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Citation: Harrison, M. D. & Broom, M. (2009). A game-theoretic model of interspecific brood parasitism with sequential decisions. Journal of Theoretical Biology, 256(4), pp. 504-517. doi: 10.1016/j.jtbi.2008.08.033

Link to published version: https://doi.org/10.1016/j.jtbi.2008.08.033

A game-theoretic model of interspecific brood parasitism with sequential decisions

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Abstract

The interaction between hosts and parasites in bird populations has been studied extensively. This paper uses game theoretic methods to model this interaction. This has been done in previous papers but has not been studied taking into account the detailed sequential nature of this game. We introduce a model allowing the host and parasite to make a number of decisions which will depend on a number of natural factors. The sequence of events begins with the host forming a nest and laying a number of eggs, followed by the possibility that a parasite bird will arrive at the nest; if it does it can choose to destroy a number of the host eggs and lay one of its own. A sequence of events follows, which is broken down into two key stages; firstly the interaction between the host and the parasite adult, and secondly that between the host and the parasite chick. The final decision involves the host choosing whether to raise or abandon the chicks that are in the nest. There are certain natural parameters and probabilities which are central to these various decisions; in particular the host is generally uncertain whether parasitism has taken place, but can assess the likelihood of parasitism based upon certain cues (e.g. how many eggs remain in its nest). We then use this methodology to model two real-world interactions, that of the Reed Warbler with the Common Cuckoo and also the Yellow Warbler with the Brown-Headed Cowbird. These parasites have different methods in the way they parasitize the nests of their hosts, and the hosts can in turn have different reactions to these parasites. Our model predictions generally match the real results well, and the model also makes predictions of the effect of changes of various key parameters on the type of parasitic interactions that should occur.

Introduction

Many species of bird parasitise others by laying their eggs in their nests (brood parasitism, e.g. Payne(1977)). It involves the introduction of an egg into a previously laid 'host' nest by a parasite. Sometimes such parasitism occurs within species (intraspecific) and sometimes the victims are other species (interspecific). Typically intraspecific parasites also form their own nest, but interspecific parasites do not, and are thus completely reliant on their hosts to raise their offspring, and are referred to as obligate brood parasites (Davies and de L. Brooke(1988)). There are six clades of birds which exploit the post-hatching care of other species; the old world cuckoos, the Clamator cuckoos, the new world cuckoos, the honeyguides, the Vidua finches and the Cuckoo-Finch Anomalospiza imberbis, and five species of cowbird (Sorenson and Payne(2005)). The reproductive biology of the brood parasites is broadly similar between species, but the behavior of their chicks differs in one key respect. Soon after hatching some parasite chicks (from the old world cuckoos, some of the new world cuckoos, the Cuckoo-Finch and the honeyguides) deliberately kill the host young, either by evicting them from the nest or by using their hooked bills to inflict lethal injuries. The remaining species do not do this, and generally at least one of their companions in the nest survives to fledge.

What is the cause of such differences in behaviour? One possibility is that species that do not kill host young either suffer from evolutionary lag or are not physically capable due to the relatively large size of host young. There is some strong evidence for evolutionary lag since the most recently evolved brood parasites tend to be those that do not kill chicks. However, there are exceptions. For example, the Brown-headed Cowbird Molothrus ater at times strategically evicts host offspring from the nest (Dearborn(1996)), and two old world cuckoo species appear to have lost the capacity to kill young.

An alternative explanation for the difference is to consider the possible costs that parasitic offspring may experience when they kill nest-mates, which might limit the evolution of host-killing (Kilner(2005)); for instance such a cost is an increased risk of desertion by the host parents (Langmore et al.(2003)). We shall consider a single interaction between a host and its parasite, which will involve potential strategic choices at different stages.

Several decisions can be made by the adult host and parasite and also by the parasite chick once it has hatched. These decisions include (for the host) ejection of the parasite egg (Payne and Payne(1998); Lowther(1995)), abandonment of the nest (Servedio and Hauber(2006)), or to continue to raise the clutch with the parasite intact (Lorenzana and Spencer(2001)). The adult parasite can decide to eject some or all of the host eggs whilst it lays a parasitic egg (Davies and de L. Brooke(1988)) or can just add the egg but otherwise leave the nest as it is (Lorenzana and Spencer(2001)).

There is a cost to the host in raising a parasite chick (Hoover(2003)), whether this be in the destruction by the parasite of its own chicks it has spent time to raise or in the increased cost of raising the parasite chick, (Kilner et al.(2004)). There are also costs in trying to resist parasitism (Davies et al.(2003)). For example, some parasites have evolved to the point where they are able to mimic the host egg to a good degree (Stokke et al.(1999)); this can cause the host to eject the wrong egg. There is also the possibility that it could also damage its own nest in trying to eject the parasite (Hoover and Reetz(2006)). Thus the host must balance the costs of resisting this parasitism with the potential benefits of resistance, the cost-benefit equilibrium (Winfree(1999)).

Significant mathematical modelling work in the brood parasitism field has been done by Takasu (Takasu(2005); Takasu et al.(1993); Takasu(1998)). Much of his work considered the dynamics of a whole population of hosts and/or parasites, focusing on the underlying genetics and the co-evolution between the host and parasite in the form of an arms race describing the adaptation of the level of rejection and mimic behaviour over time. Evolution typically occurs in the following stages. Firstly hosts neither recognize nor reject parasites and there is no mimicry. Then hosts establish defenses against eggs that look different. Since there is no mimicry the parasites may become extinct. Finally parasites evolve better mimicry forcing the host to raise rejection levels or give up rejection completely due to the associated costs. Takasu considers the possible outcomes from this co-evolutionary process in parasite and host behaviour, and in egg appearance. He also looks into the evolution of the host-parasite interaction over a succession of breeding seasons, as opposed to just one interaction or even one single breeding season. For related modelling work tying in both intraspecific and interspecific parasitism, see Yamauchi (1995).

Previous models of this behaviour have used game theoretical methods, for example (Maruyama and Seno(1999); Broom et al.(2008); Davies et al.(1996); Robert and Sorci(2001)). Pagel et al (1998) have provided a model of the evolution of ejector and non-ejector host birds, mostly in relation to cuckoos. Rodrguez-Girons and Lotem (1999) and Lawes and Marthews (2003) discuss the egg rejection problem with regards to parasitism rate and egg mimicry. Zink (2000) has modelled the behaviour of intraspecfic brood parasitism, looking at when this is beneficial to co-operative or solitary breeding . Schmidt and Whelan (1999) discuss the impact of nest predatation and brood parasitism and what level of defence should be allocated to each..

Some of these models are sequential in the sense that the parasite makes a decision, and the host reacts to that decision. Our intention is to capture the more complex interplay of host and parasite, which in reality involves a number of stages. We identify the sequence of events in the host-parasite interaction to create a game in the extensive form, which is then solved numerically.

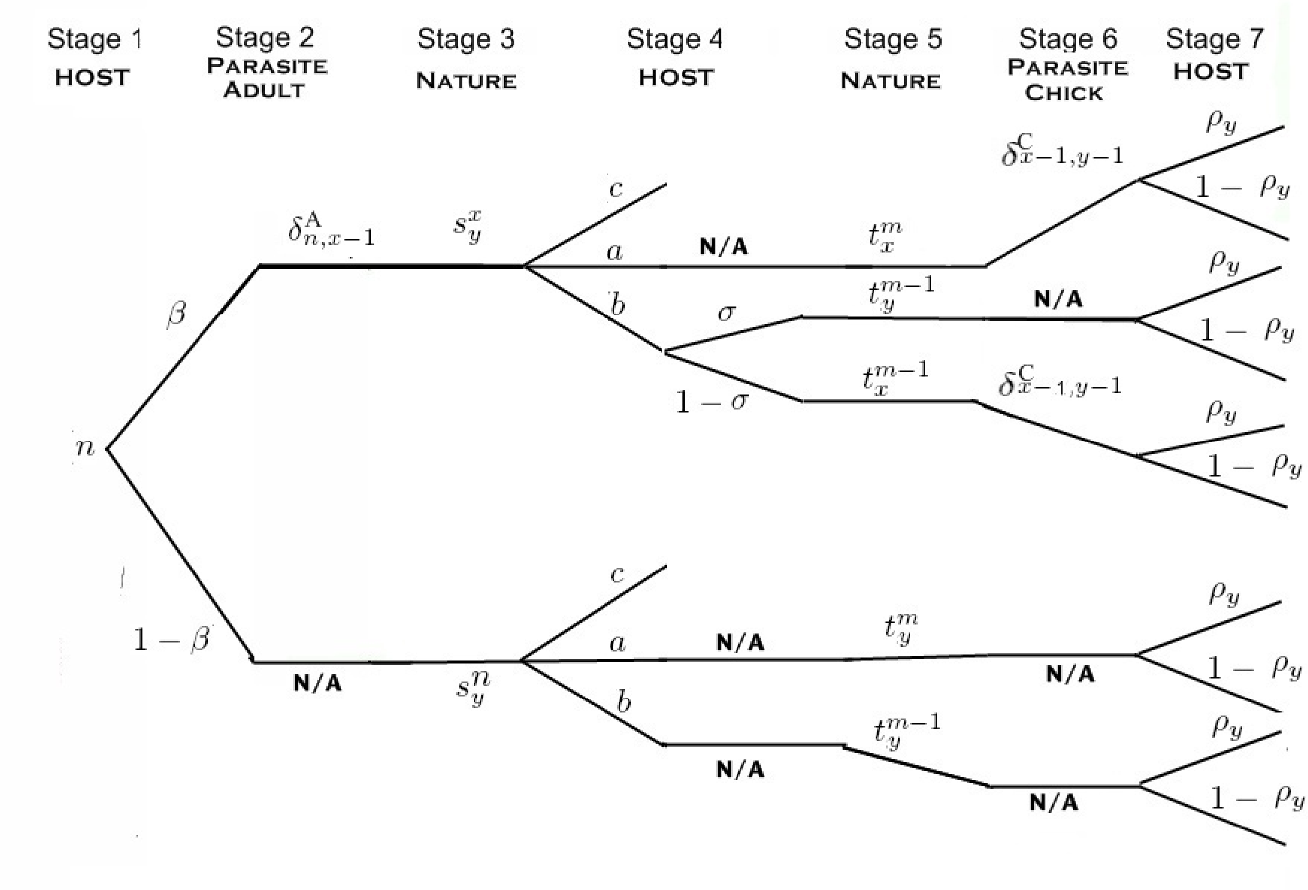

Fig. 1. Diagram of Decisions by Host and Parasite

The Model

We define the interaction in Figure 1. The first stage is a decision by the host bird at the beginning of the game to lay a certain number of eggs. After this occurs there is a period of time in which a single parasite can visit the nest. If it does then it decides whether to lay an egg. If it does lay an egg it also has the option to eject some of the host eggs from the nest. If it does not lay an egg then the host may continue just as if the parasite had not been there. Following this the host can make one of three decisions; it can abandon the nest, eject an egg in an attempt to remove the parasite and continue to nurture the nest, or just continue to nurture the nest. This then goes on to the hatching stage; once the eggs hatch the parasite chick makes another decision whether to destroy/eject/bury any number of the host chicks or unhatched eggs. The final decision is that of the host whether to raise the brood depending on the number of chicks in the nest and the likelihood that it is raising a parasite.

