A game theoretical model of kleptoparasitism with incomplete information

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Abstract Kleptoparasitism, the stealing of food from one animal by another, is a common natural phenomenon that has been modelled mathematically in a number of ways. The handling process of food items can take some time and the value of such items can vary depending upon how much handling an item has received. Furthermore this information may be known to the handler but not the potential challenger, so there is an asymmetry between the information possessed by the two competitors. We use game-theoretic methods to investigate the consequences of this asymmetry for continuously consumed food items, depending upon various natural parameters. A variety of solutions are found, and there are complex situations where three possible solutions can occur for the same set of parameters. It is also possible to have situations which involve members of the population exhibiting different behaviours from each other. We find that the asymmetry of information often appears to favour the challenger, despite the fact that it possesses less information than the challenged individual.

1 Introduction

The phenomenon of kleptoparasitism, or food-stealing, is common in animals of many types, for example mammals [7,9], fish [10] invertebrates [13,26], and especially in birds; see [2,8] for review papers. A good recent review over the range of species is in [14]. There is now a significant theoretical literature on the subject [1,3,5,12,18,20, 27].

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The theoretical model of Broom and Ruxton [3] is the basis for much of the recent work in this area [15,16,6]. One of the assumptions of this and later models is that both individuals have equal knowledge of the handling process of food items so far. If food has been discovered at sea and is subsequently flown to feed chicks on the shore [19], then this may be reasonable, since both defender and challenger will know the distance to land. However, it will often be the case that potential parasites will chance upon their victim and not know the length of handling effort that has gone into the process, for instance with food items with tough shells which need to be breached. This may still not affect the optimal choice of individuals if there are a variety of shells of different toughness, so that perhaps a handler cannot tell its remaining handing time based upon how long it has handled the food. However, there are some food types where this information is very valuable.

This brings us on to the model of Broom and Ruxton [4] where two food types with different properties were considered. One type, the 'apple', could be consumed gradually as soon as it was found. Thus the longer it had been handled, the less valuable it was. Searching individuals could observe the handling state and choose whether to attack, with defenders always defending food items. Evolutionarily Stable Strategies (ESSs) were found where behaviour was described by a single critical value; for the apple model individuals would challenge if there was sufficient food remaining. Here we will develop the work from [4] to consider the apple model when the defender knows the handling time, but the challenger does not. A key question is whether this asymmetry of information is likely to benefit the handler or its challenger.

In the following section we describe the model and how in has been developed from the key earlier models. We go on in later sections to find the ESSs for our model. We investigate six possible strategies, considering monomorphic populations where all members of the population play identically, finding when each is an ESS and which of these can coexist for identical parameters. We show that only three of these strategies can yield monomorphic ESSs, which we shall also refer to as pure ESSs. We also find that it is possible that there is no monomorphic ESS, and that mixtures of different strategies are possible, with some individuals choosing to challenge and others not. Such solutions principally occur when the defensive behaviour in a population would vary greatly depending upon whether challenges were often or rarely made. We finally discuss the consequences of these different results both from a theoretical and a practical perspective.

2 The Model

Following on from [3–5], we consider a population of foragers with a population density of P. Individuals belong to one of four subpopulations, depending upon their activity. They are either searching for food (S), handling a food item (H), fighting for food as a challenger(C) or resisting that challenge (R). We use these labels both for the activity and the population density involved in that activity. These activities are mutually exclusive and every fight involves a challenger and a resister, so that $R = C$ and

$$S + H + R + C = S + H + 2C = P$$

The rate at which searchers encounter prey items and handlers (which they can potentially challenge) are $\nu_f f$ and $\nu_h H$ respectively.
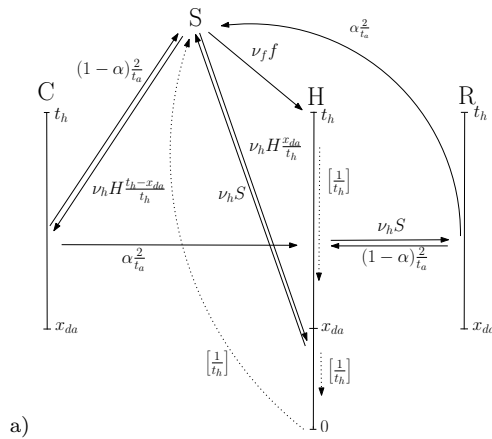
Fig. 1 Transition diagram for the model in the more complex case when challenges occur. Solid lines represent direct movements between states e.g. individuals move from S to the initial handling position at rate $\nu_f f$. Dotted lines represent a deterministic transition through the handling states; if uninterrupted by challenges an individual covers a distance [1] down the handling line per unit time, until it reaches 0 when it instantaneously moves to S. In this case handlers resist if and only if the value of the food item is at least x_Y.

We define $H(x)$ as the population density (strictly the density function of the density) of handlers with a food item which has remaining handling time x, so that t_h represents newly found items. When handling progresses undisturbed, the handing state changes with time, so that after length of time t has elapsed, a newly found food item moves from $H(t_h)$ to $H(t_h - t)$. When a handler reaches state $H(0)$ handling is completed, and it resumes being a searcher.

The time is the inner characteristic of the individual food item and it can be regarded as the actual size of the item (visible to the handler only). The size (and the time) decreases from t_h for a whole item to 0 when the item is already eaten. Arriving at time t means that the item is of such a size that it would take time t to eat it (if undisturbed by any fights). Also the time for the item "stops" when two individuals fight over the item (as during that time, the size of the item remains constant).

