Behavioral Ecology Vol. 14 No. 1: 23–33

Evolutionarily stable kleptoparasitism: consequences of different prey types

M. Broom[a] and G. D. Ruxton[b]
[a]Centre for Statistics and Stochastic Modelling, School of Mathematical Sciences, University of Sussex, Brighton, UK, and [b]Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK

We present two elaborations of the model of Broom and Ruxton that found evolutionarily stable kleptoparasitic strategies for foragers. These elaborations relax the assumption that the distribution of times required to handle discovered food items is exponential. These changes increase the complexity of the model but represent a significant improvement in biological realism. In one elaboration, handling takes a fixed interval, t_h, at the end of which the whole value of the food item is obtained. We liken this to peeling then consuming a small orange. The other elaboration also assumes that handling takes a fixed interval, t_h, but this time the reward from the food item is extracted continuously throughout the handling period. We liken this to eating an apple. Both models predict that increasing food density, the ease with which food items can be discovered, or the length of aggressive contests all act to make kleptoparasitism less common. The difference between the evolutionarily stable strategy solutions of the apple and orange models provides a clear prediction of our theory. When prey items require handling before yielding a lump sum at the end, then kleptoparasitic attacks will be focused on prey items near the end of their handling period. However, if prey items yield reward continuously during handling, then attacks should be biased toward newly discovered food items. Another key difference between the model predictions is that kleptoparasitism increases with forager density in the apple model, but decreases in the orange model. *Key words:* aggression, evolutionarily stable strategy, food stealing, game theory, intraspecific interference. *[Behav Ecol 14:23–33 (2003)]*

Animals often forage in close proximity to conspecifics (Giraldeau and Caraco, 2000). This may simply be because the food source is patchily distributed, or it may be because grouping brings some benefit to foragers (Pitcher and Parrish, 1993). This benefit need not necessarily be shown in enhanced rates of food consumption but may relate to antipredatory or other benefits (e.g., Bednekoff and Lima, 1998; Proctor and Broom, 2000; Roberts, 1996). Indeed, individuals in a group may experience reduced feeding rates due to their proximity to others. There are many mechanisms by which such interference effects can be shown, such as increased prey depletion (Driessen and Visser, 1997; Free et al., 1997) or enhanced avoidance behavior by prey (Selman and Goss-Custard, 1988).

Another circumstance under which average prey consumption rates can decline is if foragers sometimes invest time in trying to steal already-discovered food items from others, rather than searching for a food item themselves. Such kleptoparasitic behavior is particularly common in birds (see Brockman and Barnard, 1979; Furness, 1987, for reviews), but it also occurs in mammals (e.g., Carbone et al., 1997; Gorman et al., 1998) and invertebrates (e.g., Iyengar, 2000; Tso and Severinghaus, 1998). In situations where food items are hidden in the environment and thus require some time investment to acquire, it may pay an individual to attempt to obtain food items by aggression, even if this also requires a time investment (Sirot, 2000). Although such parasitic behavior benefits the individual, it necessarily leads to a reduction in the time that individuals invest in searching for new prey items and so leads to an overall decrease in food uptake rates. There is empirical evidence that animals use aggression flexibly in a way that reflects a changing trade-off between costs and benefits (Goss-Custard et al., 1998; Vines, 1980). Further, the attractiveness of kleptoparasitism to an individual will depend on the frequency with which other group members use this tactic. Thus behavior is potentially complicated, and any model selected to represent it must be game theoretic in character. In a recent article (Broom and Ruxton, 1998), we introduced an individual-based model of a group of foraging animals, where individuals could obtain food either by searching themselves or by stealing the discoveries of others. This model was used to explore how evolutionarily stable stealing strategies were affected by ecological conditions.

A key assumption of the model of Broom and Ruxton (1998) is that prey items require a certain amount of handling before the individual can extract energetic reward from them. This handling time affords kleptoparasites the opportunity to strike. The original model assumed that handling a prey item took a time that was randomly drawn from an exponential distribution with mean t_h. At the end of this time, all the food reward was obtained. This assumption was made for analytic convenience. Simplification occurs because an exponential distribution of handling times implies that a given handling event has a constant probability per unit time of coming to an end. Hence the amount of previous handling that a food item has received has no bearing on its instantaneous likelihood of yielding its reward. Although this assumption gives considerable simplification, its biological applicability is limited. Here we present two elaborations of the original model that relax this assumption. In one elaboration, handling takes a fixed interval, t_h, at the end of which the whole value of the food item is obtained. Consuming such a food item is similar to peeling then eating a small orange, and we label this the "orange model." The other elaboration also assumes that handling takes a fixed interval, t_h, but this time the reward from the food item is extracted continuously throughout the handling period. For simplicity we assume that this reward

---

Address correspondence to G.D. Ruxton. E-mail: g.ruxton@bio.gla.ac.uk. M. Broom is also a member of the Centre for the Study of Evolution at the University of Sussex.

Received 6 July 2001; revised 14 April 2002; accepted 14 April 2002.

extraction rate is constant. An example of this type of consumption is eating an apple, and we call this the "apple model."

As in the original model, we assume that aggressive interactions over a contested food item involve an investment of time by both contestants. Now, in contrast to the previous model, an individual's decision to enter into a contest should be based on how much handling the food item has already received. In the original model, all food items had an equal worth; whereas under the orange model, the more an item has already been handled (the more peel that has been removed), the more valuable it is. In contrast, under the apple model, the longer a prey item has been handled (the more of its flesh that has been consumed), the less valuable it is.

Here we explore the consequences of these alternatives on evolutionarily stable stealing behavior. For comparative purposes, we have kept other model assumptions and nomenclature as close to that of Broom and Ruxton (1998) as possible.

The general model framework

We consider a population of foragers with a constant population density, P. The population is divided into three subpopulations according to activity: the density searching for food items, S, the density handling a food item, H, and the density involved in an aggressive interaction, A. These activities are mutually exclusive, so that

$$S + H + A = P. \tag{1}$$

We use these labels interchangeably for the density of individuals involved in a particular activity and to identify the activity itself. The rate at which searchers encounter prey items and handling conspecifics are, respectively, $v_f f$ and $v_H H$, where f is the population density of food items. Upon encountering a food item, a searcher immediately switches to being a handler. We define $h(x)$ as the population density of handlers that are handling a food item that still requires a further handling time, x. Strictly, this is the density function of the density of handlers; i.e., the density of handlers with further handling time between x and $x + \delta x$ is $\delta x h(x)$, where $0 < x \leq t_h$, and

$$H = \int_{x=0}^{t_h} h(x)\ dx. \tag{2}$$

Thus, on encountering a food item, a searcher becomes a handler [entering $h(t_h)$]. It remains a handler for a time, t_h, or until it is encountered by another searcher that decides to contest for the food item. We assume that the probability in each encounter that the searcher decides to be aggressive is $p(x)$, where x is again the remaining handling time of the handler's food item. If the searcher decides not be to aggressive, then it carries on searching; otherwise both the searcher and the handler switch to the aggressive subpopulation.

We define $a(x)$, in the same way as $h(x)$, as the population density of those involved in an aggressive interaction over a food item that still requires a further handling time x, and

$$A = \int_{x=0}^{t_h} a(x)\ dx. \tag{3}$$

We assume that all handlers are equally likely to be encountered, independently of the value of x. When a searcher encounters a handler in state $h(x)$ and decides to contest the food item, then they both switch to state $a(x)$. They remain in this state for a time drawn from an exponential distribution with mean $t_a/2$ (the factor of two is used to make subsequent expressions tidier). After this, one individual (the loser) returns to searching, and the other (the winner) returns to handling in state $h(x)$. For simplicity, we assume that each individual has a 50% chance of winning. Finally, on reaching $h(0)$, a handler switches back to being a searcher.

