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How to Detect a Cuckoo Egg: A Signal-Detection Theory Model for Recognition and Learning

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abstract: This article presents a model of egg rejection in cases of brood parasitism. The model is developed in three stages in the framework of signal-detection theory. We first assume that the behavior of host females is adapted to the relevant parameters concerning the appearance of the eggs they lay. In the second stage, we consider the possibility that females make perceptual errors. In the final stage, females must learn to recognize their own eggs through an imprinting process. The model allows us to make a number of predictions concerning the egg types that should be rejected in different circumstances: egg rejection should increase as the parasitism rate increases and egg mimicry deteriorates; host females' erroneous ejection of their own eggs should be expected for intermediate levels of egg mimicry but not for very good or very poor mimicry; host females would benefit most from learning to recognize their own eggs when individual variability in egg characteristics is much lower than the population variability; and, when egg mimicry is poor or individual variability is very low, females should attempt to imprint on the first egg they lay, before they can be parasitized, but, when mimicry is good and individual variability is relatively high, females must use an extended learning phase. The model provides a framework to study how the enigmatic acceptance of parasitic eggs can be explained by adaptive discrimination mechanisms.

Keywords: great reed warblers, brood parasitism, Bayesian learning, signal-detection theory.

The enigmatic acceptance of brood parasites like cuckoos and cowbirds by their hosts has been the focus of several discussions (Rothstein 1975*b*, 1982*b*, 1990; Davies and Brooke 1989*b*; Brooker and Brooker 1990, 1996; Marchetti 1992; Moksnes et al. 1993; Lotem et al. 1995; Lotem and Nakamura 1998). Excluding a few exceptions (Smith 1968), brood parasitism is detrimental. The lack of rejection of parasitic eggs and chicks has been explained as a result of an evolutionary lag (Rothstein 1975*a*, 1975*b*; Davies and Brooke 1989*b*) or, alternatively, as a situation in which the cost of rejection exceeds its benefits (Zahavi 1979; Rohwer and Spaw 1988; Lotem et al. 1992).

Rejection of parasitic eggs may be costly as a result of egg breakage during egg ejection (Davies and Brooke 1988; Rohwer and Spaw 1988), loss of time or a nesting site (Petit 1991; Moksnes et al. 1993), a Mafia behavior by the parasite (Zahavi 1979; Soler et al. 1995), and recognition errors (Molnar 1944; Davies and Brooke 1988; Marchetti 1992). The first three types of costs are unlikely to justify acceptance when parasitized hosts lose the entire brood. However, in cuckoo hosts, mistaken ejections of their own eggs when the host is not parasitized can make rejection worse than acceptance (Davies and Brooke 1989*b*; Lotem et al. 1992, 1995; Davies et al. 1996). The risk of recognition errors is especially relevant in host-parasite systems where egg mimicry has evolved.

Experiments suggest that the mechanism of egg recognition in passerines is based on an imprinting-like process (Rothstein 1974, 1978; Lotem et al. 1995). Naive breeders should tolerate a range of egg types and learn to recognize as their own the types they see in their nests. On the basis of this experience, hosts should narrow their range of tolerance and reject unfamiliar egg types. Acceptance of cuckoo eggs can therefore arise in the host population as a result of the need of naive breeders to learn to recognize their own eggs. Additional evidence that the cost of errors has shaped the mechanism of egg recognition is provided by hosts that are more likely to reject odd eggs when they observe a cuckoo near the nest (Davies and Brooke 1988; Moksnes and Røskaft 1989; Moksnes et al. 1993; Davies et al. 1996) and by the stimulus summation mechanism found in some cowbird hosts (Rothstein 1982*a*).

Despite the increasing attention given to the mechanism of egg and nestling recognition as a key factor in under-

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standing cuckoo-host coevolution (e.g., Krebs and Davies 1997), a theoretical framework to explore the subject is still lacking. Previous models of brood parasitism consider under which conditions rejection of cuckoo eggs will be more adaptive than acceptance, but they include the error probability as a constraint rather than as a result of host behavior (Davies and Brooke 1989*b*; Takasu et al. 1993; Lotem et al. 1995; Davies et al. 1996). Hence, these models can only illustrate for what range of error probabilities acceptance is better than rejection. They cannot be used to explore what mechanism, or what kind of decision rules, should be applied by hosts. To study the evolution of recognition mechanisms, one should develop a model in which egg variability and cuckoo egg mimicry are the constraints and which allows the host to develop a fitness-maximizing strategy (Getty [1996] provides a related model for mate selection). Initial attempts in that direction were presented in a graphical model by Lotem et al. (1995, fig. 9) and by considering the problem of egg recognition within the framework of signal-detection theory (Davies et al. 1996; see also Reeve 1989 for similar approach to kin recognition; Getty [1995] clarifies the relationships between signal-detection theory and Reeve's model).

Our aim in this article is to provide a theoretical framework to determine the optimal strategy for egg recognition in a cuckoo host, considering both innate and learned recognition. The model belongs to the signal-detection theory (SDT; Green and Swets 1966) tradition and is developed in a general setting so that it can be used to study inter- and intraspecific brood parasitism. For concreteness, we focus our discussion on great reed warblers (*Acrocephalus arundinaceus*) parasitized by the common cuckoo (*Cuculus canorus*), and the numerical results we present are made on the basis of the parameter values estimated from this system.

The Model

Rationale

To explain our model we start by considering the following example in the context of SDT (see Davies et al. 1996 for a similar account). A great reed warbler (hereafter referred to as GRW) female faces a clutch of eggs. She must decide whether to incubate the whole clutch or to eject one or more eggs (throughout the article we assume that only females decide whether to reject or to accept a cuckoo egg). Assuming that cuckoo eggs are, on average, darker than GRW eggs, the GRW female could have a decision rule of the form: "reject all eggs darker than some criterion C." By modifying the value of C, she changes the probability that different outcomes take place (fig. 1): when C increases, fewer eggs are rejected. As a consequence, the likelihood of accepting parasitic eggs increases, and the likelihood of the host female rejecting her own egg decreases. The likelihoods and relative costs of these mistakes (a false rejection or the acceptance of a parasitic egg) are not the same and the expected fitness, $W(C)$, of a GRW female is a function of the criterion she uses. It is possible to calculate the criterion value C^* that maximizes the expected fitness. Note that females are not classified as "accepters" or "rejecters": rather, all females reject eggs provided that the likelihood that they are cuckoo eggs is high enough.

