J. Math. Biol. 48, 529–544 (2004)
Digital Object Identifier (DOI):
10.1007/s00285-003-0244-4

Mathematical Biology

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A framework for modelling and analysing conspecific brood parasitism

Received: 20 December 2002 / Revised version: 2 September 2003 /

Abstract. Recently several papers that model parasitic egg-laying by birds in the nests of others of their own species have been published. Whilst these papers are concerned with answering different questions, they approach the problem in a similar way and have a lot of common features. In this paper a framework is developed which unifies these models, in the sense that they all become special cases of a more general model. This is useful for two main reasons; firstly in order to aid clarity, in that the assumptions and conclusions of each of the models are easier to compare. Secondly it provides a base for further similar models to start from. The basic assumptions for this framework are outlined and a method for finding the ESSs of such models is introduced. Some mathematical results for the general, and more specific, models are considered and their implications discussed. In addition we explore the biological consequences of the results that we have obtained and suggest possible questions which could be investigated using models within or very closely related to our framework.

1. Introduction

A common phenomenon amongst bird populations is brood parasitism; that is the laying of eggs in the nest of another individual without taking part in the subsequent processes of incubation and/or caring for the hatchlings. This behaviour takes two forms. Obligate interspecific brood parasitism is where a species specialises in laying eggs in the nests of birds of another species; in this case the parasite birds do not build a nest and lay all their eggs parasitically. Conspecific (or intraspecific) brood parasitism is where the host is from the bird's own species. Conspecific brood parasitism has been categorised into three types by Davies (2000). The first case involves individuals that attempted to nest normally but whose nest was destroyed, say by weather or predators. If such a female has begun the process of egg-laying, then she may not have time to rebuild the nest, and she may turn to parasitism to "make the best of a bad job". In the second case, some individuals have made no

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Key words or phrases: Evolutionarily stable strategy – Unified model – Parasite – Egg-dumping

attempt to nest themselves but instead choose pure parasitism as in the interspecific case.

The final situation is one where parasitic individuals build nests that are not destroyed, and as well as laying eggs in their own nest, they lay some of their eggs parasitically. The advent of molecular techniques such as DNA fingerprinting has greatly aided field study of this behaviour. At the latest count (Eadie et al. 1998), conspecific brood parasitism behaviour has been recorded in 185 species.

There have been several attempts to model conspecific brood parasitism. Andersson (1984) and Eadie & Fryxell (1992) developed game-theoretic models of the second case, where parasitic birds are pure parasites. Later models have considered the third, more common, situation where parasitism is only part of a bird's behaviour and it forms its own nest as well. The first of these models was by Lyon (1998) and was followed by Robert and Sorci (2001), Broom and Ruxton (2002) and Ruxton and Broom (2002). Each of these models attempted to answer different questions about this parasitic behaviour, but there is a lot in common between them. The aim of this paper is to introduce an overall framework for the modelling of conspecific brood parasitism that incorporates the current models and can make general predictions about a wide range of possible behaviours. In particular it is of great interest under what conditions brood parasitism should occur at all, and what effect the presence of parasitism has on the number of host eggs and the total number of eggs laid. A description of each of the models and how they fit into the overall framework is given in Appendix B.

We intend this paper to be of use to modellers by providing a flexible framework for describing a wide range of brood parasitic systems. If a specific system can be cast as a special case of our general model, then the paper will supply useful tools to ease the analysis of the system. We also intend it to be of interest to those seeking to compare the assumptions and predictions of previous models. Representing two models as special cases of our general model should greatly aid comparison. Lastly, and equally importantly, we intend it to be of use to those whose interest in brood parasitism is more empirical. Our model describes several key features which we believe are central to many brood parasitic systems and consequently of great biological interest. This should allow investigators to identify those features of either host or parasite behaviour of a particular system that must be measured (and the accuracy required) in order to gain an understanding of the mechanisms underlying aspects of parasitism in that system.

2. The model

2.1. Laying strategies

Birds lay eggs in their own nest and in other nests as parasite eggs. There are various choices that the birds could make (including complex sequential ones depending upon the number of eggs in their own and other nests, time and so on) which could generate a wide range of possibly complicated payoff functions and egg distributions. We focus on the fundamental question of how many eggs a bird should lay in its own nest, and how many it should lay parasitically. To make progress we assume that birds make an initial choice of the number of host eggs that they lay *x,* and the number of parasite eggs *y* which they spread randomly among other nests. These numbers cannot be altered after laying has commenced so that sequential strategies, as mentioned above, do not occur.

In such circumstances, what is the fitness of an individual playing a particular strategy (x, y)? This involves contributions from three different terms; the cost of laying the eggs, the value to a bird of eggs laid in its own nest and the value to it from parasite eggs. It is assumed that these three terms are additive and independent. This is reasonable in the case of the cost function, which just depends upon the number of eggs laid, not when and where they were laid. The independence of the other two terms relies on a bird not being able to enhance success in its own nest at the expense of its parasite eggs, or vice versa, except by altering the values of x and y (e.g. by deciding to lay all its host eggs first). If this was possible then the range of strategies would be greatly increased as birds would have to choose the order in which they laid their eggs and what strategies would be effective would depend upon which ordering strategies other birds followed. We assume that all birds in a population will behave in a similar way in respect of the order of laying i.e. there is an evolutionarily stable ordering for any strategy (x,y), if all birds play this strategy, and the birds adopt this laying order. When considering possible invading strategies, we in essence assume that they also adopt a similar ordering.

