

# AVIAN BROOD PARASITISM: INFORMATION USE AND VARIATION IN EGG-REJECTION BEHAVIOR

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Hosts of avian brood parasites often vary in their response to parasitized clutches: they may eject one or several eggs, desert the nest, or accept all the eggs. Focusing on hosts exposed to single-egg parasitism by an evicting brood parasite, we construct an optimality model that includes all these behavioral options and use it to explore variation in rejection behavior. We particularly consider the influence of egg mimicry and external cues (observations of adult parasites near the nest) on optimal choice of rejection behavior. We find that several rejection responses will be present in a host population under a wide range of conditions. Ejection of multiple eggs tends to be adaptive when egg mimicry is fairly accurate, external cues provide reliable information of the risk of parasitism, and the expected success of renesting is low. If the perceived risk of parasitism is high, ejection of one or a few eggs may be the optimal rejection response even in cases in which hosts cannot discriminate between eggs. This may have consequences for the long-term outcome of the coevolutionary chase between hosts and parasites. We propose an alternative evolutionary pathway by which egg ejection may first arise as a defense against brood parasitism.

**KEY WORDS:** Conditional strategy, cuckoo, evolutionary arms race, external cue, multiple-egg ejection, nest desertion.

The ejection of dissimilar eggs and desertion of complete clutches containing dissimilar eggs are well-studied host defenses against avian brood parasitism; defenses which in turn have selected for parasite countermeasures such as mimicry of host eggs (reviewed by Johnsgard 1997; Rothstein and Robinson 1998; Davies 2000). There is considerable variation, both between and within host populations, with respect to the frequency and the mode of egg rejection (i.e., ejection or nest desertion). When eggs are experimentally introduced to a nest, the same egg will often induce different responses: some may eject the egg, some may abandon the nest, whereas others show no reaction to the presence of the foreign egg (Rothstein 1975a; Davies and Brooke 1988; Moksnes et al. 1991; Lotem et al. 1995; Stokke et al. 1999). Ejection of multiple eggs has been observed in a number of studies, but is

often thought to reflect accidental damage to eggs not singled out for ejection rather than a strategic host response (Davies and Brooke 1988; Moksnes et al. 1991; Lotem et al. 1995; Moskát and Honza 2002).

Many adaptive explanations have been proposed to explain variation in rejection behavior. Rejection is likely to evolve only if the expected benefit of reducing parasitism risk outweighs the expected cost of occasionally rejecting or breaking own eggs (Davies and Brooke 1989b; Lotem and Nakamura 1998). Evicting brood parasites tend to reduce host fitness more than nonevicting brood parasites, which may explain the higher tendency to reject eggs among hosts of the former (Moksnes et al. 1991). Ecological constraints such as a short breeding season can limit the opportunity for renesting, and thereby decrease the benefits of deserting a

potentially parasitized nest (Moksnes et al. 1993). On the other hand, physical constraints that render hosts less able to grasp or puncture eggs for removal, or that cause hosts to more often damage own eggs when attempting to do so (Rohwer and Spaw 1988; Davies and Brooke 1989a; Antonov et al. 2006), may leave desertion and renesting as the only beneficial option of rejection (Davies and Brooke 1989a; Moksnes et al. 1991).

Some of the variation in host responses to parasitized nests can be attributed to differences in the amount of information a host has concerning the presence and identity of parasitic eggs. Information embedded in the appearance of host and parasite eggs (such as size, color, or patterning) may underlie variation in the host response: hosts facing a parasitic egg that happens to closely resemble eggs of their own clutch will more likely accept it than hosts facing a parasite egg with a more crude resemblance (Davies and Brooke 1988; Bártol et al. 2002). Similarly, if a host's ability to single out a parasitic egg is facilitated by low variation in own egg appearance, we may expect variation in rejection behavior to parallel differences in intraclutch variation (Stokke et al. 1999; Moskát et al. 2008). Flexible rejection strategies and learning may also contribute to variation in rejection behavior. For instance, if discrimination is influenced by the learning of own egg characteristics in the first clutch (Lotem et al. 1992), individual hosts may respond differentially to deviating eggs in later clutches, even if they use the same basic mechanism for egg rejection. An additional source of variation can arise if hosts use information from external cues in their egg-rejection decisions. Several experimental studies show that hosts are more likely to reject eggs when they have observed adult parasites near their nest, suggesting that they use these observations as indicators of a high risk of parasitism (Davies and Brooke 1988; Moksnes and Røskaft 1989; Moksnes et al. 1993; Bártol et al. 2002). The risk of being parasitized may also vary with other factors, such as the time of season (Brooke et al. 1998), nest location (Øien et al. 1996; Hauber and Russo 2000; Røskaft et al. 2002; Antonov et al. 2007), and time spent near the nest (Davies et al. 2003), although it is uncertain to which extent hosts utilize these sources of information.

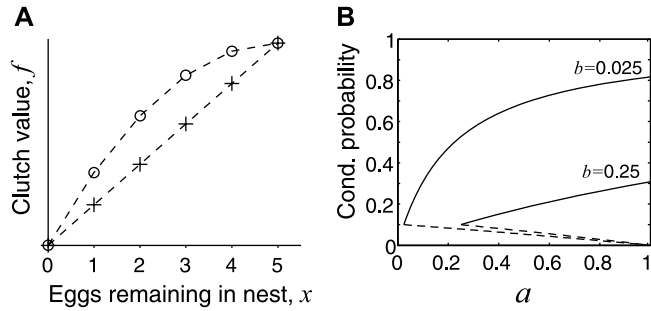
Much of the advances in the field of avian brood parasitism have been made due to a close interaction between theory and data. In this study, we construct a model that serves to predict which rejection responses one would observe given that hosts make optimal use of all the information available to them concerning their risk of being parasitized. The model extends upon the Bayesian recognition approach taken by Rodríguez-Gironés and Lotem (1999), in which the host takes into account the appearance of all the eggs in her nest, but differs from former models of egg rejection in two important ways. First, we allow for a wider range of host behavioral options: hosts are free to accept all eggs, to desert the clutch and renest, or to eject a single or any inter-