While rejecting any egg with pigmentation greater than some criterion C^* might seem to be a sensible rule, this rule does not maximize fitness: the appearance of the entire clutch must be considered to decide which eggs must be rejected. (The decision whether or not to reject an egg will depend on the comparison of expected payoffs with and without rejection, and this latter payoff cannot be calculated without considering the entire clutch.) There is, indeed, evidence that the decision to reject or accept an egg is not independent of how the rest of the clutch looks (Lotem et al. 1995). Besides, many host species reject the parasitic egg a few days after parasitism (Rothstein 1975*a*; Alvarez et al. 1976; Davies and Brooke 1989*a*), and this delay is longer when the eggs are mimetic (Lotem et al. 1995). Davies and Brooke (1989*a*) suggested that this delay might be needed to allow the host to inspect more eggs, or the whole clutch, before making a decision. The existence of these data prompted us to develop a new model that yields maximal fitness when host females must decide whether to reject an egg from the entire clutch.

Terminology

It will be convenient to clarify at this point that the terminology we will use throughout the article differs from standard SDT terminology in two ways. Signal-detection theory was initially developed to study optimal strategies in the detection of signals. In a given trial, subjects might or might not be presented with a signal, and their task is to determine in which trials the signal was present. Within this context, the following terminology was introduced: a "hit" refers to a signal trial where the subject correctly identified the signal. "Misses" are signal trials where the subject did not detect the signal. "False alarms" are empty trials where the subject thought that the signal was present, and "correct rejection" are empty trials correctly identified as such. Notice that, in our model, correct rejection of a cuckoo egg does not correspond to correct rejections in the SDT terminology; instead, it is analogous to hits.

Many SDT users classify misses and false alarms as perceptual errors. This makes sense if we assume that trials are physically different and that the overlap in the per-

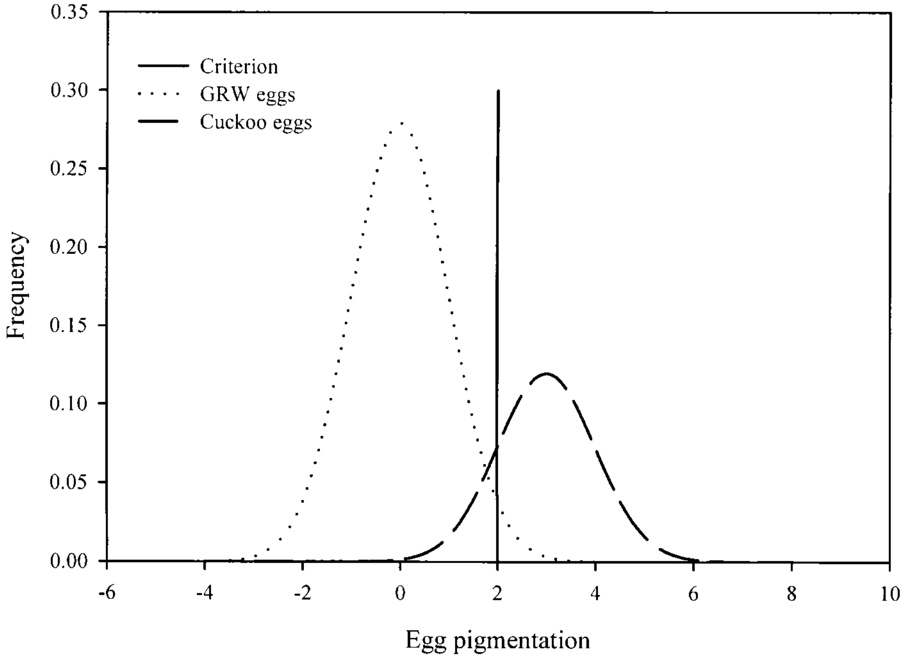

Figure 1: Frequency distribution of great reed warbler (GRW) and cuckoo egg pigmentations and a rejection criterion. The difference in area under each curve reflects a parasitism rate smaller than 50%. When eggs darker than the criterion ($c = 2$ in the figure) are rejected, the probability of accepting a cuckoo egg is given by the area of the cuckoo distribution (*dashed line*) to the left of the criterion (*solid vertical line*), while the probability of rejecting a GRW egg is given by the area of the GRW distribution (*dotted line*) to the right of the criterion. Notice that this figure represents the four possibilities for a single egg, while fitness is determined by the outcome of the entire clutch.

ception of signal and empty trials comes from noise in the perceptual process. In many cases (including the problem at hand), however, things are more complicated: there may be an overlap between the distribution of stimuli used in empty and signal trials, so that misses and false alarms are unavoidable even in the absence of perceptual errors. Thus, if a cuckoo egg is perfectly mimetic, if it really differs from a GRW egg only in its genetic composition, a female that accepts this egg (a miss) can hardly be blamed for committing a perceptual error. For this reason, when talking about perceptual errors, we do not refer to misses and false alarms but to the presence of noise in the perceptual process.

In most applications of SDT, four outcomes are considered: there may or may not be a signal and the subject may or may not detect it. When we consider a single egg, these four possibilities map to its being a cuckoo or a GRW egg, accepted or ejected. However, in this article, we will concentrate on the case in which at most one egg in the clutch is a parasitic egg and and in which the female ejects at most one egg (the extension of the model to multiple parasitism and/or egg ejection is immediate). In this case, rather than following the fate of each individual egg, it is simplest to look at the overall outcome of the clutch, since there are only five possibilities: if the clutch is not parasitized, the GRW may accept all eggs (acceptance of her own clutch) or eject one of them (unparasitized, eject own egg); if the clutch is parasitized, the GRW may eject the cuckoo egg (ejection of cuckoo egg), eject instead one of its own eggs (parasitized, eject own egg), or accept all eggs (parasitized, accept all eggs). Notice that the ejection of wrong eggs in parasitized nests results from the combination of two mistakes: failure to identify the cuckoo egg and rejection of the host's own egg. Readers familiar with SDT should strive to keep in mind the above definitions.

