{k-1}\nu_{h_i}G_{i,k}\frac{1}{i+1}\right) - \sum_{i=1}^{k-1}t_h\nu_f f\nu_{h_1}S_k\sum_{l=i+1}^{\infty}\frac{1}{l(l+1)}\prod_{j=2}^{l}\rho_{j,k}\\
&= \left(\sum_{i=1}^{k-1}\nu_{h_i}G_{i,k}\frac{1}{i+1}\right) - \sum_{i=1}^{k-1}\sum_{l=i+1}^{k-1}\frac{1}{l(l+1)}\nu_{h_l}G_{l,k}\\
&= \left(\sum_{i=2}^{k-1}\nu_{h_i}G_{i,k}\frac{1}{i(i+1)}\right) + \frac{1}{2}\nu_{h_1}G_{1,k}\\
&= (1-\pi_2)\,\nu_{h_1}G_{1,k}.
\end{aligned}$$

Moreover, using (6) and the fact that $p_j = 0$ for $j \geq k$, we get

$$t_c\sum_{i=2}^{k-1}\upsilon_{h_i}G_{i,k} = \frac{F_T - 2G_T}{S}.$$

Since $G_{1,k} = H_k$, for $k > 1$ (20) and (21) become

$$t_c\nu_f f > \frac{1}{k+1}\left(\frac{P}{S_k} - t_h\nu_f f\right) + t_c\nu_{h_1}H_k\left(\pi_{2,k} - 1 - \frac{1}{k+1}\right) \tag{23}$$

$$t_c\nu_f f < \frac{1}{k}\left(\frac{P}{S_k} - t_h\nu_f f\right) + t_c\nu_{h_1}H_k\left(\pi_{2,k} - 1 - \frac{1}{k}\right). \tag{24}$$

It follows directly from (20) that V_1 cannot be invaded by V_2 if and only if

$$t_c\nu_f f > \frac{1}{2}.$$

It is easy to see from (21) that the conditions for all other ESSs imply that $t_c\nu_f f < \frac{1}{2}$ so that when V_1 is an ESS, so that no fighting is a stable solution, it is the only ESS.

4.3. Overlapping regions and multiple ESSs

We start to consider the possibility of multiple ESSs with a range of numerical examples. Table 3 shows the different group sizes for the ESS strategy for varying $\nu_f f$ with other parameters fixed (note that for $\nu_f f = 0.31$ there are two ESSs and both of these are given). Here we can see that the ESS value of k decreases with the rate of foraging $\nu_f f$.

Figure 2 shows the range of values of $\nu_f f$ for which each of the strategies V_i are ESSs for $i = 1, \ldots, 10$. We are particularly interested in the overlaps between the regions, when there are multiple ESSs, and we explore this concept both analytically and numerically in the following sections.

4.3.1. Overlaps between V_k and V_{k-1} for $k \geq 3$. Assume that $k \geq 3$ and consider (20) for V_{k-1} and (21) for V_k to be an ESS. In view of the obser-

$\nu_f f$	0.1	0.21	0.31	0.31	0.41	0.51
ESS	k=7	k=4	k=3	k=2	k=2	k=1
S_k	0.749	0.644	0.577	0.596	0.540	0.662
H_k	0.082	0.135	0.179	0.185	0.221	0.338
$G_{2,k}$	0.035	0.053	0.065	0.110	0.119	0
$G_{3,k}$	0.015	0.021	0.038	0	0	0
$G_{4,k}$	0.006	0.013	0	0	0	0
$G_{5,k}$	0.003	0	0	0	0	0
$G_{6,k}$	0.001	0	0	0	0	0
$G_{7,k}$	0.0009	0	0	0	0	0

Table 3. Group sizes for ESSs as $\nu_f f$ varies, other parameter values: $t_h = 1, t_c = 1, \nu_h = 1, P = 1$.

vation at the end of Section 4.2.2, it is clear that if

$$\frac{1}{k} + t_c \sum_{i=1}^{k-2} \nu_{h_i} G_{i,k-1}(\frac{1}{k} - \pi_{i+1,k-1}) < \frac{1}{k} + t_c \sum_{i=1}^{k-2} \nu_{h_i} G_{i,k}(\frac{1}{k} - \pi_{i+1,k}), \quad (25)$$

or equivalently (by (23) for V_{k-1} and (24) for V_k) if

$$\begin{aligned} &\frac{1}{k}\left(\frac{P}{S_{k-1}} - t_h \nu_f f\right) + t_c \nu_{h_1} H_{k-1}\left(\pi_{2,k-1} - 1 - \frac{1}{k}\right) \\ &\qquad < \frac{1}{k}\left(\frac{P}{S_k} - t_h \nu_f f\right) + t_c \nu_{h_1} H_k \left(\pi_{2,k} - 1 - \frac{1}{k}\right) \end{aligned} \quad (26)$$

then both V_k and V_{k-1} can be ESSs for the same parameters.