The problem we must solve when looking at this model is the fact that at any stage the host does not know where it is on the game tree. For example if there are four eggs in the nest in the middle of the game, are they all host eggs, or is one of them a parasite? It will make its decision based upon the probability that there is a parasite given the number of eggs observed. Thus the standard dynamic programming methods will not work as information sets contain more than a single point on the tree, and we have a game of imperfect information where not only is the position on the tree uncertain, but the probability of being in certain positions depends upon earlier decisions. There is thus an interaction between earlier and later decisions, with the optimal choice in each depending on that in the other.

$\boxed{\text{S1}}$ This is the first and overall main decision by the host, which is the choice of how many eggs (n) to lay at the beginning of the cycle, which can theoretically be anything from one upwards. Of course in practice there will be a certain maximum number the host will be able to lay, but at this stage we shall allow for any number, and the host will be prevented from laying large numbers by increasingly prohibitive costs. At this point the host will incur a laying cost which we shall call $C_L(n)$. Biologically speaking this cost represents the use of resources in laying eggs in the current nest at a cost to other activities which may affect survival or the ability to lay more eggs at a later date when perhaps the situation is better for the host.

$\boxed{\text{S2}}$ The value β is the probability that a parasite visits the nest and lays an egg. In the case where there is no parasite we skip to S3. Stage 2 is the decision as to whether the adult parasite will destroy some, all or none of the host eggs and lay one of its own. This decision by the parasite will be denoted as $\delta^A_{n,x-1}$, where a value for $\delta^A_{n,x-1}$ will be given for all $x \in (1, n+1)$. These values will signify the probability that if the adult parasite sees n eggs it will destroy $n-x-1$ to leave x (including its own), therefore $\sum_{x=1}^{n+1} \delta^A_{n,x-1} = 1$. It will usually be the case that for one value of x, $\delta^A_{n,x-1} = 1$ and for the rest this will be zero. If it does destroy down to a total of x eggs it will incur the cost $C_{DA}(n-x-1)$, the cost of destruction for the adult parasite. This relates to the fact that the parasite must make an effort in order to destroy some of the host eggs; this could relate to a loss of energy or time. The loss of time could be important as this may lead to the parasite being discovered by the host. Similarly, the more the nest is disturded, the greater the chance of alerting the host.

$\boxed{\text{S3}}$ This is the first of two natural destruction stages, and it affects both host eggs and the one parasite egg (if there is such an egg). If there are x host eggs in the nest and no parasite then the probability that y host eggs survive is given as s^x_y. If the nest has $x-1$ host eggs plus a parasite, we set the probability that y of those eggs are left after S3 again as s^x_y. If y eggs are left in total at this point then we assume that the parasite has a probability of survival of $\frac{y}{x}$ (i.e. the parasite has the same chance of survival as each host egg). This means that the overall probability of survival for the parasite is $\sum_{y=0}^{x} s^x_y \frac{y}{x}$.

Natural destruction could occur due to nest predation, bad weather or poor parental care. If it is predation, usually the whole nest will be lost, and an alternative idea would be to simplify our model by allowing only no or full destruction. However, we want to maintain the flexibility of a more general model.

$\boxed{\text{S4}}$ This is a decision that occurs by the host before hatching. This occurs a while after laying when some natural destruction may have occurred and is in the time-period after which any parasite must have arrived (a later parasite's egg would not hatch, because host incubation is too far advanced). The host makes one of three decisions:

(a) Leave the nest alone, so choosing $a = 1$. This means that the host will do nothing and leave the nest as it is.
(b) Eject one egg ($b = 1$). If the host believes there may be a parasite then it can eject one egg, which will be the correct egg (the parasite) with probability σ, if there is indeed a parasite.
(c) Abandon the nest ($c = 1$).

We label the number of eggs remaining at the end of this stage m.

$\boxed{\text{S5}}$ This is the second natural destruction stage and has the same basis as S3, however we label the probability of destruction as t^m_x.

$\boxed{\text{S6}}$ This is a decision by the parasite chick to destroy a number of the eggs or chicks. We use the term $\delta^C_{x-1,y-1}$ to define the decision to destroy $x-y$ eggs (i.e. $\delta^C_{x-1,y-1} = 1$ iff $x-y$ are destroyed, and otherwise $\delta^C_{x-1,y-1} = 0$), so leaving $y-1$ host eggs (so y eggs in total) in the nest if there are $x-1$ host eggs in the nest at this stage. If it does this then as before it will incur the cost $C_{DC}(x-y)$. This cost could be described as before both in terms of the amount of energy exerted to destroy or eject an egg, or the time in which it takes to eject an egg. The time factor may be important because it may result in detection by the adult which we would then assume may kill the parasite chick or abandon the nest.

$\boxed{\text{S7}}$ This is the final decision of the host whether to raise the full brood or not. If the number of eggs that have made it to this stage is y, then it will incur a cost of $C_R(y)$ if it chooses to raise. The parasite will receive a reward depending on how many host eggs there are in the nest. This is denoted as $R_P(y-1)$. The host will receive a reward depending on how many of its own eggs make it to this stage, denoted $R_H(y)$. The host's decision will be denoted by ρ_y, the probability that given there are y chicks in the nest at this final stage, the host will raise them. In most cases this probability will

TABLE I

TABLE OF PARAMETERS

Parameter	Description
$R_H(x)$	Reward to the host for having x chicks in the nest at the end of the game
$R_P(x)$	Parasite reward when there are x host chicks with the parasite at the game's end
$C_R(x)$	Cost to the host for raising x chicks in the nest at the end of the game
$C_L(x)$	Cost to the host for laying x eggs in the beginning of the game
C_a	Cost of abandoning the nest in the middle of the game
C_b	Cost of abandoning the nest at the end of the game
C_E	Cost to the host if it chooses to eject an egg
$C_{DA}(x)$	Cost to the parasite adult for destroying x host eggs
$C_{DC}(x)$	Cost to the parasite chick for destroying x host chicks
ξ	The relative demand on resources of a parasite chick to a host chick
β	Probability that a parasite will visit the nest and lay an egg
s_y^x	Probability that if there are x eggs all but y will be destroyed (Adult Game)
t_x^m	Probability that if there are m eggs all but x will be destroyed (Chick Game)
σ	Probability that the host correctly recognizes the parasite if it chooses to eject in S4
n	Decision of the number of eggs to lay in S1
ρ_y	Decision to raise or not if there are y chicks left at the end
a	Decision to leave the nest alone in S4 (i.e. $a = 1 \Rightarrow$ nest is left alone)
b	Decision to eject one egg in S4 (i.e. $b = 1 \Rightarrow$ eject one egg)
c	Decision to abandon the nest in S4
$\delta_{n,x-1}^A$	Decision by the parasite adult to destroy $n - x$ eggs leaving $x - 1$ host eggs
$\delta_{m-1,x-1}^C$	Decision by the parasite chick to destroy $m - x$ chicks leaving $x - 1$ host chicks

either be one or zero. Where $\rho_y = 1$ it means that the host will always raise if there are y chicks in the nest and where $\rho_y = 0$ it means that the host will never raise if there are y chicks in the nest. The fitness cost to raising the parasite may be higher for a host parent than the cost of raising a chick of its own, this extra cost being denoted by ξ, so that the cost of the parasite chick is equivalent to ξ host chicks. Thus if there is a parasite the cost to the host becomes $C_R(y - 1 + \xi)$. This cost represents the physical exertion the host must put out in order to feed and otherwise raise the brood. Obviously the larger the brood the more food it will have to gather and the harder it will be to get the whole brood raised, and this cost may be in decreased probability of successful raising of the brood, or in its own survival chances.

Note that we allowed egg ejection in Stage 4 but not in Stage 7. As shown in Planque et al (2001) chick-rejection is not cost effective and is also not seen in nature. So for the purposes of simplicity we discard the possibility of ejecting the chick.

Breaking the model down

As we stated earlier this cannot be broken down using the standard dynamic programming methods directly, however it is possible to solve this problem numerically, by feeding forward information from the start of the game with various possibilities, and finding consistent solutions when feeding back from the end of the game in the standard way. This is illustrated in Figure 2. In order to compute this model we break it down into two games. One which runs from S4 to S7 which we shall call the Chick Game and another which runs from S1 to S4 which we shall call the Adult Game. This will mean there is an interaction between the games at S4, where the decision in S4 will be determined by the outcomes and decisions in the stages after this. The decisions made in S1 and S2 will be determined by the expected outcome of the given decision in S4.

The Chick Game

In this game we require the probability that a parasite chick has made it to stage S4; we call this probability α, which we evaluate in the next section. We finally look at the decision made in S7 and in particular the value of $r(x)$, the expected reward for raising a clutch containing x chicks given that y eggs made it to the start of the chick game (whether this contains a parasite being unknown to the host) . To do this we break down the value of r(x) into four possibilities; firstly where there was no parasite and then when there is a parasite combined with the three possible host decisions given by $a = 1$ ($b = 0$), $b = 1$ ($a = 0$) and $a = b = 0$ (meaning that $c = 1$ and the decision to abandon was taken). For example $H_a(x)$ is the expected reward to a host if it chooses to raise a clutch of size x, conditional on there originally having been a parasite and the host having made the decision to raise at stage 4. This factors in the various possible events between stages 4 and 7 which could have led to the clutch size reaching x (natural as well as parasite induced) to find the probability of there being a parasite present.