A related assumption is that any parasite egg contributes an amount equal to the mean payoff of all parasite eggs in the population to the parasite i.e. no bird's eggs do generally better than others (for example by laying fewer host eggs and so laying their parasite eggs earlier). The mechanism used can be one of many. Birds may lay parasite eggs completely at random, laying a single egg in each nest. This presupposes that nests are relatively easy to find; they may not be, and birds may have to lay eggs in nests as they find them. Alternatively birds may lay all their parasite eggs in a single nest. The assumption is that each bird uses the same method and that the expected value to each egg is the average of that for all parasite eggs in the population.

2.2. *Rewards, costs and distributions*

We proceed to outline the reward and cost functions, which contribute to the overall payoff to a bird playing a given strategy. This payoff also depends upon the distribution of clutch sizes and of eggs within the different nests, and the relevant functions are also given.

(1) Birds pay a cost depending upon the number of eggs z that they lay, $C(z)$. Clearly $C(z)$ is an increasing function. It is assumed that egg production does not get any easier as extra eggs are laid (and may become more costly as resources diminish) so that the derivative of $C(z)$, $C'(z)$, is a non-decreasing function.

(2) If a nest contains a total of t eggs then if the i th egg is laid by the owner of that nest (i.e. is a host egg) its value to its parent, measured by the probability that it hatches into a chick which survives to adulthood, is $h(i,t)$ (see (5) for an explanation of the value of such an egg to its parent if it is a parasitic egg).

It is often the case that the earlier laid eggs have an advantage, hence *h(i,t)* decreases with *i*.

(3) $f(x,t)$ is the probability that a randomly chosen nest contains a total of t eggs, x of which are host eggs. Thus, after the laying process is completed and assuming a large population, it is the proportion of such nests. The value of *f(x,t)* will depend upon the laying rules assumed. In particular we specify that $f(x,t) = d(x)g_x(t)$ where *d(x)* is the probability that a random nest contains x host eggs and $g_x(t)$ is the probability that given a nest contains x host eggs, it contains t eggs in total.

(4) $p_{x,t}(i)$ is the probability that given a nest contains x host eggs and t eggs in total, the i th egg is a host egg.
Terms (3) and (4) will depend upon the strategies adopted by the birds in the population, but also possibly on the times that birds start laying and the order that they lay in (parasite or host first, or some mixed order).

(5) The fitness of parasite eggs is multiplied by a reduced survival parameter η, so that the value of a parasite egg in position i in a nest with a total of t eggs is $\eta h(i,t)$. This may be due to the possibility of an egg being rejected by its host, or factors other than egg rejection that impede the hatching or survival of the chick, or a combination of the two. We specify the probability that an egg is not rejected by the host, as γ. Thus we have that $\eta \leq \gamma \leq 1$.

2.3. The general payoff function

The net reward to a bird playing (x^*,y^*), will be given by the general form

$$V(x^*, y^*) = U(x^*; \underline{x, y}) + y^* W(\underline{x, y}) - C(x^* + y^*) \quad (1)$$

where $U(x^*; \underline{x, y})$ is the expected value of the bird's own nest, depending upon the number of eggs it lays itself and the strategies of other birds. The mixture of strategies in the population is given by the probability vector of strategies played, $\underline{x, y}$, indicated by a probability associated with each strategy (given by a single choice of x and y). Similarly $W(\underline{x, y})$ is the expected value of a parasite egg in this population.

The three terms involved in the payoff function are as follows.

(a) The cost that it pays for laying a total of $x^* + y^*$ eggs is C ($x^* + y^*$), as above.

(b) The value of the eggs in a bird's own nest is found by finding the value to the host of its x^* eggs given that the total number of eggs is t and then finding the weighted average over all possible values of t, which gives us

$$U(x^*; \underline{x, y}) = \sum_{t \geq x^*} g_{x^*}(t) \sum_{i=1}^{t} p_{x^*,t}(i) h(i,t) \quad (2)$$

(c) To find the expected value of a parasite egg we first find the conditional probability that an egg is in position i in a nest with x hosts and a total of t eggs (event A) given that it is a parasite egg (event B).

$$\mathrm{P[A|B] = P[A \cap B]/P[B]}$$

P[A ∩ B] is the probability that a random egg is a parasite in position *i* in a nest with *x* host eggs out of a total of *t*, which is the ratio of the number of such eggs and the total number of eggs. Letting *N* be the (very large) number of nests this becomes

$$\frac{(1 - p_{x,t}(i))Nf(x,t)}{\sum_{x,t\geq x} Nf(x,t)t} \tag{3}$$

Similarly P[B] is the total proportion of parasite eggs

$$\frac{\sum_{x,t\geq x} \sum_{i=1}^{t} (1 - p_{x,t}(i))Nf(x,t)}{\sum_{x,t\geq x} Nf(x,t)t} \tag{4}$$