We will consider two possibilities. First, suppose that $\pi_{2,k-1} > \pi_{2,k}$. We already observed at the end of Section 4.2.1 that in this case $\pi_{i,k-1} > \pi_{i,k}$, for all i. We also know that $G_{i,k-1} > G_{i,k}$ and that both $\frac{1}{k} - \pi_{i+1,k-1}$ and $\frac{1}{k} - \pi_{i+1,k}$ are negative for $i \leq k-2$. Hence, (25) is true.

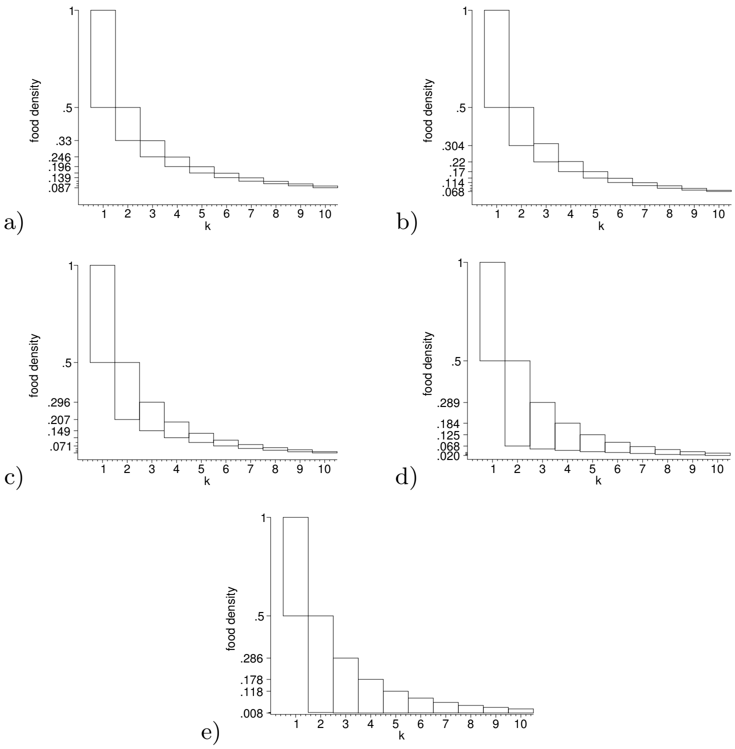

Fig. 2. Ranges of $\nu_f f$ for specific V_k to be ESS. a) $P = 0.1$, b) $P = 1$, c) $P = 10$, d) $P = 100$, e) $P = 1000$. Other parameter values are $t_h = 1, t_c = 1, \nu_h = 1$.

Now suppose that $\pi_{2,k-1} < \pi_{2,k}$. Since $S_{k-1} > S_k$ the left hand side of (26) is negative. Since $H_k < H_{k-1}$ and we are assuming that $\pi_{2,k-1} < \pi_{2,k}$, the right hand side of (26) is positive. Hence (26) holds.

Thus there is an overlap between the regions where V_k and V_{k-1} are ESSs, $k \geq 3$, and these two strategies are both ESSs for some level of the foraging rate $\nu_f f$ irrespective of the values of the other parameters.

4.3.2. Small overlaps for small population sizes. For small populations, there is very little overlap between the regions where ESSs occur (e.g. see

Figure 2a). Note that for $P \approx 0$ we obtain the conditions for V_k to be an ESS to be

$$\frac{1}{k+1} < t_c \nu_f f < \frac{1}{k}, \quad k \geq 2$$

and so there is always a unique ESS in the limit (with a tiny overlap on the boundaries for small P).

4.3.3. Large overlaps for large population sizes. When the population is large, the overlaps between regions for the ESSs can be very large, and there can be multiple ESSs. Moving from Figure 2a to Figure 2e, we can see the overlaps increasing in size. The extreme example of Figure 2e, where the population size is very large and thus the level of fighting is unrealistically high, shows that all strategies $V_2, \ldots, V_{10}$ are ESSs for some low values of $\nu_f f$, and indeed other strategies V_i with $i > 10$ are also ESSs for some of these values. Thus it is possible in our model that there are multiple ESSs.