mediate number of eggs. (Rodríguez-Gironés and Lotem (1999) did indicate that their model could be used to study ejection of multiple eggs, but this was not considered further.) Second, we explicitly model the use of an external cue that is informative of the risk of parasitism. As discussed by Davies et al. (1996), external cues will leave hosts in different informational states which in turn may lead to different responses. The model predicts optimal egg rejection for hosts that are behaviorally flexible and subject to single-egg brood parasitism. We explore the variation in rejection behavior that arises under different ecological conditions, by varying factors such as the level of parasitic egg mimicry, the rate of parasitism, the cost of renesting, and the reliability of the external cue. The patterns of rejection behavior predicted under the Bayesian egg-rejection model are then briefly compared to those predicted by a simple discrimination threshold.

## *The Model*

We consider systems of brood parasitism in which the parasite chick kills off all the host offspring, such as in most species of parasitic cuckoos, so that acceptance of a clutch containing a parasitic egg will result in complete failure of a nesting attempt. Many brood parasites remove one host egg before laying their own egg (Rothstein and Robinson 1998; Davies 2000), and we make the standard assumption that parasitized and unparasitized nests contain the same number of eggs and that only one of the eggs in a parasitized nest will contain a parasite (Davies et al. 1996; Rodríguez-Gironés and Lotem 1999; Servedio and Lande 2003; Takasu 2003; Stokke et al. 2007). As a consequence, the model is not directly applicable to systems in which parasite chicks are raised together with host chicks or in which parasitized nests typically contain several parasite eggs (e.g., many cowbird systems, Davies 2000).

To incorporate a potential benefit of desertion in the model, we assume that hosts can renest and lay a replacement clutch. Parameters that influence the rejection decision at the current nest, such as parasitism rate, degree of parasite egg mimicry, will also influence the reproductive value to be expected from replacement clutches. To account for this interdependency in a consistent and transparent manner when exploring the model, we will let the expected reproductive value of the replacement clutch emerge from the model parameters rather than being kept constant at some (arbitrarily) specified value. We chose the simplest scenario that allows for this, in which hosts are able to rear only one brood to completion within a season, but have time to renest once and lay a replacement clutch if they decide to desert their first clutch. Because the recruitment of offspring from later broods may be lower than from earlier broods for reasons other than parasitism (e.g., Verboven and Visser 1998; Naef-Daenzer et al. 2001), we allow for the recruitment of a replacement clutch to be lower than



**Figure 1.** (A) The expected reproductive value of an unparasitized clutch of initial size  $n = 5$  eggs, as a function of the eggs remaining after ejection. Linear clutch value function ( $f(x) = x$ ): “+.” Concave clutch value function ( $f(x) = [n^2 - (n - x)^2]/n$ ): “o.” (B) The conditional probability of being parasitized when the external cue is observed (solid lines), and when it is not (dashed lines), as functions of  $a$  (= probability of observing the cue when parasitized) for two different choices of  $b$  (= probability of observing the cue when not parasitized). The population wide rate of parasitism is  $P = 0.1$ .

that of an otherwise identical first clutch. The best host response is that which maximizes reproductive output within a season.

The host lays  $n$  eggs and can eject  $i$  of those eggs, where  $0 \leq i \leq n$  (ejection of  $n$  eggs amounts to desertion). Let  $f(x)$  be the expected reproductive value of raising an unparasitized first clutch with  $x$  eggs remaining after egg ejection. We will refer to  $f$  as the clutch value function and assume that it is positive and increasing for  $0 \leq x \leq n$  (Fig. 1A). The simplest representation of  $f$  is linear, that is,  $f(x) = cx$ , for some positive constant  $c$ . Alternatively, and perhaps more realistic,  $f$  is strictly concave because a parent that ejects an egg is likely to be able to invest more in the remaining offspring.

**AN ALGORITHM FOR OPTIMAL REJECTION**

We start by presenting the algorithm for egg rejection given that all available information has already been used to determine for each egg the probability that it contains a parasite. Let  $P$  denote the long-term average rate of parasitism in the host population. A clutch of  $n$  eggs can be in  $n + 1$  different states: there might be a parasite in the clutch, which can be in any of the  $n$  eggs, or there might not be a parasite in the clutch. Probabilities can be assigned to each of these possible states from the rate of parasitism alone. In Bayesian terminology, these will be the prior probabilities. The prior probability that egg  $j$  contains a parasite is  $P/n$ , and the prior probability that no egg contains a parasite is  $1 - P$ . After taking all the available information into account, however, such as egg appearance, the number and timing of observed visits by adult parasites to the nest, and nest location, an updated posterior probability can be assigned to each of the  $n + 1$  possibilities. Details of how these probabilities are updated will follow. For now, let’s just assume that  $p_1, p_2, \dots, p_n$  are the resulting posterior proba-

bilities that the parasite is in egg 1, 2, . . . ,  $n$ , respectively, where eggs are labeled such that the probabilities  $p_j$  are in descending order (i.e., egg number 1 is most likely to contain a parasite). The posterior probability of parasitism,  $p_{tot}$ , is simply the sum of the posterior probabilities that a parasite is in each of the individual eggs, that is,  $p_{tot} = \sum_{j=1}^n p_j$ . The posterior probability of parasitism is the perceived risk of parasitism for a given clutch, and may of course deviate strongly from the average rate of parasitism in the population.