Three models are developed in this article. In model 1, we assume that females make no perceptual errors and that each individual female behaves from the beginning in a way that is adapted to the appearance of her own eggs. In model 2, we study the implications of perceptual errors (such as misjudging differences in egg size or pigmentation). In model 3, females need to learn how their own eggs look. Although the equations involved in the models may at times seem cumbersome, it cannot be overemphasized that we nowhere make the assumption that birds are making these or related calculations. In fact, the decision process that the host females must follow to determine whether to incubate or reject a given egg may be extremely simple (cf. "Discussion").

Model 1: Baseline

We start with the most basic model in which it is assumed that host females have perfect information regarding all relevant statistical parameters. The assumptions of this model are as follows.

Eggs vary in a unidimensional quantity, such as pigmentation or size. This quantity is represented by x. For narrative simplicity, we will refer to x as the pigmentation of the egg. (It should be noted that real eggs do not differ on a unidimensional space, but on a multidimensional one. The generalization of the model to the multidimensional case is immediate.)

Host females make no perceptual errors: if an egg has pigmentation x, females perceive it as having pigmentation x and not $x' \neq x$.

The eggs of a GRW vary in pigmentation according to the probability density function (PDF) $\rho_{rw}(x)$. Without lack of generality, we will assume that the average pigmentation of GRW eggs is 0.

The eggs of a cuckoo vary in pigmentation according to the PDF $\rho_c(x)$, and we assume that $\rho_{rw}(x) \neq \rho_c(x)$. We will further assume that the average pigmentation of cuckoo eggs, c, is greater than or equal to 0. In other words, we assume that cuckoo eggs are darker than GRW eggs.

A random proportion α of GRW clutches are parasitized by cuckoos.

Female cuckoos remove a GRW egg from the nest at laying, and we will assume that they take one egg at random. Although it might be argued that cuckoos would benefit from removing eggs with particular characteristics (Brooker and Brooker 1990), there is no evidence that they select the egg they remove (Davies and Brooke 1988). Female cuckoos may be forced to act in this way because of the need to lay their own egg as soon as possible in order not to be detected (Davies and Brooke 1988; Moksnes and Røskaft 1989).

The expected payoff (increase in fitness) for a GRW female who lays N eggs and ejects m of them is $W_{u,\,N-m}$, if none of the eggs she incubates is a cuckoo egg, and $W_{p,\,N-m}$, if there is a cuckoo egg among the eggs that are incubated. These values of expected fitness include any cost of rejection, such as the possibility of breaking other eggs in the ejection process. In calculating the expected payoffs, we will assume that rejection of parasitic eggs always takes place by ejection, since this allows us to study the optimal decision without having to consider future clutches (Davies et al. 1996).

In order to estimate the likelihood that a particular egg has been laid by a cuckoo, we need not worry about which particular cuckoo may have laid the egg: there is no fitness difference between being parasitized by one cuckoo or another. As a result, the PDF $\rho_c(x)$ relevant for the calculations is the population distribution. On the other hand, to estimate the probability that there is a cuckoo egg in a nest, we need to know how the eggs of the individual host female look, not what the distribution of egg pigmentation in the entire host population is. For this reason, the relevant $\rho_{rw}(x)$ is the PDF of the individual female. In models 1 and 2, we assume that the behavior of each female in the population is adapted to her own PDF. This assumption will be relaxed in model 3.

A GRW female faces a clutch of N eggs, with pigmentation $x_1, x_2, \ldots, x_N$ (hereafter denoted as $\boldsymbol{x}_N$). With the above assumptions, it is possible to calculate the probabilities that a clutch with pigmentation $\boldsymbol{x}_N$ has or has not been parasitized by a cuckoo. We denote these probabilities by $\Pr(p|\boldsymbol{x}_N)$ and $\Pr(u|\boldsymbol{x}_N)$, respectively. It is equally possible to calculate the probabilities that, after ejecting the ith egg, there is or there is not a cuckoo egg between the remaining $N-1$ eggs. These probabilities we denote by $\Pr(p|\boldsymbol{x}_{N-i})$ and $\Pr(u|\boldsymbol{x}_{N-i})$, respectively. The knowledge of the different probabilities (calculated in app. A) allows us to calculate the expected payoff from accepting all eggs,

$$W_{\text{acc}} = \Pr(u|\boldsymbol{x}_N) \times W_{u,N} + \Pr(p|\boldsymbol{x}_N) \times W_{p,N}, \tag{1}$$

and from ejecting the ith egg,

$$W_{\text{rej},\,i} = \Pr(u|\boldsymbol{x}_{N-i}) \times W_{u,N-1} + \Pr(p|\boldsymbol{x}_{N-i}) \times W_{p,N-1}. \tag{2}$$

Clearly, the optimal decision is to reject the ith egg if the expected payoff from rejecting it exceeds the payoff from accepting all eggs:

$$W_{\text{rej},\,i} > W_{\text{acc}}. \tag{3}$$

Model 2: Perceptual Errors

Assumptions are as in model 1, except for the presence of perceptual errors. An egg of pigmentation x is perceived as having pigmentation x' with probability $\varepsilon(x, x') \geq 0$.

Model 3: Learning

Assumptions are as in model 1, except that females must learn how their own eggs look. Specifically, we will assume that the eggs of a particular female have x values normally distributed, with mean μ and variance σ^2. The variance is constant for all females, but the mean is not. Instead, individual means are normally distributed around some value ν, with variance Σ^2. (The normality assumption is not necessary for the model, but it greatly simplifies the calculations.)

Results and Discussion

Inequality (3) can be applied to decide whether the ith egg in a particular brood should be ejected or incubated. All the terms involved in this inequality can be easily computed with a hand calculator. In general, however, we will be interested in global or average results: How often will a cuckoo egg be incubated? How many mistakes will host females make? These questions can, in principle, be answered by calculating the probability that the left-hand side of the inequality is greater or smaller than the right-hand side. But, since each side of inequality (3) involves a sum of irrational fractions, calculating the probability that one side is greater than the other is rather difficult; in practice, then, the easiest way to obtain information about global properties is by simulating the process of laying, parasitism, and egg ejection.