The outcome for the host in the chick game given there is no parasite in the nest is

$$H_0(x) = at_x^y(R_H(x) - C_R(x)) + bt_x^{y-1}(R_H(x) - C_R(x)) - cC_a \tag{1}$$

The outcome for the host in the chick game given there is a parasite in the nest and the decision at Stage 4 is a=1 is

$$\begin{aligned} H_a(x) = \sum_{z=x}^{y} t_z^y(\frac{z}{y}\delta^C_{z-1,x-1}(R_H(x-1) - C_R(x+\xi-1)) \\ + t_x^y\left(1 - \frac{x}{y}\right)(R_H(x) - C_R(x)) \end{aligned} \tag{2}$$

The outcome for the host in the chick game given there is a parasite in the nest and the decision at Stage 4 is b=1 is

$$\begin{aligned} H_b(x) &= \sigma t_x^{y-1}(R_H(x) - C_R(x)) \\ &+ (1-\sigma)\Bigg(\sum_{z=x}^{y-1} t_z^{y-1}\frac{z}{y-1}\delta^C_{z-1,x-1}(R_H(x-1) - C_R(x+\xi-1)) \\ &+ t_x^{y-1}(1 - \frac{x}{y-1})(R_H(x) - C_R(x))\Bigg) \end{aligned} \tag{3}$$

The outcome for the host in the chick game if the decision at Stage 4 is c=1 is

$$H_c(x) = -C_A$$

Therefore

$$r(x) = (1-\alpha)H_0(x) + \alpha(aH_a(x) + b(H_b(x) - C_e) + (1-(a+b))H_c(x)) \tag{4}$$

We can also work out the outcome for the parasite in *Stage 6* given the different decisions, where we assume that m eggs have made it to *Stage 5*. We also assume that x eggs have made it to *Stage 6* with the parasite surviving with probability $\frac{x}{n}$. So the outcome for the parasite if it chooses to destroy $x-y$ eggs to leave y is

$$\Pi_{x,y} = \rho_y R_P(y) - C_{DC}(x-y) \tag{5}$$

where $\Pi_{x,y}$ is the reward to a parasite chick given that it survived to *Stage 6* as one of x eggs and chooses to destroy down to a total of y. In general we will use the symbol Π to represent the reward to the parasite. In particular in addition to $\Pi_{x,y}$, we define Π to be the overall reward to the parasite at the start of the game, $\Pi(x)$ as the expected reward for the parasite if x eggs are in the nest at the start of the Chick game and Π_Γ as the expected reward to the parasite chick given that it survives to *Stage 6* and that it plays the strategy vector Γ (prior to the number of surviving eggs being known).

We can then use this in turn to find the optimal decision for the host in Stage 4.

The Adult Game

We have to use backward induction again to evaluate the Adult Game and we need to look at S4 and with this the Chick Game. In particular we need to work out the decision made at S4 by the host. The host will then make the decisions in the later stages based upon the outcomes from the Chick game. This outcome depends upon the value of α. Using conditional probability we can deduce

$$\alpha = P(Parasite|\, x\, eggs) = \frac{P(Parasite\,\&\, x\, eggs)}{P(x\, eggs)}$$

There are different possibilities of how there came to be x eggs at *Stage 3*, given that n host eggs were laid.

Firstly, there was no parasite in the nest at all and all the destruction was natural, occurring with probability

$$\alpha_0 = (1-\beta)s_x^n$$

Secondly, there was a parasite and the destruction was caused in part by the parasite and in part by nature with the parasite egg not destroyed, occurring with probability

$$\alpha_1 = \beta \sum_{k=x-1}^{n} \delta_{n,k}^A s_x^{k+1} \left(\frac{x}{k+1}\right)$$

Thirdly, there was a parasite and the destruction was caused in part by the parasite and in part by nature with the parasite egg destroyed

$$\alpha_2 = \beta \sum_{k=x}^{n} \delta_{n,k}^A s_x^{k+1} \left(1 - \frac{x}{k+1}\right)$$

This means we have

$$\alpha = \frac{\alpha_1}{\alpha_0+\alpha_1+\alpha_2} \tag{6}$$

This will then give us an outcome for S4 onwards and thus we can find the decision made at S4 by the host. From this we can work out the best decision for the parasite at S6 and so on. We get the following outcome for the parasite if it destroys down to x eggs at Stage 2

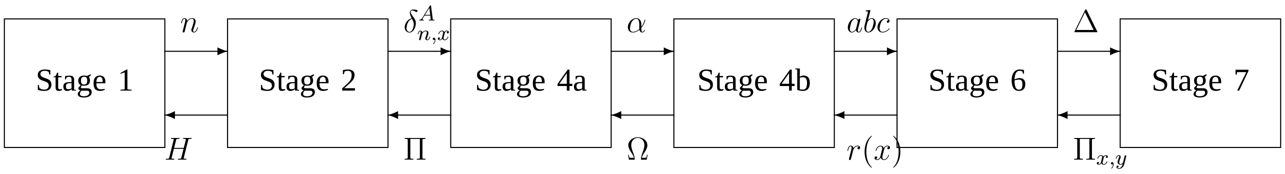

Fig. 2. Stages of the computer program

$$P(n,x) = \sum_{y=0}^{x} s^x_y \frac{y}{x}(a_y\Pi(y-1) + b_y(1-\sigma)\Pi(y-2)) - C_{DA}(n-x-1) \tag{7}$$

where $a_y = 1$ means that the decision from the host in S3 is to leave the nest alone and $\Pi(x)$ is as described above. If the host will never raise a brood this could result in a negative outcome for the parasite, however this also results in a game where the host will never raise any of its own chicks, which would most likely mean a nest will not be formed in the first place. This scenario is unlikely, therefore, to correspond to any real situation; in particular the parasite will not make a decision which the host will follow by not raising.

Once we know the decision by the parasite we can also work out the decision from the host in S1.

$$H(n) = (1-\beta)\sum_{y=0}^{n} s^n_y\Omega(y) + \beta\sum_{x=0}^{n}\delta^A_{n,x}\sum_{y=0}^{x} s^x_y\Omega(y) \tag{8}$$

where $\Omega(x)$ is the expected reward to a host in Stage 4 when there are x eggs.

Computing the Model

Real clutch sizes can be large (up to about 30 chicks for some species) so the set of possible sequences of events can be extremely large. We have written a set of programs using MATLAB version 7 to compute our solutions. We created six programs with one feeding information into another, starting from the end of the game first and working backwards. This is illustrated in Figure 2. The arrows pointing left to right represent information being fed into later stages of the program, those from right to left represent the dynamic programming method of finding optimal decisions based upon later ones.

Stage 7

In this part we have all the information necessary to calculate the values of $r(x)$ for the host as shown in the previous section. This will also allow us to find the optimal values of ρ_x for each of the possible values of x. All we need to do is compare each $r(x)$ to $-C_b$. If it is bigger then we set $\rho_x = 1$, and if it is not then $\rho_x = 0$.

Stage 6

Assume that m eggs have reached *Stage 4* and if i eggs are left after natural destruction then the parasite will choose to destroy leaving γ_i host chicks. We denote Γ as the vector

$$\Gamma = [0, \gamma_1, \gamma_2, \ldots, \gamma_{m-1}] \tag{9}$$

We need to find the best choice of Γ for the parasite. The easiest way to do this (mathematically) is to feed all possible values of Γ

$$\begin{array}{cccccc}
0 & 0 & 0 & \dots & 0 & 0 \\
0 & 0 & 0 & \dots & 0 & 1 \\
\vdots & & & & \vdots & \\
0 & 1 & 2 & \dots & m-2 & m-2 \\
0 & 1 & 2 & \dots & m-2 & m-1
\end{array}$$

into the *Stage 7* program to calculate the expected outcome for every possible decision. Then we select the one which gives the best outcome for the parasite chick.

Note that there is a relationship between the γ's and the δ^C's. The γ's are the actual number of host chicks the parasite will choose to destroy given a number i whereas the δ^C's represent a binary decision. I.e. Does the parasite destroy down to x eggs if there are i in the nest. So if $\gamma_i = x$ then this means $\delta^C_{i,x} = 1$ with $\delta^C_{i,y} = 0$ for all $y \neq x$.

Definition 1: We define Γ^* as the value of the vector Γ which yields the largest outcome for the parasite chick.

However since there are $m!$ possible variations of Γ, this poses problems for use on a computer. If $m = 8$ this means we have to run the code 40320 times, which takes approximately 3 minutes using a standard PC. However potentially we need to be able to calculate for much larger values of m, up to about 30 since some hosts will lay this many eggs, and we would have to run the code 2.6525×10^{32} times. We use an alternative process instead, as follows.

Initially we choose

$$\Gamma = [0, 0, 0, \dots, 0]$$

and calculate the best outcome for place $m-1$

$$\begin{array}{cccccc}
0 & 0 & 0 & \dots & 0 & 0 \\
0 & 0 & 0 & \dots & 0 & 1 \\
\vdots & & & & \vdots & \\
0 & 0 & 0 & \dots & 0 & m-2 \\
0 & 0 & 0 & \dots & 0 & m-1
\end{array}$$

We select the best of these for the parasite $(0, 0, \dots, \gamma'_{m-1})$ and move to the $m-2^{th}$ position.

$$\begin{array}{cccccc}
0 & 0 & 0 & \dots & 0 & \gamma'_{m-1} \\
0 & 0 & 0 & \dots & 1 & \gamma'_{m-1} \\
\vdots & & & & \vdots & \\
0 & 0 & 0 & \dots & m-3 & \gamma'_{m-1} \\
0 & 0 & 0 & \dots & m-2 & \gamma'_{m-1}
\end{array}$$

We continue down the zero, obtaining

$$\Gamma' = (\gamma'_0, \gamma'_1, \dots, \gamma'_{m-1})$$

This lowers the amount of γ's we check from $m!$ to $\sum_{x=0}^{m-1} x = \frac{m(m-1)}{2}$ or in the case of $m = 30$ from 2.6525×10^{32} to 435.

We proceed to show that (under reasonable conditions) this estimated $\gamma^{'}$ is the same as the *true* γ for our system.

