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Evolutionarily stable stealing: game theory applied to kleptoparasitism

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We present an individual-based model of a group of foraging animals. Individuals can obtain food either by discovering it themselves or by stealing it from others (kleptoparasitism). Given that challenging another individual for a discovered food item costs time (which could otherwise be spent searching for an undiscovered item), attempting to steal from another may not always be efficient. We show that there is generally a unique strategy that maximizes uptake rate—always or never challenging others. For any combination of parameter values, we can identify which strategy is appropraite. As a corollary to this, we predict that small changes in ecolgical conditions can, under some circumstances, cause a dramatic change in the aggressive behavior of individuals. Further, we investigate situations where searching for undiscovered food and searching for potential opportunities for stealing are mutually exclusive activities (i.e., success at one can only be improved at the expense of the other). Using game theory, we are able to find the evolutionarily stable strategy for investment in these two activities in terms of the ecological parameters of the model. *Key words:* evolutionarily stable strategy, food contests, foraging behavior, functional response, interference, game theory. *[Behav Ecol 9:397–403 (1998)]*

Kleptoparasitism occurs when one individual steals food from another. Interspecific and intraspecific kleptoparasitism are widespread among vertebrates and are particularly well documented for birds (see Brockman and Barnard, 1979, Furness, 1987, for reviews). Here we focus on intraspecific kleptoparasitism and how it affects food uptake rates of individuals.

The food uptake rate of an individual (which is generally a function of food availability and competition from other foragers) is often termed the "functional response." Recently, Ruxton and Moody (1997) developed a functional response based on a mechanistic description of food stealing (first described by Holmgren, 1995). Their model assumed that individuals search for food items, and on discovery of a food item, a finite amount of time was required to process that item before ingestion (e.g., for some wading birds this could be the time taken to open a shell of a mollusk). During this handling time, if another individual happens upon the handler then a contest for the prey item ensues. This contest always produces a clear winner, but both contestants must invest a finite amount of time in the challenge. This time "wasted" in contests leads to an interference effect, where average uptake rates decline with forager density (Holmgren, 1995; Ruxton and Moody, 1997). However, a key, implicit assumption in Ruxton and Moody's model was that a searching individual that detects a handler always challenges it for its food item. This may not always be the most time-efficient strategy. Under some circumstances it may pay individuals to pass up such an opportunity and invest the time that would have been spent in that contest in other activities, such as searching for an undiscovered food item of its own. The first aim of this article is to extend the model of Ruxton and Moody (1997) and to ask, If individuals can pass up opportunities to kleptoparasitize, then under what circumstances should they do so? In other words, what is the optimal strategy for the use of kleptoparasitism?

A second assumption of Ruxton and Moody (and many other studies that have derived functional responses from mechanistic models; e.g., Beddington, 1975; Holmgren, 1995; Ruxton et al., 1992), is that searching for food items and searching for conspecifics handling food (and thus for opportunities for kleptoparasitism) are separate activities that can be varied independently. In fact, it seems likely that the effectiveness of these related activities could be linked, so that individuals will often only be able to enhance their effectiveness at one at the expense of the other. As an example, we return to wading birds feeding in an aggregation. If prey detection occurs by sight, then, to optimize prey detection, the bird should focus downward within the strike zone of its bill. However, it can only observe conspecifics by looking sideways. There is a trade-off between effectiveness in these two activities. For our purposes, it does not matter if the bird resolves this by dividing its time between scans for a prey and other birds, or whether it can observe both simultaneously and divides its concentration. Our suggestion is that individuals have a finite capacity for searching, which they must split between searching for undiscovered and discovered prey items. Our second aim is to answer the question of how individuals should optimize this split, and how this optimal split is affected by ecological parameters.

The foraging model

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

$$S + H + A = P. \qquad (1)$$

We use these labels interchangeably for the density of individuals involved in a particular activity and to identify the activity

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itself. Let us consider the rules of transition between these states. The rates 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. The rates v_f and v_H can be thought of as the rates at which space is searched multiplied by the probability of detecting an individual within that searched space, to give the encounter rate. (Initially we will consider these to be independent constants; later we will allow searchers to differentially allocate search effort to either prey or handlers.) Upon finding a food item, a searcher switches to being a handler. It now requires an uninterrupted period in which to handle this food item before being able to ingest it. We assume that this time is drawn from an exponential distribution with mean t_h (see Lendrem, 1983, 1986b for a biological justification for this distribution). If during the handling time a searching individual challenges the handler for its food item, then both individuals move to the aggressive interaction subpopulation *(A)* for the duration of their contest. This lasts for a time drawn randomly from an exponential distribution with mean $t_a/2$ (the factor is halved to keep subsequent calculations as tidy as possible). After this, one individual (the loser) returns to searching, while the other (the winner) returns to handling. We assume that each participant in a fight is equally likely to emerge the winner or loser. So far, these rules mirror those of Ruxton et al. (1992) and subsequent works. The key difference is now introduced: on meeting a handling individual, a searcher is not forced to take up an opportunity to fight (as previous works assume), but rather it chooses whether to fight or continue searching. The probability that it will enter into a potential fight is defined as a constant, p. (Later we will explore how individuals should set p so as to maximize their food intake rate.) Armed with these rules, we can construct a set of equations describing the rates of movement between the three subpopulations (see Ruxton et al., 1992, for a similar procedure).

