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Rapid convergence to an equilibrium state in kleptoparasitic populations

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Abstract. Previous papers have modelled the behaviour of populations which are subject to kleptoparasitism, and found those ecological situations in which kleptoparasitism should occur. Individuals were considered to be in one of several states, and an equilibrium distribution for the population was found. It was then assumed, for analytical purposes but without proof, that the population was actually in that equilibrium. In this paper, we show that the equilibrium is a stable one, and that it is reached in a relatively short time for all reasonable values of the ecological parameters. Thus, a population may be expected to spend most of the time in equilibrium, and this assumption of these previous works is justified.

1. Introduction

"Kleptoparasitism" may be defined as the stealing by one animal of food that has been caught by another (Rothschild and Clay 1952). For the kleptoparasite, therefore, it provides an alternative source of food, in place of, or in addition to, catching its own prey. In particular, aggressive kleptoparasitism is defined (Giraldeau and Caraco 2000) as the situation in which an attacker uses force to gain the food for its own use e.g. an eagle supplanting other eagles from the carcass of a salmon (Hansen 1986).

Observations of kleptoparasitism have been reported amongst many different animal populations, including insects (Jeanne 1972), fish (Grimm and Klinge 1996), mammals (Kruuk 1972), and, most commonly, birds, as we see below. The behaviour may be inter-specific (members of one species stealing from members of another) or intra-specific (members of a species stealing from each other).

Observations of birds acting as kleptoparasites are amongst the most detailed, and an extensive review (Brockmann and Barnard 1979) gives a list of observations of kleptoparasitism by birds. It is noted there that this behaviour is much more

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common in some orders of birds than others, and it is especially prevalent amongst sea-birds.

More recent observations include the sighting of gulls attacking each other for food (Steele and Hockey 1995), oystercatchers feeding on cockles (Triplet et al 1999) and skuas attacking albatrosses and giant-petrels (Spear et al 1999).

1.1. Models

Various authors have attempted to construct mathematical models to describe the phenomenon of kleptoparasitism. This is done in order to understand why it happens, and what advantage it gives to the animal. In particular, we can ask why it occurs in some situations, and among some species, and not in others - what are the conditions which determine whether or not it is an advantageous strategy for an animal to adopt? On initial consideration, it is a surprising form of behaviour, because it seems to disadvantage the population - time is wasted fighting over food which could be spent finding more new food. However, when we consider individuals, it is seen that it can be more profitable, in terms of food intake rate, to capture food from another individual, rather than search for it directly. The models attempt to explain under what environmental conditions kleptoparasitism is more likely to occur.

The models made so far have been of various kinds:

1. Holmgren (1995) constructed a simulation model for intraspecific kleptoparasitism, in which the animals were modelled as particles, moving at constant speed in initially random directions. They behaved in a deterministic manner, fighting whenever one searching for food met another one already handling. The animals were distinct, thus allowing the simulation of a group in which the individuals differ in their dominance over each other.
2. Ruxton and Moody (1997) took a special case of Holmgren (1995), in which all the animals were identical, to develop a model, in which the proportions of searchers, handlers and fighters within the population were modelled by differential equations. They found analytical solutions for the equilibrium state of the population.
3. Broom and Ruxton (1998) then extended the Ruxton and Moody (1997) model in various ways. In particular, they allowed for the possibility that a searcher, finding a handling animal, may or may not choose to attack it, and they found in what circumstances an attack would be made.

1.2. Equilibrium and stability

The models above indicate that a population participating in kleptoparasitism will have an equilibrium state, in which the numbers of searchers, handlers and those fighting over food are constant. For the purpose of analysis, it had then been assumed that the population was actually in this equilibrium state.

The aim of this paper is to show that this equilibrium state is stable, and that the population rapidly converges to the equilibrium. This clearly has important ecological consequences. If we think, for example, of a population of birds at the beginning of the day, when all are initially searching for food, then it is of interest to know whether the equilibrium will have been reached before the end of the day - do the population spend most of the day in the equilibrium state, or are they still progressing towards it by nightfall? If the time period for convergence to equilibrium is of the order of one day, then equilibrium will never be achieved, because at the end of the day the birds will return to their nests, and start again the next day from their initial state of all searching, and none handling or fighting. We aim to find out whether it does indeed take a day or more to reach equilibrium, or whether equilibrium is reached considerably more quickly; if the time taken is short compared to one day, then the birds will spend most of the day in the equilibrium population proportions.