Thus

$$\mathrm{P[A|B]} = \frac{(1 - p_{x,t}(i))f(x,t)}{\sum_{x,t\geq x} \sum_{i=1}^{t} (1 - p_{x,t}(i))f(x,t)} \tag{5}$$

The value of a parasite egg in this position is $\eta h(i,t)$. Summing over all possible positions gives the value of a random parasite egg as

$$\begin{aligned} W(\underline{x,y}) &= \frac{\sum_{x,t\geq x} \sum_{i=1}^{t} (1 - p_{x,t}(i))f(x,t)\eta h(i,t)}{\sum_{x,t\geq x} \sum_{i=1}^{t} (1 - p_{x,t}(i))f(x,t)} \\ &= \frac{\eta \sum_{x} d(x) \sum_{t\geq x} g_x(t) \sum_{i=1}^{t} (1 - p_{x,t}(i))h(i,t)}{\sum_{x} d(x) \sum_{t\geq x} g_x(t) \sum_{i=1}^{t} (1 - p_{x,t}(i))} \end{aligned} \tag{6}$$

A bird playing strategy (x^*, y^*) lays y^* such eggs. Combining this with the expected reward from its own nest and the cost of laying its eggs, the payoff to a bird playing (x^*, y^*) is thus

$$\begin{aligned} V(x^*, \mathrm{y}^*) = {} & \sum_{t\geq x^*} g_{x^*}(t) \sum_{i=1}^{t} p_{x^*,t}(i)h(i,t) \\ & + \eta y^* \frac{\sum_{x} d(x) \sum_{t\geq x} g_x(t) \sum_{i=1}^{t} (1 - p_{x,t}(i))h(i,t)}{\sum_{x} d(x) \sum_{t\geq x} g_x(t) \sum_{i=1}^{t} (1 - p_{x,t}(i))} - C(x^* + y^*) \end{aligned} \tag{7}$$

This provides us with a reward function for any distribution of other strategies; explicitly in the case of host strategies through the function $d(x)$ but also implicitly for the different parasite strategies as long as the laying mechanisms are sufficiently well defined to work out the precise form of the other functions of the model; $g_x(t)$ is obtained from the distribution of the number of parasite eggs in hosts' nests, and $p_{x,t}(i)$ from the ordering of these eggs within the nests. In practice, however, the actual strategies used in a population will only be those that are successful; in particular we shall restrict ourselves to finding ESSs of the model.

2.4. The ESSs of the system

To find the ESSs of this system, we assume that almost all birds play strategy (x^e, y^e) and a small number (proportion ε) choose the alternative strategy (x^*, y^*). Let $y^m = (1-\varepsilon)y^e + \varepsilon y^*$, the average number of parasite eggs per nest. Since birds are assumed to use the same laying mechanism regardless of how many parasite eggs they lay, the parasite numbers only depend on the total y^m, and not on the particular contributions of the different birds. Further denote $U(x, y)$ as the reward from its own nest to a bird which lays x eggs in this nest in a population where the *average* number of parasite eggs laid per bird (and so per nest) is y and $W(x, y)$ as the expected reward to a random parasite egg in a nest with x host eggs where the average number of parasite eggs laid per bird is y. Note that the payoff to parasite eggs is affected by which type of host is encountered, so the expected reward to a parasite is a weighted average of the two possible rewards.

The general expression for the payoff to a bird playing this alternative strategy in equation (1) now becomes

$$\begin{aligned} V(x^*, \mathrm{y}^*; x^e, y^e) = U(x^*, y^m) + y^*((1-\varepsilon)W(x^e, y^m) \\ +\varepsilon W(x^*, y^m)) - C(x^* + y^*) \end{aligned} \tag{8}$$

We shall in fact simplify this expression further to become

$$V(x^*, \mathrm{y}^*; x^e, y^e) = U(x^*, y^e) + y^* W(x^e, y^e) - C(x^* + y^*) \tag{9}$$

so that the vector of possible alternative strategies $\underline{x, y}$ has been replaced by the specific strategy (x^e, y^e), on the assumption that the value of ε is negligible. This simplification has no effect on the ESS conditions, except in one particular case, which is analysed in Appendix A. The optimal strategy to play in such a population is the one that maximises the payoff $V(x^*, \mathrm{y}^*; x^e, y^e)$. (x^e, y^e) is an ESS if it is the optimal strategy in a population playing (x^e, y^e).

There are four possible types of solution, namely $(x^e > 0, y^e > 0)$, $(0, y^e)$, $(x^e, 0)$, and $(0, 0)$.