$$\frac{dS}{dt} = \left(\frac{H}{t_h} - v_f Sf\right) - \left(pv_H SH + \frac{A}{t_a}\right) \tag{2}$$

$$\frac{dH}{dt} = \left(-\frac{H}{t_h} + v_f Sf\right) - \left(pv_H SH + \frac{A}{t_a}\right) \tag{3}$$

$$\frac{dF}{dt} = 2pv_H SH - \frac{2A}{t_a}. \tag{4}$$

If the population is allowed to reach a dynamic equilibrium, then we can solve Equations 1–3 (Equation 4 can be derived from Equations 1–3 and so provides no further information) to obtain a quadratic equation for the fraction of individuals which are handling at any one time

$$\left(\frac{H}{P}\right)^2 pD + \left(\frac{H}{P}\right)(C + 1) - C = 0, \tag{5}$$

where, for convenience, we have defined the following

$$C = t_h f v_f \tag{6}$$

$$D = t_a P v_H. \tag{7}$$

The roots of Equation 5 are given by

$$\frac{H}{P} = \frac{-(C + 1) \pm \sqrt{(C + 1)^2 + 4pCD}}{2pD}. \tag{8}$$

(Because $pCD \geq 0$ and $C > 0$, only the root where we add the square root term will be positive.) An individual's uptake rate is the rate at which it makes the transition from handler back to searcher (which is the rate at which it gains food items). Because all individuals are intrinsically identical, each individual's uptake rate is the same as the population per capita rate of food items consumed (γ), which is given by

$$\gamma = \frac{H}{t_h P}. \tag{9}$$

Circumstances where kleptoparasitism is a good or bad strategy

We can ask how individuals should set p (their propensity to take up opportunities to steal food) so as to maximize their uptake rate. Consider a searcher that has just come upon a handler and so has the option to attempt to steal the handler's food item. If the searcher takes this option, then before having a chance of capturing the food item, it must invest an average time of $t_a/2$, at the end of which it will only have a 50% chance of success. Hence, for this option (taken with probability p), the rate at which searchers become handlers is half of $2/t_a$ (i.e., $1/t_a$). Now, if the option to attack is rejected (with probability $1 - p$), then the searcher must find a food item for itself, this occurs at rate $v_f f$. Hence for any value of p, the mean time (τ) taken for a searcher that has just encountered a handler to begin handling a food item itself is given by

$$\tau = \frac{1 - p}{fv_f} + pt_a. \tag{10}$$

This can be rearranged to give

$$\tau = \left(\frac{1}{fv_f}\right) + p\left(\frac{t_a f v_f - 1}{fv_f}\right). \tag{11}$$

The optimal value of p is the one that minimizes τ. There is a simple straight-line relation between τ and p. If $t_a f v_f > 1$, then this straight line has a positive gradient (i.e., τ increases with p). Hence under these conditions the optimal value of p to play is zero. That is, under these conditions searchers should always turn down opportunities to contest for a food item. By similar arguments, when $t_a f v_f < 1$, then searchers should always take opportunities to fight for food. In the boundary case, where $t_a f v_f = 1$, then accepting or turning down the chance to contest both produce a food item in exactly the same average time, and so it does not matter which value of p an individual adopts; all will be equally effective.

We argue above that individuals should either never contest for food or contest for food at every opportunity. Which tactic works best depends on food availability and fight duration. If food is easy to find or aggressive encounters are of long duration, than all encounters should be avoided; if food is hard to find or encounters are short lived, then all opportunities for food stealing should be adopted. There is a critical point at which this switch occurs. Notice that the optimal value of p is independent of the forager density, P. This will be true whenever third parties have no influence on the outcome of a contest between two individuals.