Why can we get multiple ESSs as described above? Consider a population where the foraging rate $\nu_f f$ is low, and the population size P is large; in particular we think about fixing $\nu_f f$ at some small value and letting P tend towards infinity. Using equation (10) and then (5), we obtain for a population playing V_k

$$\begin{aligned} P &\approx S_k + \frac{(k-1)(k-2)}{2}\nu_f f S_k + \nu_f f S_k^2 \\ G_{i,k} &\approx \nu_f f S_k, \qquad i = 1, \ldots, k-1 \\ G_{k,k} &\approx \nu_f f S_k^2, \end{aligned}$$

which as P becomes large, also implies that $\nu_f f S_k^2 \approx P$. In turn the average rate of becoming a handler in the population is thus approximately

$$\frac{S_k \nu_f f}{P} + \frac{\nu_f f S_k^2}{k t_c P} \approx \frac{1}{t_c k}.$$

If an individual changed their strategy to V_{k+1}, then they would acquire food almost always by finding food directly, or by challenging a group of size k and then winning the contest (with probability $1/(k+1)$), since there are many such groups and they are the only individual who will challenge. Thus their overall rate of becoming a handler is approximately

$$\frac{S_k \nu_f f}{P} + \frac{\nu_f f S_k^2}{(k+1) t_c P} \approx \frac{1}{t_c (k+1)} < \frac{1}{t_c k}$$

Thus such an individual will do worse than the rest of the population, and so cannot invade.

If an individual changed their strategy to V_{k-1}, then it would spend more time searching than the other population members. Almost surely, at the end of the search, it would join a group of size $l < k-1 < k$ (which will almost certainly become a group of size k) at rate $(k-2)\nu_f f S$ instead of rate $(k-1)\nu_f f S$. Its rate of finding food is again approximately $1/t_c k$ multiplied by the probability of being in one of these large groups. Since this probability is less for this individual than for the population, it does worse and cannot invade.

Thus for our given small value of $\nu_f f$ and any non-large value of k (except $k = 1$ where there are no fights), V_k is an ESS. There is a range of ESSs, V_2 up to V_K, and we can find situations where K is arbitrarily large.

k\P	0.1	1	10	100	1000
1	[.5,∞)	[.5,∞)	[.5,∞)	[.5,∞)	[.5,∞)
2	[.330, .500)	[.304,.500)	[.207, .500)	[.068, .500)	[.0100, .500)
3	[.246, .329]	[.220, .314]	[.149, .296]	[.053, .289]	[.0078, .286]
4	[.196, .245]	[.170, .222]	[.113, .194]	[.046, .184]	[.0077, .178]
5	[.163, .195]	[.137, .17]	[.089, .136]	[.039, .125]	[.0079, .118]
6	[.139, .162]	[.114, .136]	[.071, .101]	[.035, .087]	[.0080, .083]
7	[.121, .138]	[.098, .113]	[.058, .078]	[.03, .065]	[.0081, .061]
8	[.108, .12]	[.085, .097]	[.049, .062]	[.025, .05]	[.0080, .046]
9	[.097, .107]	[.075, .084]	[.041, .051]	[.023, .039]	[.0078, .036]
10	[.087, .096]	[.068, .074]	[.035, .042]	[.02, .032]	[.0075, .028]

Table 4. Ranges of $\nu_f f$ where specific V_k is an ESS with varying P; other parameter values: $t_h = 1, t_c = 1, \nu_h = 1$.

This type of situation can be observed for example in Figure 2e for small (but not too small) $\nu_f f$.

Table 4 shows the range of $\nu_f f$ where specific V_k are ESSs for different values of P, following on from Figure 2. The cases with multiple ESSs required the combination of little food and large populations, leading to intense contests and very little consumption, which of course is not realistic. However, for more realistic population sizes, there will be overlaps, but perhaps not more than two or three ESSs for any given value of $\nu_f f$.