Theorem 1: If $R_H(x-1) - C_R(x-1+\xi) < 0$ then $\Gamma^* = \Gamma^{'}$, for all $1 \leq x \leq m$.

The condition $R_H(x-1) - C_R(x-1+\xi) < 0$ for all x means that the parasite has a sufficiently large detrimental effect that the host will always have a negative outcome. Thus if the host was certain that there was a parasite present, abandonment would be the best policy.

Note that Γ^* and $\Gamma^{'}$ are not always equal because the chick rejection strategy of the parasite chick affects the probability that a nest with a certain number of chicks actually contains a parasite. Accordingly, any elements of the parasite strategy set can affect a decision of the host against any number of chicks.

Proof: The proof is by induction.

1) First of all we prove that if $[0, \gamma_1, \gamma_2, \ldots, \gamma_{m-1}]$ is the true solution that the first cycle will produce $[0, 0, 0, \ldots, 0, \gamma_{m-1}]$ in the *quick* solution. i.e. $\gamma'_{m-1} = \gamma_{m-1}$.
If we set $\Gamma^* = [0, \gamma_1, \gamma_2, \ldots, \gamma_{m-1}]$ (the true solution) and $\Gamma' = [0, 0, 0, \ldots, 0, \gamma'_{m-1}]$, we get the following outcomes for Π_γ and $\Pi_{\gamma'}$.

$$\begin{aligned}\Pi_{\Gamma^*} &= \sum_{x=1}^{m} t_x^m \sum_{y=1}^{x-1} \delta^C_{x-1,y-1}(\rho_y R_p(y-1) - C_{DC}(x-y)) \\ &= t_m^m(\rho_{\gamma_{m-1}+1} R_p(\gamma_{m-1}) - C_{DC}(m-\gamma_{m-1})) \\ &\quad + t_{m-1}^m(\rho_{\gamma_{m-2}+1} R_p(\gamma_{m-2}) - C_{DC}(m-1-\gamma_{m-2})) \\ &\quad + \cdots + t_1^m(\rho_{\gamma_1} R_p(0) - C_{DC}(0))\end{aligned} \tag{10}$$

$$\begin{aligned}\Pi'_{\Gamma} &= \sum_{x=1}^{m} t_x^m \sum_{y=1}^{x-1} \delta^{C'}_{x-1,y-1}(\rho_y R_p(y-1) - C_{DC}(x-y)) \\ &= t_m^m(\rho_{\gamma'_{m-1}+1} R_p(\gamma'_{m-1}) - C_{DC}(m-\gamma'_{m-1})) \\ &\quad + \sum_{x=0}^{m} t_x^m(\rho_1 R_p(0) - C_{DC}(x-1))\end{aligned} \tag{11}$$

where the δ^C's come from the γ's in Γ^* and the $\delta^{C'}$'s come from the γ''s in Γ' as previously described. The only place where both γ_{m-1} and γ'_{m-1} appear is in the first term of each expression. So the best choice of γ'_{m-1} will be the same as the true value as long as $\rho_{\gamma_{m-1}+1} = \rho_{\gamma'_{m-1}+1}$.
So we must look at the host outcome in Stage 7. Without loss of generality we assume $a = 1$ (an almost identical argument works for $b = 1$). We also need only to look at the parts where the decision of the parasite affects the decision in this final stage. Note if $\rho_x = 0\ \forall x \in (0, y)$ then it is clear that $\gamma_y = \gamma'_y = y$ since the host will never raise.
Here the outcome for the host is $r(x) = H_0(x) + \alpha H_a(x)$ where

$$H_0(x) = (1-\alpha)\left(a t_x^m (R_H(x) - C_R(x))\right) \tag{12}$$

is not affected by the parasite and

$$\begin{aligned}H_a(x) = &\sum_{z=x}^{m} t_z^m \frac{z}{m} \delta^C_{z-1,x-1}(R_H(x-1) - C_R(x+\xi-1)) \\ &+ t_x^m (1 - \frac{x}{m})(R_H(x) - C_R(x)).\end{aligned} \tag{13}$$

The only part of $r(x)$ affected by the parasite is $\sum_{z=x-1}^{m} t_z^m \frac{z}{m} \delta_{z-1,x-1}^C (R_H(x-1) - C_R(x+\xi-1))$ and we shall denote $r(x)$ minus this expression by r_{NP}. In addition we shall also assume $r_{NP} > 0$, since otherwise unparasitised nests would not be profitable.
With the given values from Γ^*, the above formula rearranges to

$$t_m^m(R_H(\gamma_{m-1}-1)-C_R(\gamma_{m-1}+\xi-1))+\sum_{x=\gamma_{x+1}}^{m-2} t_{x-1}^m \frac{x-1}{m} \delta_{x,\gamma_x-1}^C (R_H(\gamma_x-1)-C_R(\gamma_x+\xi-1)) \tag{14}$$

We also assume that this is bigger than $C_b - r_{NP}$, since otherwise $\rho_{\gamma_{m-1}} = 0$, which contradicts our assumption that the host will raise. Looking at the value for Γ', we only need consider

$$t_m^m(R_H(\gamma'_{m-1}-1) - C_R(\gamma'_{m-1}+\xi-1)) \tag{15}$$

Therefore we get out the same result for $\rho_{\gamma_{m-1}}$ as long as

$$t_m^m(R_H(\gamma_{m-1}-1) - C_R(\gamma_{m-1}+\xi-1)) \geq C_b - r_{NP} \tag{16}$$

Since we have assumed $R_H(\gamma_x-1) - C_R(\gamma_x+\xi-1) < 0$, the summation part of (14) is also negative, meaning the inequality in (16) holds.

2) Now we must perform the induction step.
Let us suppose that we have found some values of Γ' and that these are identical to the equivalent terms in Γ^* i.e. all the $\gamma'_i = \gamma_i$ for all $i \in (x, m-1)$. We then consider γ'_{x-1} from

$$\Gamma' = [0, 0, \ldots, \gamma'_{x-1}, \gamma_x, \ldots, \gamma_{m-1}] \tag{17}$$

The new value for $\Pi_{\gamma'}$ is

$$\Pi_{\Gamma'} = \sum_{y=1}^{m} t_y^m \sum_{z=1}^{y-1} \delta_{y-1,z-1}^C (\rho_z R_p(z-1) - C_{DC}(y-z)) \tag{18}$$

Since we know all of the values of $\delta_{y-1,z-1}^C$ we can substitute these in giving

$$\begin{aligned}\Pi_{\Gamma'} \quad &= \sum_{y=x}^{m} t_x^m(\rho_1 R_p(0) - C_{DC}(y-1)) \\ &+ t_x^m(\rho_{\gamma'_x+1} R_p(\gamma'_{x-1}) - C_{DC}(m-\gamma'_{x-1})) \\ &+ \sum_{y=1}^{m} t_x^{y-1}(\rho_1 R_p(0) - C_{DC}(y-1))\end{aligned} \tag{19}$$

We can break this up into the first term, which is the same as in the *true* solution, and the second and third terms, which could (potentially) affect the decision of the host in Stage 7. We again have a situation where we need to check if $\gamma_y = \gamma'_y$. We shall look at the outcome for the host for Γ^*, and again w.l.o.g. we assume $a = 1$ and only look at the part which involves the parasite

$$\begin{aligned}&\sum_{z=x}^{m} t_z^m \frac{z}{m}(R_H(\gamma_{x-1}-1) - C_R(\gamma_{x-1}+\xi-1)) \\ &+ t_x^m \frac{x}{m}(R_H(\gamma_{x-1}-1) - C_R(\gamma_{x-1}+\xi-1)) \\ &+ \sum_{z=0}^{x+1} t_{z+1}^{m+1} \frac{z+1}{m+1}(R_H(\gamma_x-1) - C_R(\gamma_x+\xi-1))\end{aligned} \tag{20}$$

which is assumed to be greater than $C_b - r_{NP}$.
We obtain the outcome for Γ' as

$$\sum_{z=x}^{m} t_z^m \frac{z}{m}(R_H(\gamma'_{x-1}-1)-C_R(\gamma'_{x-1}+\xi-1)) \tag{21}$$

$$+t_x^m \frac{x}{m}(R_H(\gamma'_{x-1}-1)-C_R(\gamma'_{x-1}+\xi-1)) \tag{22}$$

which is the same as the expression for Γ^* in equation (20) except for terms which, under the assumption of the theorem, do not affect the optimal decision. Hence the theorem is proved.

■

Stage 4b

Now we calculate which is the best choice for the host in *Stage 4*. We know the value of α which is fed in by *Stage 4a*. We assume $a = 1$ then work out the outcome for both host and parasite in the later stages, then assume $b = 1$ and do the same. Finally we compare the expected outcomes for the host against each other and against $-C_A$ (the outcome for $c = 1$) to work out the best choice, which is the one with the largest outcome.

Stage 4a

Given the decision for the host in *Stage 1* and for the parasite in *Stage 2*, we now need to know the expected outcome for both in the chick game. For this we need to work out the outcome for both in the later stages for every possible number of eggs which can reach these later stages. For every $y \in (0, x)$ (where $x - 1$ is the number of host eggs the parasite chooses to leave) we calculate a value for α based upon the equations in the previous section, then use this and feed it into the later games. We then take all these values and work out both $H(n)$ and $P(n, x)$.

Stage 2

Given the value for n from *Stage 1* we just work out which value of x maximizes the outcome for $P(n, x)$.

Stage 1

For this stage we set a sensible maximum for the number of host eggs to lay. Then we calculate the expected outcome $H(n)$ for each n.

Example Calculations

Stage 6

Since *Stage 7* is just a calculation we can look initially at *Stage 6*. At this stage we have a value for n and α, we assume that all $n = 4$ eggs have made it as well as a parasite with probability $\alpha = 0.1$. We also

TABLE II

WORKED EXAMPLE VARIABLES.