$(x^e > 0, y^e > 0)$ is an ESS only if

$$\frac{dV_{x=x^e}(x, \mathrm{y^e}; x^e, y^e)}{dx} = 0, \quad \frac{dV_{y=y^e}(x^e, \mathrm{y}; x^e, y^e)}{dy} = 0 \tag{10}$$

which are the equilibrium conditions, and

$$\frac{d^2V_{x=x^e}(x, \mathrm{y^e}; x^e, y^e)}{d^2x} < 0, \quad \frac{d^2V_{y=y^e}(x^e, \mathrm{y}; x^e, y^e)}{d^2y} < 0 \tag{11}$$

which are the one dimensional stability conditions. Finally we need the two dimensional stability condition, given by

$$\frac{d^2V_{x=x^e}(x, \mathrm{y}^{\mathrm{e}}; x^e, y^e)}{d^2x} \frac{d^2V_{y=y^e}(x^e, \mathrm{y}; x^e, y^e)}{d^2y} > \left(\frac{d^2V_{x=x^e, y=y^e}(x, \mathrm{y}; x^e, y^e)}{dxdy} \right)^2 \tag{12}$$

Note that although these conditions are necessary, whether they are sufficient for an ESS depends upon the type of evolution allowed by the system. In particular the conditions are sufficient if mutations can only lead to slightly differing strategies. If they can lead to large differences, then sufficiency is given if in addition, there is no other turning point of the payoff function. The same proviso applies to the boundary solutions. The solutions that we have found are the *local ESSs* of the system (see Pohley and Thomas, 1983). This is a somewhat weaker concept than an ESS and the implications of using this idea are discussed in Section 3.

$(0, y^e)$ is an ESS only if

$$\frac{dV_{y=y^e}(0, \mathrm{y}; 0, y^e)}{dy} = 0 \tag{13}$$

which is the equilibrium condition, and

$$\frac{dV_{x=0}(x, \mathrm{y}^{\mathrm{e}}; 0, y^e)}{dx} < 0, \quad \frac{d^2V_{y=y^e}(0, \mathrm{y}; 0, y^e)}{d^2y} < 0 \tag{14}$$

which are the stability conditions.

$(x^e, 0)$ is an ESS if

$$\frac{dV_{x=x^e}(x, 0; x^e, 0)}{dx} = 0 \tag{15}$$

which is the equilibrium condition, and

$$\frac{dV_{y=0}(x^e, \mathrm{y}; x^e, 0)}{dy} < 0, \quad \frac{d^2V_{x=x^e}(x, 0; x^e, 0)}{d^2x} < 0 \tag{16}$$

which are the stability conditions.

$(0, 0)$ is an ESS if

$$\frac{dV_{x=0}(x, 0; 0, 0)}{dx} < 0, \quad \frac{dV_{y=0}(0, \mathrm{y}; 0, 0)}{dy} < 0 \tag{17}$$

which are both stability conditions.

We now return to the general expression for the payoff function given in equation (9); in particular we find all the above derivatives and show that all equilibria are also ESSs.

$$\frac{dV(x, \mathrm{y}; x^e, y^e)}{dx} = U'(x, y^e) - C'(x + y) \tag{18}$$

where $U'(x, y^e)$ is the first derivative of $U(x, y^e)$ with respect to x.

$$\frac{dV(x,\mathrm{y};x^e,y^e)}{dy} = W(x^e,y^e) - C'(x+y) \tag{19}$$

$$\frac{d^2V(x,\mathrm{y};x^e,y^e)}{dx^2} = U''(x,y^e) - C''(x+y) \tag{20}$$

$$\frac{d^2V(x,\mathrm{y};x^e,y^e)}{dy^2} = -C''(x+y) \tag{21}$$

$$\frac{d^2V(x,\mathrm{y};x^e,y^e)}{dxdy} = -C''(x+y) \tag{22}$$

Now since $U(x^*, y^e)$ is the reward to a nest-builder who lays x^* eggs in its own nest and y^e is the number of parasite eggs laid by other birds, the fact of within-nest competition means that $U(x^*, y^e)$ should decrease with y^e and while it may increase with x^* it should do so at a decreasing rate. Thus $U'(x^*, y^e)$ decreases with x^* which in turn implies that $U''(x, y^e) < 0$. Similarly, since $W(x^e, y^e)$ is the reward to a parasite egg in such a population it should decrease with both x^e and y^e. Further, we have stated that $C''(z) \geq 0$. If $C''(z) > 0$ for all z, then these conditions together ensure that any strategy that satisfies the equilibrium condition to be an ESS, also satisfies the stability conditions as well, whether it is an internal or a boundary strategy (subject to the sufficiency comments mentioned above; see Section 3). Similarly if $C''(x^e + y^e) > 0$ then if (x^e, y^e) is an equilibrium, it is also an ESS. In fact if $C''(x^e + y^e) = 0$, as in Broom and Ruxton (2002) and Ruxton and Broom (2002), then the equilibrium (x^e, y^e) is still stable and thus an ESS, but more careful analysis is required to show this, and this is given in Appendix A.

Note that in Broom and Ruxton (2002) and Ruxton and Broom (2002) it is assumed that this reward from a bird's own nest always increases with the number of eggs, whereas Robert and Sorci (2001) generally have this decreasing for sufficiently large x^*.