The aim of this article is to consider the evolutionary stable strategy (or strategies) for kleptoparasitism under both the apple and orange models. The derivation of these strategies requires considerable, but straightforward, mathematical manipulation. We give this derivation in full in the Appendix, and simply quote the important results from this in the following sections.

The apple model

In the original model of Broom and Ruxton (1998), the evolutionarily stable strategy (ESS) was to always challenge a discovered handler if the parameter combination $t_a v_f f$ were less than unity, and never challenge if it were greater than unity. In the dividing case (when $t_a v_f f$ was identically equal to one), then all strategies for deciding whether to challenge yielded the same reward.

In the apple model, it is easy to see that always challenging will never be an ESS. Because challenging involves an investment of time, challenging for an almost exhausted apple would not be efficient. If we denote $p(x)$ as the probability of competing for a prey item that still requires handling for a time x, then $p(x)$ should always tend to zero as x tends to zero.

Let us now consider the other extreme case, of discovering a handler with a prey item that has received no previous handling. Although the investment in a contest is the same for all prey items, the reward from winning a contest is highest for a prey item that has received no previous handling. Thus, if challenging for previously unhandled prey items is not optimal, nor is challenging for any prey items. That is, if $p(t_h) = 0$ is part of the ESS, then no prey items should be contested, and the ESS is $p(x) = 0$ for all $x \in [0,t_h]$.

Manipulation of Equation A10b of the Appendix shows that if $t_a v_f f > 1$, then the strategy $p(x) = 0$ for all $x \in [0,t_h]$, so that no kleptoparasitism occurs, is an ESS. This is exactly the condition for no parasitism to occur in the original model. This is logical becuase the apple model makes challenging for already partially handled food items less attractive than in the original model. A partially handled prey item now yields less reward for the same investment in an aggressive encounter. Hence, under circumstances when challenging was unrewarding in the original model, it will remain so under the apple model.

We now turn our attention to the situations where kleptoparasitism can be selected for. By analogy with the original model, we can see that, if challenging is ever a good strategy, then challenging for a prey item that has only just been discovered should be selected for; in other words, we expect $p(t_h) = 1$. In the opposite extreme, contesting for an almost exhausted food item does not make sense; hence, $p(0) = 0$. By analogy with the original model again, we would expect that there is a critical amount of handling remaining in a food item (X_a). On discovering a handler in state $h(x)$, a searcher should always be aggressive if $x > X_a$, and never aggressive if $x < X_a$. In the dividing case, where $x = X_a$, all strategies of choosing whether to be aggressive are equally successful. Thus, the ESS can be described fully by finding the evolutionarily stable value of X_a.

Equation A10a of the Appendix gives a cubic equation, the three roots of which are the candidate values of X_a:

$$DX_a^3 - X_a^2[t_h(D + 1)] + X_a[t_h t_a(C - 1)] + t_a^2 t_h C = 0, \tag{4}$$

where $C = t_h v_f f C$ and $D = t_a v_H P$.

When $t_a v_f f < 1$, it is easy to show (see Appendix) that there is always and only one root of Equation 4 between 0 and t_h.

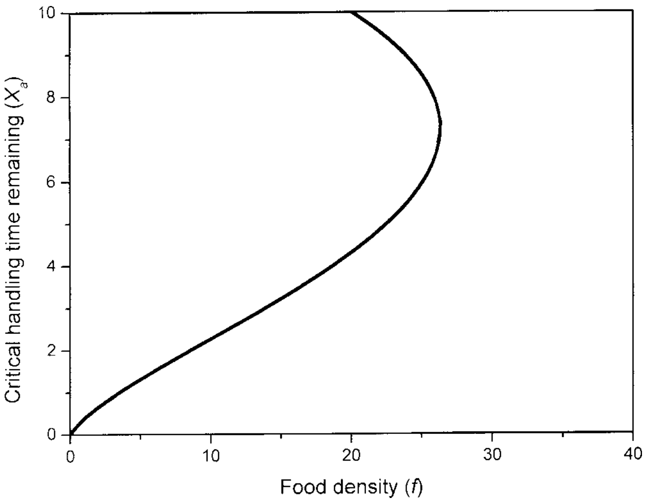

Figure 1
Numerical solution of Equation 4 to find the critical handling time remaining on a food item in the apple model (X_a) as a function of food density f. At the ESS, if a searcher encounters a handler with a food item with remaining handling time above X_a, then it challenges for that food item, otherwise it does not challenge. For f <, 20, there is only a single value of $X_a \in (0,t_h)$, and so only a single ESS where kleptoparasitism occurs. For f >, 20, then $X_a = t_h$ is always an ESS. There can also be two other equilibrium values of $X_a \in (0,t_h)$ for intermediate values of f: The upper kleptoparasitic equilibrium is always unstable and the lower always stable (i.e., an ESS). Other parameter values: $P = 20$, $t_a = 5$, $t_h = 10$, $v_f = 0.01$, $v_H = 0.05$.

This value must be found numerically. Following Broom and Ruxton (1998) and Holmgren (1995), a baseline set of parameter values $f = 30$, $P = 20$, $t_a = 5$, $t_h = 10$, $v_f = 0.01$, and $v_H = 0.05$ are used in our numerical calculations. These references can be consulted for biological justifications for these values. However, further simulations (not shown) suggest that our results remain qualitatively unchanged for a wide variety of plausible parameter combinations. In each figure, the parameters other than the one of the x-axis are held at their default values, except where specified.

The ESS value of X_a can be seen in Figure 1 for a range of food densities (f values). As one would expect, X_a increases, and so kleptoparasitism becomes less frequent, as food density increases. The condition $t_a v_f f > 1$ translates into $f < 20$ for the default parameter values. In this situation, as expected, we find only one ESS value of X_a.

The situation is more complex when $t_a v_f f > 1$ (e.g., when f is > 20 in Figure 1). First, we have discussed above that in this situation never challenging is always an ESS. However, for some combinations of parameter values satisfying $t_a v_f f > 1$, there can be two roots of Equation 4 between 0 and t_h. The higher of these turns out be unstable, but the lower is stable (see the Appendix) and is thus an alternative ESS to the one where no kleptoparasitism occurs. This can be understood as follows. When $t_a v_f f > 1$, if the dominant strategy in the population is one of not challenging handlers, then a mutant that does kleptoparasitize performs less well than the others. Thus, the population should stay at the ESS of never attempting kleptoparasitism. However, now consider a situation where $t_a v_f f$ is still > 1, but for some reason, kleptoparasitism is common in the population. This might occur, for example, if ecological conditions have recently changed such that $t_a v_f f$ moved from just less than 1 to just greater than 1. Under these circumstances, the expected reward obtained from discovery of a previously undiscovered food item is less than under conditions where no parasitism occurs. This may make the alternative strategy of kleptoparasitism more attractive. In this way, the population can move toward the alternative ESS, where some kleptoparasitism continues to occur.

As we can see from Figure 1, the alternative ESS that allows kleptoparasitism when $t_a v_f f > 1$ is a smooth extension of the ESS when $t_a v_f f < 1$. Hence, it is no surprise that X_a increases and kleptoparasitism becomes less common as food density increases. The upper (unstable) equilibrium appears at $X_a = t_h$, when we cross the boundary at $t_a v_f f = 1$. It then decreases with increasing food density. At a critical food density (i.e., when $t_a v_f f$ is sufficiently bigger than unity), the upper and lower kleptoparasitic equilibria coincide. For food densities greater than this, the sole ESS is one where all opportunities for kleptoparasitism are spurned.