Parameter
$R_H(x) = x$
$C_R(x) = 0.25e^{\frac{x}{2}}$
$C_L(x) = \frac{x}{100}$
$C_A = 0$
$C_e = 0.26$
$R_P(x) = e^{\frac{-x}{10}}$
$C_{DA}(x) = \frac{x}{100}$
$C_{DC}(x) = \frac{x}{100}$
$\sigma = 0.68$
$\beta = 0.06$
$s_n^n = 0.99$ and $s_x^n = \frac{0.01}{n} \forall x < n$
$t_n^n = 0.99$ and $t_x^n = \frac{0.01}{n} \forall x < n$

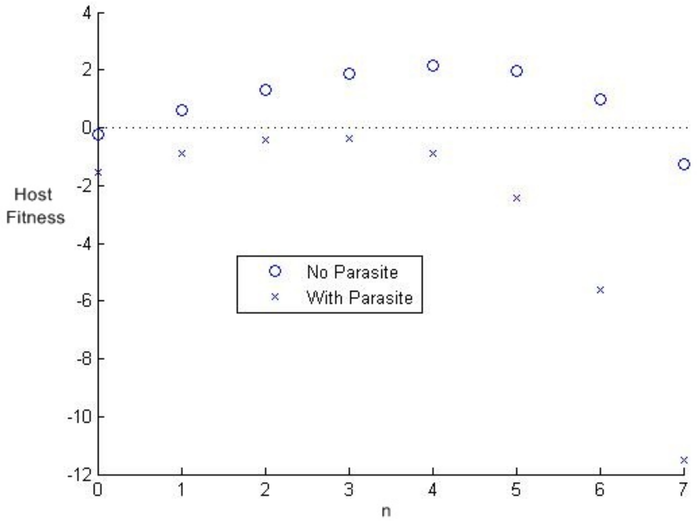

Fig. 3. Graph of host fitness for a given final number of host chicks for both the cases with and without a parasite chick, i.e. Comparing $R_H(X) - C_R(X)$ with $R_H(X-1) - C_R(X-1+\xi)$ where $R_h(x) = x, C_R(x) = 0.25e^{x/2}, \xi = 2$

assume that $a = 1$.

So now we need to work out the best γ for the parasite chick. We start off by looking at

$$\Gamma = [0, 0, 0, 0]$$

meaning that the parasite will destroy all the host eggs in every situation. For this we get the following value for r.

$$r = [-0.0752, 0.0030, 0.0043, 1.9607, 0]$$

where this is the vector containing the values for $r(x)$ for each x from one to five (four hosts and a parasite), the value for five being zero because here the parasite always destroys the host's eggs. These are the expected outcomes for the host for each x; the outcome for 5 chicks is zero because there can never be five chicks due to the earlier parasite decision.

TABLE III

Outcomes of varying elements of γ

Γ	r	ρ	Host Outcome	Parasite Outcome
First Check				
$[0,0,0,0,4]$	$[0, 0.0010, 0.0030, 0.0043, 1.9607, -0.1673]$	$[0,1,1,1,1,0]$	1.9691	0.0079
$[0,0,0,0,3]$	$[0, 0.0010, 0.0030, 0.0043, 1.9160, 0]$	$[0,1,1,1,1,0]$	1.9244	0.7314
$[0,0,0,0,2]$	$[0, 0.0010, 0.0030, -0.0049, 1.9607, 0]$	$[0,1,1,0,1,0]$	1.9648	−0.0119
$[0,0,0,0,1]$	$[0, 0.0010, -0.0237, 0.0043, 1.9607, 0]$	$[0,1,0,1,1,0]$	1.9661	−0.0218
Second Check				
$[0,0,0,3,3]$	$[0, 0.0012, 0.0030, 0.0043, 1.9160, 0]$	$[0,1,1,1,1,0]$	1.9245	0.7309
$[0,0,0,2,3]$	$[0, 0.0012, 0.0030, 0.0043, 1.9160, 0]$	$[0,1,1,1,1,0]$	1.9245	0.7311
$[0,0,0,1,3]$	$[0, 0.0012, 0.0030, 0.0043, 1.9160, 0]$	$[0,1,1,1,1,0]$	1.9245	0.7312

TABLE IV

Outcome for different Stage 4 Decisions

Stage 4 Decision	Best Γ	Host Outcome	Parasite Outcome
a	$[0,0,0,0,3]$	1.9244	0.7314
b	$[0,0,0,0]$	1.7468	0.9583
c	NA	0	0

This equates to the following ρ

$$\rho = [0, 1, 1, 1, 0]$$

where we give the value $\rho_y = 1$ if it will raise and $\rho_y = 0$ if it does not. Thus in this case the host will raise if the nest contains 2,3 or 4 eggs, but not 1; (note that 5 eggs cannot occur here). The outcome for the host is 1.9680 and the parasite's outcome is $-.0397$. We then need to compare this to the outcome for values of Γ where the entry in the final position is different. We see that the best outcome for the parasite in this case is

$$\Gamma = [0, 0, 0, 0, 3]$$

So we move on and check this against values of Γ with 3 in the final position, for the different possibilities in the penultimate position. The best outcomes occurs for our original Γ. Note that it appears as if the outcome for the host does not change at all (see Table III). However, this is because of the rarity in which the differing strategies lead to different behaviour in practice, and there are in fact small differences. For examples the strategies $[0, 0, 0, 3, 3]$ and $[0, 0, 0, 2, 3]$ only lead to different behaviours with probability $\alpha \times t_3^4 \times 3/4 = 0.06 \times 0.01 \times 0.75 = 0.00045$ for our example. In fact it turns out that this chosen value of Γ is the best choice overall for the parasite.

Stage 4b

Suppose that we again assume that $\alpha = 0.1$. We need to work out which is the best choice at Stage 4, and so we need to find the outcome for a, b, or c.

It is clear from Tables IV and V that the host will choose a in this case. It is worth noting that the parasite reward for $b = 1$ is the largest of the three possibilities in this example, which is initially surprising as this is when the host attempts to remove the parasite by ejecting a single egg. The reason for this is that the parasite only records this outcome if the host chooses to eject, guesses incorrectly and destroys one of its

TABLE V

OUTCOME FOR DIFFERENT STAGE 2 DECISIONS WHEN $n = 4$

δ decision	Parasite Outcome
δ_0^A	-0.0350
δ_1^A	0.8533
δ_2^A	0.7811
δ_3^A	0.7162
δ_4^A	0.3032

TABLE VI

OUTCOME FOR DIFFERENT STAGE 1 DECISIONS

n	Host Outcome
1	0.4237
2	1.1694
3	1.6824
4	1.9187
5	1.7380
6	1.4959

own, meaning the parasite will have less destruction to do. In reality the parasite will receive $1 - \sigma$ times this reward. But this is not calculated until Stage 2.

Stage 4a

Here we calculate the value of α going into this second half. For example assuming $n = 4$ and that the parasite adult does not choose to destroy any eggs, we get

$$\mathcal{A} = [0.0299, 0.0442, 0.0581, 0.0002, 1.0000]$$

Where A is a vector where the entries are the probabilities that there is a parasite given different values of $m \in (0, 5)$. In this case $a = 1$ and the outcome for the host is 2.1403 and for the parasite is 0.9583, with the chosen Γ being the decision for the chick to destroy everything.

Stage 2

As an example we assume in this case that the number of eggs laid is 4, so we need to look at the parasite outcome for the different δ^A's, as we can see in Table V. Thus the parasite decides to leave just one host egg.

Stage 1

Choosing 6 as a maximum for n in this example, we just look at the outcome for each of the possible n (see Table VI). This gives us $n = 4$ as our best choice for the host.

Results

In this Section we describe two real interactions between a host and its parasite. In each case we use

TABLE VII

REAL WORLD EXAMPLE VARIABLE TABLE.

Parameter
$R_H(x) = x$
$C_R(x) = 0.25e^{\frac{x}{2}}$
$C_L(x) = \frac{x}{100}$
$C_A = 0$
$C_e = 0.26$
$R_{cuckoo}(x) = e^{-0.1x}$
$R_{cowbird}(x) = \frac{50-(x-2.25)^2}{50}$
$C_{DA}(x) = \frac{x}{100}$
$C_{DC}(x) = \frac{x}{100}$
$\sigma_{cuckoo} = 0.68$
$\sigma_{cowbird} = 0.98$
$\beta_{yellow} = 0.64$ $\beta_{reed} = 0.06$
$s_n^n = 0.99$ and $s_x^n = \frac{0.01}{n} \forall x \neq n$
$t_n^n = 0.99$ and $t_x^n = \frac{0.01}{n} \forall x \neq n$

real parameter values as much as we can and make use of other evidence to estimate further parameters indirectly. These then generate predictions of behaviour for the two cases. We further consider varying a range of parameters to allow for different estimates and examine the effect. We will look at two interactions between host and parasite, the first the Yellow Warbler (host) and the Brown-Headed Cowbird (parasite), the second the Reed Warbler (host) and the Common Cuckoo (parasite).

Yellow Warbler vs Brown-Headed Cowbird

This is an interesting interaction because the Brown-Headed Cowbird is a species that does not generally eject any host chicks after hatching, however on occasions they have been seen doing so (Davies and de L. Brooke(1988)), so it is clear that they are capable of it. Thus although cowbirds do not (usually) in reality destroy chicks in this situation, our model allows them the option to do so. Parasitism occurs for the Yellow Warbler in a high (64%) in (Tewksbury et al.(2002)), and so we choose $\beta = 0.64$. Other studies (Banks and Martin(2001); Barber and Martin.(1997)) show similar statistics. The Yellow Warbler makes correct guesses as to which egg in the nest is the parasite (if it chooses to eject) 98% of the time, so we choose $\sigma = 0.98$. From studies of the warbler/cowbird interaction it is shown that it is approximately (2-2.5) times harder to raise a cowbird chick than a warbler chick; we shall use $\xi = 2.25$. According to studies done by (Davies and de L. Brooke(1988)) the reed warbler host loses an average of 0.26 of its own eggs during ejection, since there is little data on this on the yellow warbler we shall assume it is the same. Since we usually set the fitness to be the average amount of host eggs left at the final stage we shall use this as our cost of ejection C_E. We also assume in this case that the cost of abandonment C_A is equal to zero.

We also need suitable values for our fitness parameters. First of all we look at the reward to the host. We always set $R_H(x) = x$, which makes sense because the fitness is just the amount of eggs we get out minus the cost it took to raise them. In this case we can set it as $0.1x$. Therefore it costs 10% of the reward from a host chick surviving to fledge to raise it.