Let  $W_{n,i}$  denote the expected reproductive success under risk of parasitism from a clutch originally counting  $n$  eggs, but from which the  $i$  eggs most likely to contain a parasite have been ejected ( $0 \leq i < n$ ). Because only an unparasitized nest will result in production of own offspring, the expected success of accepting all eggs is  $W_{n,0} = (1 - p_{tot})f(n)$ . Ejection of eggs will reduce both the clutch size and the probability of a parasitic egg remaining in the nest, so that after the ejection of the  $i$  eggs most likely to contain a parasite, the expected reproductive output is

$$W_{n,i} = \left( 1 - p_{tot} + \sum_{j=1}^i p_j \right) f(n - i). \tag{1}$$

Because the probability of not being parasitized will be a concave increasing function of the number of ejected eggs,  $W_{n,i}$  will be unimodal in  $i$  for any increasing concave choice of  $f(x)$ . Thus, the optimal number of eggs to reject can be found through iteration. After ejecting  $i$  eggs, it will be beneficial to eject yet another one if and only if  $W_{n,i+1} > W_{n,i}$ . (We ignore the unlikely knife-edge case where  $W_{n,i+1} = W_{n,i}$  for some  $i$ , in which the host will be indifferent to ejecting  $i$  or  $i + 1$  eggs.) The optimal number of eggs to eject,  $i^*$ , is reached when both  $W_{n,i^*+1} < W_{n,i^*}$  and  $W_{n,i^*} > W_{n,i^*-1}$  hold. The expected reproductive success from the remaining  $n - i^*$  eggs can then be compared with the expected success of a replacement clutch, which we will refer to as “the benefit of renesting” or  $W_{renest}$ , the details of which we shall return to in the next section. The rejection algorithm is illustrated by a simple numerical example in Box 1.

We shall consider the case in which the host can obtain information about the risk of parasitism from two sources: an external cue and the appearance of the eggs that make up the clutch. The external cue is assumed uncorrelated with parasite egg phenotype and thus only provides information on whether a parasitic egg is likely to be present (or not) in the current nest, whereas egg appearance is informative of each individual egg’s probability of containing a parasite.

**INCORPORATING AN EXTERNAL CUE**

We will, for the sake of simplicity, assume that external cues are either present or absent and thus leaves the hosts in one of two discrete informational states (cf. Holen and Johnstone 2006).

**Box 1**

Consider a host with clutch size  $n = 5$  that cannot discriminate between own and parasite eggs. The sight of an adult parasite on the nest suggests that there is an 80% risk that the nest is parasitized ( $p_{tot} = 0.8$ ). Under the assumption that parasitized clutches contain only a single parasite egg, the probability that a randomly drawn egg contains a parasite is  $p_{tot}/n = 0.16$ . For simplicity, let the reproductive value  $f$  of an unparasitized clutch be proportional to the number of eggs  $x$  remaining in it, and scaled so that  $f(x) = x$ . On the same scale, and accounting for risk of future parasitism, nest failure, and reduced recruitment, let the benefit of renesting be 1.25. The expected payoff from accepting all eggs is given by  $W_{5,0} = (1 - p_{tot})n = (1 - 0.8)5 = 1$ , so a renesting attempt will be favored over full acceptance. Hosts that eject one egg will do better because  $W_{5,1} = (1 - p_{tot} + p_1)(n - 1) = (1 - 0.8 + 0.16)4 = 1.44$ . The best option, however, will be to eject two eggs and incubate the remaining three:  $W_{5,2} = (1 - p_{tot} + p_1 + p_2)(n - 2) = (1 - 0.8 + 0.16 + 0.16)3 = 1.56$ . Ejection of three and four eggs will yield lower payoffs: 1.36 and 0.84, respectively. These simple calculations show that hosts suffering parasitism from perfectly mimetic eggs can benefit from ejecting multiple eggs after having observed an adult parasite near the nest.

Let  $a$  and  $b$  be the fraction of parasitized and unparasitized hosts, respectively, that observe the external cue during the egg laying period. By convention, we assume that the external cue is more likely to be present in the surroundings of parasitized hosts than unparasitized hosts, so that  $a > b$ . The probability that a randomly drawn host observes a cue is  $\Pr(cue) = Pa + (1 - P)b$ . Using Bayes' rule, the conditional probability that a host is parasitized given that it has observed the cue is then  $\Pr(parasitized | cue) = Pa/[Pa + (1 - P)b]$ , which is higher than  $P$ . Likewise, the conditional probability that a host is parasitized given that it has not observed the cue is  $\Pr(parasitized | no cue) = P(1 - a)/[P(1 - a) + (1 - P)(1 - b)]$ , which is lower than  $P$ . If  $a$  increases and/or  $b$  decreases, the cue becomes more informative and the conditional probabilities of parasitism will deviate more from  $P$  (Fig. 1B).

The optimal rejection behavior in the current clutch can be identified through backwards induction, that is, by first determining the expected reproductive success of the final renesting attempt. It follows from our assumptions that there is nothing to gain from deserting a replacement clutch, and to simplify matters further we assume that the observation of an external cue when laying the first clutch is not instructive of the risk of parasitism (or the probability of observing the cue) in a replacement clutch, and

that the population-wide rate of parasitism remains unchanged between first and second nests. The optimal rejection response, excluding the option of desertion, can then be worked out for the cases in which a cue is and is not observed in the renesting attempt, and based on this the benefit of renesting can be determined (details follow below). To account for other factors that reduce overall recruitment from later clutches, we also introduce a discount factor  $s$ , where  $0 \leq s \leq 1$ , so that the expected reproductive output from an unparasitized replacement clutch containing  $x$  eggs is  $s \cdot f(x)$ . We note that the method of backwards induction could, with additional assumptions, be extended to any number of renesting attempts.