Figure 2a explores the effect of varying the parameter determining the lengths of conflicts over food items (t_a). The condition $t_a v_f f < 1$ translates into $t_a < 5$ for the parameter values used. Below this, there is a single ESS with individuals attempting kleptoparasitism only if the food item (if won) can subsequently be handled for an amount of time exceeding a critical value, X_a. Not surprisingly, X_a increases when t_a increases, and so contests require more time. For t_a values a just > 5, there can be an ESS allowing kleptoparasitism. This can be understood in exactly the same way as discussed above for Figure 1. Similarly, Figure 2b can be understood in an entirely analogous fashion because the condition $t_a v_f f < 1$ translates into $v_f < 0.01$. Figure 2c demonstrates the effect of varying the density of foragers. Generally, increasing predator density makes kleptoparasitism more attractive. The same is true when v_h is increased, making finding handlers easier (Figure 2d). This can be understood most easily by considering that increasing either forager density or the rate at which handlers can be discovered makes finding unhandled prey items less attractive because subsequent parasitism is more likely. Obtaining food by kleptoparasitism is affected similarly, but this effect is less because after food has been handled for a certain amount of time it stops being attractive to potential kleptoparasites because its intrinsic value decreases with handling. Notice also that when values of P or v_h are sufficiently low that kleptoparasitism is not strongly favored, then when $t_a v_f f > 1$, the alternative kleptoparasitic ESS never exists, and so the ESS where all kleptoparasitic opportunities are rejected is the only ESS. Figure 2e demonstrates that increasing the time taken to handle a food item (t_h) increases kleptoparasitism. This is not surprising because increasing the handling time increases the value of food items, but yet the cost of competing for a food item (controlled by t_a) remains unchanged.

The orange model

In the orange model, we can see that challenging for a prey item that has only just been discovered should not be selected for (unless challenging is always optimal). In the opposite extreme, if an ESS contains any kleptoparasitism, then contesting for an almost completely handled food item should be attractive. We would thus again expect that there is a critical amount of handling remaining in a food item (X_o). On discovering a handler in state $h(x)$, a searcher should always be aggressive if $x < X_o$, and never aggressive if $x > X_o$. In the dividing case, where $x = X_o$, all strategies of choosing whether to be aggressive are equally successful. We now seek an expression for X_o. The Appendix demonstrates that this can be found by simultaneous solution of the equations below for r and X_o:

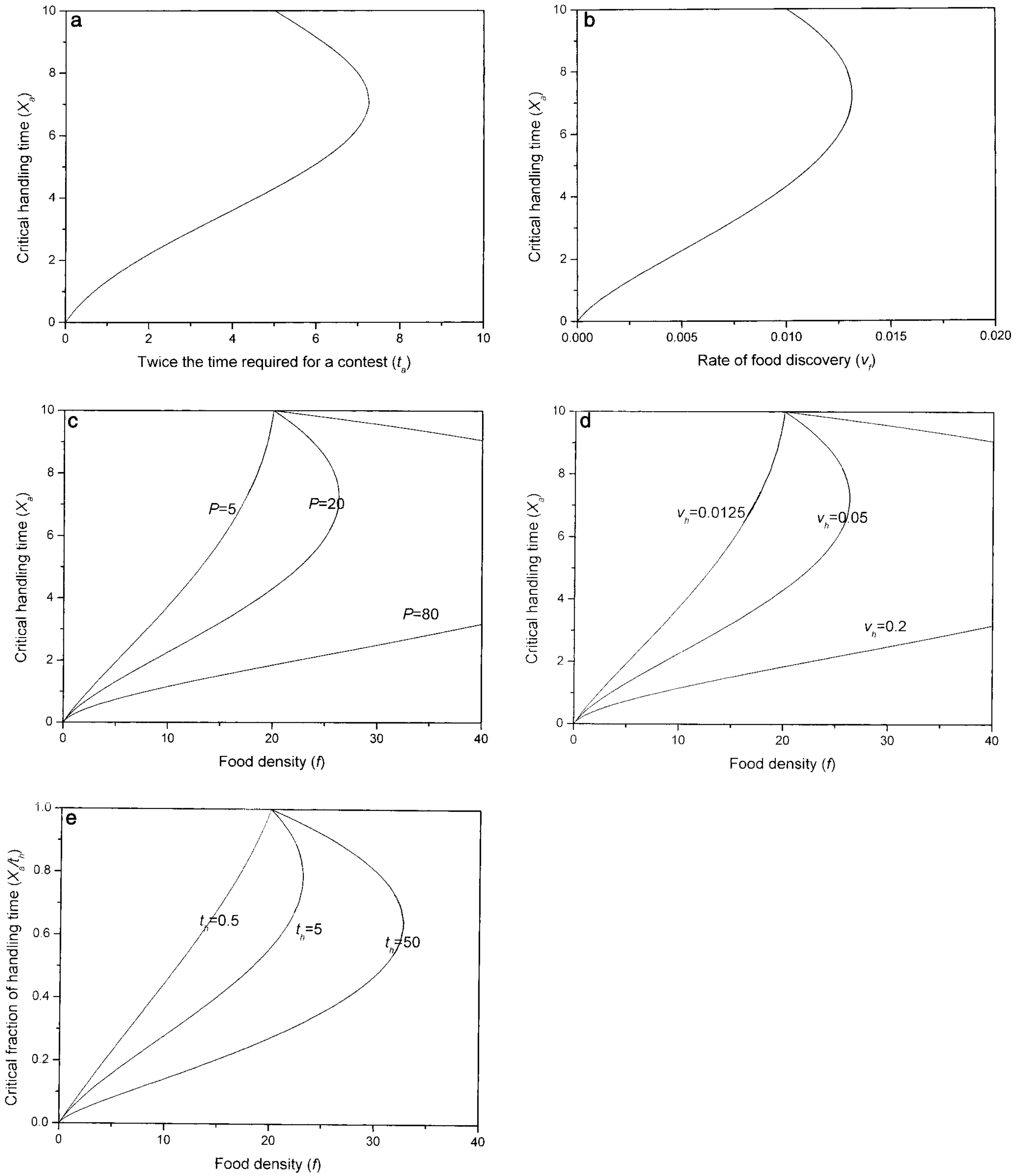

Figure 2

The apple model. (a) As for Figure 1, except that the time required for a contest (t_a) is varied. (b) As for Figure 1, except that the rate of food discovery (v_f) is varied. (c) Figure 1 reproduced for three values of the density of foragers (P). (d) Figure 1 reproduced for three values of the rate of finding handlers (v_h). (e) Figure 1 reproduced for three values of the time required to handler a food item (t_h). Note that comparison under the changing values of t_h requires that we plot X_a/t_h rather than simply X_a. Unstated parameter values: $f = 30$, $P = 20$, $t_a = 5$, $t_h = 10$, $v_f = 0.01$, $v_H = 0.05$.

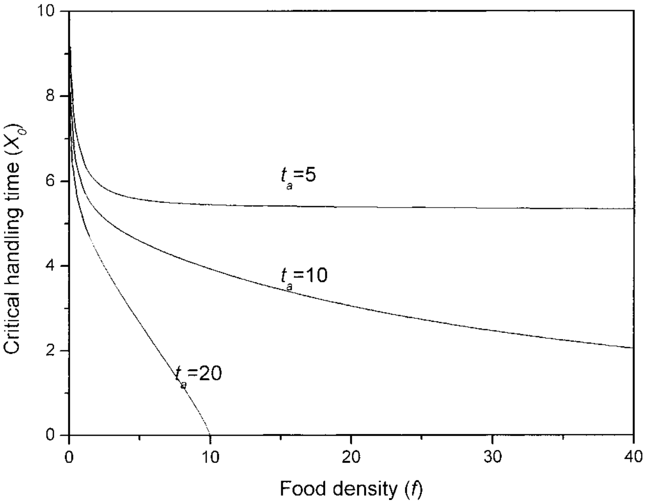

Figure 3
Numerical solution of Equations 5a and 5b of the orange model to find the critical handling time remaining on a food item (X_o) as a function of food density f and time taken in an aggressive contest (t_a). At the ESS, if a searcher encounters a handler with a food item with remaining handling time below X_o, then it challenges for that food item, otherwise it does not challenge. Other parameter values: values $P = 20$, $t_h = 10$, $v_f = 0.01$, $v_H = 0.05$.