It has been shown in studies that a parasite does best with approximately 2-2.5 host chicks in the nest (Kilner et al.(2004)). For this reason we shall in this first example make the payoff graph for the parasite the following.

$$R_P(x) = \frac{50 - (x - 2.25)^2}{50}$$

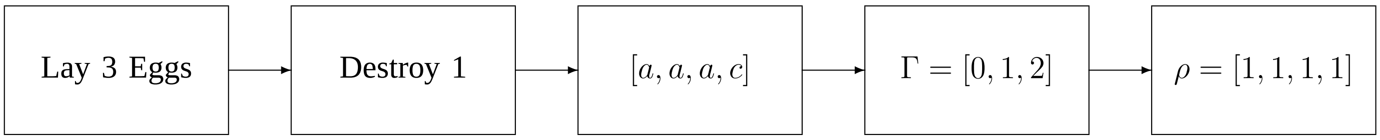

Fig. 4. Stages of the game for the cowbird

Clearly this has a maximum at 2.25. The destruction costs for both the adult cowbird and the cowbird chick are set at 0.01per host chick destroyed (just a small nominal cost). It has not proved possible to find experimental evidence for an explicit functional form for the fitness cost $C_R(x)$ to the host in raising a clutch. We choose a form that has plausible features, namely a small cost for small clutches and an increasing incremental cost for each extra egg for larger clutches. Different forms to the one chosen are possible, but as long as they maintain these general features, then we contend that the results would not be greatly affected. We get the following outcome for the cowbird game

- $\Omega = 1.1476$
- $\Pi = 0.9678$

where the stages are as described in Figure 4.

This solution means that the host will lay three eggs; if a parasite visits the nest it will destroy one of the host eggs and lay one of it's own (it does this because the host will abandon the nest should it see four in the nest). These results follow that of (Tewksbury et al.(2002)), where evidence of one egg being removed by the parasite adult was found. Once the chicks have hatched, no matter what has happened with natural destruction, the parasite will not destroy any of the host chicks and the host will then raise the brood whatever the amount in the nest. This is what we find happens in nature with real cowbirds.

Reed Warbler vs Common Cuckoo

Note that the Common Cuckoo has a very different behaviour to Cowbirds (Kilner and Davies(1999); Haas and Haas(1998)) in that it destroys all of the host chicks (Davies(2000); Davies and de L. Brooke(1988)). We assume that all the natural elements are the same for this game as for the one with the Cowbird and Yellow Warbler, including the rewards and costs to the host, except in the case of the parasitism rate, which is much lower here. The only things that we are going to change are the fitness equation for the cuckoo and the raising cost to the host of the parasite chick ξ. Unlike for the cowbird, there is no evidence that the cuckoo would benefit from the presence of host young, so we set the value of $R_P(x)$ accordingly.

$$R_p(x) = exp(-0.1x)$$

As shown in Kr$\ddot{u}$ger and Davies(2004) a common cuckoo bird is over four times the size of its hosts, so we set $\xi = 4.377$, the average value found. We get the following outcome, with the game described in Figure 5. Cuckoos are better mimics than Cowbirds and it has been shown that the ejection success of the Warbler versus the Cuckoo is only 68%, so we set $\sigma = 0.68$.

- $\Omega = 1.5784$
- $\Pi = 0.7162$

We initially have the same story happening as with the Cowbird, where the host will lay four eggs and if a parasite visits the nest it will destroy one of the host eggs and lay one of its own. However after the chicks hatch behaviour is different, when the Cuckoo chick will destroy all of the host's young no matter how many there are left in the nest. This is again the behaviour of real cuckoos. It should be noted that we

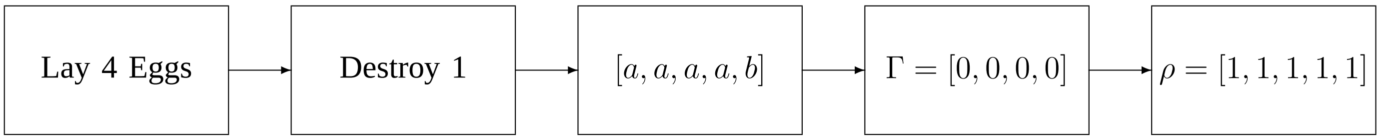

Fig. 5. Stages of the game for the cuckoo

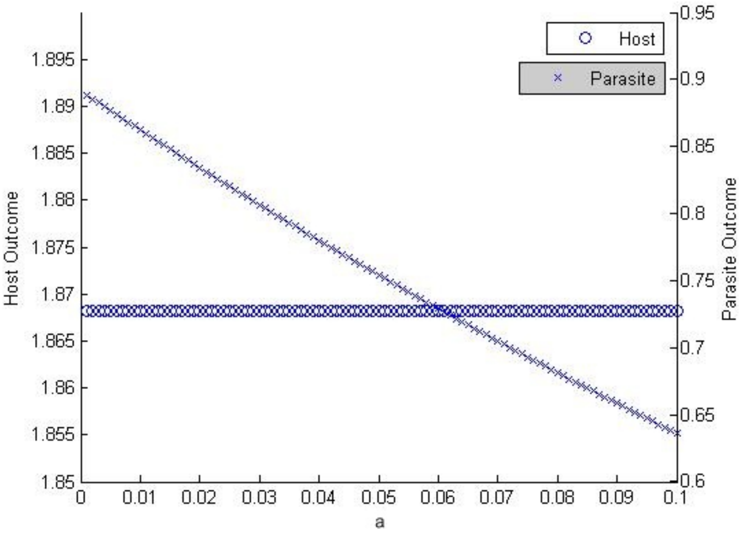

Fig. 6. The parasite reward function $R_P(x) = e^{-\lambda x}$ with $\xi = 3$. Other parameters are $\beta = 0.06, \sigma = 0.68, R_H(x) = x, C_R(x) = 0.25e^{x/2}, C_{DC}(x) = C_{DA}(x) = 0.05x$

can obtain the type of behaviour associated with the cowbird, described above, with the same exponential shape of reward as in the cuckoo, providing that the rate of decay is sufficiently slow.

Differing Parameters

The parasite reward $R_p(x)$

In Figure 6 the values of C_{DA} and C_{DC} have been increased from their default values to consider a situation where behaviour varies for plausible values of λ (λ being the tolerance of a parasite to having host chicks in the nest with it. The higher the value of lambda, the worse for the parasite it is to have host chicks being raised alongside it). The pattern of the outcomes is the same, except that these occur for larger values of λ in this figure than they would if we had used the default values. The reward for the parasite steadily decreases over time, whereas the host reward marginally increases but as we can see from the scale, this reward is not changed a lot. In fact from the figure it is not clear that there is any strategic change at all, as there are no significant jumps in the rewards to parasite or host; however such strategic changes do occur. There are always four host eggs laid, and if a parasite visits, it will always eject a single host egg. In the region between $\lambda = 0.05$ and $\lambda = 0.06$, there are in fact three points where a decision change has been made. These occur at roughly $\lambda = 0.0515$, $\lambda = 0.053$ and $\lambda = 0.055$. This is a transitional period between typical cowbird behaviour (low λ) and typical cuckoo behaviour (high λ). For values less than $\lambda = 0.0515$ we get that the parasite ejects one egg in Stage 2 but does not eject any in Stage 6. For $\lambda \in (0.0515, 0.053)$ the parasite will eject in Stage 6 if it has only a single nest-mate (the others being lost through natural destruction). For $\lambda \in (0.053, 0.055)$ the parasite will eject all in Stage 6 if there is only one or two others. For any value of λ higher than 0.055 the parasite will eject all three of the host chicks.

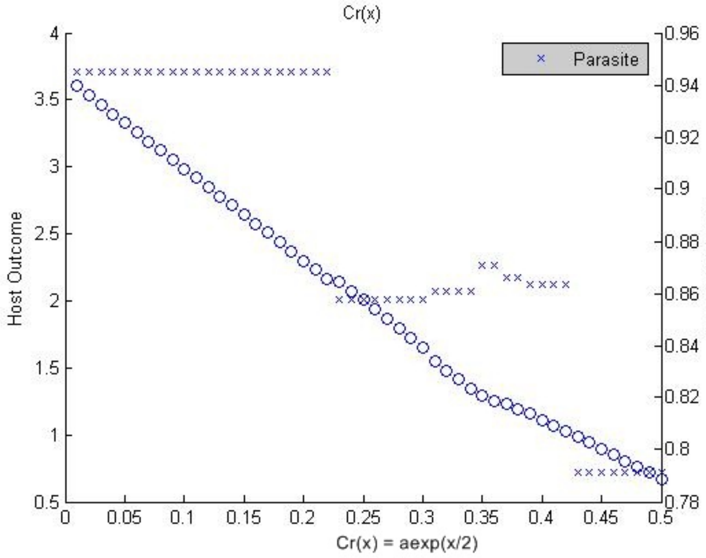

Fig. 7. The cost function to the host of raising Cuckoo chicks $C_R(x) = \mu e^{\frac{x}{2}}$. Other parameters are $\beta = 0.06, \sigma = 0.68, R_H(x) = x, R_P(x) = e^{-0.1x}, C_{DC}(x) = C_{DA}(x) = 0.1$,$\xi = 4.377$

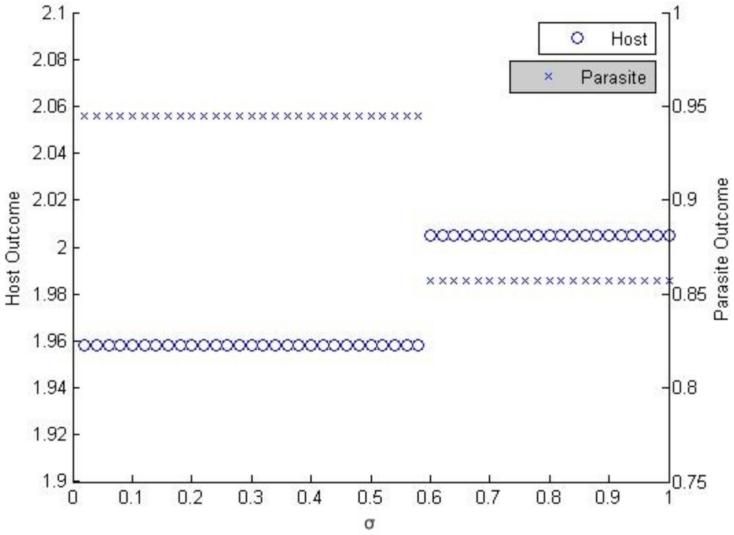

Fig. 8. The probability that the host correctly recognises the Cuckoo chick σ. Other parameter values are $\beta = 0.06, R_P(x) = e^{-0.1x}, R_H(x) = x, C_R(x) = 0.25e^{x/2}, C_{DC}(x) = C_{DA}(x) = 0.1$,$\xi = 4.377$

The raising cost of the host $C_R(x)$

The value of μ in Figure 7 relates to the cost to the host of raising a chick; the higher the value of μ, the greater this cost is. The outcome for the host differs greatly depending on the cost of raising, as we would expect. However there is a change in the parasite's outcome which is not necessarily as we would expect, since this does not have a direct relation to $C_R(x)$. This reward is not smooth and jumps at certain points, these being caused by a change in the host's behaviour. When the value of μ reaches 0.35 the host then chooses to only lay three eggs which is why we see a slight raise in the parasite outcome which then slowly dies away.