When a forager finds a handler it may decide to challenge for the food item (or not) and the challenged handler may decide to resist the challenge (or not). When a contest occurs, it takes place for an exponential time of mean duration $t_a/2$. The forager moves to state $C(x)$ and the handler to $R(x)$. The challenger wins and becomes a handler in state $H(x)$ (the defender becoming a searcher) with probability α, and otherwise the defender wins, becoming the handler in state $H(x)$, and the challenger resumes being a searcher. If there is no challenge there is no change in the states, and if a challenge is not resisted the challenger and handler swap states with no time lost. A summary of the key transition rates of the model is given in Figure 1.

It was shown in [4] that if the population is in equilibrium, then the handlers would be uniformly spread between the range of handling states from t_h to 0, since each item has to pass through each of the stages before being consumed, and this is also true for the different stages of the contesting states R and C. Thus, challengers are equally likely to find food items in all states of being handled. In our model, like previous ones such as [3–5], there is a balance between transitions from fighting states (C and R) to

non-fighting states (S and H) and between non-fighting states so that

$$H = \nu_f f t_h S \tag{2.1}$$

Handlers are aware of how much of their food item remains, and they are able to surrender it if challenged. Searchers can challenge for a food item, but do not know its value prior to making a challenge; thus there is asymmetric information. Challengers make a decision to challenge based upon no knowledge of the value of the food item challenged for, whereas defenders will have a precise knowledge of the handling time elapsed.

An individual's strategy can be summarised as a pair. Firstly, since as a searcher, it cannot observe the current handling state of its potential victim, it must simply decide whether to challenge (Y) or not (N). Secondly as a handler, it must decide which food items are worth defending; it will decide food items are worth defending if and only if they are worth above a certain value. Thus individuals' strategies are labelled (N, x) or (Y, x). We look for evolutionarily stable strategies; in particular we will find the optimal value of x, x_Y, when the population challenges, and then check for stability against a non-challenging mutant individual. We do the same for the optimal value of x, x_N, for a non-challenging population, and then check for stability against a challenging mutant. The value of x_N (or x_Y) may be equal to either t_h or 0, and we will write in terms of finding solutions (N, t_h), $(N, 0)$ or (N, x_N), where the third of these implies a value such that $0 < x_N < t_h$ (and similarly for challenging populations and x_Y).

When there are no challenges the uptake rate of the population, which is equal to H/P, is the maximum possible and it is given by the Holling ratio [11]

$$h_H = \frac{\nu_f f t_h}{1 + \nu_f f t_h} \tag{2.2}$$

If every searcher-handler encounter results in a fight, the uptake rate is h_r, the positive root of

$$h_r^2 t_a \nu_h P + h_r(1 + t_h \nu_f f) - \nu_f f t_h = 0 \tag{2.3}$$

We assign a value of t_h to a food item; thus since the item takes precisely this time to handle, the mean consumption rate during handling is 1 (in fact this is the actual rate, since food is consumed continuously at constant rate). Thus in each case the handling ratio $h = H/P$ is also the mean consumption rate of the population. We shall also use the following notation to summarise the important collections of parameters b and γ which feature in our solutions.

$$b = \frac{\nu_h P}{\nu_f f t_h} \tag{2.4}$$

$$\gamma = \frac{t_a \nu_f f}{2(1 - \alpha)} \tag{2.5}$$

γ is the ratio of the rate of finding food as a searcher and the rate of moving back to the handling position as a defender in a contest, and is thus key to the decision on whether to defend an item or not. It has featured as a key parameter in a number of earlier papers, including [3,5]. The parameter b can also be expressed as the ratio $\nu_h S/(H/P)$ the ratio of the rate that a given handler is found by potential challengers and the overall rate of reward in the population, which is again important for decisions of attack and defence.

3 Results

3.1 Summary

There are six potential solutions which are $(N, t_h), (N, x_N), (N, 0), (Y, t_h), (Y, x_Y)$ and $(Y, 0)$. As it becomes less valuable to be holding an item nearer to the end of the handling period, x_N and x_Y represent the critical remaining handling time, when defence occurs if and only if the remaining time is *longer* than this. Note that for populations which contain only non-challenging individuals, we still consider the strategy of when to defend against occasional challenging mutants, imagining a continuous supply of such individuals at very low frequency.

The strategies $(N, t_h), (N, 0)$ and $(Y, 0)$ are never stable. If every individual in the population adopted the strategy (N, t_h), there would never be fights, and so a mutant challenger would always invade. If every individual adopted $(N, 0)$ or $(Y, 0)$, the individuals would be willing to fight for items of zero value, and so individuals playing higher values of x_N or x_Y would invade.

3.1.1 Strategy (N, x_N)

$(N, x_N), 0 < x_N < t_h$, is in equilibrium with respect to a change in critical defensive time if

$$\gamma < 1 \tag{3.1}$$

where the equilibrium value of x_N is given by

$$x_N = \gamma t_h \tag{3.2}$$

This is stable against invasion by a mutant challenger if

$$3\gamma^2 - 2\gamma + \frac{\alpha}{1 - \alpha} < 0 \tag{3.3}$$

If (3.3) holds then clearly (3.1) must also hold, and thus (3.3) is the sole condition for (N, x_N) to be an ESS. Note that if there are never any challenges, the defensive strategy would of course be irrelevant. We assume that there will be a low level of challenges even in a nominally non-challenging population, either as a result of occasional mutant challengers or behavioral aberrations by some individuals. This seems reasonable for any real populations with the potential to challenge, and any such very low level is enough to maintain a unique defensive strategy.