All the results presented are made on the basis of normal PDFs for GRW and cuckoo eggs. Throughout, we assume that at the population level, both distributions have equal variance. Average pigmentation is 0 for GRW eggs and c for cuckoo eggs. In all figures, 10,000 clutches of five eggs (the median clutch size in GRW) were simulated to calculate each data point, with egg pigmentation following $\rho_{\mathrm{rw}}(x)$. In a proportion α of the 10,000 clutches (randomly selected), an egg was removed and replaced with a cuckoo egg, and GRW females followed their optimal strategy (inequality [3]) to decide whether an egg should be rejected. Payoffs (expected number of chicks raised) for the different possible outcomes are given in table 1. They are calculated on the assumptions that cuckoo chicks eject from the nest other eggs or chicks, and in 20% of egg ejections by the host, accidental egg breakage leads to nest desertion (Lotem et al. 1995), to which we assigned a payoff of 2.5 (somewhat arbitrarily). Note that, although table 1 includes only three different payoffs, the distinction between five possible outcomes is relevant because when the parasitic chick does not eject all host eggs, the different outcomes are associated with different payoffs and because the five different outcomes reflect different processes and provide information about the behavioral strategy followed by the host. (This difference is related to the concept of receiver-operating-characteristic curves in SDT. For lack of space, we will not discuss them here, but see Getty 1995.)

Table 1: Payoff of the different possible outcomes

Outcome	Payoff
Acceptance of own clutch	5.0
Ejection of cuckoo egg	3.7
Unparasitized, eject own egg	3.7
Parasitized, eject own egg	0
Parasitized, accept all eggs	0

Model 1: Baseline

The Outcomes of Host Behavior. Figure 2 shows the frequency of occurrence of the different outcomes as a function of parasitism rate when the average cuckoo egg pigmentation was $c = 2$ (fig. 2*A*) and as a function of average cuckoo egg pigmentation, c, when 20% of the clutches were parasitized (fig. 2*B*). The strategy of GRW females basically changes from "accept all eggs" at low levels of parasitism to "reject the egg with highest pigmentation" at high levels of parasitism. With a constant rate of parasitism (fig. 2*B*), no eggs are rejected when there is perfect mimicry ($c = 0$). As the mimicry deteriorates, cuckoo eggs become more easily detected and rejection appears. At intermediate levels of mimicry, rejection entails some costs: GRW females sometimes reject one of their eggs. As the mimicry deteriorates even further, rejection of their own eggs disappears; for very poor mimicry, females always reject the cuckoo eggs and never their own. Note, however, that the ejection of their own eggs at intermediate levels of parasitism is more than offset by the accompanying increase in rejection of cuckoo eggs.

The results of the simulation in figure 2*A* confirm predictions by previous models, according to which rejection should increase with the probability of being parasitized (Davies and Brooke 1989*b*; Takasu et al. 1993; Lotem et al. 1995; Davies et al. 1996). The best evidence that hosts behave according to this prediction is that reed warblers (*Acrocephalus scirpaceus*) are more likely to reject the oddest egg from the clutch after seeing a cuckoo near the nest (Davies et al. 1996).

Egg rejection becomes common as egg mimicry deteriorates (fig. 2*B*). It is only for good and intermediate mimicry levels (when some but not all the cuckoo eggs are rejected) that females will sometimes eject their own eggs from unparasitized nests. In accordance with this result, there is evidence for ejection of their own eggs only from host species known to be parasitized with mimetic eggs (Molnar 1944; Marchetti 1992; Davies et al. 1996). When mimicry is extremely good, the model predicts that no rejection should be observed (fig. 2*B*; cf. discussion of fig. 3*B*).

