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Intraspecific brood parasitism can increase the number of eggs that an individual lays in its own nest

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Intraspecific brood parasitism involves laying eggs in the nest of another individual of the same species without subsequently caring for the eggs or hatchlings. Where individuals lay in their own nest as well as parasitically, previous works predicted that parasitism leads to fewer eggs being laid in an individual's own nest, compared with the equivalent situation without parasitism. This is predicted to occur both to reduce the effects of competition from parasitically laid individuals and because parasitism can be used to reduce competition between siblings. Here, we present a quantitative model of this situation. This model indicates that the brood-reduction prediction does not hold universally. For some plausible parameter combinations, parasitism causes an increase rather than a decrease in the number of eggs laid by an individual in its own nest. This occurs because parasitism becomes a less profitable tactic as more eggs are laid by nest owners due to increasing within-nest competition. Increasing clutch size will also increase competition between the host's own offspring, but can still be advantageous if the induced reduction in parasitism is sufficient.

Keywords: clutch size; evolutionarily stable strategy; conspecific brood parasitism

1. INTRODUCTION

Intraspecific brood parasitism is the laying of eggs in the nest of another individual of the same species without taking part in the subsequent processes of incubation and/or caring for the hatchlings (Yom-Tov 1980). This occurs in fishes, insects and amphibians (Wcislo 1999; Wisenden 1999; Andersson & Ahlund 2001), but is particularly well-documented in birds (Davies 2000; Yom-Tov 2001). In the case where individuals lay in their own nest as well as parasitically, Lyon (1998) predicted that parasitism leads to fewer eggs being laid in an individual's own nest, compared with the equivalent situation without parasitism. This is predicted to occur both to reduce the effects of competition from parasitically laid individuals and because parasitism can be used to reduce competition between siblings. Previously, this hypothesis has only been justified by qualitative verbal arguments; here we present a game-theoretic model that allows predictions of the evolutionarily stable numbers of eggs that individuals should lay in their own nest and parasitically.

2. METHODS

In our model, we define an individual's strategy by two values H and P , where H is the number of eggs laid in that individual's own nest and P is the number of eggs that it lays parasitically. We assume that parasitic eggs are evenly spread throughout the available nests, such that each nest contains H host eggs and P

parasitic ones. This effectively postulates that parasites have some mechanism, such as egg counting, which avoids them laying in nests that already contain many eggs. No individual lays more than one parasitic egg in any one nest other than their own. It is assumed that the worth of an egg is independent of its position in the sequence of eggs deposited in the nest, so that the ordering of the eggs in the nest is unimportant. This is an assumption for the sake of clarity only and is not necessary to produce the results that follow. The worth of an egg does, however, depend on the number of other eggs in the nest. We define $f(x)$ as the worth of an egg in a nest that contains x eggs in total. We assume that $f(x)$ has the following properties:

$$f'(x) = \frac{df(x)}{dx} < 0. \quad (2.1)$$

This means that the worth of an egg decreases as the total number of eggs in the nest increases.

$$\frac{d(xf(x))}{dx} > 0. \quad (2.2)$$

Every new egg that is added to the nest increases the total worth of eggs in the nest.

$$\frac{d^2(xf(x))}{dx^2} < 0. \quad (2.3)$$

Each new egg added to the nest increases the total worth of eggs in the nest by less than the preceding egg.

Each egg costs C to produce. Parasitically laid eggs are accepted by the host with probability γ , otherwise they are rejected and provide no worth. Individuals seek to maximize the worth of the eggs that they lay minus the costs of laying these. Because the worth of an egg declines with increasing number

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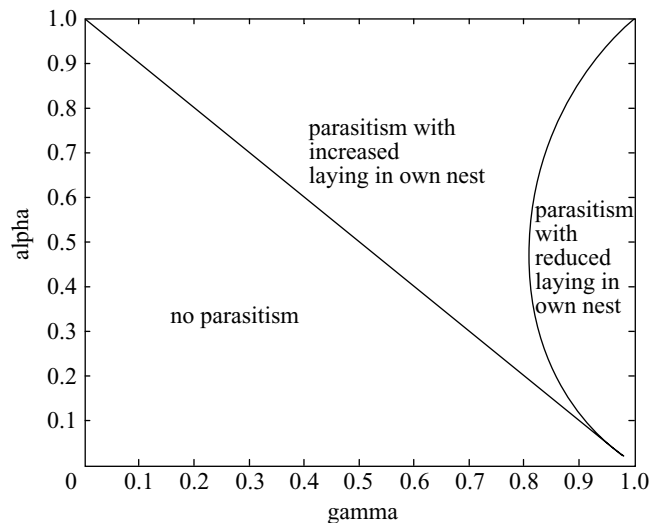