3.1.2 Strategy (Y, t_h)

(Y, t_h) is stable against a change in critical defensive time if

$$\gamma > \frac{1 - \exp(-t_h \nu_h P / (1 + t_h \nu_f f))}{t_h \nu_h P / (1 + t_h \nu_f f)} = \frac{1 - \exp(-t_h b h_H)}{t_h b h_H} \tag{3.4}$$

and is always stable against a mutant non-challenger, since handlers never resist.

3.1.3 Strategy (Y, x_Y)

$(Y, x_Y), 0 < x_Y < t_h$, is in equilibrium with respect to a change in critical defensive time if

$$\left(b + \frac{1}{t_a h^2}\right) t_h \exp\left(-hbt_h + \frac{(1 + t_h \nu_f f)(h_H - h)}{t_a h \nu_f f}\right) - \frac{\gamma bh(2 - h)}{(1 - h)^2 \nu_f f} > 0 \qquad (3.5)$$

where h is a solution of

$$1 - \exp\left(-hbt_h + \frac{(1 + t_h \nu_f f)(h_H - h)}{t_a h \nu_f f}\right) - \frac{\gamma h^2 b}{(1 - h)\nu_f f} = 0 \qquad (3.6)$$

and the equilibrium value x_Y is given by

$$x_Y = t_h - \frac{(1 + t_h \nu_f f)(h_H - h)}{b t_a h^2 \nu_f f} \qquad (3.7)$$

This is stable against a mutant non-challenger if

$$\gamma \left(1 + \frac{1 - \exp\left(-\alpha(t_h - x_Y)bh\right)}{\alpha\left(\exp(x_Y bh) - 1\right)}\right) < 1 \qquad (3.8)$$

3.1.4 A mixture of Challengers and Non-challengers

If (3.1) holds but (3.3) does not (so that the potential non-challenging solution is unstable against individuals which challenge), (3.5) holds but (3.8) does not (so that the potential challenging solution is unstable against individuals which do not challenge) and (3.4) does not hold, then there is no pure ESS. Here challengers invade non-challengers and non-challengers invade challengers so that we will have a mixture of such individuals in the population. Whenever these conditions occur, there is an equilibrium mixture where both groups employ the same defensive strategy.

3.2 Combinations of solutions and the influence of the parameters

Figure 2 shows the possible patterns that can occur in a challenging population. We can see that there can be at most one value $x_Y < t_h$ so that the strategy (Y, x_Y) is stable; and the strategy (Y, t_h) can be stable as well. There is a total of three possible pure strategy solutions (N, x_N), (Y, x_Y) and (Y, t_h). We can see in Figure 3 that all eight combinations of these solutions are possible. For parameters such that $\alpha < 1/4$, P is large and $\frac{t_a}{2}$ is slightly bigger than $\left(\frac{1}{3} - \sqrt{\frac{1}{9} - \frac{\alpha}{3(1-\alpha)}}\right)\frac{1-\alpha}{\nu_f f}$ all three ESSs occur, and for parameters such that $\alpha < 1/4$, P is relatively small and $\frac{t_a}{2}$ only slightly bigger than $\left(\frac{1}{3} + \sqrt{\frac{1}{9} - \frac{\alpha}{3(1-\alpha)}}\right)\frac{1-\alpha}{\nu_f f}$ none of them occur.

Note that for N strategies to be stable there is quite a small region, so the asymmetry of knowledge with the defender knowing more seems to lead to an advantage to the challenger, with solutions of types (Y, x_Y) and (Y, t_h) occurring for a wider range of parameters than (N, x_N).

The parameter range of the different solutions is not always straightforward. The non-challenging solution (N, x_N) can only occur for sufficiently small challenger winning probability α (e.g. as in Figure 3). It also requires intermediate values of fight time
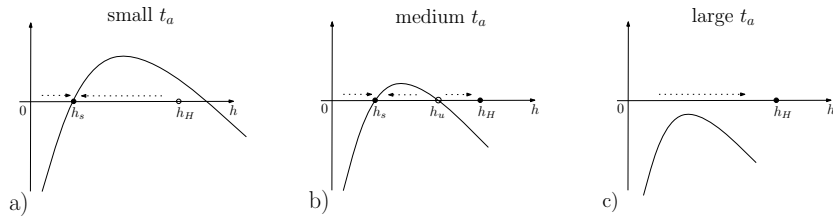
Fig. 2 The schematic graph of the function on the left hand side of (3.6) and its relationship to the stability of the value x_Y (the values x_Y is increasing with h by (3.7)) where h_H is the Holling handling ratio and thus the maximum possible value of h. When a function is positive, defending longer is optimal and vice versa. As the parameter $\frac{t_a}{2}$ grows, one gets a) one stable root $x_Y < t_h$ ($h_s < h_H$), b) one stable root $x_Y < t_h$ and another stable state t_h, c) only one stable state t_h.
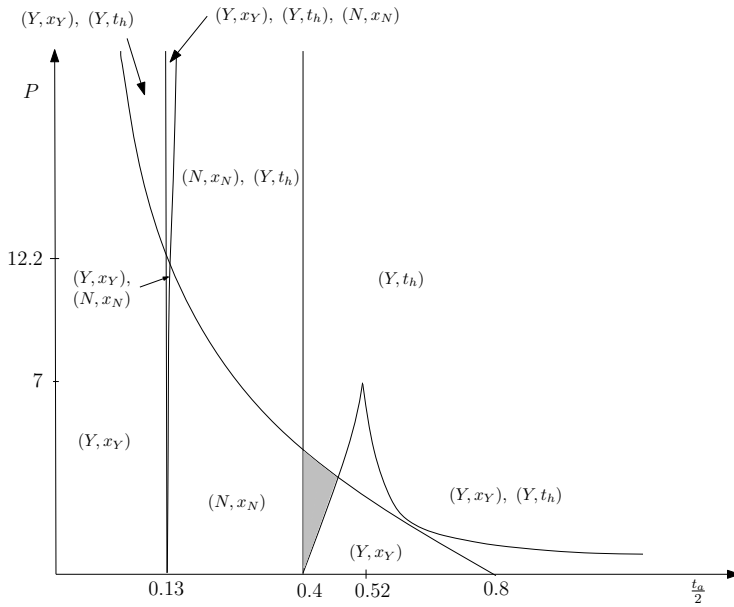

