A game theoretical approach to conspecific brood parasitism

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We constructed a game theoretical model to predict optimal patterns of egg laying in systems where individuals lay in the nests of others as well as in their own nests. We show that decreasing the effect of position within an egg-laying sequence on the worth of an egg should lead to reduced parasitism. Indeed, parasitism can only flourish if the worth of an egg to its biological parent declines with the total number of eggs laid in that nest. Further, we found that increasing the intrinsic costs of egg production should lead to an increased propensity for conspecific brood parasitism. The model also predicts that variation in hosts' ability to reject parasitic eggs has little effect on parasitism until this ability is well developed. *Key words:* conspecific brood parasitism, egg dumping, host–parasite systems, intraspecific parasitism, parental care. *[Behav Ecol 13:321–327 (2002)]*

Yom-Tov (1980) defines conspecific brood parasitism as the laying of eggs in the nest of another individual of the same species without taking part in the subsequent processes of incubation and caring for the hatchlings. At the latest count (Eadie et al., 1998), such behavior had been recorded in 185 species. The recent advent of molecular techniques such as DNA fingerprinting has greatly aided field study of this behavior. This may explain why, unusually for behavioral ecology, empirical study greatly dominates theoretical underpinning of this subject. Hence we begin to redress this imbalance by using a game theoretical approach to explain the observation of parasitism by individuals that also raise a brood themselves.

Davies (2000) described three different kinds of conspecific brood parasitism. The first type involves individuals that attempt to nest normally but whose nest is 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 type, some individuals make no attempt to nest themselves but instead choose pure parasitism. Clearly, the success of such a strategy depends on the number of individuals adopting it. The more parasites there are, the more competition there is between them for fewer nests. Such a situation can best be understood using game theory, as applied to this problem by Andersson (1984) and Eadie and Fryxell (1992). The final type of brood parasitism occurs when parasitic individuals build nests that are not destroyed and lay eggs in their own nests, but also lay some of their eggs parasitically. This is the type that concerns us here, and it was first considered theoretically by Lyon (1998).

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. This constraint on the investment that parents can make means that every egg laid in the home nest yields a lower fitness increment than the last. In the absence of the option to parasitize, the optimal number of eggs to lay is n, where the $n + 1$ egg would be the first to yield a negative fitness increment. However, if the average fitness increment that a parent can obtain from a parasitic egg is some positive value (P), then the optimal number of eggs to lay in an individual's own nest changes. Now an individual should lay n_1 eggs in its own nest, when the $n_1 + 1$ egg is the first to provide a fitness increment below P, all subsequent eggs should be laid parasitically. Lyon's key prediction was that n_1 would be less than n; in other words, the opportunity to parasitize would force a reduction in the optimal clutch size laid in an individual's own nest.

One important simplification in this argument is the assumption that the benefit gained from a parasitic egg (P in Lyon's model) is a constant. In practice, the worth of a parasitic egg will depend on both the number of eggs that individuals lay in their own nest and the amount of parasitism. However, both of these will be influenced by the worth of parasitism. To cope with this interdependence, a game theoretical model is required. The aim of this study was to develop such a model. This model should predict the optimum numbers of eggs laid in an individual's own nest and laid parasitically and predict how these numbers are influenced by ecological variables, such as the costs of egg production and strength of competition between nest mates.

Model assumptions

First, we assume that the worth (as defined by Lyon, 1998) to the genetic mother of the ith egg laid in a nest that has an eventual clutch size of T is given by

$$f(i, T) = \frac{V\beta^{i-1}}{1 - \alpha^T},$$ (1)

where $V > 0$ and $0 < \alpha < \beta < 1$. The biological basis for this assumption, and the meaning of the parameters, can be understood as follows. Each egg laid is less valuable than the last;

indeed, its worth is always a constant fraction, β, of that of the preceding egg:

$$\frac{f(i + 1, T)}{f(i, T)} = \beta < 1. \qquad (2)$$

This can be thought of as an effect of competition, with earlier-laid eggs leading to dominant individuals likely to be able to outcompete nest mates for food. The smaller the final clutch size, the larger the worth of an egg in a given position:

$$\frac{f(i, T)}{f(i, T + 1)} = \frac{1 - \alpha^{T+1}}{1 - \alpha^{T}} > 1. \qquad (3)$$

Hence the parameter α is used to control the effect of final clutch size on the worth of eggs in individual positions in the laying sequence. This can be thought of in terms of finite resources leading to more intense competition in larger clutches. There is a cost to parasitism implicit in this assumption: parasitism leads to increased clutch sizes and so reduces the worth of all eggs in the clutch because of increased competition. The extent of this effect is controlled by the value of α.

The total worth of a clutch is given by

$$\sum_{i=1}^{T} f(i, T) = \left(\frac{V}{1 - \beta}\right)\left(\frac{1 - \beta^{T}}{1 - \alpha^{T}}\right), \qquad (4)$$

which (because $\alpha < \beta$) increases with T. The theoretical maximum worth of a clutch is obtained by allowing the clutch size T to tend to infinity:

$$\sum_{i=1}^{\infty} f(i, T) = \frac{V}{1 - \beta}.$$

Hence the parameter V scales the overall worth of a given clutch of eggs to parental fitness. For example, it will be lowest in species where individuals make several breeding attempts during their life span and highest in those where reproduction occurs only once.