Implications for the functional response

If the food density is high, such that $t_a f v_f > 1$, then the optimal strategy is $p = 0$. Substituting this into Equation 5 gives

$$\frac{H}{P} = \frac{C}{C + 1}. \tag{12}$$

Substituting this into Equation 9, and substituting for C gives the uptake rate (γ) as

$$\gamma = \frac{t_h f v_f}{t_h (t_h f v_f + 1)}. \tag{13}$$

This can be rearranged to give

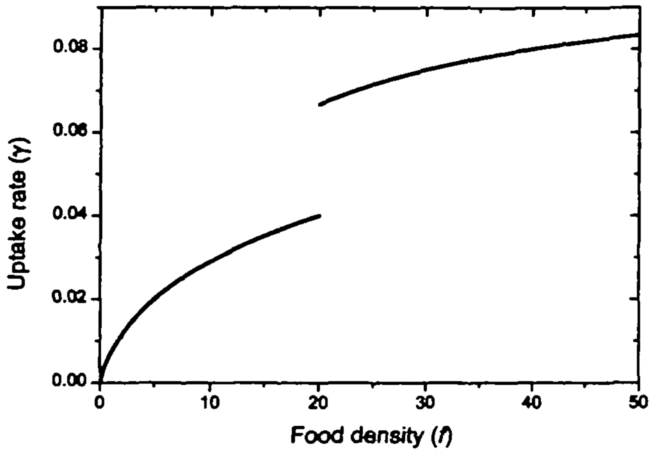

Figure 1
The food uptake rate (γ) as a function of food density (f). For f values < 20, $t_a f v_f < 1$, kleptoparasitism occurs at every opportunity, and uptake rate is calculated using Equations 8 and 9; for f values > 20, $t_a f v_f > 1$, kleptoparasitism never occurs, and uptake rate is calculated using Equations 9 and 12. Other parameter values are taken from Holmgren (1995): $P = 20$; $t_a = 5$, $t_h = 10$, $v_f = 0.01$, $v_H = 0.05$.

$$\gamma = \frac{\left(\frac{1}{t_h}\right)f}{f + \frac{1}{v_f t_h}}, \tag{14}$$

which is the classical type II saturating function first derived by Holling (1959). However, if the food density drops such that $t_a f v_f < 1$, then the optimal strategy is given by $p = 1$. In this case, Equation 8 shows that the uptake rate takes on a considerably less tidy form:

$$\gamma t_h = \frac{-(C+1) + \sqrt{(C+1)^2 + 4CD}}{2D}. \tag{15}$$

However, Ruxton and Moody (1997) argue that in the limit $(C+1)^2 \gg 4CD$ (which might occur when predator density, P, is very low), this expression is well approximated by

$$\gamma t_h = \frac{\left(\frac{1}{t_h}\right)f}{f + \frac{1}{v_f t_h} + \frac{t_a f v_H P}{t_h f v_f + 1}}. \tag{16}$$

This is simply Equation 14 with an extra term in the denominator. Hence, *we predict a dramatic step change in both behavior and uptake rate as food becomes more difficult to find* (or equivalently fights for food take less time). If food is plentiful, then no kleptoparasitism will take place. As the food density is gradually decreased, the uptake rate declines in a smooth fashion according to Equation 14. But as soon as the food supply drops below a critical value, kleptoparasitism will occur whenever the opportunity arises. This step change in behavior is accompanied by a sudden drop in uptake rate (as illustrated in Figure 1). After this sudden change occurs, further gradual reductions in the food supply will result in a smooth decline in uptake rate. This general prediction of a step change in behavior and uptake rate is independent of whether we make the simplifying assumption that $(C+1)^2 \gg 4CD$. Further, we can calculate the size of this step (in the general case, without making the simplifying assumption) The step is given by $\gamma_{p=0} - \gamma_{p=1}$; substituting using Equation 8 gives

$$t_h(\gamma_{p=0} - \gamma_{p=1}) = \frac{C}{C+1} - \left[\frac{\sqrt{(C+1)^2 + 4CD} - (C+1)}{2D}\right]. \tag{17}$$

If we form the parameter group

$$Y = \frac{2CD}{(C+1)^2}, \tag{18}$$

then it is easy to show that

$$\frac{t_h(\gamma_{p=0} - \gamma_{p=1})}{\gamma_{p=0}} = \frac{(1+Y) - \sqrt{1+2Y}}{Y} \approx \frac{Y}{2}. \tag{19}$$

The smaller Y, the better this approximation. Notice from the above that, although the Ruxton and Moody limit was useful for illustrative purposes to show that there is a step change in uptake rate, it is actually the limit where the step size is least impressive.

How should individuals optimize their searching?