Fig. 3 The regions of ESSs. The grey triangular region is a region with no pure ESS. The regions are for parameter values $t_h = 1, \nu_h = 1, \nu_f f = 1, \alpha = 0.2$.

$t_a/2$ and foraging rate $\nu_f f$; if fights are short or the foraging rate low then it is worth challenging even if the probability of success is low, and if they are high it is also worth challenging because a challenged individual is unlikely to defend its item. Interestingly, the population density P has no effect on the existence of this solution, as in any such population the only fights will be caused by mutant individuals. Population density does, however, affect the existence of the other solutions; the denser the population, the more challenges an individual can expect to face. The challenging and no resisting solution (Y, t_h) occurs for sufficiently dense populations, sufficiently large fighting time and sufficiently low foraging time. It is also more likely to occur when the probability of the challenger winning is larger. The challenging strategy where individuals will defend

sufficiently good food items (Y, x_Y) occurs for sufficiently low fight times, but also for high $\frac{t_a}{2}$ and low population density. Most of these results are individually intuitive, although the possible combinations of solutions and the complex shape of Figure 3 are not. Previous models, such as those from [16] had several possible combinations of solutions, but the behaviour in this model is surprisingly rich, with only small changes in parameter values being able to lead to a range of different combinations of solutions.

4 Analysis

4.1 General method

Let $h(\Sigma, x; \Sigma_p, x_p)$, denote the long term foraging rate (i.e. expected food consumption divided by the total time used) of an individual using a strategy (Σ, x) in the population where everybody else uses a strategy (Σ_p, x_p). Here $\Sigma \in \{Y, N\}$ is the challenging strategy and $x \in [0, t_h]$ is the defending strategy. We are looking for evolutionarily stable strategies which are pairs (Σ_p, x_p) such that if every individual in the population adopts such a strategy, it is then the optimal strategy, i.e.

$$h(\Sigma, x; \Sigma_p, x_p) < h(\Sigma_p, x_p; \Sigma_p, x_p)$$

for any $(\Sigma, x) \neq (\Sigma_p, x_p)$ (in fact when $\Sigma_p = N$ all defensive strategies do equally well in the absence of challenges, and so we allow a very small background level of mutant challenges).

Thus, given (Σ_p, x_p) we need to consider the optimal invading strategy (Σ_o, x_o) such that

$$h(\Sigma_o, x_o; \Sigma_p, x_p) = \max\{h(\Sigma, x; \Sigma_p, x_p), \Sigma \in \{Y, N\}, x \in [0, t_h]\}$$

We will see in the subsequent sections that formulae for $h(\Sigma, x; \Sigma_p, x_p)$ can be complicated and finding the maxima of these functions can be commensurably difficult. Thus, we introduce an additional measure and show how to use it to find the optimal strategy. Let $R_c(\Sigma, x; \Sigma_p, x_p)$ denote the average feeding rate of an individual during and after the challenge that arrived at time t just slightly larger than x, up until the end of its interaction with that particular food item. Clearly, $R_c(\Sigma, x; \Sigma_p, x_p)$ does not depend on an individual's challenging strategy and thus whenever the strategy of the population will be clear from the context, we will use $R_c(x)$ only. In more detail, $R_c(x)$ is the amount of food eaten divided by the total amount of time during the event that starts by a challenge at time $t > x, t \approx x$, continues by a fight (for an average time $t_a/2$) and, in the event of the handler winning the fight, continues with the handler eating the food item until the item is eaten in full or the handler is challenged again (when it immediately concedes without a fight).

Universal principle: Let the population consist of individuals using strategy (Σ_p, x_p) and let one individual use a challenging strategy Σ. If x_o is the optimal defensive strategy the individual can use, then

$$x_o \geq x \text{ if and only if } h(\Sigma, x; \Sigma_p, x_p) \geq R_c(x). \tag{4.1}$$

To understand the principle, note that $R_c(x)$ does not count the consumption before the encounter. What matters is that right now at time $t \approx x$ the individual is challenged

and it should decide whether it is worth defending (yielding feeding rate $R_c(x)$) or giving up (yielding feeding rate $h(\Sigma, x; \Sigma_p, x_p)$).