(We may note here that equilibrium may be approached exponentially, and thus it is never completely attained; we are interested in the practical situation where the vast majority of the population has reached the equilibrium state. If the approach to equilibrium is via an exact exponential decay with a time constant T, then after a low multiple of T the deviation from the equilibrium values will be very small. Thus, for example, after time $Tln100 \approx 4.6T$ the difference between the starting value and the equilibrium value will have decreased to $(1/e)^{ln100} = 1\%$ of its initial level.)

Clearly, if conclusions about animal behaviour are based on treating the population as if it is in equilibrium, then it is important to determine whether this is reasonable, or whether the population spends all of its time far from equilibrium. (It should be noted that this statement is equally true of any biological system, and that methods used here may have more general application.)

2. Stability and convergence to equilibrium

2.1. Convergence to equilibrium in the absence of kleptoparasitism

In this situation, which is a special case of the Ruxton and Moody (1997) model, without kleptoparasitism, the population density P (a constant) is comprised of searchers, density S, foraging for their own food, and handlers, density H. The density of food is f, also assumed to be constant. It is assumed that searchers randomly explore a certain volume per unit time, with a rate ν_f of finding any prey that is within this volume, thus finding food at a total rate of $\nu_f f S$; this gives the rate at which searchers become handlers. It is also assumed that the length of time required to handle food follows an exponential distribution, with mean time t_h, so that the rate at which handlers again become searchers is H/t_h. Thus, the equation for the net rate at which handlers become searchers is

$$dS/dt = H/t_h - \nu_f f S.$$

However, since $H + S = P$, and writing $C = \nu_f f t_h$,we have

$$dS/dt = P/t_h - (C + 1)S/t_h,$$

which is a linear first-order differential equation, with solution

$$\begin{aligned} S &= P/(C + 1) + PCe^{-(C+1)t/t_h}/(C + 1), \\ H &= PC/(C + 1) - PCe^{-(C+1)t/t_h}/(C + 1), \end{aligned}$$

using $S(0) = P$.

The number of searchers and handlers approach the equilibrium values $S^* = P/(C+1)$, $H^* = PC/(C+1)$ via exponential decay, with a time constant of $t_h/(C+1)$. This is clearly lower than t_h, the handling time for prey, and so we see that equilibrium is reached very quickly. This result is perhaps a surprising one, as it does not appear to involve the rate of finding prey, $\nu_f f$. The reason is that when $C(= \nu_f f t_h)$ is small, then $H^* = PC/(C+1) \approx PC$ is also small, so that little time is required to reach H^* starting from $H = 0$. In fact, the time required for H to get close to equilibrium is of the order of $PC/(S\nu_f f) \simeq P\nu_f f t_h/(P\nu_f f) = t_h$, as given by the formula $t_h/(C+1)$, when C is very small.

The fact that our explicit solution for H and S shows exponential decay to the steady state also makes it clear that this equilibrium is a stable one - any disturbance from it would similarly decay exponentially back to the equilibrium.

We comment at this point that the equilibrium solution obtained here is an example of the Type II functional response identified by Holling: the uptake rate

$$\frac{H}{t_h P} = \frac{C}{t_h(C+1)} = \frac{(1/t_h)f}{f + 1/\nu_f t_h}.$$

2.2. *The Ruxton-Moody model*

In this model (Ruxton and Moody 1997), as modified by Broom and Ruxton (1998), the total population, with density P, is partitioned into three sets: searchers, handlers and those fighting over food, with densities S, H, and A respectively. In addition to foraging for food, and handling it, (as in the previous section), searchers also explore a volume per unit time, looking for other handlers and having a certain rate ν_h of finding them. They thus find them at a rate $\nu_h HS$. We will assume here that all such encounters lead to a contest for the food item, and that the lengths of these contests have an exponential distribution with mean $t_a/2$. At the end of the contest, losers become searchers and winners become handlers. The length of time required to handle food is also assumed to come from an exponential distribution, with mean time t_h.

These rates of change between the groups can then be expressed as the differential equations:

$$\begin{aligned}
dS/dt &= H/t_h + A/t_a - \nu_f f S - \nu_h HS \\
dH/dt &= -H/t_h + A/t_a + \nu_f f S - \nu_h HS \\
dA/dt &= -2A/t_a + 2\nu_h HS
\end{aligned}$$

together with

$$S + H + A = P.$$

The equilibrium values S^*, H^* and A^* of S, H and A can be found by setting the time derivatives equal to zero. It is found that

$$\begin{aligned}
S^* &= \frac{-(C+1) + \sqrt{(C+1)^2 + 4Ct_a P\nu_h}}{2Ct_a\nu_h} \\
H^* &= CS^*,
\end{aligned}$$

and then $A^* = P - S^* - H^*$.