In the last section, we allowed individuals to vary their likelihood of attempting kleptoparasitism whenever they encountered a handling individual. However, the rate at which they encountered handlers ($v_H H$) was fixed. We will now allow individuals to vary both v_H and p. It seems biologically plausible that both v_f and v_H should be bounded above, and further that v_H can only be increased at the expense of decreasing v_f (i.e., if individuals devote more energy to searching for handlers, then their ability to search for food will decrease). Mathematically, we express this by fixing two constants, α and β, such that

$$\frac{v_f}{\alpha} + \frac{v_H}{\beta} = 1. \tag{20}$$

An individual's strategy is now defined by the pair $\{v_f, p\}$; once this is chosen, v_H is obtained from Equation 20. After this choice has been made, we have a system exactly like that described earlier. We know that for such systems the optimal value of p to play is either 0 or 1, for any combination of v_f and v_H. Note that this is true for any population at equilibrium, even if some individuals choose different v_f values, since Equation 10 shows that the optimal p for an individual depends only on the v_f chosen by that individual (not on that of others). Hence we need only consider two strategies: where individuals always or never attempt kleptoparasitism when the opportunity arises.

We distinguish between two types of individual. Those that maximize their prey-finding ability by setting $v_f = \alpha$ (the highest possible value), we refer to as "insular" because using this strategy is equivalent to ignoring all other foragers. In this case, $v_H = 0$, handlers can never be detected, and hence the value of p chosen is irrelevant. Individuals that set $v_f < \alpha$ in order to give themselves some potential to detect opportunities for food stealing are termed "aggressive." We know that it is only sensible to play this strategy in conjunction with setting $p = 1$. Hence we assume that all aggressive individuals play $p = 1$, and so potentially optimal strategies reduce to a single value, that of v_f that maximizes uptake rate.

If we consider a fixed population of density P and allow individuals to adopt either strategy, then we can ask the following questions: Under what circumstances should all individuals play $\{\alpha\}$? Under what circumstances should all individuals play $\{v_f < \alpha\}$; and what v_f should they play? We confine the bulk of our mathematics to the appendixes and present the main results here. Essentially, we search for evolutionarily stable strategies (ESSs). A strategy is an ESS if, when every individual plays it, then no individual can increase its pay-off by switching to any other strategy (see Appendix A for a more formal definition).

We already know that if $t_a f u_f > 1$, then individuals do best by declining any chances they have to kleptoparasitize. Thus, when

$$t_a f\alpha > 1, \tag{21}$$

"insular" $\{\alpha\}$ is an ESS, and an individual will always do worse by playing any other $\{u_f < \alpha\}$. We show in Appendix C that it is the only ESS.

We now turn our attention to the case where Equation 21 does not hold. How should handlers divide their energies between searching for food and other handlers? Clearly this depends on the relative ease with which the two can be found (and, once found, captured). In the extreme case where handlers are scarce or hard to find, it is still optimal for foragers to devote all their energies to food finding and play $\{\alpha\}$ even though Equation 21 does not hold. Appendix B demonstrates that $\{\alpha\}$ is an ESS when Equation 21 does not hold, providing

$$P < \frac{2(1 + t_h f\alpha)}{\beta t_h(1 - t_a f\alpha)}. \tag{22}$$

Let us examine this inequality more carefully. Clearly, this equality is satisfied if predator density (P) is very small. This makes intuitive sense; if there are few other predators about, then there is little point in investing energy in searching for them, and hence the optimal strategy will be $\{\alpha\}$. Similarly, the inequality can also always be satisfied by making β low enough: β is the maximal value that v_H can take, and so it is a measure of how likelihood of encountering handler (for given search effort). There is less point in investing energy searching for conspecifics, if these are hard to find. It is clear that increasing aggressive interaction time (t_a) makes it more likely that Equation 22 will be satisfied. This occurs because increasing t_a increases the fraction of individuals in the aggressive interaction subpopulation and hence reduces the number of handlers an individual would be able to interact with (as we do not allow individuals to be involved in more than one contest simultaneously).

Increasing either f or α makes satisfying Equation 22 more likely because they both make finding food easier. If the handling time is very short ($t_h \to 0$) then Equation 22 will be satisfied. In this limit, the fraction of individuals handling at any one time is vanishingly small. Hence, there is no point in looking for handlers. There are two situations to consider as we allow t_h to increase. First,

$$2f\alpha \geq \beta P(1 - t_a f\alpha). \tag{23}$$

in this case Equation 22 is satisfied for all values of t_h. In this case, the total population of predators is so small (or they are so hard to detect), that no matter how many of them are handling, it is not worth investing effort in looking for handlers. Second,

$$2f\alpha < \beta P(1 - t_a f\alpha). \tag{24}$$

Now, if t_h is bigger than a critical value; i.e.,

$$t_h > \frac{2}{\beta P(1 - t_a f\alpha) - 2f\alpha}, \tag{25}$$

then Equation 22 is not satisfied. When this occurs, the population size is sufficiently big that if a large t_h causes a large fraction of individuals to be handling, then it is optimal for searchers to make some investment in looking for them.