For a host that does not discriminate between eggs the posterior probabilities,  $p_1, p_2, \dots, p_n$ , will all equal  $\Pr(parasitized | cue)/n$  when the external cue is observed, and  $\Pr(parasitized | no cue)/n$  when it is not. The benefit of renesting is equal to the sum of the expected successes of a replacement clutch when the cue is observed and when it is not, weighted by the probability of either event

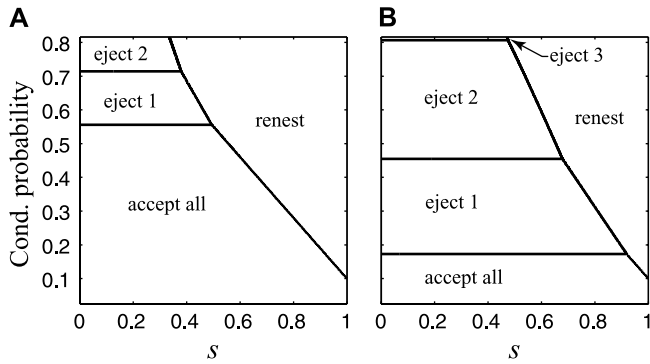
$$W_{renest} = s \cdot \Pr(cue) \cdot \max_i \left\{ \left( 1 - \frac{n-i}{n} \Pr(parasitized | cue) \right) f(n-i) \right\} + s \cdot \Pr(no cue) \cdot \max_i \left\{ \left( 1 - \frac{n-i}{n} \Pr(parasitized | no cue) \right) f(n-i) \right\}.$$

Subsequently, the optimal rejection response in the first clutch can be identified, recognizing that the host should opt for desertion whenever the benefit of renesting exceeds that of incubating the  $n-i^*$  eggs remaining in an optimally reduced first clutch.

In absence of egg discrimination, the optimal rejection behavior is as follows. When the conditional probability of parasitism is low, the host should accept all the eggs in the nest (illustrative examples are provided in Fig. 2). If the conditional probability of parasitism is high and the benefit of renesting is high, the host may do best by deserting. If the conditional probability of parasitism is high and the benefit of renesting is low, the host may do better by ejecting eggs, and the number of eggs that should be ejected increases with the perceived risk of parasitism. Note that egg rejection will be favored despite the fact that each host egg will have an equally high chance of being ejected as the parasite egg. Because the cost incurred by partial clutch reduction is lower under a concave clutch value function, the parameter region where partial clutch reduction is favored widens in Figure 2B.

**INCLUDING EGG DISCRIMINATION**

Now consider the case in which hosts in addition take egg appearances into account before making their egg-rejection decisions. Let the variable  $z$  represent the egg trait of importance for



**Figure 2.** The optimal rejection response when there is no egg recognition for a clutch of size  $n = 5$  under (A) a linear clutch value function and (B) a concave clutch value function (cf. Fig. 1A). The conditional probability of being parasitized (y-axis) will vary according to cue informativeness and whether the cue has been observed or not. To produce this plot we have set  $b = 0.025$ ,  $P = 0.1$  and let  $a$  vary (cf. Fig. 1B). The parameter  $s$  is a discount factor for the relative value of a replacement clutch. See main text for additional information.

discrimination. Each of a host's  $n$  eggs is drawn from a continuous distribution with density function  $\varphi_h(z)$ , whereas parasitic eggs are drawn from a continuous distribution with density function  $\varphi_p(z)$ . Let  $p'_1, p'_2, \dots, p'_n$  denote the probabilities of parasitism conditional on the presence/absence of the cue, and let  $z_1, z_2, \dots, z_n$  be the observed phenotypic values of the eggs in the nest, where subscripts correspond to those of the conditional probabilities. Bayes' theorem for probability densities (e.g., Papoulis 1984) can then be used to calculate the posterior probability of each egg containing a brood parasite, using the conditional probabilities as priors. We obtain an equation that corresponds to equation (A10) in Rodríguez-Gironés and Lotem (1999):

$$p_j = \frac{p'_j \varphi_p(z_j) \prod_{k \neq j} \varphi_h(z_k)}{\sum_{k=1}^n \left( p'_k \varphi_p(z_k) \prod_{m \neq k} \varphi_h(z_m) \right) + (1 - p'_{tot}) \prod_{k=1}^n \varphi_h(z_k)} \quad (2)$$

The numerator of equation (2) is simply the prior probability density (conditional on the cue) that egg  $j$  originates from a parasite and all the other eggs originate from the host, and the denominator is the sum of the analogous probability densities for all  $(n + 1)$  possible clutch states. Note that the posterior probabilities produced by equation (2) will have to be ordered into a decreasing sequence according to magnitude and correspondingly reindexed before entering the rejection algorithm previously outlined.