If $h(\Sigma, x; \Sigma_p, x_p) < R_c(x)$, then the individual is better off entering the contest than conceding it at x, and indeed also after some small further depletion of the resource. Consequently, $x_o < x$. If $h(\Sigma, x; \Sigma_p, x_p) > R_c(x)$, the individual is better off conceding than entering the contest at x, and indeed should concede if challenged a little sooner than at x. Thus, $x_o > x$.

A direct consequence of the universal principle is that, for the optimal value,

$$h(\Sigma_o, x_o; \Sigma_p, x_p) = R_c(x_o) \tag{4.2}$$

In order to check that a given strategy (Σ_p, x_p) is an ESS, we need to consider optimal defending for an individual using challenging strategy Σ_p and also for an individual using challenging strategy $\Sigma \neq \Sigma_p$. The first means that the defending strategy is optimal, i.e. the value x is stable against its change. Using the universal principle and (4.2), the necessary condition for it is

$$h(\Sigma_p, x_p; \Sigma_p, x_p) = R_c(x_p) \tag{4.3}$$

This condition is necessary, but not always sufficient. For the case $\Sigma_p = N$ we will see that it is sufficient, as it is not possible to have more than one root of the equation (4.3). However, when $\Sigma_p = Y$, there can be two, but no more than two, roots of (4.3) (see Figure (2)). When there are two roots, the lower one is stable and the higher unstable, so that finding the smallest $x_p > 0$ which satisfies (4.3) always gives the unique optimal value.

In the population of non-challengers using strategy (N, x_p), a single challenger will not be challenged itself and thus its defensive strategy is irrelevant. In the population of challengers using strategy (Y, x_p) where x_p is stable against its change, the individual (N, x_o) invades if and only if $h(N, x_o; Y, x_p) > h(Y, x_p; Y, x_p)$ which, by (4.2) and (4.3), happens if and only if $R_c(x_o) > R_c(x_p)$. Clearly, R_c is monotone in x (the expected uptake rate over the duration of an item which will never subsequently be defended after the first attack is clearly increasing with the size of the item at the moment the attack occurs; see also (4.6) below), and thus (N, x_o) invades if and only if $x_o > x_p$ which is by the universal principle (4.1) equivalent to $h(N, x_p; Y, x_p) > R_c(x_p)$. It means that we need to consider invasion by (N, x_p) individuals only.

4.2 Feeding rate during the contest at the critical time

Assume that the density of challenging searchers in the population is S_C and consider an individual using strategy (Y, x) or (N, x) that defends the item until time x. Assume it is currently handling a food item and that it has been challenged at time $t \approx x, t > x$. We will calculate its feeding rate during this contest which is the total amount of food eaten divided by the total amount spent by eating and fighting for it.

The individual engages in a fight for an average time $\frac{t_a}{2}$. It wins the fight with probability $(1 - \alpha)$ and resumes eating. From that moment, challenges arrive to the handler as a Poisson process of rate $\nu_h S_C$.

When $S_C > 0$, the expected amount of food consumed (and time taken to consume it) until the handler is finished or found by a searcher is given by

$$E_F(t) = t \cdot Pr(\text{not found at all}) + \int_0^t \tau Pr(\text{found at time } t - \tau) \mathrm{d}\tau$$

$$
\begin{aligned}
&= t \int_t^\infty \exp(-\nu_h S_C \tau) \nu_h S_C \mathrm{d}\tau + \int_0^t \exp(-\nu_h S_C \tau) \nu_h S_C \tau \mathrm{d}\tau \\
&= t \exp(-\nu_h S_C t) + \left(-t \exp(-\nu_h S_C t) + \int_0^t \exp(-\nu_h S_C \tau) \mathrm{d}\tau \right) \\
&= \frac{1}{\nu_h S_C} (1 - \exp(-\nu_h S_C t))
\end{aligned}
\tag{4.4}
$$

where the second use of $Pr()$ above is a probability density function (of the time at discovery). Note that when $S_C \approx 0$,

$$
E_F(t) \approx t \tag{4.5}
$$

Since $t \approx x$, then when our individual is found again, it will not resist but give up the food. Consequently, from the event of being challenged at time $t \approx x$, the handler spends time $t_a/2$ fighting and possibly (with probability $(1-\alpha)$) additional time $E_F(x)$ eating (terminated by the next challenge, which is not resisted, or complete consumption of the food item); and at the same time, it eats $E_F(x)$ amount of the item. Thus its feeding rate is

$$
R_c(x) = \frac{(1-\alpha)E_F(x)}{(1-\alpha)E_F(x) + \frac{t_a}{2}} \tag{4.6}
$$

4.3 The long term foraging rate

4.3.1 Homogenous populations

If there are no challengers in the population (or $S_C \approx 0$), the foraging rate will be the Holling handling ratio from (2.2). In the population where everybody adopts a strategy (Y, x), the handlers defend their food with the probability $1 - \frac{x}{t_h}$ and thus, by e.g. [6], the long term handling ratio is the positive root of

$$
h^2 t_a \nu_h P \left(1 - \frac{x}{t_h} \right) + (1 + t_h \nu_f f)h - \nu_f f t_h = 0 \tag{4.7}
$$

if $x < t_h$ (and is otherwise the Holling ratio), which gives equation (3.7). It follows that

$$
\frac{-hx\nu_h P}{t_h \nu_f f} = \frac{t_h}{t_a h} - \frac{1 + t_h \nu_f f}{t_a \nu_f f} - h \frac{\nu_h P}{\nu_f f}
$$

4.3.2 A single non-challenger amongst challengers

Let us consider an individual using a strategy (N, x) in the population where the density of searching challengers is S_C (the defensive strategy of challengers, x_p is irrelevant for this calculation and can be arbitrary). The individual finds food at rate $\nu_f f$, and this food is completely unhandled, and so worth t_h. Challenges then occur at rate $\nu_h S_C$. If the individual still has the food at time x, then from that moment, by (4.4),

$$
E_F(x) = \frac{1 - \exp(-\nu_h S_C x)}{\nu_h S_C}
$$

is eaten, on average, and no time is lost by fighting (if a challenge occurs, the individual surrenders the food).