For a non-boundary ESS we need

$$U'(x^e, y^e) = C'(x^e + y^e) = W(x^e, y^e) \tag{23}$$

We return to our more explicit functional form and the reward function of equation (7). If almost all birds play (x^e, y^e), and the rest (a proportion ε) play the alternative strategy (x^*, y^*), then the value of the function $d(x)$ is given by $d(x^e) = 1 - \varepsilon$, $d(x^*) = \varepsilon$, and $d(x) = 0$ for all $x \neq x^e, x^*$. As the number playing the alternative strategy becomes a vanishingly small proportion of the population, the value of $d(x)$ is given by $d(x^e) = 1$ and $d(x) = 0$ for all $x \neq x^e$. This gives the following expression for the payoff function

$$V(x^*\mathrm{y}^*) = \sum_{t \geq x^*} g_{x^*}(t) \sum_{i=1}^{t} p_{x^*,t}(i) h(i,t)$$
$$+ \eta y^* \frac{\sum_{t \geq x^e} g_{x^e}(t) \sum_{i=1}^{t} (1 - p_{x^e,t}(i)) h(i,t)}{\sum_{t \geq x^e} g_{x^e}(t) \sum_{i=1}^{t} (1 - p_{x^e,t}(i))} - C(x^* + y^*) \tag{24}$$

which yields ESS conditions

$$\sum_{t \geq x} \frac{d(g_x(t))_{x=x^e}}{dx} \sum_{i=1}^{t} p_{x^e,t}(i)h(i,t) + \sum_{t \geq x} g_{x^e}(t) \sum_{i=1}^{t} \frac{d(p_{x,t}(i))_{x=x^e}}{dx} h(i,t)$$
$$= C'(x^e + y^e) \tag{25}$$

and

$$\eta \frac{\sum\limits_{t \geq x^e} g_{x^e}(t) \sum\limits_{i=1}^{t} (1 - p_{x^e,t}(i))h(i,t)}{\sum\limits_{t \geq x^e} g_{x^e}(t) \sum\limits_{i=1}^{t} (1 - p_{x^e,t}(i))} = C'(x^e + y^e) \tag{26}$$

We thus have a formula for the payoff to any strategy against a population playing an alternative strategy in quite general terms and formulae which can be used to find the ESSs of any particular system provided that the form of the functions which make it up are known. See Appendix B for a discussion of particular models to see how this works in practice.

2.5. *Some questions and answers*

Firstly we shall consider the possibility of multiple ESSs, using our most general modelling form. Let us suppose that there are two solutions to equation (23), (x_1^e, y_1^e) and (x_2^e, y_2^e). Since $C'(x^e + y^e)$ does not decrease with the sum of x^e and y^e, but $W(x^e, y^e)$ decreases with both of them it is not possible for $x_1^e \leq x_2^e, y_1^e < y_2^e$ or for $x_1^e < x_2^e, y_1^e \leq y_2^e$ so that any such pair of solutions must be of the form $x_1^e < x_2^e, y_1^e > y_2^e$. A similar argument can also be used to show that this applies to boundary solutions as well as internal ones. Of course this does not rule out there being many such solutions. That such a pair of solutions can exist is easy to demonstrate, as is shown below, and the consequences of this are discussed briefly in Section 3. Consider the following (not necessarily realistic) functions

$$U(x, y) = \frac{6\ln(x)}{y}, \quad W(x, y) = \frac{1}{x} + \frac{1}{y}, \quad C(z) = \frac{1}{16}z^2$$

which leads to the following equilibrium conditions

$$\frac{6}{x^e y^e} = \frac{1}{x^e} + \frac{1}{y^e} = \frac{1}{8}(x^e + y^e) \tag{27}$$

It is easy to show that there are precisely two ESSs to this system, namely $x_1^e = 2, y_1^e = 4$ and $x_2^e = 4, y_2^e = 2$.

It is possible to show that there is a unique ESS under certain restrictions. The lack of a position effect ($h(i, t)$ does not depend on i) in Robert and Sorci (2001) and Ruxton and Broom (2002) leads to considerable simplification. Following Robert and Sorci (2001) by setting $h(i,t) = s(t)$, the general payoff function to a bird with strategy (x, y) in a population who play (x^e, y^e) is given by

$$V(x,\mathrm{y}) = \sum_{t\geq x} g_x(t)xs(t) + \eta y \frac{\sum\limits_{t\geq x^e} g_{x^e}(t)(t-x^e)s(t)}{\sum\limits_{t\geq x^e} g_{x^e}(t)(t-x^e)} - C(x+y) \tag{28}$$

(since $\sum_{i=1}^{t} p_{x,t}(i) = x$)

Further simplification is yielded by the fact that every nest contains exactly the same number of parasite eggs, giving

$$V(x,\mathrm{y}) = xs(x+y^+) + \eta ys(x^e+y^+) - C(x+y) \tag{29}$$

where y^+ is the number of parasite eggs per nest and takes different values in the two models, namely $y^+ = \eta y^e$ in Ruxton and Broom (2002) and $y^+ = y^e$ in Robert and Sorci (2001).

To find any non-boundary solution (neither x^e nor y^e equal to zero), we set the two derivatives of $V(x,\mathrm{y})$ equal to zero and $x = x^e$, $y = y^e$ giving

$$x^e s'(x^e+y^+) + s(x^e+y^+) = C'(x^e+y^e) = \eta s(x^e+y^+) \tag{30}$$

Boundary conditions:

Following on from equations (13–17) the conditions for ESSs at the boundary are as follows.

$x^e = y^e = 0$ if $s(0) < C'(0)$

$x^e > 0,\ y^e = 0$ if $x^e s'(x^e) + s(x^e) - C'(x^e) = 0$ and $\eta s(x^e) < C'(x^e)$

$x^e = 0,\ y^e > 0$ can only occur if $s(y^+) < C'(y^e)$ and $\eta s(y^+) = C'(y^e)$. Since η cannot exceed 1, this is impossible.