$$t_a - t_h\left(\frac{C+1}{C}\right) + X_a = (1 + rt_a)\left\{X_o + \left(\frac{2}{r}\right)\left[1 - \exp\left(\frac{rX_o}{2}\right)\right]\right\} \tag{5a}$$

$$X_o C t_a^2 r^2 + t_a t_h r(C + 1) - Dt_h = 0. \tag{5b}$$

The Appendix also demonstrates that there is an ESS where all kleptoparasitic opportunities are spurned providing

$$(t_a - t_h)v_f f > 1. \tag{6}$$

For the original model and the apple model, the equivalent condition was

$$t_a v_f f > 1. \tag{7}$$

It can be seen that Equation 6 is a more restrictive condition than Equation 7. Thus, if kleptoparasitism is predicted never to occur in the orange model for a given combination of parameter values, then never attempting kleptopararsitism would also be the optimum strategy in the other two models with the same parameter values. The attraction of kleptoparasitism in the orange model, in comparison to the other two, is to be expected from consideration of the biology. In the orange model, the effective value of a prey item increases with the handling it has already received, in the original model its value stayed constant, and in the apple model it declined.

Notice that if $t_a < t_h$, then, from Equation 6, the strategy of rejecting all parasitic opportunities is never an ESS. Thus, in this case, unlike both the original and apple models, some kleptoparasitism will always be seen regardless of how easy it is to find unhandled food items. Such a situation is illustrated for the situation where $t_a = 5$ (and default value $t_h = 10$) in Figure 3. However, in general, increasing food density (f) makes kleptoparasitism less attractive, as we would expect, and providing $t_a > t_h$, never kleptoparasitizing will eventually become an ESS providing f is increased such that Equation 6 is satisfied. In our exploration below of the effect of varying parameter values, we generally consider $t_a = 20$, rather than the previous default value of 5, because this allows us to satisfy Equation 6 for some parameter combinations and allows us to display the fullest extent of the behavior of the model.

The Appendix also demonstrates that if $tafv_f$ is sufficiently < 1, then the critical handling time, X_o, will tend to t_h, and the ESS will be to always accept opportunities to kleptoparasitize. Notice that in the original model the condition for always challenging to be the best strategy was simply that $tafv_f$ was < 1. The condition for the orange model is more strict. Thus, if always challenging is the best strategy (for a given set of parameter values) in the orange model, then it would also be the best strategy in the analogous original model. However, under some circumstances, the original model will predict always challenging as the best strategy, but the analogous orange model will predict on optimal strategy where recently discovered prey items are not competed for. We can see in Figure 3 that for the default set of parameter values, X_o only tends to t_h as the food density f becomes very low.

Figure 4a shows that increasing the duration of contests makes kleptoparasitism less attractive, as would be expected. Eventually, for $t_a > 15$, no kleptoparasitism occurs. The situation is simpler than the equivalent graph for the apple model (Figure 2a) because there is only ever one ESS for a given combination of parameters. Similarly, increasing the rate of food discovery (v_f) decreases the attractiveness of kleptoparasitism, and indeed beyond a critical value of discovery rate, no aggression occurs (see Figure 4b). At the opposite extreme, we see that the at low values of v_f, the response is very nonlinear. As v_f increases from very low values, X_o drops very quickly, then the rate of this decrease is significantly reduced. Unlike the apple model, Figure 4c shows that the rates of kleptoparasitism observed should decline with increasing predator density (P). Specifically, increasing P decreases X_o. When forager numbers are high, then capturing items that still require a lot of handling becomes unattractive because the chance of still having possession of this item when handling has been completed is reduced. Of course, this effect also makes finding entirely unhandled food items less attractive, although (as Figure 4c shows) this effect is less strong due to no time being wasted in contesting the item in this case, and so kleptoparasitism becomes disfavored. The line for $P = 5$ in Figure 4c shows a situation where the ESS is to accept all opportunities to kleptoparasitize (for f values less than around 3.0). The decreasing value of X_o with increasing ease of finding handlers (increasing v_h) shown in Figure 4d can be understood similarly to the effect of varying P.

The effect of changes in the value of t_h is more complicated. If t_h is low, then kleptoparasitism can be very attractive. For $t_h = 2.5$ in Figure 4e, the ESS is to accept all kleptoparasitic opportunities when the food density is less than approximately 12. Parasitism is promoted because, if a food item is won in a contest, then because of the short handling time, another forager in unlikely to challenge before the reward for that item is obtained. However, if food density is high, then parasitism becomes less favored simply because spending time searching for food is more profitable than spending time in aggressive encounters. In contrast, if the handling time of a food item is increased, then X_o declines because of the increasing danger that a food item won in one aggressive interaction will then be lost in another interaction before handling is complete. Generally, the lower the food density, the more attractive parasitism is, but this is not universally true, as can be seen from the line with $t_h = 40$ in Figure 4e.

DISCUSSION

For the apple model, we found that increasing either the food density in the environment, the ease with which food items could be found, or the investment required in trying to steal