Before time x, the handler fights and wins the fight with probability $(1 - \alpha)$, thus successful challenges occur at rate $\alpha S_C \nu_h$, and so the individual still has food at time x with probability

$$p_c(x) = 1 - \int_0^{t_h - x} \alpha S_C \nu_h \exp(-\alpha S_C \nu_h \tau) \mathrm{d}\tau = \exp\bigl(-\alpha S_C \nu_h (t_h - x)\bigr)$$

The expected gain in food from the beginning of handling up to time x is

$$E_I(x) = (t_h - x)p_c(x) + \int_0^{t_h - x} \tau Pr(\text{lost at } t_h - \tau) \mathrm{d}\tau$$

$$= (t_h - x) \exp\bigl(-\alpha S_C \nu_h (t_h - x)\bigr) + \int_0^{t_h - x} \tau \alpha S_C \nu_h \exp(-\alpha S_C \nu_h \tau) \mathrm{d}\tau$$

$$= \frac{1 - \exp(-\alpha S_C \nu_h (t_h - x))}{\alpha S_C \nu_h}$$

where as before, the expression using $Pr()$ is a probability density function. Finally given an individual has spent an average time $E_I(x)$ handling when subject to potential challenges that it will resist, and such challenges occur at rate $\nu_h S_C$, it has spent, on average, the time

$$t_I(x) = \nu_h S_C \frac{t_a}{2} E_I(x)$$

resisting.

The feeding rate for this individual is thus

$$h(N, x; Y, x_p) = \frac{E_I(x) + p_c(x)E_F(x)}{(\nu_f f)^{-1} + E_I(x) + t_I(x) + p_c(x)E_F(x)}$$

4.4 A non-challenging population

The strategy $(N, 0)$ is never optimal. If it were, by (4.3), the feeding rate at that population would be

$$h(N, 0; N, 0) = R_c(0) = 0$$

which is a contradiction of the fact that the feeding rate is the (nonzero) Holling ratio.

Now consider the strategy (N, x), $0 < x \le t_h$. By (4.3), it is stable against a change in the defensive time if

$$h(N, x; N, x) = R_c(x)$$

where, by (4.6) and (4.5)

$$R_c(x) = \frac{(1 - \alpha)x}{(1 - \alpha)x + t_a/2}$$

Since $h(N, x; N, x) = h_H = \frac{\nu_f f t_h}{1 + \nu_f f t_h}$, it is best to fight if $x > \min\{1, \gamma\}t_h$. If $\gamma > 1$ the feeding rate from defending is always worse than the average foraging rate, and food should be discarded at any challenge, no matter its value i.e. choose $x_N = t_h$.

In order to find out whether challenging among non-challengers using strategy (N, x) is beneficial, we do not need to know the long term feeding rate of the challenger. All we need is an expected feeding rate from the beginning of a random challenge. First realize that (N, t_h) is never stable. Indeed, if food is always surrendered, an individual

who always challenges will invade, since any challenge presents them with free food, and an uptake rate of 1 for the interaction. We may thus consider $0 < x < t_h$ only.

With probability $(t_h - x)/t_h$ there will be a fight costing time $t_a/2$, and the reward will be won, and subsequently kept, with probability α. With probability x/t_h the handler will give the food up immediately, and there will be no time lost. The expected food gained through such a contest is

$$\alpha \left(\frac{(t_h - x)}{t_h} \right) \frac{t_h + x}{2} + \frac{x}{t_h} \frac{x}{2} = \frac{1}{2t_h} (\alpha t_h^2 + (1 - \alpha)x^2)$$

The expected time taken is this plus the expected extra contest time, giving

$$\frac{1}{2t_h} (\alpha t_h^2 + (1 - \alpha)x^2) + \frac{t_h - x}{t_h} \frac{t_a}{2}$$

Challenging is not beneficial if the challenger feeding rate is greater than the Holling ratio (2.2), the rate that would result from non-challenging, i.e. if

$$\frac{\nu_f f t_h}{1 + \nu_f f t_h} > \frac{\frac{\alpha t_h^2 + (1-\alpha)x_N^2}{2t_h}}{\frac{t_a}{2} \left(1 - \frac{x_N}{t_h} \right) + \frac{\alpha t_h^2 + (1-\alpha)x_N^2}{2t_h}}$$

which rearranges to

$$3\gamma^2 - 2\gamma + \frac{\alpha}{1 - \alpha} < 0$$

which is condition (3.3). Thus condition (3.3) together with $\gamma < 1$ is required for stability. Note that the above inequality is equivalent to

$$(3\gamma - 1)^2 < \frac{1 - 4\alpha}{1 - \alpha}$$

We thus need α to be small and γ to take intermediate values (the largest range of α when this condition is satisfied occurs when $\gamma = 1/3$). In particular if either $\alpha > 1/4$ or $\gamma > 2/3$ stability cannot occur.