If there is a non-boundary solution, this yields two equations for the number of eggs that should be laid as hosts and parasites. The total number of eggs in a nest is given by $T = x^e + y^+$. We can find the optimal value of x^e from this total using the equation (30), namely

$$x^e = \frac{(1-\eta)s(T)}{-s'(T)} \tag{31}$$

The second equality from (30) is

$$C'(x^e+y^e) = \eta s(x^e+y^+) \tag{32}$$

It is clear from these two equations that there is a unique solution to this system since we know that $C'(x^e+y^e)$ is non-decreasing with x^e and y^e and that $s(x^e+y^+)$ is decreasing with both of these terms (since y^e is increasing with y^+), giving a unique value of $T = x^e + y^+$ and so a unique x^e. There may be no such solution, which occurs when the optimal value of x^e from equation (31) is larger than T, which then gives a unique boundary solution with $y^e = 0$ and x^e the solution of the single equation from the above boundary conditions.

Although we provide conditions for three types of boundary ESS, two of these are of little biological interest. The condition where it pays birds to lay no eggs at all is clearly not relevant, and arises only because of the simplified nature of the model. Similarly the ESS where eggs are only laid parasitically is of little interest, since it is plainly illogical for birds to invest in building a nest that they do not use themselves, and even less logical for them to bring up a brood that they can be certain contains none of their own offspring. Again, this ESS arises only from the simplified nature of our model. The boundary ESS where all eggs are laid in the bird's own nest is of biological interest, as this condition can be used to explore the ecological conditions required for the evolution of parasitism. The fact that we provide a mechanism for deriving an analytic expression for the conditions required for parasitism to evolve should allow comparison of the predictions of this expression with the known distribution of intra-specific parasitism within the range of avian species.

The prediction that there may be multiple non-boundary conditions for a specific system may also be of biological importance. Different local populations of a species can display markedly different levels of intra-specific brood parasitism. Previously, this difference has been interpreted as indicative of between-population differences in local ecological conditions. The possibility of multiple ESSs provides an alternative explanation for this phenomenon. It would be useful to explore the likelihood of multiple ESSs occurring in more specific cases of our general model.

A possible special case of our framework involves the assumption that the value of an egg laid in a nest is independent of the number of eggs added to that nest subsequently (i.e. $h(i, t)$ is independent of *t),* allowing considerable model simplification. It is highly unlikely that this assumption is reasonable for passerine species whose offspring require parental feeding for some time after hatching. However, it may be a reasonable assumption for some non-passerines that produce precocial young,which are able to feed themselves from the moment of hatching. Further development of the consequences of this assumption for model predictions may provide an insight into the apparently higher rates of intra-specific brood parasitism among species with precocial young.

3. Discussion

In this paper we have developed a generalised model of conspecific brood parasitism that incorporates a range of already existing models as special cases. The framework that has been created is useful for two reasons. Firstly it helps when comparing existing models with each other and more clearly establishing the assumptions of the models, both explicit and implicit. Secondly, our work provides a basis for new models to start from. To fit into the framework, a new model will have to explicitly state a key set of assumptions in order to find the simpler versions of the general expressions introduced in Section 2 leading in turn to new versions of our equations, especially (7) and (24). In particular it is shown in this paper how to find the ESSs for models fitting into this framework thus providing a (possibly considerable) saving in effort. The approaches of the papers described in Appendix B to finding the ESSs were quite varied, and a common approach is useful for comparative purposes.

Note that there have also been other models considering conspecific parasitism. For example the model of Ruxton et al. (2001) which was designed to test a hypothesis of (Yom-Tov, 1980) about the use of pale eggs as a signal. This model introduced an asymmetry between host birds, which puts it outside of our framework. Another example is given in Yamauchi (1993), which describes how quantitative genetic modelling can be applied to the co-evolution of anti-parasitism traits such as egg rejection along with parasitic traits.

A further work (Yamauchi 1995) describes how this framework can be extended to consider both inter-specific and conspecific brood parasitism simultaneously.

The equations and inequalities 10-17 define all the local ESSs of our model i.e. those strategies, which cannot be invaded by a mutant playing a strategy sufficiently close to the original, and are thus not necessarily actual ESSs. These will be the only solutions of interest if either new mutants only change their strategies by small amounts or if the payoff function to a mutant can have only a single turning point (this second criterion is certainly satisfied for some simplifications of the generalised model such as that described in Section 2.5). It should be noted that it is possible to have other more complex situations for which this is not true. For a good overview of the issues raised by different types of stability see Hofbauer and Sigmund (1998).

We have shown that there is not necessarily a unique ESS in our most general model, and it is not hard to produce a system with any specified number of ESSs. How realistic is it for there to be multiple solutions? None of the papers discussed in Appendix B have non-unique ESSs and it is shown in Section 2.5 that two recent papers (Robert and Sorci, 2001, and Ruxton and Broom, 2002) are examples of a specific subset of our new framework where there is always a unique ESS. However this may be due to the simplifying assumptions made, and more complicated interactions between x and y in the payoffs, egg positions and nest size distribution may generate multiple solutions in realistic cases. It will be interesting to see if new models of situations, which fit into our framework are developed that possess multiple ESSs.