2.2.1. *Stability of equilibrium when kleptoparasitism takes place*

To see whether this equilibrium is stable, we consider a small perturbation of the population from the equilibrium, so that

$$\begin{aligned} H &= H^* + \epsilon h, \\ S &= S^* + \epsilon s, \\ A &= A^* - \epsilon h - \epsilon s. \end{aligned}$$

Putting these expressions for H, S and A into the equations, and neglecting terms in ϵ^2, we get the set of coupled linear equations

$$\begin{aligned} ds/dt &= -(C/t_h + 1/t_a + \nu_h H^*)s + (1/t_h - 1/t_a - \nu_h S^*)h \\ dh/dt &= (C/t_h - 1/t_a - \nu_h H^*)s - (1/t_h + 1/t_a + \nu_h S^*)h \end{aligned}$$

which we rewrite, for clarity, as

$$\begin{aligned} ds/dt &= as + bh \\ dh/dt &= cs + dh \end{aligned}$$

These are in the standard form for a set of homogenous linear differential equations, and the solutions for h and s will be of the form $Ae^{m_1 t} + Be^{m_2 t}$, where m_1 and m_2 are the two solutions of the auxiliary equation

$$m^2 - (a+d)m + ad - bc = 0.$$

The roots are given by

$$m = (a + d \pm \sqrt{(a+d)^2 - 4(ad - bc)})/2 = (a + d \pm \sqrt{(a-d)^2 + 4bc})/2$$

We can see immediately that

$$ad - bc = 2(C+1)/(t_a t_h) + 4C\nu_h S^*/t_h$$

is positive. This tells us that the discriminant in the solution of the quadratic equation is less than $(a+d)^2$, and so $\sqrt{(a+d)^2 - 4(ad-bc)} < |a+d|$. In addition, we see that

$$a + d = -(C+1)/t_h - 2/t_a - (C+1)\nu_h S^*$$

is negative. Re-writing the discriminant as

$$((C+1)(1/t_h - \nu_h S^*) - 2/t_a)^2 + 4(C-1)^2 \nu_h S^*/t_h$$

clearly shows that it is positive and thus both values of m are real and negative. The solutions for h and s can therefore both be written as $Ae^{-\alpha t} + Be^{-\beta t}$ with $\alpha, \beta > 0$. This shows that both h and s decay exponentially to zero; thus, any small disturbances of the population when it is in its equilibrium state decay to zero, and so the equilibrium state is stable.

2.2.2. Convergence to equilibrium

The non-linearity of the system of differential equations makes a complete analytical solution very difficult (perhaps even impossible) to find. Thus, we have to use indirect means to study the convergence of the system, and, indeed, to show that it does converge.

The pattern of the coefficients of S and H in the original equations suggest that it may be helpful to consider the combinations $S + H$ and $S - H$. We make this transformation, and also take the opportunity to change the origin, by defining

$$x = (S + H - S^* - H^*)/P,$$

and

$$y = (S - H - S^* + H^*)/P.$$

We then get

$$dx/dt = -(2/t_a + \nu_h S^*(C + 1))x - \nu_h S^*(C - 1)y - \nu_h P(x^2 - y^2)/2$$

and

$$dy/dt = -(C - 1)x/t_h - (C + 1)y/t_h$$

and note that

$$x(0) = (P - S^* - H^*)/P = A^*/P$$

and

$$y(0) = (P - S^* + H^*)/P = 1 + (C - 1)S^*/P.$$

The equilibrium values of x and y are each 0, by construction.

The fact that H, S, H^* and S^* all lie in the interval $[0, P]$ enables us to put limits on x, y and combinations of x and y. Thus, we have

$$-1 \leq x \leq 1$$

and

$$-2 \leq y \leq 2.$$

We can, additionally, form tighter bounds by reverting to the original variables. If we consider $x + y = 2(S - S^*)/P$, we find

$$-2S^*/P \leq x + y \leq 2S/P \leq 2,$$

and also since $x - y = 2(H - H^*)/P$, then

$$-2H^*/P \leq x - y \leq 2H/P \leq 2.$$

We illustrate these inequalities in Figure 1, where the valid region is the polygon ABDEI.