Figure 1. The entire range of evolutionarily stable strategies for the model. This is a function of both the probability of a parasitic egg being accepted (γ) and the strength of competition effects within nests (α).

(because of competition within nests) but the cost of an egg remains constant, this means that the number of eggs that individuals lay is limited by this trade-off.

3. RESULTS

Details of the analysis of this model are given in electronic Appendix A, available on The Royal Society's Publications Web site. For a general $f(x)$, we demonstrate that parasitism should never lead to individuals decreasing the number of eggs that they lay in total. In order to explore how these eggs are divided between an individual's own nest and those of other individuals, we need to specify an exact form for $f(x)$. We choose the general form

$$f(x) = Ax^{-\alpha}, \quad (3.1)$$

where $0 < \alpha < 1$. This fulfils all of the conditions of equations (2.1)–(2.3). Increasing α causes the value of an egg to decrease more rapidly with increasing final clutch size. For this form for $f(x)$, the evolutionarily stable strategy (ESS) is independent of the parameters A and C that scale the worth and cost of eggs, respectively. Parasitism can lead to individuals either laying more or fewer eggs in their own nest. The key parameters that determine which of these situations occurs are the probability that a parasitic egg is not destroyed by the nest owner (γ) and the strength of competition between eggs or hatchlings (α). The results for all possible combinations of α and γ are displayed in figure 1. In particular, at very high levels of γ , the number of eggs that an individual should lay in their own nest is reduced (compared with the situation where there is no parasitism, see figure 2). However, as γ decreases, this changes and individuals should switch to increasing the number of eggs that they lay in their own nest. The risk of a parasite egg being rejected is higher with decreasing γ , so that parasitic laying is made less attractive by sufficiently reducing their potential benefits relative to this increased risk. For low values of α , there is little competition between nest mates and so little incentive to parasitize, so that unless γ is large there is no parasitism at all.

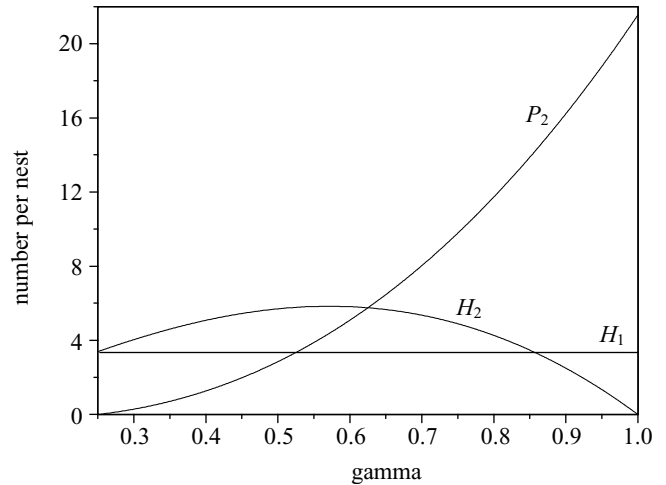


Figure 2. The evolutionarily stable values from the number of eggs that individuals should lay in their own nest (H_2) and parasitically (P_2), as a function of the probability of a parasitic egg being accepted (γ), using $A/C = 10$ and $\alpha = 0.75$. For $\gamma < 0.25$, parasitism is unattractive and all individuals will lay eggs in their own nest only. In situations where parasitism is unattractive or impossible, the evolutionary stable number of eggs an individual should lay in its own nest (H_1) can be calculated from equation (A 15) as 3.4. When $0.25 < \gamma < 0.85$, then parasitism causes individuals to lay more eggs in their own nest (as much as $H_2 = 5.8$ eggs for $\gamma \approx 0.56$). For $0.85 < \gamma \leq 1$, parasitism causes an individual to lay fewer eggs in their own nest. The value of A/C (the ratio of the worth on an egg to its costs) was chosen entirely arbitrarily. This parameter group simply scales the values of H_1 , H_2 and P_2 , but as equation (A 21) demonstrates, it has no effect on the magnitudes of these relative to each other, and hence has no effect on the qualitative predictions of the model.