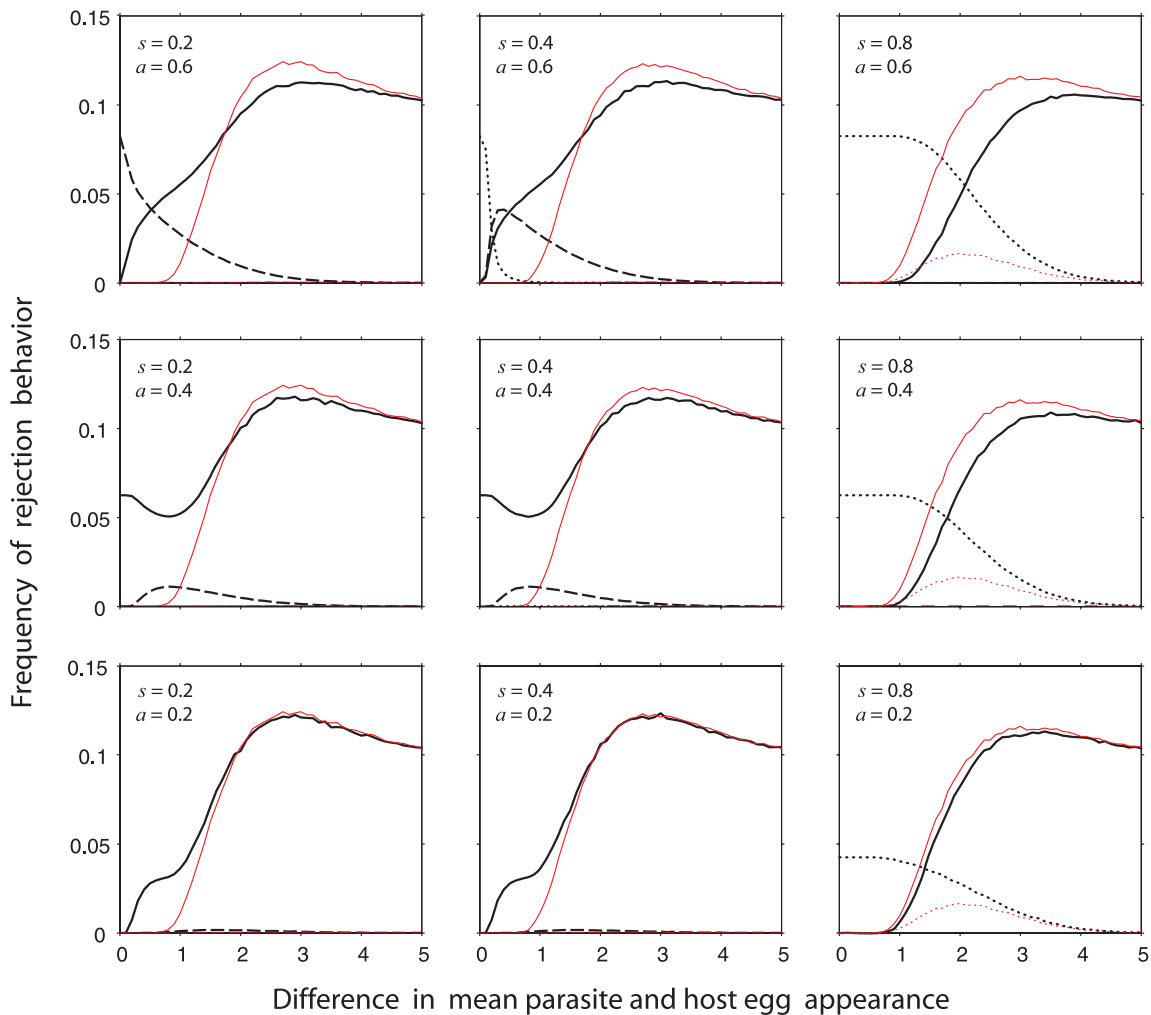
**NUMERICAL EXPLORATION**

To gain insight into the full model we simulate optimal rejection under different combinations of parameters  $P$ ,  $a$ ,  $b$ , and  $s$ , using a simple linear nest value function  $f(x) = x$ . For each parameter

combination, we explore the model for various levels of mimicry by increasing the difference between the mean egg appearance of hosts and parasites from zero (perfect mimicry) to five standard deviations (readily distinguishable). The egg trait distributions of both host and parasite are assumed normal with unit variance. Technically, for each level of mimicry we create a large number of host nests by randomly drawing  $n$  host eggs from the host distribution, so that all hosts share the same underlying mean egg phenotype, and host eggs vary within each clutch. We then parasitize a fraction  $P$  of the nests by replacing one of the eggs with an egg drawn from the parasite distribution. We add the observation of an external cue to a fraction  $a$  of the parasitized nests and to a fraction  $b$  of the unparasitized nests, by assigning to each egg the host's perceived probability of it being parasitic conditional on the cue:  $\Pr(\text{parasitized} | \text{cue})/n$ . For the remaining nests (at which the cue is not observed) the eggs are assigned the conditional probability  $\Pr(\text{parasitized} | \text{no cue})/n$ . The conditional probabilities are then updated using egg appearance by applying equation (2) to each nest, before finally employing the rejection algorithm. The benefit of reneesting is established in each case by first running separate simulations of replacement clutches.

Illustrative examples of the results under a moderate parasitism rate and a typical clutch size are given in Figure 3. The panels display the frequency of nests at which each rejection behavior occurred for different levels of egg mimicry. These frequencies are averaged over four different host states: hosts that are parasitized/unparasitized in presence/absence of the cue. Figure 4 presents the frequencies within each host state for the same parameters as in the top center panel of Figure 3. To facilitate an assessment of the influence of the external cue, the figures also show the frequency of rejection behaviors of hosts that do not make use of the external cue (red lines).

The results from an extensive exploration of the parameter space can be summarized as follows. The influence of the external cue is, as expected, higher when egg mimicry is fairly accurate. Despite the limited opportunity for egg discrimination when mimicry is good, a relatively high prevalence of egg rejection is often maintained. Hosts who experience intermediate to high levels of mimetic accuracy are also those that display the largest amount of variation in rejection behavior, all else being equal. Under these circumstances, it will often be the case that there are several eggs that to some extent resemble a parasite, and the presence of an informative external cue may elicit ejection of multiple eggs. Unless parasitism rates are very low and/or the cue provides little information concerning the risk of parasitism, several rejection responses are then likely to co-occur in the same population (in addition to acceptance). We note that ejection of multiple eggs may also occur in hosts that do not make use of the cue, although at very low frequencies. Not surprisingly, nest desertion will tend to be adopted more often when the expected



**Figure 3.** The frequencies of nests at which the host ejects one egg (solid lines), ejects two eggs (dashed lines), and deserts (dotted lines), under different combinations of the informativeness of an external cue ( $a$ ) and the discount factor of replacement clutches ( $s$ ). Black lines: Rejection behavior of hosts that use information from both an external cue and egg appearance. Red lines: Rejection behavior of hosts that use information from egg appearance only. Parasite egg mimicry decreases along the x-axis, and the presence of different rejection behaviors at any point signifies behavioral variation. Comparison between panels reveals change in patterns of variation due to differences in the value of a replacement clutch (increases towards the right), and the amount of information conveyed by the external cue (increases upwards). The fraction of nests not accounted for by the lines corresponds to hosts that do not reject eggs, whose frequency can be calculated as one minus the sum of the frequencies of the rejection behaviors. Rejection behavior was recorded for 50000 simulated nests at increments of 0.1 along the x-axis (units in standard deviation of host egg distribution), using a linear clutch value function. See main text for additional information.  $P = 0.1$ ,  $b = 0.025$ ,  $n = 5$ .