Second, we assume that the probability that the owner of a nest does not reject a newly laid parasitic egg is a constant $\gamma \in (0, 1)$.

Third, we assume that the fitness cost of laying an egg is also a constant (C) and is greater than zero. The effect of this cost on the relative payoffs of different strategies depends only on its size relative to the available reward, and so we will work with a variable (R), which is the maximum worth of a clutch divided by C:

$$R = \frac{V}{C(1 - \beta)}.$$

The fourth assumption is that all individuals begin laying on the same day.

The final assumption is that each individual lays a single egg each day. A given individual's strategy is defined as $\{n_1, n_2\}$, indicating that it lays its first n_1 eggs in its own nest, then lays another n_2 eggs. Each of these is placed in the nest of another individual, chosen at random from the available population, independently for each egg. Effectively, each laying sequence is split into two rounds: in the first, all individuals lay in their own nests; in the second, any remaining eggs are laid parasitically. It is generally true that parasites lay their parasitic eggs before laying eggs in their own nests (Davies, 2000), but the key biological feature that we need to capture is that parasitic eggs are not the first to be laid in a nest. Females reject alien eggs placed in their nests before they have started their own laying (Davies, 2000). Hence, in our model, we assume that parasitic eggs are always laid after all of the host's eggs. This slightly underestimates the effectiveness of real parasitism, but we believe it is an acceptable compromise between analytic tractability and biological realism.

The evolutionarily stable strategy

We now find the evolutionarily stable strategy (ESS) of our model. The concept of an ESS was introduced by Maynard Smith and Price (1973; see also Maynard Smith, 1982). If a system possesses a unique ESS, then (usually) the population should settle on playing that strategy by natural selection; if there are multiple ESSs, then the one that the population chooses depends on the initial conditions of the system and chance (see Hofbauer and Sigmund, 1988, 1998, for a detailed discussion of the dynamics of biological systems). It has not been possible to prove that our game always yields a unique ESS. However, in every case that we consider, we have been able to find only one ESS, despite often considering several potential candidates.

Suppose all N individuals in the population play $\{n_1, n_2\}$. Every nest contains n_1 of the owner's eggs and a number of parasitic eggs. If N is large, because parasitized nests are chosen at random, then the number of parasitic eggs in any given nest will be closely approximated by a Poisson distribution; in other words, the probability of a given nest having j parasitic eggs is given by

$$P(j) = \frac{(\gamma n_2)^j \exp(-\gamma n_2)}{j!}, \qquad j = 0, 1, 2, \ldots \qquad (5)$$

and the average number of such eggs in a nest is γn_2.

To find the ESS (or more properly, as discussed above, ESSs), we now need to consider two pair of strategies in competition: $\{n_1, n_2\}$ versus $\{n_1, n_2 + 1\}$ and $\{n_1 + 1, n_2\}$ versus $\{n_1, n_2\}$. The way the model has been formulated, the choice of whether to lay one more (or less) parasitic egg and whether to lay one more (or less) egg in an individual's own nest are independent. In addition, because increasing n_1 or n_2 both reduce the worth of extra eggs, if laying more than one extra egg is beneficial, then laying exactly one extra certainly will be, and so these two competitions are the only ones we need consider.

Laying an extra egg parasitically costs an extra amount, C. It is laid after all the other eggs and will be the last egg laid in a nest that already contains $n_1 + j$ eggs, where j is drawn from the Poisson distribution of Equation 5. Thus the worth of this egg is

$$\gamma E[f(n_1 + j + 1, n_1 + j + 1)]$$

$$= \gamma \sum_{j=0}^{\infty} \left(\frac{V\beta^{n_1+j}}{1 - \alpha^{n_1+j+1}}\right)\left[\frac{(\gamma n_2)^j \exp(-\gamma n_2)}{j!}\right]$$

$$= \gamma V \beta^{n_1} \exp(-n_2 \gamma)$$

$$\times \left\{\sum_{j=0}^{\infty}\left[\frac{(n_2\gamma)^j}{j!}\right]\beta^j[1 + \alpha^{n_1+1}\alpha^j + \alpha^{2(n_1+1)}\alpha^{2j} + \cdots]\right\}$$

$$= \gamma V \beta^{n_1} \exp(-n_2 \gamma)$$

$$\times \left\{\sum_{j=0}^{\infty}\frac{(n_2\gamma\beta)^j}{j!} + \alpha^{n_1+1}\sum_{j=0}^{\infty}\frac{(n_2\gamma\beta\alpha)^j}{j!}\right.$$

$$\left. + \alpha^{2(n_1+1)}\sum_{j=0}^{\infty}\frac{(n_2\gamma\beta\alpha^2)}{j!} + \cdots\right\}$$

$$= \gamma V \beta^{n_1} \exp(-n_2 \gamma)\left\{\sum_{k=0}^{\infty}\exp(n_2\gamma\beta\alpha^k)\alpha^{k(n_1+1)}\right\}. \qquad (6)$$