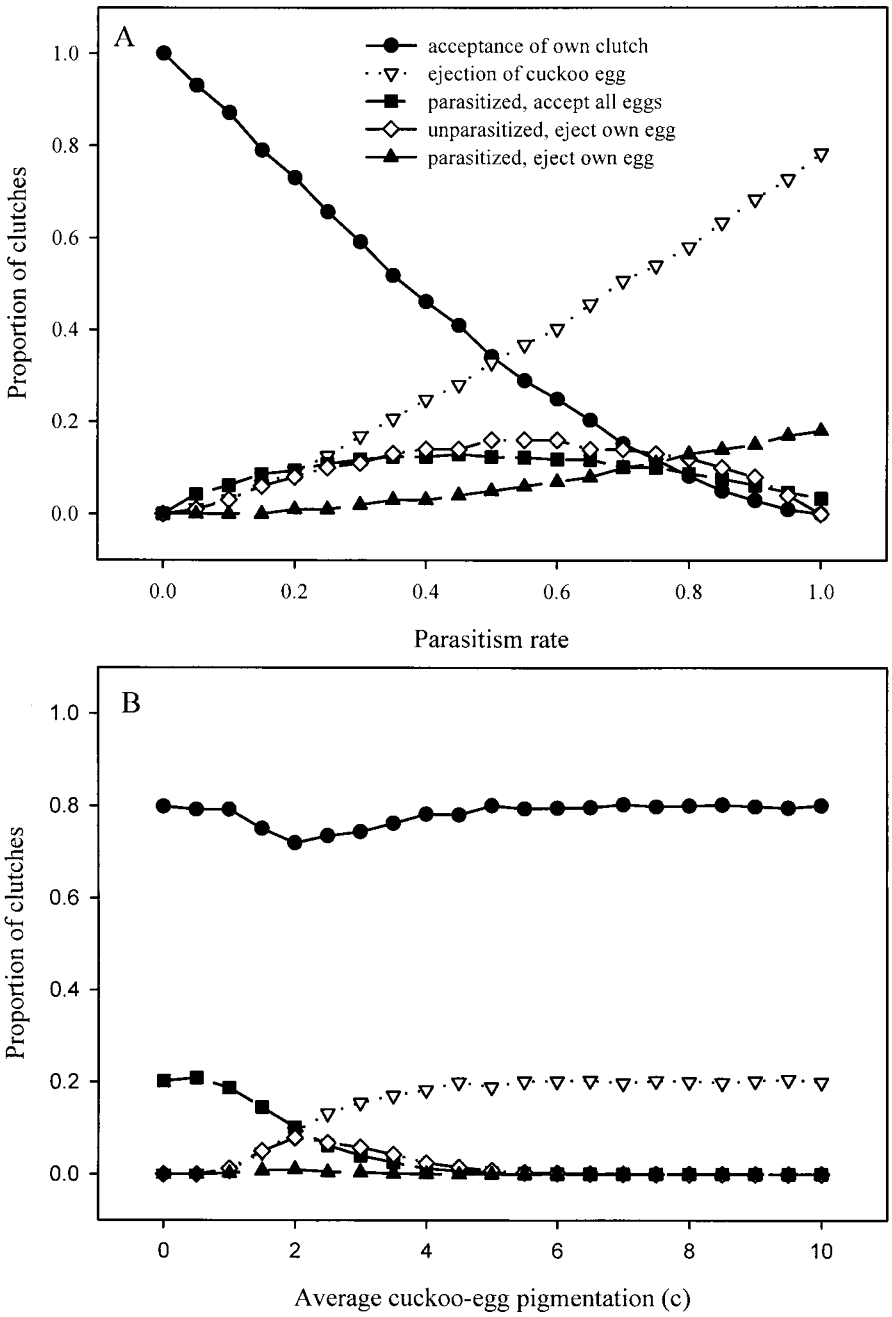

Figure 2: Proportion of clutches (out of 10,000) where the different outcomes occurred. The five lines represent the GRW females' frequencies of acceptance of their own clutches, rejection of cuckoo eggs, parasitized clutches with no egg ejected, unparasitized clutches with one GRW egg ejected, and parasitized clutches with a GRW egg ejected instead of the cuckoo egg. *A*, Average cuckoo egg pigmentation $c = 2$; *B*, 20% of the clutches parasitized.

Host Decision Rules. The pigmentation of the eggs that are rejected gives us an indication of the rules that the GRW females may be following. With the level of egg mimicry fixed (fig. 3*A*), eggs are rejected only if they are extremely odd (dark) when parasitism is rare, but at higher levels of parasitism the darkest egg is always rejected, regardless of how odd it actually is.

A more complex picture emerges when we study pig-

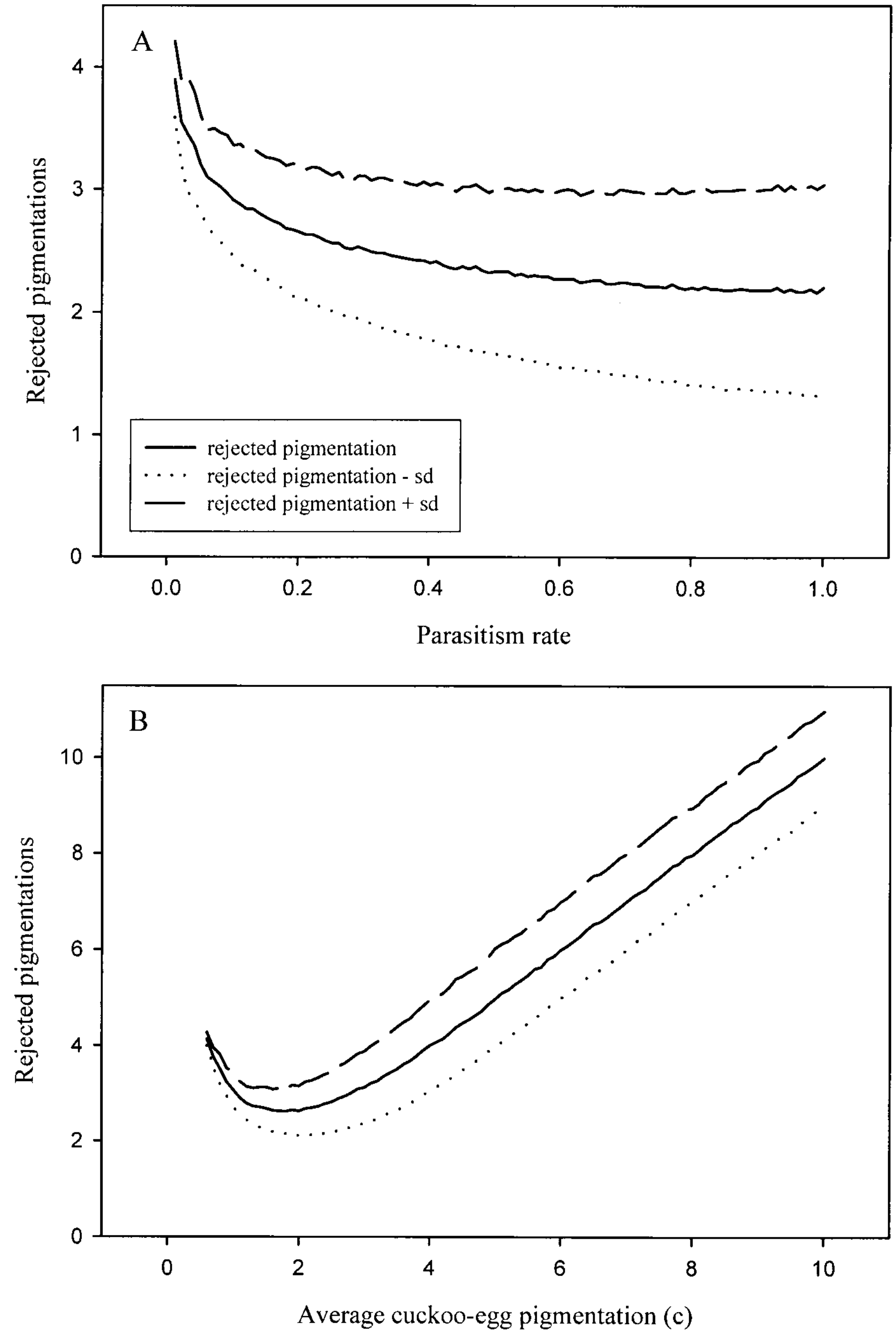

Figure 3: Pigmentation of rejected eggs (*A*) as a function of parasitism rate when $c = 2$ and (*B*) as a function of cuckoo egg pigmentation with a parasitism rate of 0.2. The central line represents average over 10,000 simulations, and the outer lines are 1 SD apart.