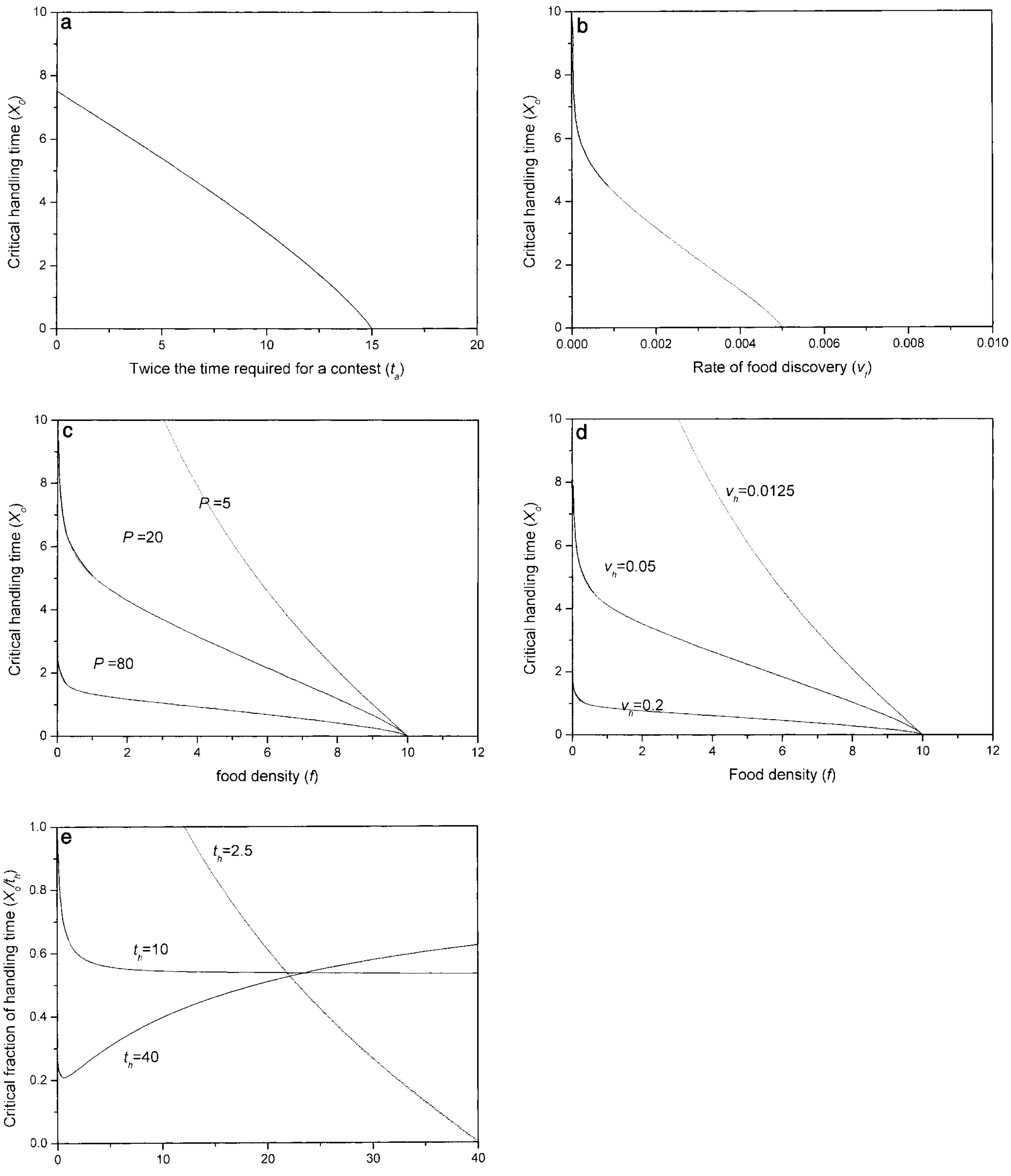

Figure 4

For the orange model. (a) As Figure 3, except that the time required for a contest (t_a) is varied. (b) As for Figure 3, except that the rate of food discovery (v_f) is varied. (c) Figure 3 reproduced for three values of the density of foragers (P). (d) Figure 3 reproduced for three values of the rate of finding handlers (v_h). (e) Figure 3 reproduced for three values of the time required to handler a food item (t_h). Note that comparison under the changing values of t_h requires that we plot X_a/t_h rather than simply X_a. Unstated parameter values: $f = 30$, $P = 20$, $t_h = 10$, $v_f = 0.01$, $v_H = 0.05$, $t_a =$, 20 except $t_a = 5$ in panel e.

from another all served to decrease the frequency with which kleptoparasitism occurs. Indeed, if any one of these is increased sufficiently, then no kleptoparasitism at all will occur, with even opportunities to steal newly discovered prey items being spurned. These results make intuitive sense, and are in accord with the previous theory of Broom and Ruxton (1998) and empirical studies (Dolman, 1995; Cresswell, 1998; Triplet et al., 1999). However, there is a significant difference between the predictions of the original and apple models. In the original model, either all kleptoparasitic opportunities would be taken or none at all. Varying one of these ecological variables had no effect unless it moved the system from one of these regimes to the other. A corollary of this was that a small change in the environment could lead to a dramatic change in the predicted behavior of individuals. In the new model, this is generally not true, and an incremental change in one of the variables leads to an incremental change in the range of handlers that are at risk from kleptoparasitism, and so to a change in the frequency of parasitism observed (see Figures 1 and 2). Notice, however, that the change in range of handler types with change in parameter values is generally nonlinear. For example, increasing food density from 10 to 11 in Figure 1 has a much smaller effect than changing from 23 to 24 (assuming the system is at the kleptoparasitic equilibrium). Abrupt changes can still occur: at $f = 24$, discovered food items are targets for kleptoparasitism for the first 25% of their handling time; whereas at $f = 25$, no kleptoparasitism occurs.

It is also possible for f values of 23 or 24 in Figure 1 to produce no kleptoparasitism at all. This is because the system exhibits alternative ESSs. Ecologically this can be interpreted as follows. When food density, for example, is low (< 20 in Figure 1), then we would expect kleptoparasitism to be common. Conversely, when food is plentiful ($f > 25$ in Figure 1), then we would expect no kleptoparasitism at all. However, for intermediate food densities, a given population may or may not exhibit kleptoparasitism. If the food density has been poorer in the past, then we might expect that parasitism will persist in this intermediate zone. However, if the system has no previous history of parasitism (perhaps because it has historically been richer in food), then we would not expect kleptoparasitism to develop in this intermediate zone, although it would if food density fell low enough. We can then have the apparently paradoxical situation where the model predicts ecologically important differences in kleptoparasitism rates between currently identical systems because these systems were different historically. Note that in this case the history in question is very recent, and we would expect to see both behaviors within a relatively short time interval. Although this argument has been framed in terms of food density, it will hold for other characteristics of the system as well.

The previous model of Broom and Ruxton predicted that the density of foragers in the environment, the ease with which handlers could be discovered, and the handling time required by a food item would all have no effect on the rates of kleptoparasitism. This is not so in the apple model. The key reason for this difference is that, in the original model, a handler could be challenged at any time during the handling process, whereas in the apple model, a food item is no longer subject to stealing after it has less than X_a handling time remaining. In the apple model, X_a decreases (and so stealing becomes more common) as forager density increases. Increasing predator numbers means that handlers are more likely to encounter searchers, and so the likelihood of a food item being stolen increases. This is true both for items that the handler found itself and for items that it stole. However, in the first case, items are vulnerable for a time $t_h - X_a$, before being safe for a time X_a; in the second case the vulnerable time will be shorter but the safe time remains the same. Hence, increasing forager numbers means that handlers will lose food items more often during the vulnerable time. If stealing is prevalent, then all food items requiring further handling (x) substantially greater than X_a have similar net worth to the current handler, since that individual is unlikely to still be the handler when $x = X_a$. The effective value of a partly consumed item thus becomes closer to that of a newly discovered item. This makes challenging for food items that are just approaching the invulnerable phase more attractive and so makes kleptoparasitism a more attractive and common strategy in the population. In the original model, there was no invulnerable period, so this effect did not apply, and forager density had no effect on kleptoparasitic behavior. Why increased detectability of handlers (increasing v_h) leads to a change in behavior (with more kleptoparasitic opportunities being accepted) in the apple model but not in the original model can be understood by similar reasoning. There is considerable empirical support for the prediction that aggression rates increase with forager density (Burger et al., 1979; Goss-Custard, 1980; Smith and Metcalfe, 1997).

Increasing the time required to handle a prey item (t_h) caused an increase in the frequency with which kleptoparasitic opportunities lead to an aggressive interaction in the apple model, but had no effect in the original model of Broom and Ruxton (1998). As reasoned above, the effective value of a part consumed item is close to that of a new item when t_h is large because, again, the current handler is unlikely still to be in position during the invulnerable final phase of handling. Thus stealing such an item is relatively more attractive than for lower t_h.

As in the apple model (and the original model of Broom and Ruxton, 1998), increasing food density, the ease with which food items can be discovered, or the length of aggressive contests all act to make kleptoparasitism less attractive in the orange model. However, unlike these previous models, increasing these does not necessarily always involve the eventual extinction of kleptoparasitism from the population. If $t_a < t_h$, then kleptoparasitism will always be attractive, no matter how bountiful the food supply. This occurs because food items only provide a reward at the end of their handling period. Hence, even if unhandled food items can be found instantaneously, kleptoparasitism may be a better option (as long as the contest is not too long), providing this yields a food item that is near to yielding its reward. The difference between the ESS solutions of the apple and orange models provides a clear prediction of our theory. When prey items require handling before yielding a lump sum at the end, then kleptoparasitic attacks will be focused on prey items near the end of their handling period; if prey items yield reward continuously during handling, then attacks should be biased toward newly discovered food items.