This is a decreasing function of both n_1 and n_2. That is, the more eggs that individuals of the "resident" phenotype lay,

the less advantageous it is for a "mutant" to lay an extra parasitic egg. This is as we would expect. For this strategy not to be advantageous, this benefit must be at most equal to C:

$$\gamma V \beta^{n_1} \exp(-n_2\gamma)\left\{\sum_{k=0}^{\infty} \exp(n_2\gamma\beta\alpha^k)\alpha^{k(n_1+1)}\right\} \leq C. \quad (7)$$

We now consider the costs and benefits to a single individual of switching to an alternative strategy where it lays the same number of parasitic eggs as the other individuals but lays one more egg in its own nest before switching to parasitism. We assume that this mutant individual lays its $n_1 + 1$ egg in its own nest before any parasitic eggs are placed in it, but that this has no effect on the eventual number of parasitic eggs laid in this nest. In addition, we assume that this also has no detrimental effect on the positioning of the individual's own parasitic eggs. These assumptions are likely not to be quite true in real systems. In reality, the number of parasitic eggs laid in the individual's nest may be less because other individuals may prefer nests with fewer eggs to parasitize. On the other hand, the individual will start laying its own parasitic eggs a day later, so that their worth will, on average, be less. Hence, these two assumptions have opposite effects on the payoff to the mutant. These simplifying assumptions are adopted because the effects are small and not additive, and they buy significant tractability to the analysis. Thus, from its own nest, the individual gains an extra amount given by

$$\sum_{i=1}^{n_1+1} f(i, n_1 + 1 + j) - \sum_{i=1}^{n_1} f(i, n_1 + j), \quad (8)$$

where j is drawn from the Poisson distribution in Equation 5.

However, the mutant individual's cost will be increased because it lays one more egg. For this strategy not to be advantageous, the benefit of laying the extra egg must be at most equal to C:

$$\sum_{i=1}^{n_1+1} f(i, n_1 + 1 + j) - \sum_{i=1}^{n_1} f(i, n_1 + j) \leq C. \quad (9)$$

Thus, for a mutant not to benefit, we require

$$\sum_{j=0}^{\infty} \frac{(n_2\gamma)^j \exp(-n_2\gamma)}{j!} V\left\{\sum_{i=1}^{n_1+1}\left(\frac{\beta^{i-1}}{1-\alpha^{n_1+1+j}}\right) - \sum_{i=1}^{n_1}\left(\frac{\beta^{i-1}}{1-\alpha^{n_1+j}}\right)\right\}$$

$$= V\sum_{j=0}^{\infty} \frac{(n_2\gamma)^j \exp(-n_2\gamma)}{j!}$$

$$\times \left\{\frac{1-\beta^{n_1+1}}{(1-\beta)(1-\alpha^{n_1+1+j})} - \frac{1-\beta^{n_1}}{(1-\beta)(1-\alpha^{n_1+j})}\right\}$$

$$= V\exp(-n_2\gamma)\left\{\frac{1-\beta^{n_1+1}}{1-\beta}\sum_{k=0}^{\infty}\alpha^{k(n_1+1)}\exp(n_2\gamma\alpha^k)\right.$$

$$\left. - \frac{1-\beta^{n_1}}{1-\beta}\sum_{k=0}^{\infty}\alpha^{kn_1}\exp(n_2\gamma\alpha^k)\right\}$$

$$\leq C. \quad (10)$$

Equations 7 and 10 can be used to find evolutionarily stable combinations of n_1 and n_2 for specified values of α, β, γ, and R. These occur at equality for the two equations when the ESS values of n_1 and n_2 are both positive. In general, these will not be integer valued. If we find that the ESS value of n_1 is 6.7, then this should be interpreted as follows. If the whole population lays six eggs in their own nests, then a mutant that lays seven would do better; conversely, if the population all lays seven eggs in their own nests, then a mutant laying six would do better. Hence, in the population at equilibrium, we would expect to find 70% of individuals laying seven eggs and 30% laying six. If Equation 10 is satisfied when $n_2 = 0$, then

the expected reward for laying a parasitic egg is less than its cost, even when no others are laying parasitically, so that the optimal strategy is $n_2 = 0$, and no parasitic eggs should be laid. If Equation 10 is not satisfied, then (n_1, n_2) is not an ESS; if Equation 7 is not satisfied, then a parasitic level greater than n_2 is favored, so that again (n_1, n_2) is not an ESS. Parasitism makes no positive value of n_1 viable, so no nest building is optimal.

Due to the complexity of Equations 7 and 10, the ESSs can generally only be found numerically. Before we do this, we explore four limiting cases, where analytical methods are effective.