The individual equations for dx/dt and dy/dt did not prove amenable to analysis, other than by numerical solution, which we consider later. However, by considering $G = x^2 + \gamma y^2$, $(\gamma > 0)$, progress can be made. G is chosen for analytical convenience, enabling us to eventually put bounds on the behaviour of x and y, and thus H and S. Clearly, G is always positive, and, in equilibrium, when

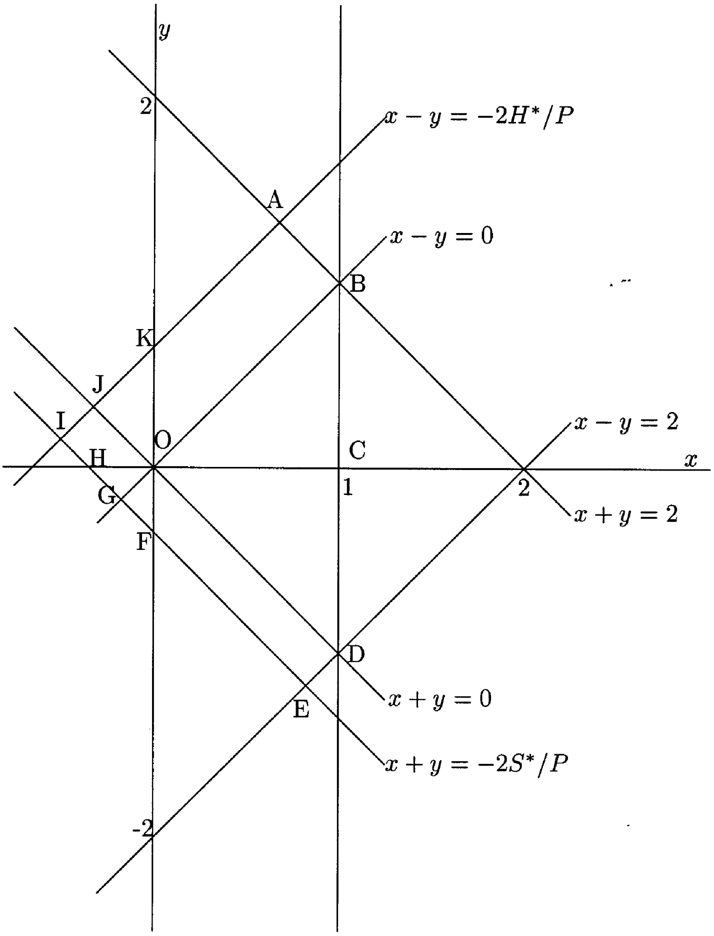

Fig. 1. Convergence regions for the function G in the plane with transformed variables $x = (S + H - S^* - H^*)/P, y = (S - H - S^* + H^*)/P$, where H^* and S^* are the equilibrium handling and searching densities; thus the equilibrium in this figure is at O.

$x = y = 0, G = 0$. We aim to analyse dG/dt, and then, by estimating the rate of convergence of G, to estimate how quickly the system approaches equilibrium.

We find

$$\begin{aligned}dG/dt &= 2x dx/dt + 2\gamma y dy/dt\\ &= -4x^2/t_a - 2C(x^2\nu_h S^* + xy\nu_h S^* + \gamma xy/t_h + \gamma y^2/t_h)\\ &\quad -2(x^2\nu_h S^* - xy\nu_h S^* - \gamma xy/t_h + \gamma y^2/t_h) - \nu_h Px(x^2 - y^2)\end{aligned}$$

Choosing $\gamma = \nu_h S^* t_h$ gives

$$dG/dt = -4x^2/t_a - 2C\nu_h S^*(x + y)^2 - 2\nu_h S^*(x - y)^2 - \nu_h Px(x^2 - y^2).$$

In the region OKABC, consider moving parallel to AB, such that $x + y = \lambda$, with $0 \leq \lambda \leq 2$, and note that in this region $x - y \geq -2CS^*/P$. This gives

$$\begin{aligned} dG/dt &\leq -4x^2/t_a - 2C\nu_h S^*\lambda^2 - 2\nu_h S^*(x-y)^2 + \nu_h x\lambda 2CS^* \\ &= -4x^2/t_a - 2\nu_h S^*(x-y)^2 - 2C\nu_h S^*\lambda y \\ &= -2CG/t_h - 2\nu_h S^*(x-y)^2 - 2CS^*\nu_h xy + (2C/t_h - 4/t_a)x^2. \end{aligned}$$

In this region, $xy \geq 0$. Also, as will be seen in 2.2.3, in order for kleptoparasitism to take place, $Ct_a < t_h$, so that $2C/t_h < 2/t_a < 4/t_a$, and so $2C/t_h - 4/t_a < 0$. Therefore $dG/dt \leq -2CG/t_h$, and thus G decays to 0 faster than e^{-2Ct/t_h} i.e. with a time period less than $t_h/2C$.

The same result applies in OFH, where again $xy \geq 0$.