Our model framework could be logically extended to represent more than one species. We have in mind a situation where the options open to bird are to lay an egg in its own nest, in a nest of another bird from its own species, or in the nest of a different species. Some birds (mainly of the cuckoo and cowbird families) are obligate brood parasites that do not build nests themselves but lay eggs in the nests of other species. Our extended model framework would allow evaluation of the conditions required for such inter-specific brood parasitism to evolve from the intra-specific case. It could also help seek an answer for why no species seems to parasitise both its own species and another species simultaneously.

Our framework demonstrates the importance of the costs of egg production for an understanding of brood parasites, and particularly identifies the importance of understanding how this cost changes with the number of eggs produced. Further empirical work to resolve the likely shape of the function $C(z)$ would be very useful. Similarly, further empirical work on the temporal arrangement of host and parasitic eggs laid in a nest would be useful, as well as measurement of the hatching (or, better yet, fledging) success of individuals from different positions within the temporal sequence.

It seems likely that birds' mechanisms for rejecting parasitic eggs have a non-zero probability of leading to the mistaken rejection of one of a bird's own eggs rather than the parasitic egg. This probability would have been substantial during the initial evolution of such ejection mechanisms. Our model framework could be modified in order to explore the feasibility of the evolution of egg rejection in the face of costs generated by such errors. Similarly, the model framework could easily cope with exploration of consequences of plausible trade-offs such as a trade-off between position on the temporal sequence of eggs in the nest and likelihood that a parasitically laid egg will be rejected. One option to a host bird is to desert a nest that it suspects has been parasitised in order to build another nest and begin laying again. As the breeding season is finite, this tactic becomes less attractive to hosts as time goes on, hence this provides selection pressure for parasites to delay parasitism in order to reduce the risk of desertion by the hosts. However, there is a counter-acting selection pressure since delaying laying means that parasitic eggs will be laid later in the temporal sequence of eggs added to the nest, and will have reduced fitness because of this. The resolution of this and other trade-offs can be effectively explored using only slight modifications to the framework presented here.

Appendix A – Stability of Equilibria

We proceed to show that all equlibria of the model are ESSs in the case when $C''(x^e + y^e) = 0$. We begin by finding revised expressions for the five derivatives of equations (18–22) using the precise reward function in equation (8). These are, respectively,

$$\frac{dV(x, \mathrm{y}; x^e, y^e)}{dx} = \frac{dU(x, y^m)}{dx} + \varepsilon y \frac{dW(x, y^m)}{dx} - C'(x + y) \tag{33}$$

$$\begin{aligned}\frac{dV(x, \mathrm{y}; x^e, y^e)}{dy} &= \varepsilon \frac{dU(x, y^m)}{dy} + ((1 - \varepsilon)W(x^e, y^m) + \varepsilon W(x, y^m)) \\ &\quad + y((1 - \varepsilon)\varepsilon \frac{dW(x^e, y^m)}{dy} + \varepsilon^2 \frac{dW(x, y^m)}{dy}) - C'(x + y)\end{aligned} \tag{34}$$

$$\frac{d^2V(x, \mathrm{y}; x^e, y^e)}{dx^2} = \frac{d^2U(x, y^m)}{dx^2} + \varepsilon y \frac{d^2W(x, y^m)}{dx^2} \tag{35}$$

$$\begin{aligned}\frac{d^2V(x, \mathrm{y}; x^e, y^e)}{dy^2} &= \varepsilon^2 \frac{d^2U(x, y^m)}{dy^2} + 2((1 - \varepsilon)\varepsilon \frac{dW(x^e, y^m)}{dy} + \varepsilon^2 \frac{dW(x, y^m)}{dy}) \\ &\quad + y((1 - \varepsilon)\varepsilon^2 \frac{d^2W(x^e, y^m)}{dy^2} + \varepsilon^3 \frac{d^2W(x, y^m)}{dy^2}) \\ &\approx 2\varepsilon \frac{dW(x^e, y^m)}{dy}\end{aligned} \tag{36}$$

$$\frac{d^2V(x, \mathrm{y}; x^e, y^e)}{dxdy} = \varepsilon \frac{d^2U(x, y^m)}{dxdy} + \varepsilon^2 y \frac{d^2W(x, y^m)}{dxdy} + \varepsilon \frac{dW(x, y^m)}{dx} \tag{37}$$

It is clear that all the equilibrium conditions are as in the simplified equations and that the only stability conditions that may be affected are those that involve equations (36) and (37), since the leading terms are of order ε. Thus the only equilibria that could be affected are $(0, y^e)$ and (x^e, y^e). Since $W(x^e, y^m)$ is decreasing with y expression (36) is negative and so if $(0, y^e)$ satisfies its equilibrium conditions it will be stable. Since both expressions (35) and (37) are negative their product is positive, and is of order ε. The square of expression (37) is also positive but of order ε^2, and so condition (12) is satisfied and whenever (x^e, y^e) is an equilibrium it is also an ESS.