However, when neither Equations 21 nor 22 hold, then $\{\alpha\}$ is no longer the best strategy. Now the optimal strategy (i.e. the unique ESS) for an individual does involve kleptoparasitism. Appendix C shows that this strategy is $u_f = U$, given by

$$U = \frac{\alpha}{1 + F}$$

$$F = \left[\frac{1 - t_a f\alpha}{2(1 + t_a f\alpha)}\right][\beta P t_h(1 - t_a f\alpha) - 2(1 + t_a f\alpha)]. \tag{26}$$

It is easy from this expression to see how varying each of the parameters affects the ESS value of U. Increasing any of β, P, or t_h causes an increase in F and hence a decrease in U. This makes biological sense, because increasing any of these parameters makes handlers easier to find and so will increase the chance that effort devoted to searching for them will be successful. Increasing f causes an increase in U because now effort devoted to searching for undiscovered prey has an increased likelihood of success. Increasing t_a also increases U; this makes sense too, since increasing t_a means that attacking handlers is a less profitable option in terms of gain rate, so switching effort from looking for handlers to looking for food is an effective strategy. Increasing α increases F such that U increases faster than α, and so U/α increases. Again, this can be interpreted in terms of the underlying biology; as α increases, food finding becomes easier, and individuals should concentrate more on finding food at the expense of looking for handlers (which has not become any easier).

We just described how the ESS value of u_f changes with changes in parameter values. We can find the effect of these changes in the ESS value of v_H by using

$$v_H = \beta\left(1 - \frac{U}{\alpha}\right). \tag{27}$$

Decreasing f, P, or t_h (or increasing t_a) all affect this equation only by increasing U, hence they all result in the optimal value of v_H decreasing. Increasing α increases U/α and so also decreases the ESS value of v_H. Finally, increasing β decreases U and so also leads to an increase in the ESS value of v_H.

DISCUSSION

At first glance, it may seem that kleptoparasitism should never be an optimal strategy in our model. Kleptoparasitism costs time which could otherwise be devoted to searching for and handling food items. Because (in our simplified model) all individuals are identical, this inevitably leads to a reduction in individual uptake rates. How can kleptoparasitism ever be a sensible strategy in our model? We claim that under some circumstances kleptoparasitism will be evolutionarily stable. Although a group of individuals that all avoid kleptoparasitism can maximize their uptake rates, this may not always be evolutionarily stable. Under some circumstances, if one individual switched to kleptoparasitism, then this individual would do better than the rest. Although others will suffer, this individual will do better. Selection works strongest at an individual level, and hence we would expect kleptoparasitism to flourish as a strategy and become more common in the group. It is for this reason that kleptoparasitism may occur in nature even in the absence of strong differences between individuals.

We predict in our model that under almost all conditions individuals should either take every opportunity to kleptoparasitize or take none at all. The consequences of this is that as a given ecological variable is changed, there will be a step change both in behavior and in uptake rate. For example, if food density is high, then it is optimal not to kleptoparasitize, so we predict no aggressive interactions between individuals. As food density is reduced, uptake rate will be reduced, but still we will see no aggressive interactions. However, as we reduce food density further, at some critical value there is a sudden change in the system. Now kleptoparasitism opportunites are always taken, aggressive intereactions become commonplace, and food uptake rates drop sharply. Further reductions in food availability will cause a further decline in uptake rate, but no further sudden changes in uptake or behavior are predicted. A similar abrupt change in behavior was predicted by classical prey-choice models (see Lendrem, 1986a, for a discussion), where a small increase in the profitability of a given prey species could cause the predator to switch from always rejecting discovered individuals of this species to always consuming them. Would we expect to see this sudden extreme change in behavior in real systems? This is quite possible, but we should add some caveats. We would not expect the change in behavior to be absolutely complete and sudden. Individuals will not know the exact ecological conditions affecting their foraging at any exact moment in time. Rather they must estimate these based on their recent experience; these estimates will not be perfectly accurate. Hence we would predict that the sharp change predicted in our model would neccesarily be a little blurred in reality. Our second caveat is that in our model all potential opportunities to kleptoparasitize are intrinsically identical because all individuals are the same. If this were not true, then selective kleptoparasitism would become a more attractive strategy. Hence, we might find that individuals do not switch from turning down all opportunities to taking all of them. Rather they would gradually increase the range of opportunies they accept, first accepting those that have lowest costs and/or greatest potential gains, and gradually accepting less and less attractive opportunities, until finally they take all options. Thus, again, this would suggest a rounding off of our predicted sharp step-change. This last hypothesis is open to experimental testing because we would predict that when food becomes less available and kleptoparasitism begins to occur, it should start with food stealing in situations were the food item is particularly valuable (e.g., because its of large size) or is particularly easy to get (e.g., because it is being handled by a competitively inferior individual).