Similarly, in the region OCDEF, moving parallel to EF, with $x - y = \lambda(0 \leq \lambda \leq 2)$, and using the fact that $x + y \geq -2S^*/P$, we get

$$\begin{aligned} dG/dt &\leq -4x^2/t_a - 2C\nu_h S^*(x+y)^2 + 2\nu_h S^*\lambda y \\ &= -4x^2/t_a - 2C\nu_h S^*(x+y)^2 + 2S^*\nu_h y(x-y) \\ &= -2G/t_h - 2C\nu_h S^*(x+y)^2 + 2S^*\nu_h xy + (2/t_h - 4/t_a)x^2. \end{aligned}$$

In this region, $xy \leq 0$, so if $2/t_h - 4/t_a \leq 0$, then $dG/dt \leq -2G/t_h$; again, if $2/t_h - 4/t_a \geq 0$ then we can rewrite the expression for dG/dt as

$$dG/dt \leq -4G/t_a - 2C\nu_h S^*(x+y)^2 + 2S^*\nu_h xy + (2/t_h - 4/t_a)x^2.$$

so that $dG/dt \leq -4G/t_a$. The same result applies in OHIK, where $xy \leq 0$.

We thus see that in some parts of the valid region convergence of G has a time period less than $t_h/2C(= 1/2\nu_f f)$ and in others it is less than $t_h/2$ or $t_a/4$ (depending on the parameter values). Thus, convergence is at least as fast as exponential, with the time period the maximum of $t_h/2$, $1/2\nu_f f$ and $t_a/4$. It is interesting to note, therefore, that the time for convergence is half of max {expected handling time, expected time to find prey, expected time to complete a fight}. The time to find another handler is not important here.

2.2.3. To kleptoparasitise or not?

Broom and Ruxton (1998) showed that kleptoparasitism should always take place in the Ruxton-Moody model if $\nu_f f t_a < 1$ i.e $Ct_a < t_h$; animals should challenge handlers whenever they find them, because either the rate at which they find their own food is low, and/or the contest times are low enough for them not to be too costly. Conversely, kleptoparasitism should never occur if $\nu_f f t_a > 1$, for the opposite reasons - food is plentiful without having to steal it, and/or fighting is very costly.

If $C > 1$ therefore, (so that $t_h/2 > t_h/2C$), and $Ct_a \leq t_h$, (so that kleptoparasitism occurs), then $t_h > t_a$ and therefore $t_h/2 > t_a/4$. The limiting factor for convergence is thus $t_h/2$. Conversely, if $C \leq 1$, (so that $t_h/2 < t_h/2C$), we must compare $t_a/4$ with $t_h/2C$. As explained above, in order for kleptoparasitism to occur, $Ct_a < t_h$, so $t_h/C > t_a$, and thus $t_h/2C > t_a/4$; therefore, convergence is faster than $t_h/2C = 1/2\nu_f f$.

Thus, for the Broom and Ruxton (1998) model, if $\nu_f f t_a < 1$ then kleptoparasitism occurs, and convergence is at least as fast as $\max\{t_h/2, t_h/2C\}$, whereas if $\nu_f f t_a > 1$ then kleptoparasitism does not occur, and in this case the time constant for approaching equilibrium is exactly $t_h/(C+1)$.

3. Numerical solution of the evolution equations

As mentioned previously, it did not prove possible to analyse the equations for x and y to the same extent as the equation for G. Whilst it was possible to find some bounds on the rates of change of x and y in the valid region, these bounds were not very helpful in producing bounds on the rate of exponential decay, as was accomplished for G.

We therefore resorted to numerical solution, by a simple difference approximation. This necessitated choosing specific values for the parameters, and we used those listed in Broom and Ruxton (1998): that is, $P = 20, t_a = 5, t_h = 10, \nu_f = 0.01, \nu_h = 0.05$, together with $f = 10$. These values were in turn taken from Holmgren (1995), where it is seen that they are essentially arbitrary; little justification is given for the values, and indeed no units are given. It is, therefore, worth discussing them at this point. P is the population density, in animals per unit area, and so we can use animals/hectare. $t_a/2$ and t_h are the mean times for a fight and for handling - they may therefore be expected to be of the order of seconds, for small prey (or possibly several minutes for larger prey). $\nu_f f$ is the rate at which prey are found within a certain area - number of prey per hectare per second- and $\nu_h H$ is the rate at which handlers are found - number of handlers per hectare per second. We can therefore see that the values above are not unreasonable using these units. However, any conclusions based on specific values need to be carefully assessed for their inherent reasonableness, as we shall see.