In contrast to the apple model, the orange model predicts that rates of kleptoparasitism should decline with increasing predator density. When forager numbers are high, then capturing items that still require a lot of handling becomes unattractive, as the chance of still having possession of this item when handling has been completed is reduced. Of course, this effect also makes finding entirely unhandled food items less attractive. However, the first effect is stronger because obtaining a food item by aggression requires a time investment in a contest that food finding does not. For example, in Figure 4c, any challenge costs an average of 20 time units to obtain a food item (the mean contest length is 10 time units, and a challenger wins with probability 0.5), whereas the total handling time is only 10 time units. The cost of this initial investment in the challenge is especially severe when the chance of successfully handling the food item is small. Thus it is better to wait for a new item without this cost (while simultaneously looking for a better challenging opportunity; i.e., for an item which requires less handling).

There was no effect of predator density in the original model of Broom and Ruxton (1998) because handling was equally likely to end at any moment, and so newly discovered items were just as valuable as those that had previously been handled for some time.

In Figure 4a, the model predicts that when the time required for an aggressive contest tends to zero, then parasites should challenge for food items that have completed at least 23% of their handling. This seems rather strange; one would expect that if aggression costs nothing, then all opportunities to challenge for a food item should be taken. This behavior highlights an implicit assumption in our model, that searching foragers should always begin handling any unhandled food items that they find. In the case where aggressive encounters have no cost, this behavior is not optimal because handling takes away opportunities to challenge for other food items (that have already been partially handled). To avoid the odd behavior of the model in this limiting case, we need to allow more flexible forager strategies where searchers can be selective about handling discovered unattended food items. However, we have not presented this elaboration because it would only be of importance in rather ecologically unrealistic conditions, such as when aggressive encounters have no cost to the participants.

It is possible that the length of a contest depends on the value of the contested item and that the individuals involved make a strategic choice about the length of time they are prepared to fight (see Ruxton and Broom, 1999); this precludes the no-cost scenario. Another such case occurs when handling times are very long, as illustrated by the case of $t_h = 40$ in Figure 4e. Again, from the discussion above, in this case the optimal strategy would allow animals to be selective about handling discovered prey items. Adding such a complication to the strategy would remove the surprising behavior shown for this limiting case in the present model where increasing food density leads to greater kleptoparasitism.

The theoretical work of Sirot (2000) makes similar predictions to the apple model presented here: Kleptoparasitism should increase with increased forager density, decreased food abundance, and increasing food item value (and handling time simultaneously). However, in Sirot's model, populations are always expected to show at least some aggression, whereas in the apple model no aggression is predicted under some circumstances. This is because Sirot's model is based on the hawk–dove methodology, and an aggressive hawk can always exploit a population of doves because it wins food items at no cost. In contrast, in our model, there is always an explicit cost to attempting to steal a food item. Another key difference between the models is that Sirot's theory assumes that an individual's decision to challenge for a prey item is independent of the state of that prey item, whereas the handling that an item has already received is an integral component of the kleptoparasitic strategy in our model. Neither approach is intrinsically biologically more realistic than the other: Sirot's applies to situations where information on the previous handling of a prey item is unavailable to potential contestants, whereas ours applies when perfect information is available. These two informational extremes probably bound the real situation where some imperfect knowledge will be available. The simulation model of Stillman et al. (1997) is more similar to the orange model, but again makes the same assumption as Sirot (2000) that no information about the current state of a handled item is used in deciding whether to challenge for it.

The key assumption of the theory developed here is that individuals are able to assess the amount of previous handling that a prey item has experienced and modify their behavior in the light of this knowledge. It is this assumption that provides the main difference between the theory presented here and that of previous works by Broom and Ruxton (1998) and Sirot (2000), where all prey items had equal worth and so no discrimination was required. It is easy to accept that the current handler (especially if that individual was the original discoverer of the food item) has good knowledge of how long it has been handled, but what of potential kleptoparasites who might challenge the present handler? The handling state may be apparent to such an individual from previous observation of the present handler, or it may get cues as to the current state of the food item through changes in the food item itself (consider the visual changes in an apple or orange as we handle them). Alternatively or additionally, such information may be obtained indirectly from the vigor with which the current handler is prepared to defend the prey item. Although we consider such discrimination to be likely, the most important development of the work presented here is the empirical testing of this idea to demonstrate its validity and explore the ecological circumstances where discrimination by potential kleptoparasites does and does not occur.

Other assumptions of the model are also open to challenge. We implicitly assume that searching for prey items and for opportunities to kleptoparasitize are completely compatible activities. That is, that the performance of one activity does not in any way impair the performance of the other. Recent empirical evidence suggest that this will not hold universally (Coolen et al., 2001). In such a situation, we would expect that individuals expand their kleptoparasitic strategy to include flexible investment between the two types of searching. A framework for this development of the theory is provided by Broom and Ruxton (1998). We also assume that contests over food items last a fixed time, t_a, after which an unambiguous winner emerges. This may be realistic for some species, but in some cases, the contest may have no defined endpoint and simply continue until one or other party decided to give up and invest time in other activities. Such situations can be modeled as a war of attrition. In these circumstances, we would expect a kleptoparasite's strategy to expand to include how long they would be prepared to fight for a prey item. Such a situation was modeled by Ruxton and Broom (1999). We would expect a complex strategy to emerge, with the amount of time that an individual is prepared to invest in a prey item depending on the reward for winning, which in turn will depend on the amount of previous handling that the prey item has experience.

APPENDIX

H, S, A, $h(x)$ and $a(x)$ are all functions of time, but for notational clarity we do not write this dependence explicitly. We can construct a differential equation for the rate of change in individuals in any aggressive subpopulation $a(x)$:

$$\frac{\partial a(x)}{\partial t} = 2p(x)h(x)Sv_H - \frac{2a(x)}{t_a}. \tag{A1}$$

As in Broom and Ruxton (1998), we assume that the population has achieved a temporal equilibrium, so that

$$\frac{\partial a(x)}{\partial t} = 0; \quad \text{i.e.,}$$

$$p(x)h(x)Sv)_H = \frac{a(x)}{t_a} \tag{A2}$$

for all values of x.

The rate of change in a given handling population $h(x)$ can be shown to be

$$\frac{\partial h(x)}{\partial t} = \frac{\partial h(x)}{\partial x} + \frac{a(x)}{t_a} - p(x)\,h(x)\,Sv_H. \qquad \text{(A3)}$$

Under the assumption of temporal equilibrium condition, we have

$$\frac{\partial h(x)}{\partial t} = 0,$$

then (combined with Equation A2), this implies that

$$\frac{\partial h(x)}{\partial x} = 0. \qquad \text{(A4)}$$

Thus $h(x)$ must be independent of x and given by

$$h(x) = \frac{H}{t_h}. \qquad \text{(A5)}$$

Substituting the result of Equation A5 into Equations A1 and A3 and integrating over the range 0 to t_h, we obtain the same equations as in Broom and Ruxton (1998), with the sole difference that p, the fixed probability of entering a contest in the original model, is replaced by

$$\frac{1}{t_h}\int_0^{t_h} p(x)\ dx.$$

Thus, in the same way, these equations can be combined to give an expression equivalent to the analogous equation of Broom and Ruxton (1998), with this sole difference, for the equilibrium fraction of individuals handling a food item:

$$\left(\frac{D}{t_h}\int_0^{t_h} p(x)\ dx\right)\left(\frac{H}{P}\right)^2 + \left(\frac{H}{P}\right)(C + 1) - C = 0, \qquad \text{(A6)}$$

where $C = t_h v_f f C$ and $D = \mathrm{t}_a v_H P$. Because C and D are always positive, this quadratic has always and only one positive root for H/P.

This is as far as we can develop the general framework; we must now consider the apple and orange models separately.

The apple model

The original model of Broom and Ruxton (1998) made the following predictions based on the value of critical parameter combination, $t_a v_f f$. If this parameter group is greater than unity, then the best strategy is $p = 0$ and no food items should be contested for; if the value is less than unity, then the best strategy is $p = 1$, and all food items should be contested; if the parameter group is equal to unity, then all strategies of whether or not to challenge handlers are equally as effective.