The probability that the host correctly rejects the parasite egg σ

Figure 8 shows the change in outcome for the host and a cuckoo parasite; we can see that the host does

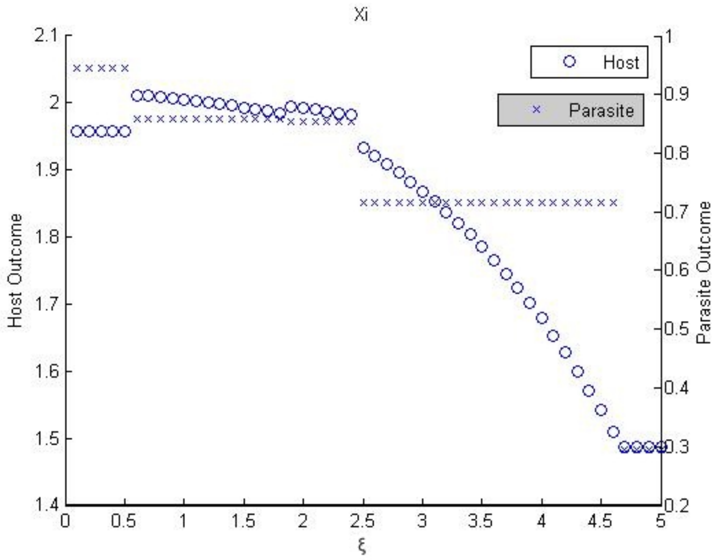

Fig. 9. The demand on resources of a parasite chick ξ for the Cuckoo. Other parameter values are $\beta = 0.06, \sigma = 0.68, R_H(x) = x, C_R(x) = 0.25e^{x/2}, R_P(x) = e^{-0.1x}, C_{DC}(x) = C_{DA}(x) = 0.1$

better when σ is high and the parasite does better when σ is low, as we would expect. There is in fact only one change in possible decisions, when the parasite adult performs the destruction for low values of σ and the parasite chick destroys the host chicks for high values of σ. There is no change in outcome for host and cowbird in their game when we change σ, so we have omitted the graph. In this case, the host never tries to evict the cowbird parasite, because it is tolerant of the host's young.

The relative cost of raising a parasite chick ξ

Here Figure 9 breaks down into different points where the parasite's decision changes as it takes into account it's own value for ξ, and the host's potential reaction. For the cuckoo example, behaviour is as follows for a different ξ.

0-0.5 For small values of ξ the adult parasite chooses to destroy all the host eggs. At Stage 4, the probability that there is a parasite given that the parasite would choose to destroy them all is 0.65. The expected outcome for the host (with $\xi = 0.2$) is 0.45, so is still positive. The host will abandon a single chick in Stage 5 if ξ goes above 0.5.

0.5-1.8 For these values of ξ the host will still allow the parasite chick through at all times except when there is just one chick. Most of the destruction this time is done by the parasite chick, with the adult destroying one egg to leave the nest the same size as when the host laid it, thus lowering the chance that the host believes there is a parasite.

1.8-2.5 The host will still abandon a single egg at Stage 4. The parasite adult ejects down to one host egg in addition to its own egg, increasing its chances of being raised.

2.5-4.5 The host will now abandon at all points unless there are the same number of eggs in the nest as it first laid, so the parasite just destroys one.

4.5+ Here the parasite strategies for adult and chick do not differ from the 2.5-4.5 range. It turns out that whatever its decision as an adult the host will attempt to destroy it by ejecting (or in some cases abandoning) in Stage 4. Thus the parasite must rely on luck, where the host fails to correctly identify it, in order to survive.

With the cowbird example there is only one change in decision which occurs at about $\xi = 4.5$ as with the cuckoo, where before this time the parasite will destroy one host as an adult then the chick will leave the nest alone. Beyond this the parasite adult and the host make the same decision as decribed in the $4.5+$ range for the cuckoo. However, the chick decision is different choosing not to destroy at any point.

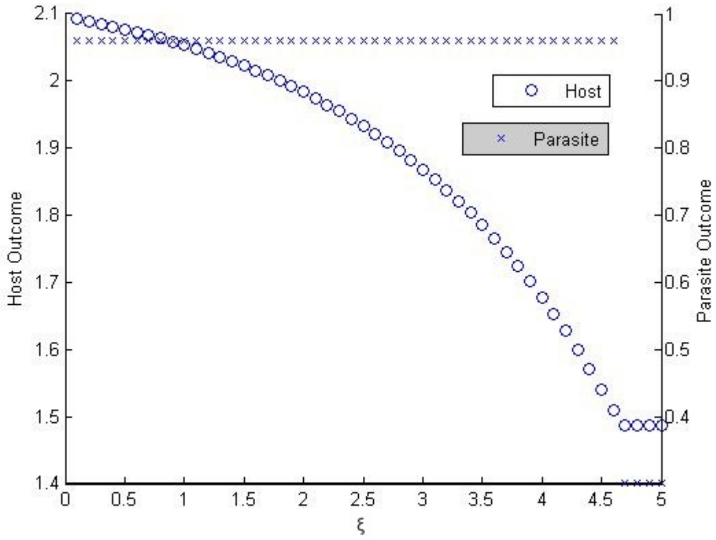

Fig. 10. The demand on resources of a parasite chick ξ for the Cowbird. Other parameter values are $\beta = 0.06, \sigma = 0.98, R_H(x) = x, C_R(x) = 0.25e^{x/2}, R_P(x) = e^{-0.1x}, C_{DC}(x) = C_{DA}(x) = 0.01x$

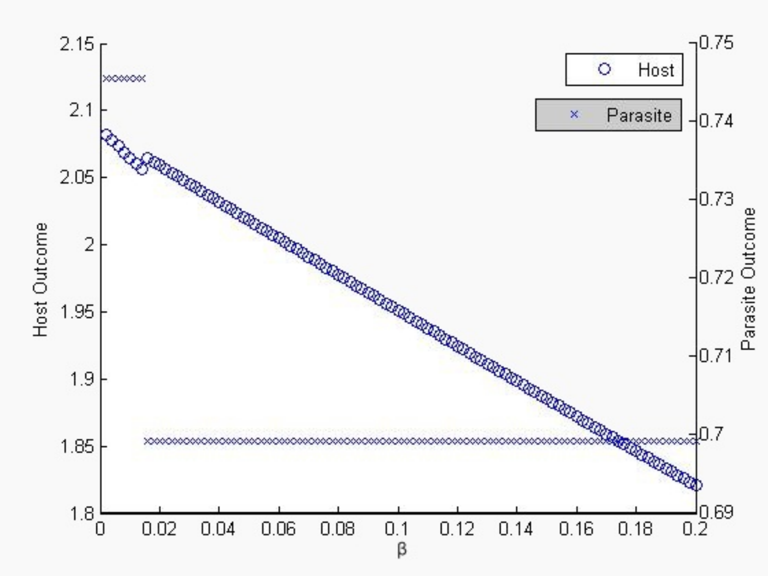

Fig. 11. The probability that a random nest is visited by a Cuckoo β. Other parameter values are $R_P(x) = e^{-0.1x}, \sigma = 0.68, R_H(x) = x, C_R(x) = 0.25e^{x/2}, C_{DC}(x) = C_{DA}(x) = 0.01x$,$\xi = 4.377$

Parasite frequency β

Varying β to see if the different values alter the decision is of especial interest because it does appear that in nature strategies do vary depending upon the level of parasitism (Brooke et al.(1998)), and this is a parameter for which reliable estimates can be found. We revert to the default value of $R_p(x)$, C_{DA} and C_{DC}. For the varying values of β we get the different outcome for the hosts as shown in Figure 11. This shows that as we would expect, the outcome for the host will decrease as the probability of a parasite arriving increases. The outcome of the parasite is independent of β, except for the effect of varying host strategy; this occurs once, with a significant reduction in the parasite outcome when β increases beyond a critical value. At below this critical value the parasite behaves the same as for low values of ξ where the adult destroys all of the host eggs.

Looking at the change in β for the cowbird in Figure 12, we see three distinct changes in outcome. For small β we get a similar outcome for the host, but where it lays four eggs. The Cowbird will eject one

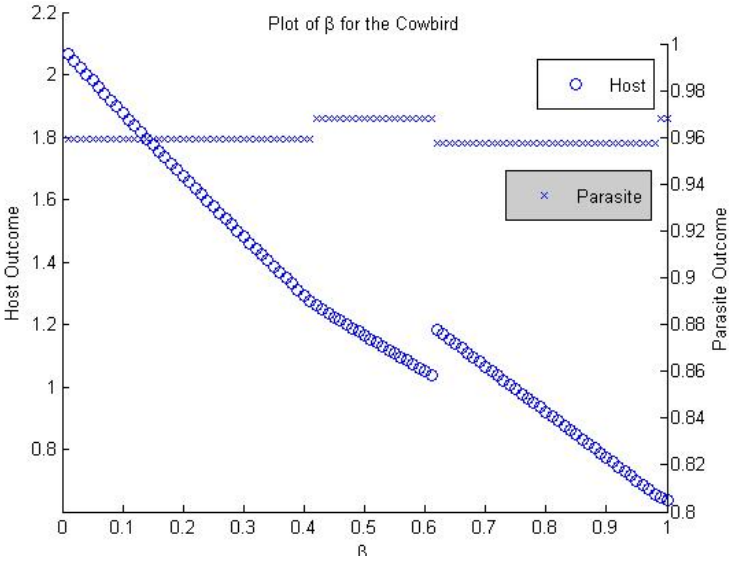

Fig. 12. The probability that a random nest is visited by a Cowbird β. Other parameter values are $R_P(x) = e^{-0.1x}, \sigma = 0.98, R_H(x) = x, C_R(x) = 0.25e^{x/2}, C_{DC}(x) = C_{DA}(x) = 0.01x$,$\xi = 2.25$

and lay one of its own, and the chick will not destroy. In the middle section the host will only lay three as described above and once β becomes high it will lay four (its preferred amount in the absence of parasitism) and then attempt to destroy the parasite in Stage 4 no matter what the parasite adult chooses to do. This is because of the high probability of it being able to identify the cowbird and the high probability of there being one visiting the nest.