3.1. $C = 1$

The above choice gives $C = 1$, which leads to a simple equation for y,

$$dy/dt = -2y/t_h,$$

so that y decays exponentially , with time constant $t_h/2$. However, the x-equation is still not tractable:

$$dx/dt = -2(1/t_a + \nu_h S^*)x - \nu_h P(x^2 - y^2)/2.$$

This equation clearly depends on P, ν_h and t_a. However, changing P or ν_h has the same effect - increasing either parameter increases the rate of encounters, and thus the amount of kleptoparasitism occurring. Indeed, by rewriting the original equations in terms of proportions of the population in each state, it is seen that only the product $\nu_h P$ occurs in the equations, and so it is immaterial whether we vary ν_h or P - each will have the same effect. We therefore carried out the numerical solution for a range of values of P and t_a, in each case keeping all the other parameters at their default values.

The results are shown in the $C = 1$ rows of Tables 1 and 2, which show the times taken for G to fall to $1/e$ of its original value; this enables comparison with the earlier analytical work.

Looking at the $C = 1$ row in each Table, we can see that the times for G to decay generally show remarkable similarity. Except for the largest values of t_a, the times are all very close to 2.5 for a wide range of values of P and t_a. The reason for this will be discussed in the following section.

3.2. $C \neq 1$

Further numerical exploration of the rate of convergence of G, for different values of P, t_a and C (by varying $\nu_f f$, but keeping $t_h = 10$) revealed some interesting effects, as shown in Tables 1 and 2.

(We should bear in mind, from 2.2.3, that in the Broom-Ruxton model, kleptoparasitism should only occur when $C \leq t_h/t_a$ i.e. $C \leq 2$ with our parameters in Table 1. Thus, the rows for $C = 3$ and $C = 10$ should not, in practice, be relevant in that model. In Table 2, the criterion for kleptoparasitism will differ in each column, as t_a changes. However, the deterministic model of Moody-Ruxton assumes that attacks always take place, for any value of C.)

Firstly, let us consider Table 1. We can see that when P is very low, the decay time for G is given, to a very good approximation, by $T = t_h/2(C + 1)$, and when P is very large, then $T = t_h/4C$ describes the data well. (Thus, when $C = 1$, the results for low and high P are the same, $t_h/4$, and this explains the numerical results for the decay of G - the times listed are all $\simeq 10/4 = 2.5$.) When $C < 1$, the times increase with increasing P, and when $C > 1$, the opposite effect occurs.

It is straightforward to understand the results for the extreme values of P. Firstly, for small P, there is actually very little kleptoparasitism, because the population density is so small that animals rarely find each other. In this case, the population behaves as if there is no kleptoparasitism, when we saw in 2.1 that the decay time for S (and H, and thus for x and y) was $t_h/(C+1)$. Since $G = x^2+\gamma y^2$, then if x, y are both proportional to $e^{-t(C+1)/t_h}$, G will be proportional to $(e^{-t(C+1)/t_h})^2 = e^{-2t(C+1)/t_h}$, and so the time period for the decay of G will be $T = t_h/2(C + 1)$ as observed.

Table 1. Time for G to decay to $1/e$ of its initial value, for varying C and P (and default values of other parameters)

C	P=0.01	P=1	P=20	P=100	P=10,000
0.01	4.9578	5.7063	16.5933	45.833	197.82
0.5	3.3347	3.4509	3.9806	4.3381	4.9102
1	2.5002	2.5125	2.4799	2.4667	2.4988
2	1.6665	1.6484	1.4852	1.3779	1.2710
3	1.2503	1.2328	1.0843	0.97465	0.85630
10	0.4545	0.4503	0.4026	0.3453	0.2665

Table 2. Time for G to decay to $1/e$ of its initial value, for varying C and t_a (and default values of other parameters)

C	t_a=0.01	t_a=1	t_a=5	t_a =10	t_a=100
0.01	4.9744	7.3778	16.5933	26.5265	102.2387
0.5	3.3366	3.5725	3.9806	4.2177	5.1355
1	2.5000	2.4914	2.4799	2.5084	2.9142
2	1.6661	1.6059	1.4852	1.4592	1.7303
3	1.2497	1.2004	1.0843	1.0557	1.3038
10	0.4547	0.4448	0.4026	0.3907	0.6068