Case 1: the worth of an egg does not decrease with clutch size

If we make the assumption that $\alpha = 0$, so that the worth of an egg depends only on the position of that egg in the nest and is independent of the total number of eggs in the nest, then considerable simplification occurs. Equation 7 becomes

$$\gamma V \beta^{n_1} \exp(-n_2\gamma)\exp(n_2\gamma\beta) \leq C. \quad (11)$$

Similarly, Equation 10 gives

$$V\left(\frac{1-\beta^{n_1+1}}{1-\beta} - \frac{1-\beta^{n_1}}{1-\beta}\right) = V\beta^{n_1} \leq C. \quad (12)$$

Because the number of parasitic eggs has no effect on the payoff to hosts, it is no surprise that this expression for n_1 is independent of n_2. Unless β and γ are both equal to 1, the left-hand side of Equation 11 is always less than that of Equation 12, so that the only solution is to satisfy Equation 12 with equality and Equation 11 with inequality, so that the optimal value of n_2 is zero, and parasitism should not take place. This makes intuitive sense because laying further eggs in your own nest does not decrease the worth of previously laid eggs, so (in this case) there is no advantage to parasitism, and individuals should lay all their eggs in their own nest.

Equation 12 can be rearranged to give the optimal number of eggs laid in an individual's own nest, namely

$$n_1 = -\frac{\ln\left(\frac{V}{C}\right)}{\ln(\beta)}. \quad (13)$$

Case 2: parasitic eggs are never rejected

If $\gamma = 1$, then for $n_2 = 0$ to be evolutionarily stable, from Equations 7 and 10, we require that

$$\frac{V\beta^{n_1}}{1-\alpha^{n_1+1}} \leq C = \frac{V}{1-\beta}\left(\frac{1-\beta^{n_1+1}}{1-\alpha^{n_1+1}} - \frac{1-\beta^{n_1}}{1-\alpha^{n_1}}\right)$$

$$< \frac{V}{1-\beta}\frac{\beta^{n_1}(1-\beta)}{1-\alpha^{n_1+1}} = \frac{V\beta^{n_1}}{1-\alpha^{n_1+1}}, \quad (14)$$

which gives a contradiction, and so $n_2 = 0$ can never be an ESS in this limit. This result, that parasitism will always be favored in our model when parasitic eggs are never rejected, is unsurprising because adding an extra egg in your own nest devalues previously laid eggs, whereas laying parasitically does not.

Case 3: the total clutch worth is independent of the number of eggs it contains

In this case $\alpha = \beta$, and so there is a fixed worth, R, to be divided between all members of the clutch, no matter how

many there are. It is clear that if $n_2 = 0$, then the left side of Equation 10 reduces to 0 because adding an extra egg to the nest does not increase the overall worth at all, so that there is no value of n_1 that generates such an ESS solution. Thus, in this case also, some parasitism is always favored. This can be explained as follows. Laying extra eggs in your own nest is especially detrimental to the original eggs because any worth obtained by the new egg corresponds with an identical drop in worth from the others, so that relatively few eggs are laid in an individual's own nest. Indeed, if there was no parasitism, a single egg would be optimal. Thus parasites will take advantage of this fact because they do not mind devaluing existing eggs.

Case 4: an egg's worth is independent of how early in the sequence it was laid

Here β takes its other extreme value, namely 1. Note that Equation 10 is no longer valid, as it required β < 1. Through similar working, we can obtain

$$V \exp(-n_2\gamma)\left\{(n_1 + 1)\sum_{k=0}^{\infty} \alpha^{k(n_1+1)}\exp(n_2\gamma\alpha^k) - n_1\sum_{k=0}^{\infty}\alpha^{kn_1}\exp(n_2\gamma\alpha^k)\right\} \le C. \quad (15)$$

In this case the type of solution depends on the value of γ. For there to be any parasitism, it is easy to show from Equation 7 that

$$\gamma \ge \frac{C(1 - \alpha)}{V} \quad (16)$$

(for there to be any egg laying at all, we require the right-hand term in Equation 16 to be less than 1). If Equation 16 is satisfied, then parasitism occurs, with the solution pair n_1, n_2 satisfying the following pair of equations (derived from Equations 7 and 15):

$$\sum_{k=0}^{\infty}\alpha^{k(n_1+1)}\exp[n_2\gamma(\alpha^k - 1)] = \frac{C}{V\gamma} \quad \text{and} \quad (17)$$

$$\sum_{k=0}^{\infty}\alpha^{kn_1}\exp[n_2\gamma(\alpha^k - 1)] = \frac{C}{V\gamma}\frac{n_1 + 1 - \gamma}{n_1}. \quad (18)$$

Hence, when the worth of an egg is independent of its position in the laying sequence, parasitism can still occur, but only if the probability of the rejection of a parasitic egg is sufficiently low (such that Equation 16 is satisfied). If this is the case, then solution of Equations 17 and 18 yields the positive ESS values of n_1 and n_2. Generally the level of parasitism will be low, even when it occurs, for sensible parameter values.