Following the argument in the section describing the apple model in the main text, if challenging is ever a good strategy, then $p(t_h) = 1$. Similarly, it must always be true that $p(0) = 0$, and so there is a critical amount of handling remaining in a food item (X_a). On discovering a handler in state $h(x)$, $p(x) = 1$ if $x > X_a$, and $p(x) = 0$ if $x < X_a$. In the dividing case, where $x = X_a$, all strategies of choosing whether to be aggressive are equally successful. We now seek an expression for X_a. If the calculated value of X_a is greater than t_h, then the optimal strategy is to never challenge. It is never the case in this model that to always unconditionally challenge is the optimal strategy. Under our argument above, we can simplify Equation A6 considerably, since

$$\int_0^{t_h} p(x)\ dx = t_h - X_a. \qquad \text{(A7)}$$

We must now find an expression for H/P in terms of X_a.

Because individuals extract food at a constant rate while handling, and if for convenience we scale this rate to be unity, then the long-term rate of food uptake is simply the fraction of time spent handling, H/P.

Let us imagine a situation where an individual is searching and encounters a handling individual of the critical type $h(X_a)$. Now, all strategies for deciding whether to challenge yield identical results, so let us assume that the focal individual always challenges, investing a time $t_a/2$. On 50% of occasions it loses the contest and returns to searching immediately. On the other 50% of times, it wins the food item. On such occasions it will always consume the remains of the food item for a time X_a, free from contest by other individuals, because the food item is no longer worth challenging for. Thus we can work out the long-term average reward rate for challenging in these circumstances easily. The ratio of the expected reward to the expected time to obtain this reward is

$$\frac{0.5X_a + 0.5(0)}{0.5t_a + 0.5X_a} = \frac{X_a}{X_a + t_a}. \qquad \text{(A8)}$$

We thus obtain:

$$\frac{H}{P} = \frac{X_a}{X_a + t_a} \qquad \text{(A9a)}$$

if $0 < X_a < t_h$. For $X_a = t_h$, we require

$$\frac{H}{P} > \frac{t_h}{t_h + t_a}. \qquad \text{(A9b)}$$

Substituting Equation A7 and Equation A9 into Equation A6 gives

$$DX_a^3 - X_a^2(t_h(D + 1)) + X_a(t_h t_a(C - 1)) + t_a^2 t_h C = 0 \qquad \text{(A10a)}$$

for $0 < X_a < t_h$ and

$$-t_h^3 + t_h^2 t_a(C - 1) + t_a^2 t_h C < 0 \qquad \text{(A10b)}$$

for $X_a = t_h$.

Equation A10a is a cubic in X_a and thus has at most three roots. The left-hand side (LHS) is negative in the limit $X_a \to -\infty$, positive when $X_a = 0$, and positive in the limit $X_a \to \infty$. If $t_a v_f f < 1$, then LHS is negative when $X_a = t_h$, and so there are exactly three roots, one of which is negative, one greater than t_h, and a unique allowable solution between 0 and t_h. Thus there is a unique solution in this case.

When $t_a v_f f > 1$, Equation A10b is satisfied, and so $p(x) = 0$ for all values of x is a solution, and no kleptoparasitism will occur. This is logical because the apple model makes challenging for already partially handled food items less attractive than the original model. A partially handled prey item now yields less reward for the same investment in an aggressive encounter. Hence, under circumstances when challenging was unrewarding in the original model, it will remain so under the apple model. Note, however, that for some parameter values Equation A10a can have two roots between 0 and t_h. Because LHS of Equation A10a is positive when $X_a = 0$, the lower root has a negative derivative, meaning that a slightly larger value of X_a (i.e., less kleptoparasitism) gives kleptoparasitism an advantage and vice versa, so that this root is a stable solution. Similarly, at the second root the derivative is positive so that such an increase in X_a gives kleptoparasitism a disadvantage and so the root is unstable. The higher of these turns out be unstable, but the lower is stable and is thus an alternative solution. If challenging is already prevalent in the population, then the expected reward of finding a food item is lower, so that the prospect of obtaining one of lower than maximum value may still be worthwhile because others will not challenge for it when its value becomes sufficiently low. See the numerical example for a demonstration of this.

Hence, for any combination of values for the ecological variables P, f, v_f, v_H, t_h, and t_a, we can find X_a and hence describe the optimal strategy for kleptoparasitism under the apple model.

The orange model

From the description of the orange model in the main text, we expect $p(t_h) = 0$, unless challenging is always optimal, and $p(0) = 1$ if challenging is ever a good strategy. There is again a critical amount of handling remaining in a food item (X_o). Thus, on discovering a handler in state $h(x)$, a searcher should always choose $p(x) = 1$ if $x < X_o$, and $p(x) = 0$ if $x > X_o$. In the dividing case, where $x = X_o$, all strategies of choosing whether be aggressive are equally successful. We now seek an expression for X_o.

Let us define $F[S]$ as the expected further time until consumption of a food reward by an individual currently searching, $F[a(x)]$ and $F[h(x)]$ are defined similarly. Hence,

$$F[S] = F[a(X_0)]. \tag{A11}$$

From the rules of our model

$$\begin{aligned} F[a(x)] &= 0.5(F[h(x)] + 0.5t_a) + 0.5(F[S] + 0.5t_a) \\ &= 0.5(F[h(x)] + F(S) + t_a). \end{aligned} \tag{A12}$$

Combining Equations A11 and A12 gives

$$F[S] = F[h(X_0)] + t_a. \tag{A13}$$

We now introduce Q as the probability that a searcher's next transition is to being an aggressor rather than a handler, and T as the expected time to that transition. Using these definitions,

$$F[S] = T + (1 - Q)F[h(t_h)] + \left(\frac{Q}{X_0}\right)\int_{x=0}^{X_o} F[a(x)]\,dx. \tag{A14}$$

A searcher meets handlers at a rate $v_H H$. At equilibrium all $h(x)$ are equally likely to be encountered, but only a fraction (X_o/t_h) of these encounters should lead to aggression. Hence, the rate of transitions to aggressive states is $(v_H H X_o)/t_h$. The rate of transition to handling is simply $v_f f$. Thus we can write

$$T = \frac{1}{v_f f + \dfrac{v_H H X_o}{t_h}} = \frac{t_h}{C + v_H H X_o}, \tag{A15}$$

Similarly,

$$Q = \frac{\dfrac{v_H H X_o}{t_h}}{\dfrac{v_H H X_o}{t_h} + v_f f} = \frac{v_H H X_o}{v_H H X_o + C}. \tag{A16}$$

It is clear that

$$F[h(t_h)] = (t_h - X_0) + F[h(X_0)] \tag{A17}$$

because a handler will not be challenged until its prey item requires less than X_o further handling. Substituting Equations A12, A13, A15, A16, and A17 into Equation A14 and rearranging gives

$$\begin{aligned} &t_a C - t_h(C + 1) + CX_o \\ &= 0.5 v_H H \int_{x=0}^{X_o} (F[h(x)] - F[h(X_o)])\,dx. \end{aligned} \tag{A18}$$

Define r as the rate of challenges on any handler holding a food item requiring less than X_o additional handling time. Then in any small time interval of length δx, the probability of being challenged is approximately $r\delta x$. If a challenge occurs with handling time x remaining, an extra time, $t_a/2$, is taken if the contest is won, and an extra time, $F[S] - F[h(x)] + t_a/2$ is taken on average if the contest is lost because the handler then reverts to being a searcher. It is easy to show that

$$\frac{d}{dx}F[h(x)] = 1 + \left(\frac{r}{2}\right)\left(\frac{t_a}{2}\right) + \left(\frac{r}{2}\right)\left(F[S] - F[h(x)] + \frac{t_a}{2}\right). \tag{A19}$$

Substituting for $F[S]$ using Equation A13 gives

$$\frac{d}{dx}F[h(x)] = 1 + rt_a + 0.5r(F[h(X_o)] - F[h(x)]). \tag{A20}$$

Now r is simply $v_H S$. However, at equilibrium the rate of individuals returning to searching from handling (H/t_h) is equivalent to those leaving searching for handling, $v_f fS$. This allows us to substitute for S and obtain

$$r = \frac{v_H H}{C} = \left(\frac{H}{P}\right)\left(\frac{D}{t_a C}\right). \tag{A21}$$

Noting that $F[h(X_o)]$ is independent of x, we make the substitution

$$y = F[h(x)] - F[h(X_0)]. \tag{A22}$$

to obtain

$$\frac{dy}{dx} = 1 + rt_a - 0.5ry. \tag{A23}$$

This can be solved using the condition that $y = 0$ when $x = X_o$ to give

$$y = \frac{2}{r}(1 + rt_a)\left[1 - \exp\left(\frac{r(X_o - x)}{2}\right)\right], \tag{A24}$$

which is negative for all $x < X_o$.