mentation of ejected eggs as a function of egg mimicry (fig. 3*B*). With perfect mimicry, no egg is rejected. With poor mimicry, cuckoo eggs are easily detected and are always rejected. In this range, the egg pigmentation of rejected eggs is approximately equal to *c*, because of the low frequency of mistakes. At intermediate mimicry levels, where egg rejection appears and becomes common, there is a range where rejected eggs become lighter as cuckoo eggs get darker. This result may first look counterintuitive. The reason for this is that when rejection starts to be adaptive, the overlap in PDFs is large and only the darkest cuckoo eggs are rejected. However, as c increases, dark cuckoo eggs become more common: the likelihood that a dark egg is a cuckoo egg is now very large, and eggs that were formerly kept are now rejected (even if this implies a higher probability of rejection of their own eggs; fig. 2*B*). As c increases even further, most cuckoo eggs will be much darker than the host eggs, and a risky decision rule will not be needed any more. (Note that the coevolutionary sequence of events is likely to be from dark cuckoo eggs to light ones, rather than the direction we followed in our explanation.) Figure 3*B* suggests, therefore, that, for similar levels of cuckoo parasitism, the highest level of intolerance toward divergent eggs should be found among hosts facing an intermediate level of mimicry, rather than perfect or nearly perfect mimicry.

A situation like this may exist. Rothstein (1990) has pointed out that in the redstart (*Phoenicurus phoenicurus*), rejection ability is surprisingly poor, considering the nearly perfect egg mimicry that this cuckoo host has to cope with. Rothstein suggested that the evolution of egg rejection may stall completely when egg mimicry becomes especially good because hosts will not be able to detect most of the cuckoo eggs (see also Kelly 1987).

Model 2: Perceptual Errors

The Effect of Perceptual Errors. The optimal behavior is to reject the most extreme egg when inequality (3) is satisfied, but now the perceived distributions of egg pigmentations, $\rho_{rw,p}(x)$ and $\rho_{c,p}(x)$, should be substituted for $\rho_{rw}(x)$ and $\rho_c(x)$ when calculating the conditional probabilities $\Pr(p|\mathbf{x}_N)$, $\Pr(u|\mathbf{x}_N)$, $\Pr(p|\mathbf{x}_{N-1})$, $\Pr(u|\mathbf{x}_{N-1})$. The perceived distributions are calculated as

$$\rho_{rw,p}(x) = \int_{-\infty}^{\infty} \epsilon(x, s) \times \rho_{rw}(s) \times ds \tag{4}$$

and

$$\rho_{c,p}(x) = \int_{-\infty}^{\infty} \epsilon(x, s) \times \rho_{c}(s) \times ds. \tag{5}$$

In the absence of any knowledge about the shape of $\varepsilon(x, x')$, we can only note that the effect of the perceptual errors will be to inflate the variance on the distribution of egg pigmentation. Host females will behave as if the PDFs of host and cuckoo eggs had a larger variance than they actually have, thus making rejection more costly and less likely than in their absence.

The existence of perceptual errors does not invalidate the results of models 1 and 3, because it only modifies the shape of the PDFs that must be used in equations (1) and (2). Because perceptual errors make rejection more costly, realistic rejection rates might be lower than those predicted by models 1 and 3, and the decision rules used by hosts should be more conservative (i.e., only more extreme eggs should be rejected).

Behavioral Strategies to Minimize Perceptual Errors. In the absence of perceptual errors, a female would reach the same decision (whether to accept or reject a given egg) no matter how often she made it. In this scenario, then, one does not need to consider when or how often females decide whether to eject or incubate their eggs. They may make this decision every time they arrive at the nest or only once midway through the incubation period—the end result would be the same. With perceptual errors, however, things are otherwise. An egg may look more cuckoo-like one day than another. The solution that we have proposed is made on the basis of the assumption that only one decision is taken. At least two other scenarios are possible. The female may make a decision every time she arrives at the nest. This strategy would minimize the likelihood of accepting a cuckoo egg but would increase the chances of a female rejecting her own egg. Therefore, the criterion for rejecting the egg would have to be more conservative than the one we have proposed. Alternatively, the female could inspect the clutch repeatedly. If inequality (3) is satisfied, her motivation to eject one egg will increase somewhat. If inequality (3) is not satisfied, the motivation to eject an egg will decrease (with the presence of perceptual errors, inequality [3] may be satisfied sometimes but not others). Ejection might take place only when the motivation to eject reaches a certain threshold. This behavior would essentially eliminate the effect of perceptual errors. Potentially, this scenario might explain why reed warblers spend such a long time studying their clutch (N. B. Davies, unpublished data), and why, as we mentioned earlier, it can take a few days for most host species to reject mimetic eggs.

Model 3: Learning

Within the assumptions of model 3, the closed form of the optimal strategy cannot be derived. According to the approximation derived in appendix B, naive females should behave as if their distribution of egg pigmentations was equal to the population distribution. With the assumptions of model 3 this implies calculating $\Pr(p|\mathbf{x}_N)$, $\Pr(u|\mathbf{x}_N)$, $\Pr(p|\mathbf{x}_{N-i})$, and $\Pr(u|\mathbf{x}_{N-i})$, using a normal distribution with mean ν and variance $\omega^2 = (\sigma^2 + \Sigma^2)$ for $\rho_{rw}(x)$. As time goes on and a female lays more and more clutches, some sort of imprinting process could allow her to accept eggs similar to the ones she has laid in the past and to reject dissimilar ones.

Can Learning Improve Recognition? Before studying learning algorithms, we consider whether birds have much to gain from learning. When the variance of egg types in the host population is considerably larger than that of a particular female, females are unlikely to have a precise genetic knowledge of their own eggs. We ask to what extent learning can improve recognition for hosts that already have innate recognition of the mean and the variance of the population egg types.