Numerical results: the general case

Equations 7 and 10 can be used to find the ESS combinations of n_1 and n_2 for specified values of α, β, γ, and R. In order to advance, we must now postulate values for these parameters. The variable γ is the probability that a host does not reject a parasitic egg. Obviously, when γ has a low value, then parasitism is greatly disfavored, so we will concentrate on the more interesting case, especially evolutionarily, where rejection is relatively unlikely, and assume that γ lies somewhere between 0.75 and 1.0. Each egg in a laying sequence is worth a fraction, β, of the last laid one, and we postulate that β is likely to lie in the range 0.7–1.0. The worth of an egg is also proportional to a factor Q, which is a function of both the total clutch size T and the parameter α according to
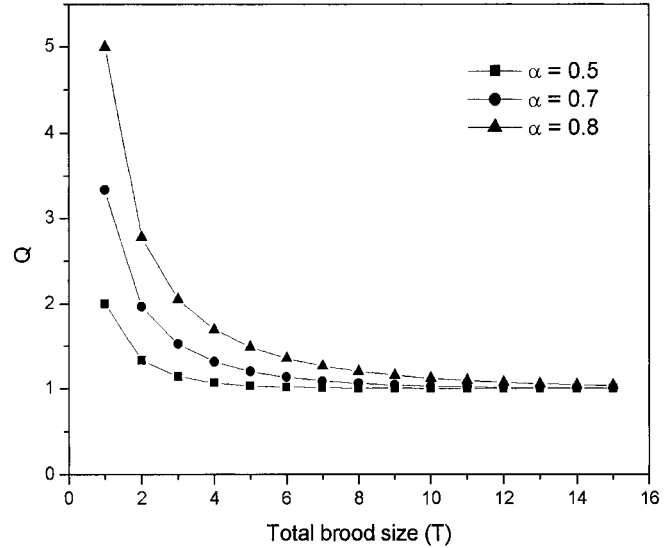
Figure 1
The factor, Q, to which the worth of an individual egg is proportional as a function of the total clutch size (T) for three values of the parameter α.

$$Q = \frac{1}{1 - \alpha^T}.$$

Figure 1 shows Q as a function of T, for three values of α: 0.5, 0.7, and 0.8. This shows that α = 0.5 represents a relatively small effect of total brood size on the worth of an individual egg in a given position and α = 0.8 represents a strong effect. We let α vary in the range 0.5–0.8. For each parameter, we set a default value that we consider to be a reasonable value. We then set each parameter at its default value, and vary the chosen value over a range of plausible values. The chosen default values are α = 0.7, β = 0.9, and γ = 0.95. Further simulations (not shown) suggest that our results are not qualitatively particular to these specific values. The variable R is the maximum possible return from a breeding event divided by the cost of laying a single egg. Because this is very difficult to evaluate, we consider it over a very wide range of plausible values from 10 to 500 and always consider several values of R as we vary the other parameters.