Another prediction of our model is that kleptoparasitism may not be observed under circumstances where it may initially appear to be an effective strategy because of a trade-off with other activities such as independent foraging. As one would expect, our model predicts that individuals will turn down opportunities to kleptoparasitize when the time cost of the interaction could better be used elsewhere. Perhaps less expectedly, it also predicts that under some circumstances kleptoparasitism will not be seen even when individual interactions would be a good time investment. These circumstances occur when kleptoparasitism opportunities are rare and when detection of these opportunities can only be obtained at a cost (in our model this cost is reduced food detection rate). Under these conditions, while individual acts of kleptoparasitism would be efficient over a short time scale, over a longer time scale the costs of being able to detect these (rare) kleptoparasitic opportunities are too high. Individuals do better by forgoing these occasional kleptoparasitic opportunities in order to devote all their resources to food searching. This general observation should be robust to changes in model formulation and should be open to experimental testing in a species where detecting food and kleptoparasitic opportunities require quite separate and distinct behaviors.

Notice that our model does not predict that individuals should ever give up searching for food completely and devote their attentions fully to stealing. A situation where all individuals gave up food searching would clearly be disastrous; no food would ever be found and so uptake rates would be zero. However, this prediction might change if there were differences between some individuals. Under these circumstances it might pay some individuals to devote themselves purely to kleptoparasitism. However, in nature, although kleptoparasitism is a major source of diet for some species (e.g., frigate birds, skuas), these species do not provision solely by kleptoparasitism. It may be that even when kleptoparasitism opportunities are superabundant, other food sources are still detected because the cost of this detection is very low. For example, although the skuas are focused on other birds as a source of food stealing opportunity, they also watch the landscape (to find their nests or to avoid crashing), and in this way they also discover other food sources (e.g., carrion or unprotected nestlings or eggs) as a by-product.

Although our model is a simple first attempt at capturing the costs and benefits of kleptoparasitic strategies, it has produced a number of interesting (and testable) predictions, as discussed above. Further extensions to the model would be interesting and biologically realistic. Our assumption that all individuals are intrinsically identical will often be inappropriate in many natural situations. Individuals could differ in their ability to find food, in their energetic requirements, and in their ability to steal food from others. In this case the strategy a bird should adopt will depend on its own abilities and requirements, but also on those of others within the population. Another intrinsic assumption of our model is that the population is well mixed and that all different pairs of individuals are equally likely to meet. Again, this may be a poor representation of some natural situations. To consider the group of wading birds one last time, this aggregation will not generally be well mixed, with birds often spending prolonged periods of time in a generally fixed position within the group. Clearly, the distance between two birds will affect the probability that kleptoparasitic opportunities will be observed. Also, the costs of attempting kleptoparasitism increase with the distance that must be traveled to reach the potential victim. Hence, a bird's strategy may now include its position within the group so as to maximize its ability to kleptoparasitize others and/or minimize its own chance of losing food. Such extensions to the model, allied to carefully controlled experimentation, would greatly increase our understanding of the evolution and operation of this ecologically interesting and important behavior.

APPENDIX A

What is an ESS?

Define the pay-off to a player playing strategy S in a population of players playing strategies $T_1, \ldots, T_n$ in proportions $\alpha_1, \ldots, \alpha_n$, respectively ($\Sigma\ \alpha_i = 1$) as

$$E[S;\ T_1(\alpha_1), \ldots, T_n(\alpha_n)].$$

Then S is evolutionarily stable (ES) against T if and only if

$$E[S;\ S(1-\epsilon),\ T(\epsilon)] > E[T;\ S(1-\epsilon),\ T(\epsilon)]$$

for all sufficiently small ϵ.

S is an evolutionarily stable strategy (ESS) if S is ES against all $T \neq S$. (See Maynard Smith, 1982, for further details.)

APPENDIX B

Mathematics: when is α an ESS?

First we set out the general equations for a mixed population playing two different strategies for ν_f : a large population (of density P_1) play $\{\nu_f\}$ and another much smaller population (of density P_2) play $\{\eta_f\}$. We intend to determine when population 1 gains a higher intake rate than population 2 playing any possible η_f. Both populations are split into searchers, handlers, and participants in aggressive interactions; i.e.,

$$S_1 + H_1 + A_1 = P_1 \tag{A1}$$

$$S_2 + H_2 + A_2 = P_2 \tag{A2}$$

$$P_1 + P_2 = P \tag{A3}$$

We can write equations for the rates of change in each subpopulation. Under the condition that $P_1 \gg P_2$, these are well approximated by a simplified form.