We will denote by omniscient a female whose behavior is precisely adapted the average pigmentation of the eggs she lays, μ. We assume that the population of GRW and cuckoo eggs are normally distributed with equal variance ($\omega^2 = 16$) and 0 mean. Individual GRW females lay eggs normally distributed, with variance σ^2 and mean μ, where μ itself is normally distributed with mean = 0 and variance $\Sigma^2 = 16 - \sigma^2$.

Figure 4 shows the fitness of a naive female, plotted as the proportion of the fitness of an omniscient female. The difference between the proportion of maximal fitness and one is a measure of the benefit a female can derive from learning. We can see that the putative advantage of learning increases as parasitism rate increases and as the variability in pigmentation of an individual female (σ^2) decreases. The latter factor can be explained as follows: the smaller the range of pigmentations in the eggs of an individual female, the less likely that a randomly selected cuckoo egg is within the range of the female and the easier it becomes for the female to detect cuckoo eggs. Hence, the narrower the range of egg pigmentations laid, relative to that of the entire population, the more interesting it becomes to know precisely what that range is.

The next question is how fine the learning process must be. Figure 5 shows (for $\sigma^2 = 1$ and $\alpha = 0.4$) the expected payoff per brood when the GRW female behaves as if her average pigmentation was different from its true value. When mimicry is good, and parasitism rates are elevated, GRW females can be severely penalized for imprinting to the wrong pigmentation.

Learning Algorithms. Although the graphic model of Lotem et al. (1995, fig. 9) illustrates that egg variability should determine the length of the learning period, it is not a realistic model of learning. Individuals are unlikely to shift from accepter to rejecter at the end of the learning period. Rather, they appear to refine their discrimination gradually. Naive GRW females were already capable of rejecting most highly nonmimetic eggs and some of the intermediate egg types, while experienced breeders reject both types at a higher rate (Lotem et al. 1995). As in most forms of imprinting, one should expect a mechanism that gradually refines preexisting preferences (Bateson 1979).

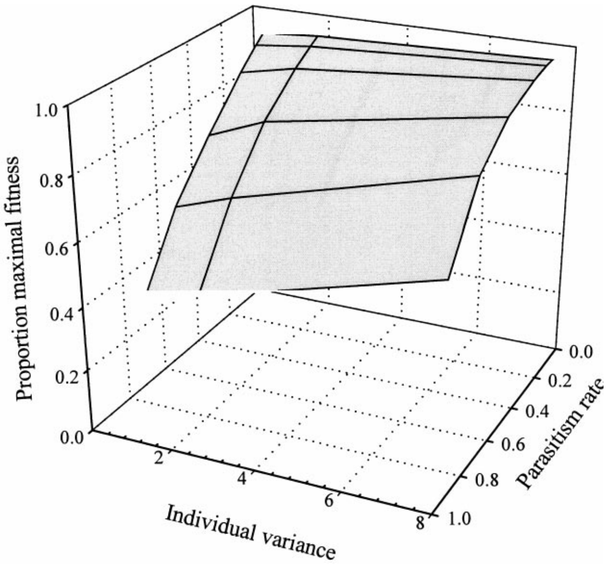

Figure 4: Fitness of a naive female relative to the fitness of an omniscient female (proportion of maximal fitness) as a function of parasitism rate (α) and individual variance (σ^2). Each node of the grid is the average over 10,000 simulations with $c = 0$ and $\omega^2 = \sigma^2 + \Sigma^2 = 16$.

With the assumptions of the model (specifically, the existence of a prior distribution for μ), an obvious choice for a learning algorithm would be Bayesian statistics (DeGroot 1986). The logic of the Bayesian learning process can be explained as follows. At the beginning of the learning process, the individual has some information—the prior distribution. In our case, this would imply that females are born with an innate template that corresponds to the optimal rejecting strategy, if egg pigmentation follows the population distribution. Some information is then acquired. In our case, the information could be framed as "k eggs have been laid, with pigmentation $x_1, x_2, \ldots, x_k$." The learning process itself consists of the modification of the earlier distribution in accordance with the information gathered. In other words, after laying k eggs the expectations of the female change. In subsequent clutches, she will expect to lay eggs similar to the initial sample.

The behavioral strategy that follows from the Bayesian learning process is calculated in appendix C. The optimal behavior is still given by rejecting an egg when inequality (3) is satisfied, but the distribution of egg pigmentations that must be used for the calculation of the conditional probabilities is no longer the population distribution, nor is it the individual distribution (which is, of course, unknown). With the assumptions of model 3, the distribution that must be used is a normal distribution. Its mean and