At the other extreme, of large P, any handler will very quickly be found by a searcher and the pair will enter a contest. Thus, the vast majority of the population will be involved in fights. From the formula for S^*, it is easy to see that $S^* \simeq H^* \simeq \sqrt{P}$ (so that $A^* \simeq P$), and so $x(0) = 1 - (C+1)S^*/P \simeq 1 - \sqrt{P}/P \simeq 1$ and $y(0) = 1 + (C-1)S^*/P \simeq 1$. Therefore, initially the population is very near B, in Fig 1, where $y = x = 1$; indeed, for all t, $x - y = 2(H - H^*)/P \simeq 1/\sqrt{P}$, so that $x \simeq y$ for all t. Returning to the equation for dG/dt, and discarding terms not involving P, we find that, when P is large

$$dG/dt \simeq -2C\nu_h\sqrt{P}4x^2 - \nu_h P 2x^2(x-y)$$

For large P, S^* is also large, and so with $y \simeq x$,we may approximate $G = x^2 + \nu_h t_h S^* y^2 \simeq \nu_h t_h S^* x^2$. Then we find

$$dG/dt = -8CG/t_h + 4CG/t_h = -4CG/t_h.$$

The time period for exponential decay is therefore $t_h/4C (= 1/4\nu_f f)$, as observed.

Table 2 shows the decay times of G for various combinations of C and t_a. Again, when t_a is small, we see a similar behaviour to that seen previously, with the time given approximately by $t_h/2(C+1)$. This is because small t_a means that contests are very short, and so food is effectively transferred, from handler to attacker, with no loss of time, and the handling ratio of the population is the same as if there had been no fighting. We thus have the same result as occurred when there was no kleptoparasitism.

At the other extreme, of large t_a, it is clear that the vast majority of the population will be involved in fighting, because once two animals have entered a contest it takes a long time to resolve (although it should be noted again that in the Broom-Ruxton model, kleptoparasitism would only occur in this case if C were very low e.g. $C < 0.1$ when $t_a = 100$). The short times seen in the table (apart from when $C = 0.01$) show that equilibrium is reached before any contests are finished - it is a question of animals getting into contests, rather than resolving the contests, which determines the time to reach equilibrium. These results are interesting, because they may be taken as an indication of a more complex model, where injuries or recovery time are needed, which might be considered to be included within t_a.

The decay time of G gives us a good indication of the decay times of x and y, and hence of H and S, the observables. In fact, if x, y have equal exponential decay, then their time to decay to 1% of their initial values will be given by a multiple 2 ln100(= 9.21) of the time taken for G to decay to 1/e of its original value. Even when x and y are not exact identical exponentials, it is found numerically that the time for the observables H and S to approach to within 1% of their equilibrium values is never more than about 10 × the decay times listed for G. Thus, for most combinations of parameters, the population is getting very near to its equilibrium state in less than one minute. Convergence is very rapid.

It is clear that when kleptoparasitism is occurring to a significant extent, due to high P or ν_h, then the time required for convergence to equilibrium $(1/4\nu_f f)$ is based on the rate of finding prey, rather than the handling time, as occurred in the non-kleptoparasitic case discussed in 2.1. The reason for the difference is that when kleptoparasitism takes place, the equilibrium value $S^* \simeq \sqrt{P}$, and so, unless P is small, there has to be a large change in the number of searchers, which requires a large time if the rate of finding prey is low; (in the non-kleptoparasitic case, $S^* = P/(C+1)$, so a significant fraction of the population remained searchers, and thus only a small change in S was required, taking a relatively short time).

Generally, the results in Tables 1 and 2 are all fractions of t_h; the deviations from this are when C is small and P or t_a is large. In these conditions, the vast majority of the population are fighting, but over a very small amount of food. Thus, each piece of food is being continually stolen from one handler to another searcher, and so on, so that the actual uptake rate is very low. It is clear that this scenario is very unlikely in reality. The combination of a low rate of finding prey and a high rate of fighting is unviable - the population will simply not survive, because there will be mass starvation. In these conditions, there is a breakdown of the assumptions on which the model is based. In all realistic conditions, the model converges within a low multiple of the handling time.

4. Other behaviours and more general systems

We have assumed that the only behaviours allowed are our rather limited list of searching, handling and fighting. Other possibilities might include resting after a meal and/or recovering after a contest. A more realistic (and inevitably more complex) model would include such factors, which could possibly affect our result about the speed at which equilibrium is attained. In order to see whether this would affect our conclusion of rapid convergence, we approximated the system as a continuous-time Markov chain with transition intensity matrix Q. In this case,

$$Q = \begin{bmatrix} -1/t_h - \nu_h S & 1/t_h & \nu_h S \\ \nu_f f & -\nu_f f - \nu_h H & \nu_h H \\ 1/t_a & 1/t_a & -2/t_a \end{bmatrix}.$$

We can see that the complicating factor in our original equations, the non-linear term $\nu_h SH$, manifests itself now as variable terms within the matrix Q.