5. Discussion

Kleptoparasitic contests involving multiple competitors are common in nature (Steele and Hockey, 1995), but have not before now been modelled mathematically. In this paper we have developed the model of Broom and Ruxton (1998) to allow for such contests. In contrast to previous models, when a group of individuals contesting a food item is observed, then it is possible for the observer to join the contest in the hope of acquiring the food item. The chance of success will decrease with the number of other competitors, and we investigate a number of possible scenarios. For a defined challenging behaviour we find the equilibrium distribution of the sizes of the population density in each of the different categories of activity; there is a single equation for the density of searchers, from which all other densities can be found.

In particular we are interested in the possible strategies of individuals, and finding the best strategies under different conditions. It should be noted that these strategies are more complex here than in most previous models. In previous models when a challenge is made (and resisted) then the contest duration is fixed, its real cost is determined by the level of foraging success that could be expected when not in the contest and the benefit of being in the contest is fixed as well (often, the contest is won 50% of the time). In our model further individuals may challenge groups and this makes the evaluation of the benefits of entering the contest more complex. It is for this reason that we see many possible strategies, and that multiple ESSs can occur for a given set of parameters.

We show that when individuals may or may not challenge groups of any size, the only viable strategies involve only challenging groups up to a certain size, and always challenging these. Thus there are an infinite number of possible strategies. Individuals display varying levels of ”Hawkish” behaviour, rather than just Hawk or Dove, or more appropriately (since all individuals resist attacks) Hawk or Retaliator (Maynard Smith, 1982). We have derived conditions as functions of our parameters for different strategies to be ESSs. It should be noted that the rate that the population acquires food (its uptake rate) decreases with the size of group individuals are prepared to challenge. Its largest value is given by the classical result from Holling (1959) when no individuals challenge, but only forage, and falls away sharply if individuals challenge handlers only (Broom and Ruxton, 1998, and see also Ruxton and Moody, 1997, when all individuals were compelled to fight).

We have proved that there is always at least one ESS. As we vary the food density we can see how the pattern of ESSs changes. From high food availability we move from never challenging to be an ESS, to challenging only handlers, to challenging handlers and fighting pairs and so on. As the availability of food declines, individuals are willing to challenge larger and larger groups. As the population moves from one situation to the next, there is an overlap region where both strategies are ESSs (except when going from no challenges to challenging handlers only). If the population size is small, the overlap is small, and in most scenarios there will be a single ESS. However, for larger populations this overlap can become substantial; in fact it can be sufficiently large for there to be three or more ESSs. It should be noted that these situations only occur for very (generally unrealistically) large populations, when competition for food is intense. They are theoretically possible however, and situations where there are three ESSs are plausible.

In previous models this overlap has not previously been observed, because only handlers could be challenged, and there is no overlap between the no challenge (V_1) and only challenge handlers (V_2) regions. It is possible to have two ESSs simultaneously, because an individual chooses to challenge a group of given size if and only if the rate that it finds food by not challenging is sufficiently poor. Unless we are considering the rate of finding food of an individual which does not challenge handlers (which is always $\nu_f f$), this rate is reduced the more others in the population are prepared to challenge, and so it can be best to challenge if all others are going to challenge, and not challenge if they are all not going to challenge. Situations with more than one ESS have been found in other models, often for similar reasons (that the strategies of others not involved in a particular contest affects this background uptake rate) but never a potentially unlimited number of ESSs as in the current paper.

The model developed in this paper predicts significantly different behaviour to those allowed in previous models in particular when food is quite rare and/or populations are large (note that the extremes of these two situations are unlikely to occur together, except for seasonal variations in food availability). When food is plentiful it pays nobody to fight, and the extra possibility of multiple contests adds nothing. If the population is small, individuals are unlikely to chance upon competing groups; thus although theoretically their strategy might be to challenge groups of size seven or less, they will rarely in practice experience such a situation. Our model is also only realistic if individuals are foraging in close proximity and it takes some time to handle the food. For instance Shealer and Spendelow (2002) examined a real situation where foragers travelled significant distances to find food, but had to return to the nest site to feed their young, and kleptoparasites waited near the nest to try to steal. Multiple fights would be possible in this situation, but the symmetry of our model would be lost, as there would be at least two distinct types of individual in the population, as modelled in Luther et al. (2007).

In this paper we have extended the original and simplest of a series of recent game theoretic models of kleptoparasitic behaviour, so that to allow for multiple contests we have re-introduced some of the original simplifications of this model. It would be of interest to develop the current model with some of the more complex features of later models. For instance in Broom et al. (2004) individuals did not have to resist challenges, and handlers had a different probability of success to subsequent challengers.

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