$$\begin{aligned}\frac{dH_1}{dt} &= -\frac{H_1}{t_h} - S_1H_1v_H - S_2H_1\eta_H + S_1v_ff + \frac{A_1}{t_a}\\ &\approx -\frac{H_1}{t_h} - S_1H_1v_H + S_1v_ff + \frac{A_1}{t_a}\end{aligned} \tag{A4}$$

$$\begin{aligned}\frac{dS_1}{dt} &= -\frac{H_1}{t_h} - S_1H_2v_H - S_1H_2v_H - S_1v_ff + \frac{A_1}{t_a}\\ &\approx \frac{H_1}{t_h} - S_1H_1v_H - S_1v_ff + \frac{A_1}{t_a}\end{aligned} \tag{A5}$$

$$\begin{aligned}\frac{dA_1}{dt} &= 2S_1H_1v_H + S_2H_1\eta_H + S_1H_2v_H - \frac{2A_1}{t_a}\\ &\approx 2S_1H_1v_H - \frac{2A_1}{t_a}\end{aligned} \tag{A6}$$

$$\begin{aligned}\frac{dH_2}{dt} &= -\frac{H_2}{t_h} - S_1H_2v_H - S_2H_2\eta_H + S_2\eta_ff + \frac{A_2}{t_a}\\ &\approx -\frac{H_2}{t_h} - S_1H_2v_H + S_2\eta_ff + \frac{A_2}{t_a}\end{aligned} \tag{A7}$$

$$\begin{aligned}\frac{dS_2}{dt} &= -\frac{H_2}{t_h} - S_2H_1\eta_H - S_2H_2\eta_H - S_2\eta_ff + \frac{A_2}{t_a}\\ &\approx \frac{H_2}{t_h} - S_2H_1\eta_H - S_2\eta_ff + \frac{A_2}{t_a}\end{aligned} \tag{A8}$$

$$\begin{aligned}\frac{dA_2}{dt} &= 2S_2H_2\eta_H + S_2H_1\eta_H + S_1H_2v_H - \frac{2A_2}{t_a}\\ &\approx S_2H_1\eta_H + S_1H_2v_H - \frac{2A_2}{t_a}\end{aligned} \tag{A9}$$

As before, Equations A4–A6 and A7–A9 only constitute two independent equations each. Setting Equations A4–A9 equal to zero for the populations in equilibrium, Equations A4–A6 are equivalent to equations 2-4 in the text with $p = 1$, and thus

$$\frac{H_1}{P_1} \approx \frac{H_1}{P} = \begin{cases}\dfrac{\sqrt{(C+1)^2 + 4CD} - (C+1)}{2D}, & D > 0\\[2ex] \dfrac{C}{C+1}, & D = 0\end{cases} \tag{A10}$$

If $v_f = \alpha$, then $v_H = 0$; i.e., $C = t_hf\alpha$, $D = 0$, which implies that

$$\frac{H_1}{P} \approx \frac{C}{1 + C}. \tag{A11}$$

Using Equations A2, A7, and A9 we can show that

$$\frac{H_2}{P_2} = \frac{\eta_ff + \dfrac{\eta_HH_1}{2}}{\dfrac{1}{t_h} + \dfrac{t_a\eta_HH_1}{2t_h} + \dfrac{\eta_HH_1}{2} + \eta_ff}. \tag{A12}$$

The strategy that performs better is the one with the highest proportion of handlers; i.e., α is better that η_f if

$$\frac{H_1}{P_1} > \frac{H_2}{P_2}. \tag{A13}$$

Combining A11, A12, and A13, we obtain

$$P(1 - t_af\alpha) < \frac{2(1 + C)}{\beta t_h}, \tag{A14}$$

which is independent of η_f. This means that if α cannot be invaded (outcompeted) by a given η_f, then it cannot be invaded by any and is then an ESS (equivalently, if it can be invaded by one, then it can be invaded by any such strategy). If $t_af\alpha > 1$, then α is always an ESS (as explained in the main text). Otherwise, if $t_af\alpha < 1$, then α is only an ESS if

$$P < \frac{2(1 + t_hf\alpha)}{\beta t_h(1 - t_af\alpha)}. \tag{A15}$$

APPENDIX C

When is $U < \alpha$ an ESS?