It is well known (Anderson 1991) that the least negative eigenvalue, λ_2 (apart from 0) of the intensity matrix leads to the exponential decay time $T = -1/\lambda_2$.

We found these eigenvalues, and hence the convergence times, for the range of parameter values used in the numerical simulations previously. We did this taking the values of S and H in Q as i) their initial values $S = P$, $H = 0$ and ii) their equilibrium values $S = S^*$, $H = H^*$; in both cases, we got results within an order of magnitude of the previous results (and usually closer) , except for the high-P-low-C regime, where we had already concluded that the model is inappropriate.

The speed of convergence in fact depends upon two key factors - the sizes of the transition rates, and the pattern of transitions between the states. For example, consider two extreme cases of n-state behaviour:

1. Firstly, that in which each state leads to just one other, and so on (as in a queue) with a final return transition i.e. searcher → handler $\rightarrow \cdots \rightarrow$ searcher, with n possible behavioural states. When all the exit-rates from states are 1, we found that $T = n^2/2\pi^2$.
2. At the other extreme, suppose that each state leads, with equal probability, to every other state. Assuming, again, an exit-rate of 1 from each state, this gives a convergence time of $T = (n-1)/n$.

We would expect that the latter would be the most efficient way of producing convergence, whilst the former model would be the slowest, and so we expect that for a general n-state system, the convergence time will depend on the number of states as

$$T \propto n^{\delta}, 0 \le \delta \le 2.$$

Thus, for example, if our model with 3 states is replaced by a more sophisticated one with 6 states, the convergence time should not increase by more than a factor of $(6/3)^2 = 4$, which will still only be of the order of minutes.

The idea that the rate of convergence of a system depends on the “topology” of that system might well have applications elsewhere, in models of other biological processes. Equally, the use of linear approximations to give an indication of the rate of convergence of a system may have wider applicability.

5. Conclusion

Previous works (Ruxton and Moody 1997, Broom and Ruxton 1998) have modelled the behaviour of a population of birds under kleptoparasitism. Individuals were considered to be in one of three states, and an equilibrium distribution of individuals among the states was found. Subsequent analysis proceeded on the assumption that the population was indeed in this equilibrium. In this paper, we have considered whether this assumption is reasonable, by looking at the time taken to converge to this equilibrium in this model.

Our model is, of course, still very idealised. We have not allowed for variation in any of the parameters once the model is running eg the amount of prey might decrease during the period when foraging is taking place. We have also assumed that the only behaviours allowed are our rather limited list of searching, handling and fighting. Other possibilities, including resting and/or recovering, would result in a more complicated model, but it seems that the convergence time might only increase as the square of the number of behavior states included in the model.

However, with our assumptions, we have found, from the analysis in the preceding sections, that the time period required to reach the equilibrium state is short, unless $\nu_f f$ is very low in a population where a great deal of kleptoparasitism is occurring (high P or high ν_h).

For a population with a low number of animals per unit volume, or where the chance of finding a handler is low, or the mean time for a contest is low, then the decay time for the variable G that we have introduced is always less than the time required to handle prey; thus, within, say, a few minutes at most, the population will have essentially reached equilibrium. As explained, this result is the same whether or not kleptoparasitism has occurred, because in these situations such a phenomenon is unlikely anyway, or has no effect - either there are so few encounters that stealing is irrelevant, or encounters are so brief that effectively there is a free transfer of food.

For populations with high density, or a high rate of finding handlers, kleptoparasitism is more significant. When it does not occur - because the fighting time, $t_a/2$, is sufficiently long to deter attacks or because the rate of finding food, $\nu_f f$, is sufficiently high to make it easy for the animal to find its own food - then we found that equilibrium is reached within a fraction of the handling time. However, when kleptoparasitism does occur, the picture is more complicated. When $\nu_f f \ll 1$, then the time period, of the order of $1/\nu_f f$, might be a very long time; the discussion in Section 2.1 is now relevant, where a slow process dominates a quicker one. We see that, if $\nu_f f$ is very low (when there is little food available, or the rate of finding it is low) then it will be difficult for searchers to become handlers, and for other searchers, in turn, to find these handlers, and so equilibrium will take longer to reach.

It is likely, however, that the combination of parameter values which produce very long times to convergence are unrealistic. All sensible parameter values will produce fast convergence, and therefore the population will indeed spend most of the time in its equilibrium state. This then validates the assumptions of previous work in this area, and conclusions reached in that work are seen to be justified.

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