Figure 2 explores the effect of the value of β on the ESS strategy. Each egg in a laying sequence is worth a fraction, β, of the last laid one. As we would expect, Figure 2a shows that increasing both β and R increases the ESS number of eggs an individual lays in its own nest. It is initially surprising that for low values of R, this number decreases with β at very high values. Perhaps even more surprising, because β has no effect on the first-laid egg in a nest, n_1 can fall below 1. This effect occurs because R and β are not independent variables. Increasing β and keeping R constant can only be achieved by increasing the cost of producing eggs (relative to their future worth). Hence, at very high β, the cost of eggs has been raised so high that any egg laying is prohibitively expensive. Generally, in Figure 2b we find that the ESS number of parasitic eggs decreases with both β and R, since increasing both of these factors make the cost of laying eggs in an individual's own nest smaller. Again, Figure 2b shows unusual behavior at high β and low R because of the non-independence of these variables. There is a critical value, which we denote R_c and define as the highest value of R for which n_2 is nonzero, and so parasitism occurs. This value decreases dramatically with increasing β (see Figure 2c).
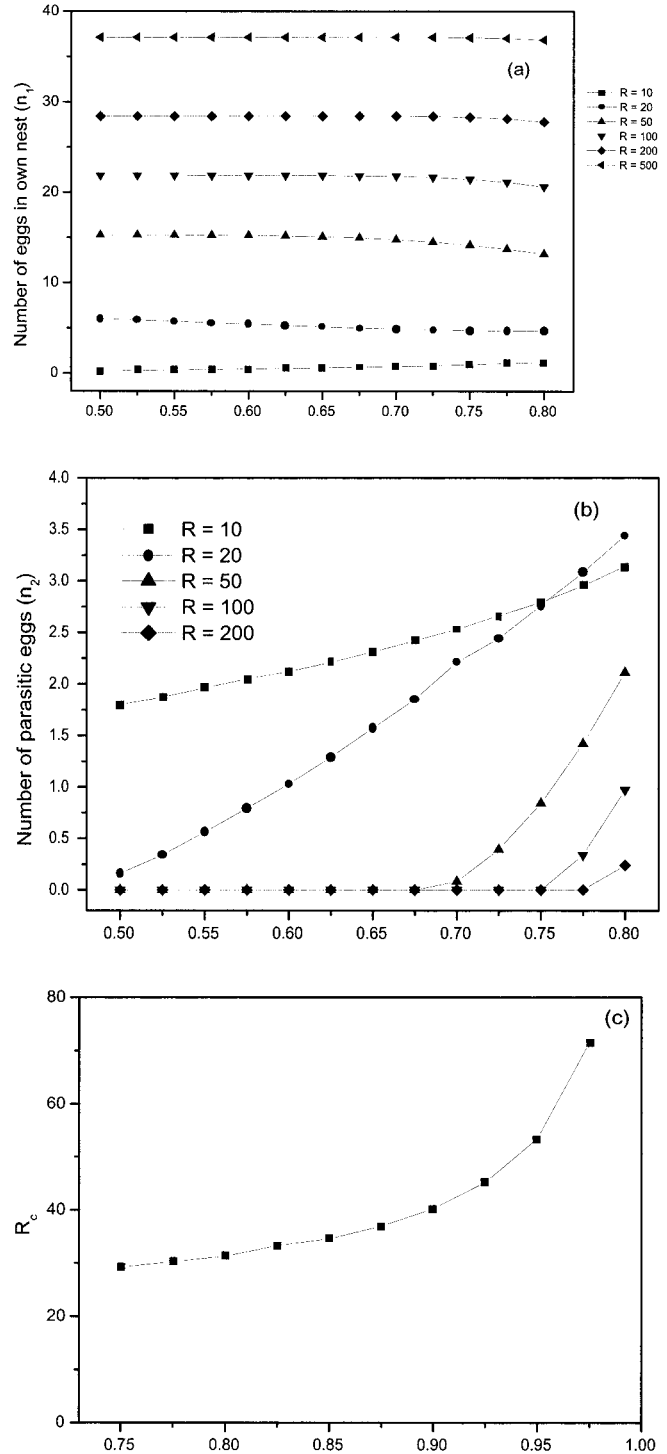
Figure 3 explores the effect of the value of α on the ESS strategy. As Figure 1 shows, at high brood sizes, the value of
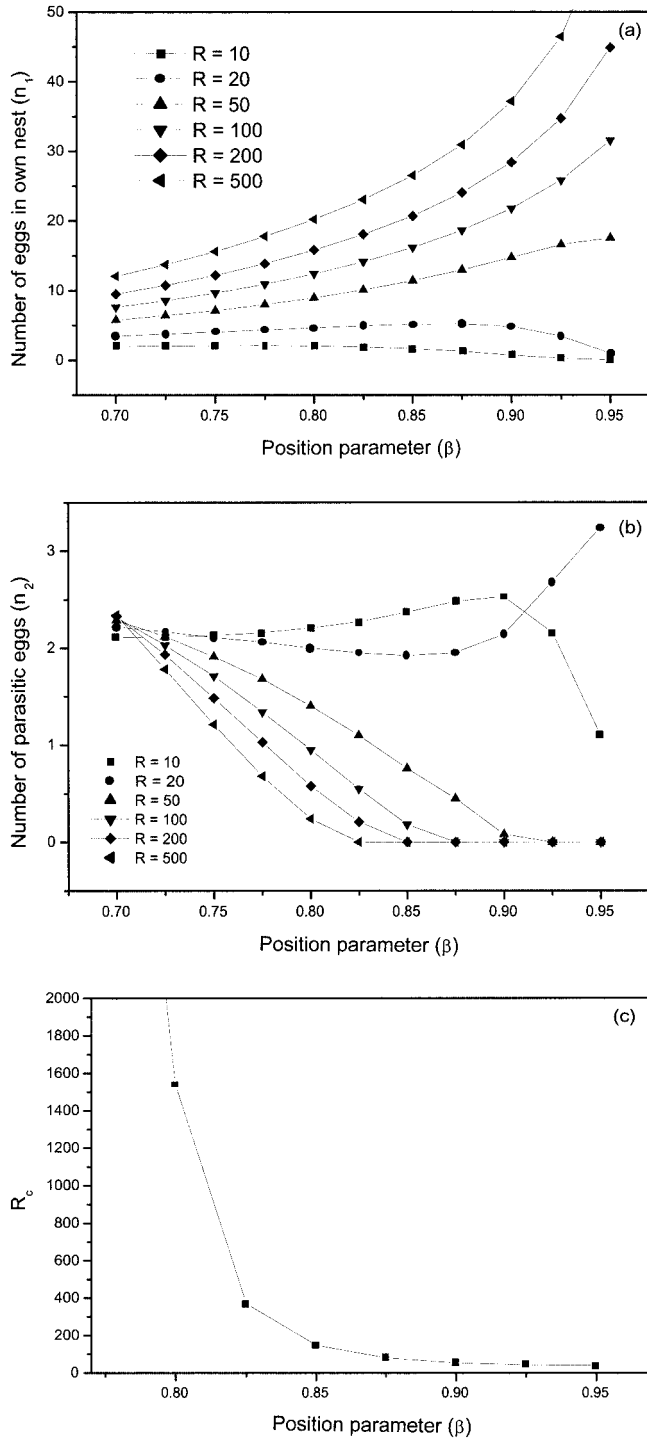
Figure 2
The effect of varying the value of β on (a) the ESS value of n_1: the number of eggs an individual lays in its own nest, (b) the ESS value of n_2: the number of eggs an individual lays parasitically, and (c) R_c, the critical value of R, above which the ESS value of n_2 is zero, and parasitism is not seen. $\alpha = 0.7$, $\gamma = 0.95$ for all panels.