4.5 A challenging population

Similarly to the case of the strategy $(N, 0)$, the strategy $(Y, 0)$ is never optimal. If it were, by (4.3), the feeding rate at that population would be

$$h(Y, 0; Y, 0) = R_c(0) = 0$$

which is contradicted by the fact that the feeding rate is, by (2.3), $h(Y, 0; Y, 0) = h_r > 0$.

4.5.1 The strategy (Y, t_h)

Since handlers are giving up the food whenever challenged, there are no fights in this population, and we have a situation similar to that of the Marauder strategy in e.g. [5, 6]. Since $P = S + H$, from (2.1) and (2.2) it follows that $S = \frac{P}{1+\nu_f f t_h}$, and thus, by the universal principle, for stability against lower x_Y values we require

$$h_H \geq R_c(t_h)$$

By (4.6) and (4.4) it yields

$$\frac{\nu_f f t_h}{1 + \nu_f f t_h} \geq \frac{\frac{1}{\nu_h S}\left(1 - \exp(-\nu_h S t_h)\right)(1 - \alpha)}{\frac{1}{\nu_h S}\left(1 - \exp(-\nu_h S t_h)\right)(1 - \alpha) + \frac{t_a}{2}}$$

which can be rearranged to

$$\nu_f f \frac{t_a}{2} \geq \frac{1 - \exp(-\nu_h S t_h)}{\nu_h S t_h}(1 - \alpha)$$

which is condition (3.4). It is clear that (Y, t_h) is always stable against a mutant non-challenger, since handlers always give up their food, so that challenging is optimal.

4.5.2 The strategy (Y, x), $x < t_h$

By (4.3), the value x is stable against its change if

$$h(Y, x; Y, x) = R_c(x).$$

By (4.6) and (4.4) again

$$R_c(x) = \frac{\frac{1}{\nu_h S}\left(1 - \exp(-\nu_h S x)\right)(1 - \alpha)}{\frac{1}{\nu_h S}\left(1 - \exp(-\nu_h S x)\right)(1 - \alpha) + \frac{t_a}{2}}$$

and combining the above two equations with (3.7) and (2.1) yields

$$1 - \exp\left(\frac{t_h}{t_a h(x)} - \frac{1 + t_h \nu_f f}{t_a \nu_f f} - h(x)\frac{\nu_h P}{\nu_f f}\right) = \frac{\frac{t_a}{2}h(x)^2 \nu_h P}{(1 - h(x))(1 - \alpha)\nu_f f t_h} \qquad (4.8)$$

which can be rearranged to give (3.6). In fact this solution is stable against changes in defensive strategy if the derivative of the left hand side of (3.6) is positive at the specified root (see Figure (2)), which yields (3.5).

Next, we must consider when (Y, x_Y), $x_Y < t_h$ is stable against an invasion of a mutant (N, x). The feeding rate, $h(N, x; Y, x_Y)$, is given by

$$h(N, x; Y, x_Y) = \frac{E_I(x) + p_c(x)E_F(x)}{1/\nu_f f + E_I(x) + t_I(x) + p_c(x)E_F(x)}$$

Using the universal principle, the mutant does not invade if and only if

$$h(N, x_Y; Y, x_Y) < R_c(x_Y)$$

This implies that

$$\frac{t_a}{2(1 - \alpha)}\left(\nu_h S E_I + \nu_h S p E_F\right) < \left(1 - \exp\left(-(\nu_h S)x_Y\right)\right)\left(\frac{1}{\nu_f f} + \frac{t_a}{2}S\nu_h E_I\right)$$

which rearranges to

$$1 > \frac{t_a \nu_f f}{2(1-\alpha)\,\alpha} \left(\frac{\alpha(1 - \exp(-x_Y bh)) + \exp(-x_Y bh)(1 - \exp(-\alpha(t_h - x_Y)bh))}{1 - \exp(-x_Y bh)} \right)$$
$$= \gamma \left(1 + \frac{\exp(-x_Y bh)(1 - \exp(-\alpha(t_h - x_Y)bh))}{\alpha(1 - \exp(-x_Y bh))} \right)$$

which is condition (3.8).

Let us now investigate the number of possible solutions of (3.6) and the consequences to the existence of stable ESSs. The right hand side of (4.8) is convex, starting at 0 for $h = 0$ and ending at ∞ for $h = 1$. The left hand side is concave, starting at $-\infty$ for $h = 0$ and ending at 1 for $h = 1$. This means that there are either two roots or there are none (except on a specific coincidence of parameters). Also, from (4.7) it follows that if we consider x_Y as a function of h, then it is an increasing function.

It is possible there is no solution of (4.8), which corresponds to (Y, t_h) being the ESS (see Figure 2c). If there are two solutions h_1, h_2 of (4.8), we have one of the following three cases

i) $h_H < h_1 < h_2$,
ii) $h_1 < h_H < h_2$,
iii) $h_1 < h_2 < h_H$.