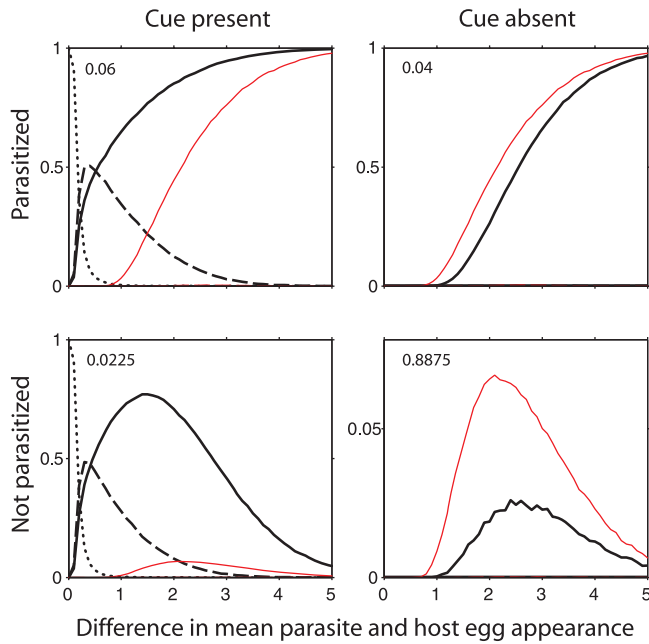
value of a replacement clutch is high. Unless the average rate of parasitism is very high, hosts that also use information from the cue will on average typically suffer more recognition errors than hosts that only use information from egg appearance, but this is weighed up for by the fact that they more often avoid successful parasitism.

Simulations with an increased clutch size ( $n = 7$ ) and a decelerating (i.e., strictly concave) nest value function (the one in Fig. 1A) have also been undertaken (not shown). Not surprisingly, these simulations confirm that either of these two factors will increase the prevalence of both single- and multiple-egg

ejection. Moreover, ejection of more than two eggs occurs more frequently.

#### REJECTION UNDER A SIMPLE DECISION RULE

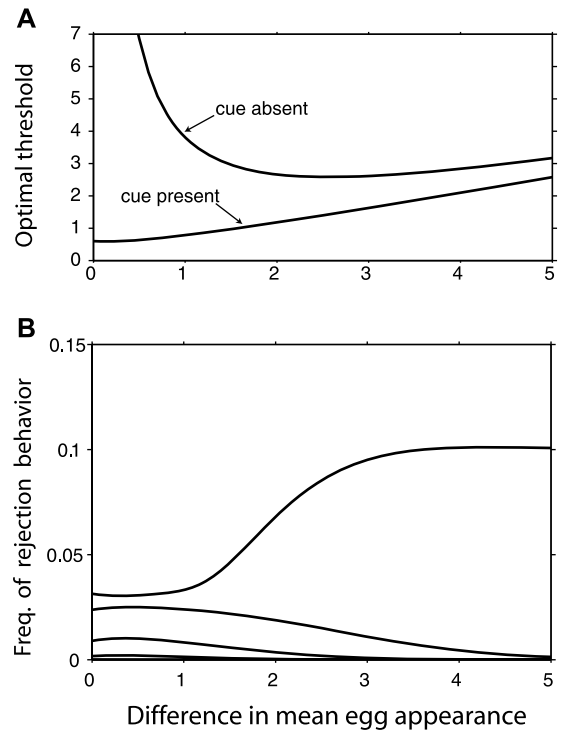
Discrimination thresholds have been fundamental to the study and understanding of animal responses to cognitive tasks (e.g., Shettleworth 1998), and are often invoked in the context of egg rejection (e.g., Lotem et al. 1995; Davies et al. 1996; Servadio and Lande 2003). How well may a simple rule of thumb, such as a threshold rule, approximate the complex Bayesian algorithm presented above? To answer this, we have reexamined egg rejection



**Figure 4.** The frequencies of nests at which the host ejects one egg (solid lines), ejects two eggs (dashed lines), and deserts (dotted lines) in relation to whether the cue was present or not, and whether the nest was parasitized or not. Black lines: hosts that use information from an external cue and egg appearance. Red lines: hosts that use information from egg appearance only. The numbers in the upper left corner of each panel gives the proportion of hosts that fall within the class. Note the change in scale in the bottom right panel. Parameters are as in Figure 3 top center panel. See main text and legend of Figure 3 for further information.

under the parameters used in Figure 4, this time using a threshold rule (Fig. 5). We assume one-sided thresholds and by convention let the mean of the parasite distribution be greater than (or, in the case of perfect mimicry, equal to) the mean of the host distribution. The hosts now adopt one of two thresholds, depending on whether the external cue was present or absent, and apply the threshold to each egg in its nest. Eggs with trait values below the adopted threshold are thus accepted whereas those above are ejected. Desertion occurs when all eggs are ejected, and in re-nesting attempts, the host again adopts one of the two rejection thresholds. The optimal thresholds under different levels of egg mimicry were found by numerical optimization. (See Supporting Information for a detailed account of the model.)