We again use Equations A1–A9 from Appendix B. Because $U < \alpha$, we obtain the solution in Equation A10 for H_1/P_1. The value of H_2/P_2 must be found. Using Equations A2, A7, and A9, we can show that

$$\frac{H_2}{P_2} = \frac{\dfrac{H_1t_hD'}{P_1} + 2t_aC'}{2t_a(1 + C') + D't_h + \dfrac{H_1\left(\dfrac{C't_aD}{C} + \dfrac{Dt_h}{C} + t_aD' - \dfrac{D't_h}{C}\right)}{P_1}}, \tag{A16}$$

where C and D are as before and

$$C' = t_hf\eta_f,$$

$$D' = t_aP\eta_H.$$

For U not to be invaded by η_f, we again need

$$\frac{H_1}{P_1} > \frac{H_2}{P_2}. \tag{A17}$$

Combining Equations A10, A16, and A17, we obtain

$$(\eta_f - U)\left\{2t_af(\alpha - U) + \left(\frac{A_1}{P}\right)[(t_af\alpha - 1)(t_hfU + 1) + 2t_af(U - \alpha)]\right\} \le 0. \tag{A18}$$

For an ESS, we require the above inequality to hold for all $\eta_f \neq U$ (unless U is equal to 0 or α), but this can only happen if

$$2t_af(\alpha - U) + \frac{A_1}{P}[(t_af\alpha - 1)(t_hfU + 1) + 2t_af(U - \alpha)] = 0. \tag{A19}$$

When a small group of η_f players is introduced, on average the population value of U changes from U to $U(1-\epsilon) + \epsilon\eta_f$. Playing against this strategy mixture is not the same as playing against a population all playing $U(1 - \epsilon) + \epsilon\eta_f$. More of the η_f players will be fighting and fewer searching (at ESS the proportions handling are roughly the same), so the effective weighting of the η_f players will be less. It is only in searching mode that the strategy differences are apparent; but still for

$\eta_f > U$, the mixture value $[U(1-\epsilon)+\epsilon\eta_f\}$ is slightly greater than U, and for $\eta_f < U$ it is slightly less. So the conditions for an ESS reduces to Equation A19 and

$$\frac{d}{dU}\left\{2t_af(\alpha - U) + \left(\frac{A_1}{P}\right)\right. \\ \left. \times\ [(t_af\alpha - 1)(1 + t_hfU) + 2t_af(U-\alpha)]\right\} < 0. \quad \text{(A20)}$$

Using Equations A4 and A5, it is clear that

$$S_1 = \frac{H_1}{C} \quad \text{(A21)}$$

and

$$\frac{A_1}{P} = 1 - \left(\frac{H_1}{P}\right)\left(\frac{C+1}{C}\right), \quad \text{(A22)}$$

which together with (Equation 5) implies

$$\left(\frac{H_1}{P}\right)^2\left(\frac{D}{C}\right) = \frac{A_1}{P}. \quad \text{(A23)}$$

Substituting this into Equation A19 gives

$$2t_af(\alpha - U)\left(\frac{C+1}{C}\right)\left(\frac{H_1}{P}\right) - (1 - t_af\alpha)(C+1)\left(\frac{A_1}{P}\right) = 0. \quad \text{(A24)}$$

(Note that is $t_af\alpha > 1$, then Equation A24 has no solutions $U < \alpha$, and so $\{\alpha\}$ is a unique ESS) Simple rearrangement of this gives

$$\left(\frac{C+1}{C}\right)\left(\frac{H_1}{P}\right)\left(\frac{t_a(\alpha - U)}{\alpha}\right)\left\{2f\alpha - \left[\beta P(1 - t_af\alpha)\frac{H_1}{P}\right]\right\} = 0. \quad \text{(A25)}$$

Substituting for the handling population steady state gives

$$\frac{2f\alpha}{(1 - t_af\alpha)\beta P} - \frac{\sqrt{(1+C)^2 + 4CD} - (1+C)}{2D} = 0. \quad \text{(A26)}$$

This can be written in a more compact form:

$$DE^2 + E - C(1 - E) = 0, \qquad E = \frac{2f\alpha}{(1 - t_af\alpha)\beta P}. \quad \text{(A27)}$$

Substituting in terms of the original parameters gives

$$g(U) = 2\alpha(1 + t_af\alpha) - U\{2(1 + t_af\alpha) + (1 - t_af\alpha) \\ \times [\beta Pt_h(1 - t_af\alpha) - 2(1 + t_af\alpha)]\} \\ = 0 \quad \text{(A28)}$$

as the condition for U to be an ESS. Note that because $t_af\alpha < 1$ and Equation 22 does not hold, the derivative of this expression is negative. It is clear that this expression is just a positive value multiplied by the expression in Equation A19 and thus any U that solves it is an ESS. The conditions for U to be an ESS are thus $g(U) = 0$ and $g'(U) < 0$. This is a similar formulation to that of Broom et al. (manuscript submitted). Rearranging this expression gives the ESS as the unique solution to

$$U = \frac{\alpha}{1 + F},$$

$$F = \left[\frac{1 - t_af\alpha}{2(1 + t_af\alpha)}\right][\beta Pt_h(1 - t_af\alpha) - 2(1 + t_af\alpha)]. \quad \text{(A29)}$$

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