If α is large then competition is severe and parasitism is both potentially highly favoured and very deleterious to the victim; in such circumstances, individuals that increase the number they lay in their own nest greatly reduce the attractiveness of parasitism. Reduced laying is most favoured by intermediate values of α and high γ (for low γ , no parasitism occurs and for medium γ it is again possible to reduce the prevalence of parasitism by laying extra eggs in your own nest).

4. DISCUSSION

We have demonstrated that the key prediction of Lyon (1998)—intraspecific brood parasitism should lead to individuals reducing the number of eggs that they lay in their own nest—need not always occur. In our simple model, such a reduction can occur for some combinations of parameter values. However, a wide range of other parameter-value combinations lead to an increase in the number of eggs laid in an individual's own nest. This situation has not, to our knowledge, been predicted before. The parasitism insurance hypothesis (see Power *et al.* 1989; Davies 2000) deals with a different but related situation: the response to parasitism of birds that can only lay eggs in their own nest. Like Lyon (1998), this theory predicts that such hosts may sometimes gain a benefit by reducing their own laying in the face of parasitism.

Our model predicts that parasitism will produce an increase in the number of eggs laid by an individual in its own nest provided that the probability that a parasitic egg is accepted (γ) is less than some critical value, generally between 0.8–0.9. Conversely, if γ is close to unity, then parasitism leading to a reduction in the number of eggs laid in an individual's own nest is predicted. When γ is close to unity, parasitism is so attractive that many parasite eggs will be laid (see figure 2), so reducing the number of eggs that you lay in your own nest is the best strategy. However, when γ is reduced, parasitism is less attractive and so increasing clutch size can further reduce the attractiveness of parasitism and thus also lessen the cost that parasitism imposes on an individual's eggs in its own nest.

One assumption of our model that warrants further scrutiny is that parasitic eggs are laid in such a way that each individual lays each of its parasitic eggs in a different nest and all nests are equally parasitized. These assumptions were made for analytical convenience. Whilst greatly simplifying the model analysis, we do not believe that our qualitative model predictions critically depend on these assumptions. They may also be a reasonable approximation to reality because parasites may gain an advantage from dispersing their eggs between nests, both through 'hedging their bets' and through avoiding competition between siblings. Seeking to reduce the competition experienced by their offspring should cause parasites to avoid using nests with abnormally large numbers of eggs already in them, and this process will lead to an evening-out of parasitism across the population.

Another simplification employed in the model is the lack of an order effect. For example, we assume that the cost of egg production is constant, although it might be expected to increase with the number of eggs that an individual has already laid. Physiologically, this may occur through depletion of essential nutrients required for egg production. We also assume that the fitness worth of an egg is a function of the final number of eggs that are laid in the nest, and not dependent on the position that that egg occupies in the laying sequence. This again is a simplification of reality, where often the earliest-laid eggs in a clutch are most likely to hatch first, a situation that often gives the chicks emerging from these a competitive advantage over other nestlings. Again, these simplifications were made for analytical convenience. Generalization of this theory to avoid making these simplifications would certainly be biologically plausible and would allow study of the control of timing of egg laying. Although such models will necessarily be much more complex than that presented here, we see no reason to expect that this complication will provide mechanisms that will lead to a reversal of the qualitative predictions given here.

In our model, all individuals are identical. This means that all individuals are parasites as well as victims of parasitism. This is not the situation seen in nature, where the fraction of conspecific brood-parasitic individuals has rarely been recorded as being above 20% of the local population. Our model is fundamentally incapable of exploring why some individuals parasitize and some do not. Models that describe populations composed of a range of phenotypes would be appropriate to explore such problems and indeed may be a useful testbed for exploring

the evolution of obligatory interspecific brood parasitism. However, the qualitative predictions of our paper are not dependent on the assumption that all individuals parasitize.