Figure 3
The effect of varying the value of α on (a) the ESS value of n_1: the number of eggs an individual lays in its own nest, (b) the ESS value of n_2: the number of eggs an individual lays parasitically, and (c) R_c, the critical value of R, above which the ESS value of n_2 is zero, and parasitism is not seen. $\beta = 0.9$, $\gamma = 0.95$ for all panels.

α has little effect. This can be seen in Figure 3a, where at high R values, the value of n_1 is sufficiently big that it is insensitive to α. But at lower brood sizes, increasing α does have a significant effect, and this can be seen in the declining brood sizes at high α values for intermediate R values. But for such intermediate R values, individuals compensate at high α val-

ues by switching to laying eggs parasitically (Figure 3b). This situation is carried to its extreme for low R values, where individuals lay more eggs parasitically and practically no eggs in their own nest.

Note that when final clutch size (T) is low, increasing α increases the worth of the eggs appreciably, so that n_1 increas-

es with α. Under these circumstances, our assumption that all individuals build a nest is likely to be false, as individuals that lay all their eggs parasitically would not build a nest. Again, there is a threshold value of R above which parasitism is not seen. As we would expect from earlier discussion, R_c increases with α.

The variable γ is the probability that a host does not reject a parasitic egg. We have already seen a pattern that at high values of R, parasitism is not observed. Hence it is no surprise that Figure 4a shows that at high R values the value of n_1 has a negligible dependency on γ. Increasing γ promotes parasitism, but the effect of this is less marked than might be expected, (see Figure 4b,c). At lower values of R, there is a tendency for n_1 to increase slightly with increasing γ. These two occurrences are linked and can be explained as follows. When γ increases, the parasitic eggs are more beneficial (to the parasite), so that it is better for the parasites to lay more eggs. Parasitic eggs have a significant detrimental effect on a host's eggs through increasing the clutch size and hence competition among nest mates for resources. If the host lays more eggs in its own nest, this reduces the advantage to parasites, thus reducing the number of parasitic eggs it is best to lay, and so indirectly helping the host's own eggs. Thus, as γ increases more host eggs are laid, and the rate of increase of parasitism is less than might be expected.

DISCUSSION

One key assumption of our model is that the worth of the ith egg placed in a nest is a function not only of its position in the laying sequence (i.e., all the eggs placed in the nest before it), but also of the final number of eggs (including all the eggs that come after it). Without this assumption, parasitism is never evolutionarily stable in our model. In this case, extra eggs do not harm existing eggs, so there is no incentive to avoid laying in your own nest; indeed, the risk of another individual rejecting your egg makes it optimal not to do so. Lyon (1998) did not make this assumption; he implicitly assumed two classes of individuals, only one of which is able to parasitize, and the other of which is only vulnerable to parasitism. We predict that when egg production is relatively cheap (high R), then brood sizes will be relatively insensitive to the strength of this effect, and parasitism will not be favored. Conversely, when eggs are relatively expensive (low R), the position effect is high (low α) and within-brood competition is strong (high β), then parasitism is highly favored. Indeed, under such conditions we predict that many individuals would opt to lay all their eggs parasitically. In this instance, our model needs some modification, as such individuals would not build nests of their own. However, this result indicates that case 1 of Davies (2000), discussed in the Introduction, where birds become obligate parasites and do not build a nest, need not be seen as a separate case to the one described here, but rather both can be adopted within a more general framework. We hope that the methodology presented here will be a useful foundation for that framework.