The variation in observed rejection behavior under a threshold rule will often exceed that of the Bayesian algorithm (Fig. 5B), simply because a sufficiently high probability of successfully rejecting a mimetic parasite requires a low threshold. As in the full model, rejection can still be maintained under perfect mimicry. Despite the obvious rejection costs, the expected payoff under the threshold rule in Figure 5 is no less than 99.7% of that of Bayesian hosts under the same circumstances. The threshold rule performs



**Figure 5.** Egg rejection under a threshold model of discrimination for different levels of egg mimicry (in units of standard deviation of host egg distribution). (A) The optimal discrimination thresholds in presence and in absence of the cue. (B) From top to bottom, the lines show the frequency of nests at which hosts eject one, two, three, and four eggs. The frequency of desertion is too low to show up in the plot.

much worse, however, when population levels of parasitism are high and/or expected recruitment from replacement clutches is high.

## Discussion

We have explored the patterns of variation in optimal egg-rejection behavior for hosts exposed to evicting brood parasites. The egg-rejection behavior adopted by hosts is assumed to be flexible, and fine-tuned to a selective environment which encompasses factors such as the average rate of parasitism across years, the distributions of host and parasite egg phenotypes, the level of egg mimicry, the reproductive value of host clutches of different sizes, the informativeness of external cues, and ecological constraints on re-nesting. Our model shows that one should in many cases expect to observe several types of rejection behavior in use within the same host population. Host individuals that are identical in every way might—depending on the information they have access to from their clutch and the external cue—choose to accept their clutch, eject one egg, eject multiple eggs, or desert the clutch and re-nest. Clutches containing one or a few eggs with parasite-like appearance will typically elicit egg-ejection, whereas more

homogenous clutches containing only host-like eggs may lead to acceptance (if the risk of parasitism is perceived to be low), or desertion/egg ejection (if the risk of parasitism is perceived to be high).

The diversity of rejection behaviors will vary with the selection regime set up by local conditions and constraints. Broadly speaking, we have found that variation in rejection behavior is more likely in populations in which the benefit of renesting is high (which favors desertion under a wider range of conditions), in which the external cue is informative (which increases the variation in perceived risk of parasitism between host individuals), and in which the clutch value function is decelerating (which favors multiple-egg ejection under a wider range of conditions). The largest amount of variation is predicted in systems in which mimetic accuracy is moderate to high, because hosts will then be more sensitive to slightly deviating eggs and the influence of external cues will be larger. There are, of course, many other sources of variation that have the potential to generate further variation in optimal rejection behavior: individual hosts may differ in age, condition, experience, and exhibit phenotypic variation in egg appearance and recognition templates, just to mention a few.

Ejection of multiple eggs will in many cases be the most effective way to reduce the odds of a parasite remaining in the nest, a possibility that has received little attention in the literature. It has been pointed out that multiple eggs may be removed from a clutch if the host accidentally damages other eggs when attempting to eject a single egg (Davies and Brooke 1988; Moksnes et al. 1991), or if the cuckoo removes or damages eggs when depositing its egg (Payne 1977), and the disappearance of more than one egg from a clutch has usually been interpreted as reflecting such costs (Davies and Brooke 1988; Moksnes et al. 1991; Lotem et al. 1995; Moskát and Honza 2002). Efforts at identifying and quantifying egg traits that are relevant for egg recognition and discrimination (Rothstein 1982; Cassey et al. 2008; Moskát et al. 2008) may provide an opportunity to test whether multiple-egg ejection is a strategic behavior or an accidental side effect: If strategic, the appearance of all the ejected eggs should deviate from the rest of the clutch and resemble parasite eggs in some consistent manner.

When will strategic ejection of multiple eggs be favored? First, we predict that multiple-egg ejection will tend to be found more often in hosts that better compensate for a reduced clutch size by redirecting parental investment originally intended for the ejected offspring to the ones that remain. Such compensation will lead to decelerating (concave) clutch value functions, which favor multiple-egg ejection for a wider range of parameters. Second, we predict that multiple-egg ejection will be found more often in systems in which the risk of parasitism correlates positively between nesting attempts because this will increase the relative benefits of single- and multiple-egg ejection over desertion for hosts that have a high perceived risk of parasitism in their current

clutch. We did not incorporate such correlations in our model, and it may thus greatly underestimate the frequency of multiple-egg ejection. A third factor that may influence the prevalence of multiple-egg ejection is clutch size: Numerical exploration using a linear clutch value function showed that multiple-egg ejection was favored more often with a larger clutch, all else being equal. This makes sense because the fraction by which the value of a clutch is reduced when an additional egg is ejected is smaller for larger clutches than for smaller clutches. Caution is needed when interpreting this result, however, because the shape of the clutch value function may differ systematically between hosts that lay clutches of different size. Lastly, it is clear that factors known to constrain single-egg ejection will also apply to multiple-egg ejection: For instance, hosts with a small bill may not benefit from egg ejection because they damage too many eggs in the process (Rohwer and Spaw 1988; Moksnes et al. 1991).

In principle, it should be possible for a host to avoid some of the costs associated with instances of multiple-egg ejection. If eggs are cheap to produce, it could actually benefit a female to lay a clutch that is larger than what she can successfully raise, and subsequently reduce it by ejection to the optimal size during incubation (or, if the parasite is nonvicting, reduce the brood to optimal size after hatching). Although admittedly speculative, a host could thereby dilute the risk of a parasite remaining in the nest without suffering a net reduction in number of own offspring. Obligate brood reduction has been observed in combination with brood parasitism (Cunningham and Lewis 2006) although a dilution effect seems unlikely in this particular case.