Substituting h_H for h in (3.6) yields equality in (3.4). Consequently, if (3.4) holds, we have either case i) or iii); and we can get case ii) only if (3.4) does not hold. Since the Holling ratio, h_H, is the maximal handling ratio, the solutions larger than this ratio are of no interest to us. Moreover, positive values of the left hand side of (3.6) correspond to lower values of x_Y being favourable and, vice versa, negative values correspond to higher values of x_Y being favourable. Hence, the root h_2 is either unrealistic (in case ii)) or unstable (in case iii)). Consequently, we can have only one stable (Y, x_Y) with $x_Y < t_h$ which will be h_1 in either ii) (see Figure 2a) or iii) (see Figure 2b); however, we can have both (Y, x_Y), $x_Y < t_h$ and (Y, t_h) being stable (Figure 2b).

4.6 A mixture of challengers and nonchallengers

As seen at Figure 3, there are cases with no ESS. Specifically, if (3.1) holds but (3.3) does not (so that challengers can invade any non-challengers adopting a stable defensive strategy), (3.5) holds but (3.8) does not (so that non-challengers can invade any challengers adopting a stable defensive strategy) and (3.4) does not hold, then there is no pure ESS. In such a situation we will have a mixture of individuals in the population. For any such mixture to be in equilibrium, both groups would have to perform equally well. This in turn means, by the universal principle, that the value of x_Y must be equal to x_N at equilibrium; in other words, all individuals would have to use the same defensive strategy. Whenever (3.3) is not satisfied challengers do better in a population wholly consisting of non-challengers and whenever (3.8) is not satisfied non-challengers do better in a population consisting wholly of challengers. Considering any population combined of challengers and non-challengers, if we slightly alter the proportion of challenging individuals, this will correspondingly alter the equilibrium defensive strategies x_N and x_Y, and hence the uptake rate of challengers and non-challengers by a small amount. Thus these uptake rates are continuous as a function of the proportion of challengers, and so there will be a mixture where the two perform

equally well. It is clear that there is an equilibrium within this region (and indeed in a larger region). Note that we have not been able to prove that this solution is unique, or that it is stable.

5 Discussion

Kleptoparasitic behaviour takes a number of forms amongst its most visible constituency, that of seabirds. From the interspecific parasitism where individuals are clearly divided into parasites and potential victims as typified in [22] to intraspecific parasitism where individuals can move interchangably between the two, which is the focus of our model. This intraspecific behaviour can take different forms, varying from mainly ground-based competition with a strong spatial element [24], [21] to aerial contests involving potentially many individuals [23]. In each case, there is a variety of key parameters which determine behaviour, for instance the availability of food [25], the duration of contests or the population density [16,23]. In this paper we have looked at kleptoparasitic models from a new perspective, that of imperfect and asymmetric information amongst the competitors for food. Thus in this paper we effectively get mixed defensive strategies not usually seen in previous work because of the different values of the food items at the time that a defensive choice is made, since defenders will decide that some items are worth defending and others are not. The assumption is that the individual handling the food will have greater information about the item in question than any challenger. The handlers of food items appear at first sight to have an advantage because of the extra information that they possess about the value of the food. In fact the model often predicts the reverse, i.e. the handlers have a disadvantage as a result of the extra knowledge of the food item size since this knowledge often leads to the small items being conceded by the handler, providing free food to the challenger.

Considering our model of continuous food consumption, there are four possible solutions identified, three of which are pure ESSs. There is a solution (N, x_N) where nobody challenges, another solution (Y, t_h) where all challenge and there is no resistance and one solution (Y, x_Y) where all challenge and there is defence of sufficiently valuable food items. It is interesting to see that for some parameter values all of these strategies can be ESSs simultaneously, so that which occurs in practice will depend upon the history of the system, and that a small change in parameter values can result in various combinations of solutions in quite a small range. It is worth noting that all eight possible combinations of these solutions (including none of them as pure ESSs) can occur for plausible parameter values. When there is no such ESS, even more complex behaviour with some individuals challenging and others not emerge.

Some of our results are consistent with previous models, for instance the solution (Y, t_h) is essentially the Marauder strategy of [15] and again occurs for dense enough populations or large fight times. The other two strategies contain defensive strategies which are analogous to mixed strategies, in the sense that sometimes the defender resists and sometimes not, and when this occurs is unknown to the challenger. The general relationship between the critical defensive time and the parameters resembles the critical attacking time from [4], in that in both cases fights are generally less likely the denser the population or the more costly fights are, but the complex interplay of the different types of solution is distinct. One implication for real populations is that behaviours that are quite different may not be the result of different environmental conditions or properties of the species involved, but rather because different solutions

are available, and which is selected is due to chance and past conditions. Thus the investigation of potentially different food types and strategic behaviour extends the range of possible natural observations that our models can predict. An interesting prediction of the model regards the circumstances when the non-challenging solution (N, x_N) occurs. This happens for intermediate values of foraging rate or contest time, provided that the chance of the defender successfully keeping the food in a contest is sufficiently high, with challenging occurring at either extreme (for large contest time or very easy food availability challenges happen because defenders will simply concede rather than fight). This will be an interesting prediction to test in real populations.

There are various ways this model can be extended. One natural extension is to consider food items of varying initial size, where the distribution of these sizes could be expected to play a critical role. More generally, in the contests in this paper, individuals are able to challenge or not, and resist or not, but then they have no option to change their strategy based upon information acquired after the start of the contest. Such information as discovering the value of the food item, or the strategy of its opponent, could affect the individual's assessment of its best strategy, and thus make it change its decision if it was able to do so. Thus there could be a sequence of potential decisions to consider, which could be a continuum, and the effect of asymmetric information in such kleptoparasitic contests is potentially complex.

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