For ease of interpretation, we defined γ as describing a disadvantage to parasites through host rejection behaviour. In reality, this parameter encapsulates the aggregate of a considerable number of mechanisms that serve to reduce the fitness of parasitically laid eggs. These include the risk that such an egg is laid mistakenly in the nest of another species, the risk that the parasite is unable to gain access to a suitable host nest and has to dump the egg, and the risk that it is placed in a nest after incubation has begun (and so will not develop fully and hatch successfully). It also incorporates costs of parasitism that are felt directly by the parasitic parent, such as the time and energy required to find and gain access to host nests. All of these factors can be incorporated into the model as a decrease in the value of γ .

Both high and low levels of acceptance of parasitic eggs have been observed in nature (Davies 2000, p. 162), so our expectation is that increased and decreased laying in a bird's own nest should occur. Our results are open to empirical testing using comparisons between different species or populations. We predict that situations where parasitism leads to a lowering of the number of eggs placed in an individual's own nest will be associated with low levels of rejection of parasitic eggs, whereas an increase in this number (relative to analogous populations with no parasitism) will be associated with higher rates of rejection. We would also expect an effect of competition between eggs or chicks in the same nest, in that very pronounced competition should increase the likelihood of the number of eggs laid in an individual's own nest increasing in response to parasitism.

Several empirical studies support the prediction of parasitism reducing the number of eggs laid in an individual's own nest. Goldeneye (*Bucephala clangula*) reduce the number of eggs that they lay in their own nest in response to parasitism (Andersson & Eriksson 1982). The study of Power *et al.* (1989) on European starlings (*Sturnus vulgaris*) found the most common number of eggs laid by a female in her own nest was five, although nests with six eggs produced the highest number of fledging chicks. Intraspecific brood parasitism was common in the study population, and the authors suggest that females would do best to lay six eggs if there were no brood parasitism. However, with parasitism present, the laying of five eggs is a better strategy because, although this reduces the number of chicks fledged from unparasitized nests, this cost is outweighed by reduced costs of parasitism. Common eiders (*Somateria mollissima*) responded to artificial brood parasitism by reducing the number of eggs that they laid in their home nest (Erikstad & Bustnes 1994).

We know of no previous work that demonstrates parasitism inducing an increase in the numbers of eggs laid in an individual's own nest. This may be connected to there having been no expectation of this effect, to our knowledge, prior to the results presented here. Another possible reason is that when our model predicts increased laying it is to make parasitism less attractive, so that if this is an effective strategy the level of parasitism associated with it must be fairly low (and hence may have been less likely

to attract study). In such cases, the threat of parasitism has increased individuals' laying in their own nest precisely to prevent that parasitism from occurring. However, reducing laying compensates for parasitism that will occur without challenging it, so that high levels of parasitism may occur in this case.

The only other modelling study we know of that has explored similar questions to those addressed here is the quantitative genetic model of Yamauchi (1993). This predicted that although parasitism would increase the number of eggs that an individual lays in total, it would have no effect on the number of eggs laid in that individual's own nest. Yamauchi acknowledges that this prediction seems at odds with observation of naturally occurring parasitism and concludes that different functional forms for some of the relationships in their model may lead to different predictions. Our model predictions are different in that either increases, decreases or no change (in the limiting region between the two) can be predicted not by changes in functional relationships but simply by changes in the values taken by parameters.

As pointed out in Yamauchi (1993), the form of the payoff function can sometimes have a large effect on the predictions made. In this paper, we picked a particular functional form for $f(x)$ for convenience to illustrate our main results, which are qualitative in nature. But how would altering this functional form affect this? It is shown at the end of electronic Appendix A that the following is true for any plausible functional form. If γ is small then no parasitism should occur and if γ is sufficiently large then parasitism occurs so that the number of eggs laid in a bird's own nest is reduced. For intermediate values of γ , there is parasitism where the number of eggs laid in a bird's own nest is increased for some values of the cost C , but not for others (there are always some values of C where this occurs). Thus, we can be confident that the phenomenon that we predict is not simply due to our specific choice of function. The independence of the incidence of parasitism on the cost C is, however, a pro-

duction of the specific functional form chosen here. We mentioned earlier in the discussion the possibility of the cost of laying an egg increasing with the total number laid. It is easy to show that this does not affect our prediction.

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