It is no surprise that our model predicts that increasing ability of hosts to reject alien eggs (decreasing γ) decreases the attractiveness of parasitism. What is more interesting is that changing from a situation where hosts reject no parasitic eggs to one where they reject 25% of them makes only a very slight difference to the levels of parasitism that the model predicts. This is due to the fact that in our model individuals must find optimal values for the number of eggs laid in their own nest and laid parasitically and that these values are linked. The detrimental effect of parasitic eggs can be severe, so that as parasitism becomes more effective, the optimal strategy is to lay more eggs in your own nest to discourage para-
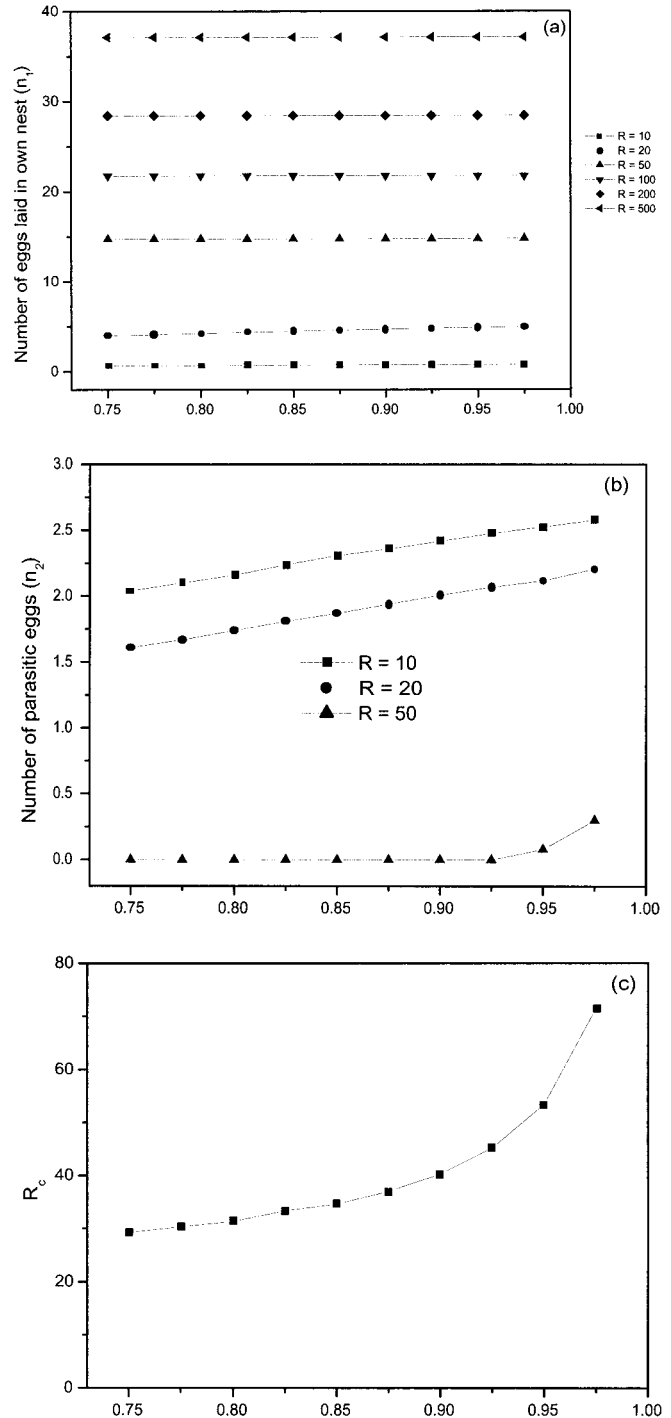
Figure 4
The effect of varying the value of γ on (a) the ESS value of n_1: the number of eggs an individual lays in its own nest, (b) the ESS value of n_2: the number of eggs an individual lays parasitically, and (c) R_c, the critical value of R, above which the ESS value of n_2 is zero, and parasitism is not seen. $\alpha = 0.7$, $\beta = 0.9$ for all panels.

sites. This effect, combined with the risk of individuals mistakenly rejecting their own eggs (Lotem, 1993), suggests that the evolution of rejection by hosts is also worthy of further theoretical effort.

Conspecific brood parasitism is not as well known to the general public as the parasitic behavior of cuckoos, but it contains many fascinating challenges for the evolutionary ecolo-

gist. Further developments of the theory must explore the consequences of intrinsic differences between individuals and host selection by parasites. However, there is still much need for empirical work if we are to fully explain the diversity of this mechanism shown by natural populations. We hope that others will challenge the predictions made here with empirical testing, either by experimental manipulation or (perhaps more amenably) by cross-species or cross-population comparisons. Some of the simplest of these to test are the following. Increasing the intrinsic costs of egg production should lead to an increased propensity for intraspecific brood parasitism. Decreasing the effect of position within a brood on the worth of an egg should lead to reduced parasitism. Variation in hosts' ability to reject parasitic eggs has little effect on parasitism until this ability is well developed.

Further, theoretical development may also be fruitful. To retain some analytic tractability, we were required to remove any temporal component to birds' strategies. Thus we imposed strict laying synchrony on all the birds. This does not happen in the real world. Allowing birds to control the timing of when to begin laying would be a very interesting development to this model. Particularly, this would allow the host availability to parasites and parasite pressure on hosts to vary over time and would naturally introduce variability in host nest attractiveness (through differential clutch size) to parasites at any given time. However, this added realism will necessarily incur costs in increased model complexity. However, an added advantage is that it will also allow relaxation of another assumption in our model, that an individual lays parasitically after laying in its own nest. Generally the reverse is true in nature. This assumption was forced on us, once we adopted the simplifying assumption of complete synchrony of breeding, because the key biological feature that we needed to capture is that parasitic eggs are not the first to be laid in a nest. Females reject alien eggs placed in their nest before they have started their own laying (Davies, 2000). Accepting the complexity produced by having a temporal component to individual's strategies would allow more realistic ordering of parasitism and laying in an individual's own nest. We are confident that the work presented here will be a useful tool in aiding understanding of such more complex models.

Another useful extension would be to explore the coevo-lution of antiparasitism traits such as egg rejection along with parasitic traits. Yamauchi (1993) described how quantitative genetic modeling can be applied to such coevolution. Further work (Yamauchi, 1995) described how this framework can be extended to consider both interspecific and conspecific brood parasitism simultaneous. Such a framework is vital if we are to understand how the type of conspecific brood parasitism described here may have provided an evolutionary stepping stone to the obligate interspecific brood parasitism famously practiced by cuckoos and cowbirds.

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