Appendix B – Specific models

We consider four models of conspecific brood parasitism which have been published recently. It is shown that all are sub-models of our more general model. In particular we show how the parameters of these models relate to the more general model. Note that the parameters in the papers referred to sometimes have different labels and we have converted them into our standard format for ease of understanding.

3.1. Model A – Lyon (1998)

The model of Lyon (1998) argued that the "worth" of an egg to its parent can be thought of in terms of a "fitness increment" defined as survival of offspring from that egg minus the costs to producing it and any negative impact that the egg or its hatchling has on the survival of siblings because of competition for limited parental care. Thus every egg laid in the home nest yields a lower fitness increment than the last. Assuming that the average fitness increment that a parent can obtain from a parasitic egg is some positive value (P), after the clutch has reached a given size the increment falls below P and it is optimal to switch to laying parasitic eggs. Lyon's key prediction was that the number of eggs laid in a bird's own nest should be less under parasitism than in the absence of parasitism. There were no explicit functional forms in the model, so that we cannot completely specify it in our terminology. However it is clear that it falls within our more generalised structure; there is a clear laying sequence (hosts before parasites), the number of eggs a bird chooses to lay is governed by some global average parasite reward so that birds do not alter their behaviour using their own immediate experience. It is also recognised in Lyon (1998) that the parasite eggs will have a negative impact on both the host eggs and other parasites and so the author is thinking in similar terms to the later papers. In particular parameters are given in terms essentially of the form of equation (9), where it can be shown that $P = W(x^e, y^e) - C(y^e)/y^e$ and the increment of the j th egg laid is $U(j, y^e) - U(j-1, y^e) + C(y^e + j - 1) - C(y^e + j)$.

To analyse such a model more fully requires more precision as to the model components, but this was not needed in the original paper.

3.2. Model B – Broom & Ruxton (2002)

This paper modelled intraspecific brood parasitism, finding the optimal laying patterns and the effects of certain key features of the environment such as the probability of egg rejection, the within-brood competition and the position effect (earlier laid eggs were considered to have some advantage over later ones). It was assumed that all host eggs were laid first after which parasite eggs were laid, with nests chosen at random, so that the number of parasite eggs in each nest follows a Poisson distribution with parameter γy^e. There was a fixed cost to lay each egg. The parameters used were as follows:

$$C(z) = Cz, g_x(t) = \frac{(\gamma y^e)^{t-x} e^{-\gamma y^e}}{(t-x)!} t \geq x,$$

$$p_{x,t}(i) = \begin{cases} 1 & i \leq x \\ 0 & i > x, \end{cases} \qquad h(i,t) = \frac{V\beta^{i-1}}{1-\alpha^t}, \gamma = \eta$$

Increasing the effect of position, within-brood competition or the cost of egg production all lead to a greater tendency to parasitise. The effect of increasing the host's ability to reject eggs reduces parasitism, but not to the level anticipated.

3.3. Model C – Robert & Sorci (2001)

The model developed in this paper is intended to show how interspecific brood parasitism might begin from intraspecific parasitism. The paper develops a relatively simple model of intraspecific brood parasitism, finding the evolutionarily stable laying strategy and showing when this should lead to an abandonment of nest building. There are no formal costs to laying eggs, but birds have a maximum number that they can lay (and so they always lay this number). Parasites (implicitly) have a general idea of how many eggs are in a nest, and it is assumed that all nests end up with the same number of parasite eggs and the position of eggs within the nest is irrelevant.

$$C(z) = \begin{cases} 0 & z \leq n \\ M & z > n, \end{cases} \qquad g_x(x+y^e) = 1, \; h(i,t) = s(t), \; \gamma = 1$$

where M is some large positive number.

Two example functions of $s(t)$ are given $s(t) = e^{-rt}$, $s(t) = 1 - at (t < 1/a)$. The value of $p_{x,t}(i)$ is irrelevant due to the fact that $h(i,t)$ is independent of *i*, so that rewards do not depend upon an egg's position in the nest. Conditions are found when it is optimal to lay no host eggs and so abandon making a nest (note that this occurs only because of the discontinuity in $C(z)$ above).

3.4. Model D – Ruxton & Broom (2002)

This paper has a specific question to consider, that of whether the threat of parasitism should be met by the host reducing the number of eggs it lays to make room for them (as has been widely suggested) or whether there are times when the reverse strategy is true. Thus the model has been made as simple as possible, and in some ways is very similar to Robert and Sorci (2001). In particular the number of parasite eggs per nest is constant and there is no effect of position. There is a fixed cost per egg, as in Broom and Ruxton (2002).

$$C(z) = Cz, \; g_x(x + \gamma y^e) = 1, \quad h(i, t) = f(t), \quad \gamma = \eta$$

An example function of $f(t)$ is given, $f(t) = At^{-\alpha}$. The value of $p_{x,t}(i)$ is again irrelevant since there is no position effect. The paper shows that for any reasonable functional form of $f(t)$ (i.e. that $f'(t) < 0$) the total number of eggs that a bird may lay is greater if there is parasitism than if there is not, and that a bird should lay more eggs in its own nest if parasitism occurs, for at least some values of C. The paper finds the conditions when egg laying should be reduced, and also when it should be increased (to deter parasites).

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