Particularly significant variables

When considering which of these changes of variables are the most significant, probably the most important thing is looking at variables which when altered produce a change of behaviour. For the parasite the most significant feature, unsurprisingly, is $R_P(x)$ (i.e. its own reward with regards to how many host chicks are in the nest). Changes in this function produce the change in decisions between the two classic behaviours, that of a cuckoo and that of a cowbird.

For the host perhaps the most significant parameter is ξ, the effective cost of raising a parasite, and all other things being equal this is the one variable that affects the host decision in the most ways (so there can be a sequence of different host strategies as ξ varies), although there is also a parasite reaction to such host changes which affects the host's outcome. As ξ increases the cost to the host of raising such a chick increases and the host becomes more aggressive with how it deals with a parasite egg, eventually trying to destroy it no matter the consequences.

Another parameter that has a significant effect on both host and parasite is σ, the probability of correctly identifying a parasite egg. The host will never attempt to evict if this probability is sufficiently low, and evicts if the likelihood of a parasite being present is sufficiently large for larger values of σ. Although this is a single change in behaviour, the outcomes for both parasite and host change markedly when this takes place.

Discussion

In this paper we have developed a model of the interaction between a brood parasite and its host which is based upon a sequence of events, representing decisions by parasite parent, parasite chick or host parent, and random acts of nature. In this way we try to use information about the sequence of real occurrences during these complex interactions in order to improve on past models and give realistic predictions of host and parasite behaviour. Although we consider a very specific sequence of interactions, the methodology is quite general and different sequences of events could be modelled in a similar way without many modifications.

The model is complex in that it has many different elements to it and the interaction between the different parameters can in some instances be difficult to interpret. However it has been shown that there is some significant alteration to the outcome of the game when the parameters are changed and each of the seven stages gives us an interaction between host and parasite that occurs in nature. We have attempted to identify the key influences of the parameters by concentrating on each in turn, although it should be noted that with this number of parameters it is very hard to identify all the possible interactions between them. A major aim of this paper is to consider the sequence of events in detail, and of course in some ways the model is still a simplification. Thus every element of the game has a significant influence, and thus is of potential importance.

A complication of this game is a lack of complete information. In particular, the host is unsure about whether there is a parasite present in the nest or not, and must rely on estimating the likelihood of a parasite based upon the current state of the nest. This lack of complete information in a game in extensive form makes it not straightforward to analyze (van Damme(1996)). This is a simplification of reality, and sometimes a host can pick up cues as to whether a parasite is present or not. For instance if the nest is disturbed by the parasite, or if the parasite egg is sufficiently different to those of the host that the host can recognise this.

The number of possible sequences of games that can occur quickly becomes very large as the initial number of eggs laid increases. In particular the vector Γ, which describes the possible choices of the parasite chick for all possible numbers of host eggs in the nest, can have $(n+1)!$ possibilities and the computing time involved in running the program this number of times is prohibitive. In fact, we use a simpler procedure which is much quicker. We have proved that the solutions obtained for the two methods are in fact the same for the game described under clearly defined conditions.

This model assumes that both players in the game know all of the rules. It also assumes that both the host and the parasite know what the other would do given what it does. For example when the parasite in *Stage 2* is choosing whether to leave four eggs and itself, then it knows what the host will do in *Stage 4* if it sees five eggs. At the final stage when the host decides whether to raise or not, it knows the number of eggs present m and has an estimate of the probability that one of these is a parasite α, acquired from information from the previous stages.

We assume in this model that only one parasite visits each nest and only lays one egg. This is to make the calculation simpler. But it is entirely plausible to include more parasites having multiple *Stage 2*s and *Stage 6*s. To adjust the model, we would need to consider how the parasites interact. Earlier models, in particular Maruyama and Seno (1999), have considered the important question *How many eggs the Parasite should lay?*

There have been a number of models addressing this classical interaction between host and parasite. Davies et al (1996) discusses a model involving how the probability of parasitism (β in our model) and recognition probability σ are the main factors in deciding whether the host should eject. This model showed similar effects to ours in that they are both indicators of what the host should do in *Stage 4*. Robert and Sorci (2001) discuss a model of how conspecific brood parasite could evolve into that of an interspecific one. This is done by assuming that a particular parasite can lay in both its own nest (say x eggs) and in other birds nests (y eggs) with a given total (n). They then found conditions under which $y = n$ and $x = 0$, which they interpreted as giving an interspecific brood parasite. Broom et al (2008) considers a model involving the interaction of two key decisions which feature in our model, the destruction of broods by parasites and the abandonment of broods by hosts. In particular hosts often abandoned single chicks for life-history reasons independently of the (relatively low) probability of parasitism, and the kind of behaviour seen as the parasite reward $R_P(x)$ varies in this paper, was also observed. A model by Servedio and Hauber (2006) has sequential elements with a game in three stages equivalent to Stages 1, 2 and 4, looking into what cases nest abandonment and egg rejection should occur. It was found that egg rejection was more favourable in Cowbird-like parasites and that nest abandonment was better for Cuckoo-like parasites.

The interaction between host and parasite is one of great intrinsic interest, and one of the particularly fascinating features is the way that the behaviour of brood parasitic young varies significantly between species. A variety of possible explanations for this have been raised. It has been suggested in (Lotem(1998)) that the destruction of nest-mates is beneficial to parasites and species which do not do this are suffering from evolutionary lag, or are prevented from killing host young due to their large size compared to the parasite young (Grim(2006)). There is some evidence to support the evolutionary lag hypothesis, since the more recently evolved parasites, such as the cowbirds, are also those that generally do not kill host young (Davies(2000)). There are exceptions, however, so this cannot be the whole story. An example is the Brown-headed Cowbird Molothrus ater which at times strategically evicts host young (Dearborn(1996)). In addition two old world cuckoos, the Asian Koel Eudynamis scolopacea and the Channel-billed Cuckoo Scythrops novaehollandiae, seem to have lost the capacity to kill young (they do not kill the host young, but their closest living relatives do (Sorenson and Payne(2005); Payne and Payne(1998))). Perhaps these cuckoos' chicks are not strong enough to evict the host young (Kr$\ddot{u}$ger and Davies(2002)), since their hosts are large. Relative size is generally not the main factor is deciding parasite behaviour, however; both the Common Cuckoo Cuculus canorus and Horsfields Bronze-cuckoo Chalcites basalis chicks can evict eggs or nestlings of twice their body weight (Payne and Payne(1998); Davies(2000)), and the Vidua and cowbird hosts generally weigh much less than twice their parasites (Kilner(2005)). Note that nest structure may limit ability to kill host young by eviction, but is unlikely to prevent killing by other means (Kilner(2005)).

We consider real examples of brood parasitism and find as many of our parameters for these situations as possible, with other parameters and functional forms chosen to be as realistic as possible. We find that the solutions from our game match with those from reality reasonably well. In particular changes in just a single parameter within the reward function for the host moves the population from one of the classic behaviours of destruction of all the host young by the parasite chick, associated with cuckoos, to the other classic behaviour of no such destruction associated with the cowbirds. Studying the behaviour of the solution as this parameter changes shows intermediate solutions which occur for small parameter ranges only. Thus perhaps real behaviour can be explained in terms of individuals making optimal choices in games under certain constraints which are the same for most brood parasitism situations, and do not need to rely on evolutionary lag and/or size restriction arguments.

Increasing the prevalence of parasitism through the parameter β has an affect on both host and parasite. Common sense would suggest that the effect on the host would be the more significant, as the number of interactions between host and parasite is proportional to this parameter, and such interactions are detrimental to the host, whereas our model assumes no interactions between parasites at all. However, in fact, the effect on the host is quite gradual, whereas the effect on the parasite reward occurs in a sudden steep jump as the host changes strategy in response to the frequency of parasites, the reward becoming less as the parasite frequency increases. See Broom et al (2008) for similar results. The effect of this parameter is of interest because it is measurable and so predictions are potentially testable, and it would be of interest whether the sequence of events that occurs in the model as β changes also happen for real situations. Similarly the cost of raising a brood should affect the host but not the parasite but in fact a steady decline for the host is accompanied again by steep (negative) jumps for the parasite, as the host changes strategy. In this model we have considered a fixed value of β only, rather than allowing it to vary as would happen if we considered a fully population dynamic model. Our approach has been to assume that the population has settled to a stable situation (or at least that this rate of change is slow enough that birds' strategies are able to change quicker than the rate of parasitism) and look for ESSs. There are likely to be situations where this is not the case, and then a more dynamic model would be valuable.

In this sequential game, there are different places where in reality the game can stop, for example abandonment of the nest by the host after the parasite has laid or at the moment of hatching. If modelled in real time there would not be arbitrary costs associated with staying in or leaving the game at a given time; the cost would be related to how much time could not be used in future activities because it is being used to participate in this game (e.g. the opportunity to start a new nest for the host). We envisage developing a model where there are multiple hosts and parasites and interactions take place in real time, so that individuals play the game as above but leave the game at different times. The reward for leaving at a given time for a host will depend upon various ecological parameters such as the time remaining to the end of the breeding season, but also the number of laying hosts per parasite in the population at that time. The parasite may visit many nests, but must do so at the right point in the laying sequence, and can only lay eggs at a certain rate (e.g. one per day). When should the hosts lay in such a population? It seems likely that they should lay together, not just because it is the best time for reasons associated with ecological parameters, but because it will dilute the effect of the parasites. These and other types of effects could be investigated when this model is further developed.

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