Substituting this into Equation A18, using Equation A21, and rearranging gives

$$\begin{aligned} &t_a - t_h\left(\frac{C + 1}{C}\right) + X_o \\ &= (1 + rt_a)\left[X_o + \left(\frac{2}{r}\right)\left(1 - \exp\left(\frac{rX_o}{2}\right)\right)\right]. \end{aligned} \tag{A25}$$

This gives us one equation in r and X_o. We can obtain another from Equation A6 because $p(x)$ is unity for $0 < x < X_o$ and zero for $X_o < x < t_h$. This gives us:

$$\left(\frac{H}{P}\right)^2\left(\frac{DX_o}{t_h}\right) + \left(\frac{H}{P}\right)(C + 1) - C = 0. \tag{A26}$$

Combining this with Equation A21 and rearranging gives

$$X_o C t_a^2 r^2 + t_a t_h r(C + 1) - Dt_h = 0. \tag{A27}$$

The right-hand side of Equation A25 is always negative for $X_o > 0$, and equal to zero when $X_o = 0$. It follows that there is no solution to Equation A25 if

$$t_a - t_h\left(\frac{C + 1}{C}\right) > 0, \tag{A28}$$

which can be rearranged as

$$t_a v_f f > 1 + C. \tag{A29}$$

If parameter values are such that Equation A29 is satisfied, then the best strategy is to never enter into aggressive interactions. The equivalent condition for the original and for the apple model is

$$t_a v_f f > 1, \tag{A30}$$

which is a less restrictive condition. Thus, the orange model predicts aggression under ecological circumstances where the other two models do not. Conversely, if aggression is predicted never to occur in the orange model for a given combination of parameter values, then always avoiding aggression would also be the optimum strategy in the other two models.

Considering the other extreme, when is it best to always challenge? If $X_o = t_h$, then the left-hand side of Equation A25 is equal to $t_a - t_h/C$ and the right-hand side is negative (let us say, equal to $-\alpha$). Thus we obtain

$$(t_a + \alpha) f v_f = 1. \tag{A31}$$

Thus, it is always best to challenge if $t_a v_f f$ is sufficiently < 1. In particular, when $t_a v_f f = 1$, there is a solution $0 < X_o < t_h$. We cannot obtain the condition when always challenging is the best strategy algebraically, this must be found numerically.

Simultaneous solution of Equations A25 and A27 can be used to find X_o. If all solutions are out with $(0, t_h)$ and $t_a v_f f$ is sufficiently < 1, then the best strategy is to always challenge. Notice that in the original model the condition for always challenging to be the best strategy was simply than $t_a v_f f$ was < 1. The condition for the orange model (Equation A29) is more strict. Thus, if always challenging is the best strategy (for a given set of parameter values) in the orange model, then it would also be the best strategy in the analogous original model. However, under some circumstances, the original model will predict always challenging as the best strategy, but the analogous orange model will predict on optimal strategy where recently discovered prey items are not competed for. Notice also that always challenging is never an optimal strategy in the apple model.

REFERENCES

Bednekoff PA, Lima SL, 1998. Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour. Proc R Soc Lond B 265:2021–2026.

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

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

Burger J, Hahn DC, Chase J, 1979. Aggressive interactions in mixed-species flocks of migrating shorebirds. Anim Behav 27:459–469.

Carbone C, DuToit JT, Gordon IJ, 1997 Feeding success of African wild dogs: does kleptoparasitism by spotted hyenas influence hunting group success? J Anim Ecol 66:318–326.

Coolen I, Giraldeau L-A, Lavoie M, 2001. Head position as an indicator of producer and scrounger tactics in a ground feeding bird. Anim Behav 61:895–903.

Cresswell W, 1998. Variation in the strength of interference competition with resource density in blackbirds, *Turdus merula*. Oikos 81: 152–160.

Dolman PM, 1995. The intensity of interference varies with resource density: evidence from a field study with snow buntings, *Plectrophenax nivalis*. Oecologia 102:511–514.

Driessen G, Visser ME, 1997. Components of parasitoid interference. Oikos 79:179–182.

Free CA, Beddington JR, Lawton JH, 1977. On the inadequacy of simple models of mutual interference for parasitism and predation. J Anim Ecol 46:543–554.

Furness RW, 1987. Kleptoparasitism in seabirds. In: Seabirds: feeding ecology and role in marine ecosystems (Croxall JP, ed). Cambridge: Cambridge University Press; 77–100.

Giraldeau L-A, Caraco T, 2000. Social foraging theory. Princeton, New Jersey: Princeton University Press.

Gorman ML, Mills MG, Raath JP, Speakman JR, 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. Nature 391:479–481.

Goss-Custard JD, 1980. Competition and interference among waders. Ardea 68:31–52.

Goss-Custard JD, Cayford JT, Lea SEG, 1998. The changing trade-off between food finding and food stealing in juvenile oystercatchers. Anim Behav 55:745–760.

Holmgren N, 1985. The ideal free distribution of unequal competitors: predictions from a behaviour-based functional response. J Anim Ecol 64:197–212.

Iyengar EV, 2000. To steal or not to steal? That is the question. Suspension feeding versus kleptoparasitism in a marine snail. Am Zool 40:1073.

Pitcher TJ, Parrish JK, 1993. Functions of shoaling behaviour in teleosts. In: Behaviour of teleost fishes (Pitcher TJ, ed). London: Chapman & Hall.

Proctor CJ, Broom M, 2000. A spatial model of anti-predator vigilance IMA J Math Appl Med Biol 17:75–93.

Roberts G, 1996. Why vigilance declines as group size increases. Anim Behav 51:1077–1086.

Ruxton GD, Broom M, 1999. Evolution of kleptoparasitism as a war of attrition. J Evol Biol 12:755–759.

Selman J, Goss-Custard JD, 1988. Interference between foraging redshank, *Tringa totanus*. Anim Behav 36:1542–1544.

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

Smith RD, Metcalfe NB, 1997. Why does dominance decline with age in wintering snow buntings. Anim Behav 53:313–322.

Stillman RA, Goss-Custard JD, Caldow RWG, 1997. Modelling interference from basic foraging behaviour. J Anim Ecol 66:692–703.

Triplet P, Stillman RA, Goss-Custard JD, 1999. Prey abundance and the strength of interference in a foraging shorebird. J Anim Ecol 68:254–265.

Tso IM, Severinghaus LL, 1998. Silk stealing by *Argyrodes lanyuensis* (Araneae: Theridiidae): a unique form of kleptoparasitism. Anim Behav 56:219–225.

Vines G, 1980. Spatial consequences of aggressive behaviours in flocks of ostercatchers, *Haematopus ostralegus* L. Anim Behav 28:1175–1183.