The Bayesian algorithm predicts the type of behavior that will be favored in a brood parasitic system, but is not the kind of simple decision rule one might expect to evolve readily in nature (Rodríguez-Gironés and Lotem 1999). A simpler decision rule based on a flexible rejection threshold (as proposed by e.g., Davies et al. 1996) mimicked many of the properties of the Bayesian algorithm, including the coexistence of several rejection behaviors within a population, use of multiple-egg ejection, and maintenance of egg ejection under perfect egg mimicry. When the rate of parasitism and the benefit of renesting were both low, the simpler algorithm even had a payoff that was close to the Bayesian one. Although a simple threshold rule will elicit suboptimal behavior under some circumstances, it is clear that other accompanying rules could arise and evolve so as to further fine-tune rejection. For instance, the addition of a rule to desert in response to a nest containing too few eggs would reduce the probability of maladaptively raising clutches after partial clutch reduction when the benefit of renesting is high. Indeed, experimental studies have found desertion to be more likely at nests that contain fewer eggs (Verboven and Tinbergen 2002). Further sophistication that would improve performance could be to adopt separate discrimination thresholds early and late in the season. A suggested alternative



to template-based recognition is an “odd-one-out” rule, often referred to as recognition by discordancy (*sensu* Rothstein 1975b), by which the most extreme egg(s) in the clutch are ejected, or highly variable clutches deserted (Marchetti 2000; Servedio and Lande 2003; Moskát et al. 2009). Such variance-based rules require that hosts have an internal representation of the maximum allowable variation in the clutch, or, as considered by Servedio and Lande (2003), the maximum allowable difference between the two most deviating eggs. An exploration of these types of rules within a Bayesian framework could prove interesting for future study.

Both the Bayesian algorithm and the threshold rule predict that egg rejection may be optimal even in the limiting case of perfect egg mimicry or complete absence of egg recognition, given that the external cue is sufficiently informative. A host may in such cases stand to benefit from ejecting one or a few randomly chosen eggs. Thus, strictly speaking, the presence of egg rejection in a host population does not in itself provide evidence that the hosts can discriminate between eggs and care should therefore be taken before inferring egg recognition abilities from egg ejection behavior. That ejection of randomly chosen eggs can be beneficial has previously not been emphasized in the brood parasitism literature, although it readily follows from several earlier models of egg rejection (e.g., Davies and Brooke 1989b; Rodríguez-Gironés and Lotem 1999). A likely reason for this not being discussed more is perhaps the implicit assumption that parasitism risk is equivalent to the population level of parasitism (but see e.g., Davies et al. 1996), which is typically too low for random ejection to be optimal.

The fact that recognition-free egg ejection can be adaptive may shed new light upon several aspects of the evolutionary arms race between host and parasites. At the proximate level, Hosoi and Rothstein (2000) argue that egg ejection behavior is less likely to evolve than nest desertion: while desertion may evolve as an extension of a general response to intruders, egg ejection requires both egg recognition and egg removal behavior to work. Although nest sanitation may act as a preadaptation for egg ejection, a pre-existing behavior for egg recognition is less likely to be found (Hosoi and Rothstein 2000). Nonetheless, egg ejection is found in a wide range of host species (Langmore et al. 2005), which seems paradoxical. We will argue, however, that egg ejection could also evolve as an extension of a general response to intruders. After encountering nest intruders such as egg predators, birds may be more alert to the presence of damaged eggs in their nest and thus have a higher propensity to remove them, which might serve a preadaptation for egg ejection. An exaggerated propensity to remove eggs in response to nest intruders could constitute an effective defense against brood parasitism, even with no egg discrimination. Natural selection might then subsequently proceed to fine-tune more exactly under which circumstances ejection should be employed

and which eggs to target. This alternative route to egg ejection could also work in systems in which the brood parasite by chance starts out with a pretty good level of egg mimicry, or in which light conditions impede the assessment of eggs.

Egg ejection without recognition may also occur late in a coevolutionary arms race. If the evolution of parasite egg mimicry proceeds to the point where the host's egg recognition machinery is virtually useless in distinguishing between the two egg types, beneficial egg ejection can still be maintained as a response to an external cue. It is important to note, however, that even though the egg recognition mechanism fails to distinguish between host and parasite eggs, the eggs that are rejected are unlikely to be chosen at random and rejection will still impose a selection pressure on egg phenotypes. For instance, hosts using a threshold rule may be under selection to adopt a low threshold in presence of the external cue, despite parasite and host eggs being equally likely to exceed the threshold. Eggs with trait values above the threshold will be ejected, thus maintaining a selection pressure on both hosts and parasites for eggs with lower trait values. This is not restricted to threshold rules. As long as rejection is not based on a true random generator (and there is no reason to believe that it ever would be), some egg appearances will be less favored and tend to be chosen for ejection more often than others, thereby imposing selection on egg appearance. This suggests that the evolution of egg appearance may never reach an “end point” characterized by accurate egg mimicry (Davies 1999), but rather continue as an indefinite coevolutionary chase (cf. the mimicry chase model by Holmgren and Enquist 1999).

## Conclusion

Our optimality approach to egg-rejection behavior has shown that variation in rejection behavior is expected under a wide range of conditions. Because hosts will differ with respect to the information they have obtained from inspecting their clutch and from external cues that are indicative of instances of parasitism, a range of different rejection responses will co-occur within the same parasitized population. Ejection of multiple eggs can represent a beneficial behavioral option and deserves more attention. The fact that natural selection may maintain a significant level of egg ejection when egg discrimination is not possible suggests that egg ejection behavior in response to adult parasites could evolve as a defense strategy prior to egg recognition. If hosts have access to reliable external cues the coevolutionary chase in egg appearance is likely to continue indefinitely.

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## *Supporting Information*

The following supporting information is available for this article:

**Appendix S1.** Avian brood parasitism: information use and variation in egg-rejection behavior.

Supporting Information may be found in the online version of this article.

(This link will take you to the article abstract).

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