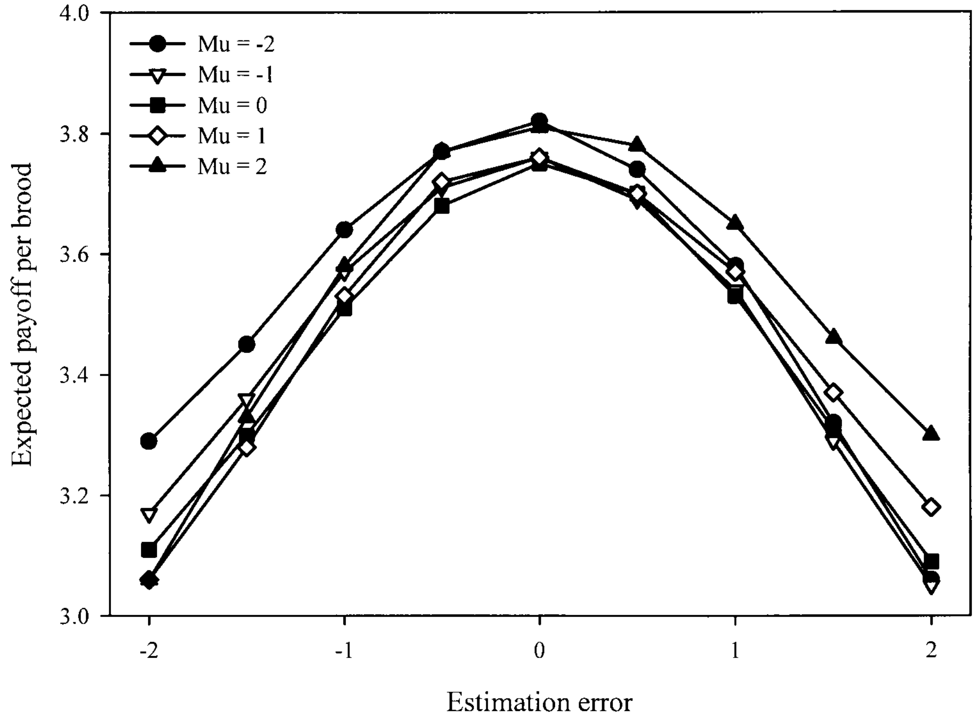

Figure 5: Expected payoff per brood (average over 10,000 simulations) for a great reed warbler (GRW) female that lays eggs with average pigmentation μ and behaves as if she laid eggs with average pigmentation μ_{est}, as a function of her estimation error ($\mu_{est} - \mu$). In all cases, 40% of nests were parasitized and $c = 0$.

variance must be estimated from the sample of eggs already laid by the female. The estimated variance (eq. [C3]) decreases hyperbolically with the number of eggs laid, k, from the population variance, $\sigma^2 + \Sigma^2$ (when $k = 0$) to the individual variance, σ^2 (when $k = \infty$). The estimated mean depends on the specific pigmentation of the eggs laid. It is a weighted average between the population mean, ν, and the average pigmentation of the eggs laid by the female, $\langle x \rangle$ (eq. [C2]).

Within the framework of Bayesian learning, a number of mechanisms can be devised. When individual variance is low relative to the population variance (fig. 6), or when there is a low level of mimicry, a single egg is sufficient for the female to identify her egg type. The best she can do is then to imprint on the first egg she lays, as soon as she lays it, in order to avoid imprinting on parasitic eggs (hereafter "misimprinting"; see Lotem 1993). With high levels of mimicry and relatively high individual variance in egg pigmentation, having a fixed learning period during which all eggs are accepted and, thereafter, a rejection phase is of little use, regardless of the duration of the learning period. A single egg does not provide sufficient information for the female to adopt an optimal rejection criterion, and extending the learning phase leads to misimprinting (M. A. Rodríguez-Gironés, unpublished data). Under these conditions, the best strategy is to reject eggs from the first clutch onward and modify the rejection criterion using the Bayesian process on the basis of the eggs left in the nest after rejection has taken place (fig. 7).

To reduce the cost of misimprinting, a host could use the median pigmentation of the clutch to update the prior distribution instead of using the mean, as suggested by the standard Bayesian process. The median clutch pigmentation is less affected than the mean by the presence of parasitic eggs. A typical result is that using the median clutch pigmentation instead of the mean is somewhat advantageous in the second breeding attempt, but the difference between both updating algorithms becomes negligible as the females get more and more experience (fig. 7).

There is evidence that hosts that accept a parasitic egg in one breeding attempt may still reject this egg type in a future breeding attempt (Lotem et al. 1995; M. Soler, unpublished data). Although this evidence can be explained as a result of perceptual errors, it is also predicted independently by the extended learning mechanism. The cuckoo egg, if accepted, would affect the new estimate of the average pigmentation. However, if the majority of host

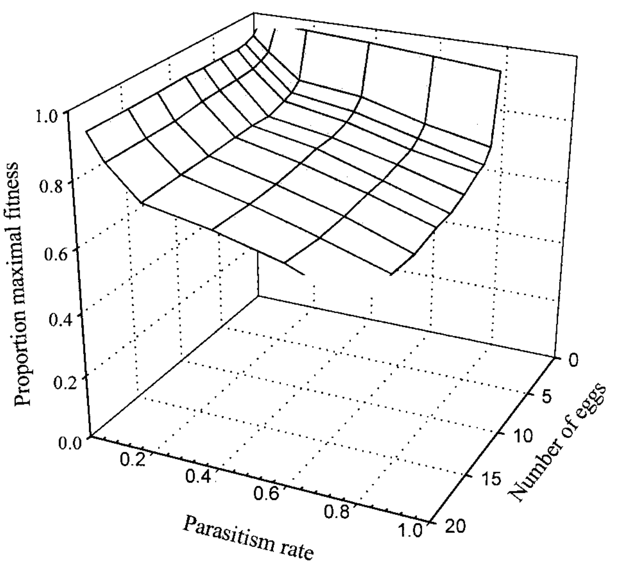

Figure 6: Fitness of a naive female at the end of the learning process relative to the fitness of an omniscient female (proportion of maximal fitness) as a function of parasitism rate (α) and the number of eggs used for learning. Each node of the grid is the average over 10,000 simulations with $c = 0$ and $\omega^2 = \sigma^2 + \Sigma^2 = 16$. The individual variance was $\sigma^2 = 0.475$.

eggs are closer than the cuckoo egg to the average pigmentation of the individual female, the latter distribution will be closer than that of the former to the real distribution of egg pigmentations. Another reason is that the variance of egg types that is tolerated by the host is assumed to decrease with the number of clutches laid (see above). Therefore, even if the estimate of the average pigmentation remained unchanged, a rejection of egg types that once were accepted is likely to occur.

The Cost of Misimprinting. For the parameter values used in the simulations, misimprinting was not particularly costly. Although females who raised a cuckoo in their first breeding attempt were more likely to do so in the future, their expected decrease in fitness was small. In their second brood, they raised an average of 0.2 fledglings less than females who had not been misimprinted. As we mentioned above, the misimprinting cost could be further reduced by estimating their own pigmentation from the median rather than the mean clutch pigmentation, but the fitness differences when using one learning rule or the other were fairly small (fig. 7). However, our results have been obtained for relatively large clutch sizes ($N = 5$) and low proportion of parasitic eggs (there was never more than one cuckoo egg in a clutch). As the proportion of parasitic eggs in a clutch increases (either by decreasing clutch size or because multiple parasitism becomes common), so does the misimprinting cost. In particular, although females may benefit from learning how their own eggs look, learning to recognize what the chicks look like might be counterproductive when the parasitic chick ejects its foster siblings from the nest (Lotem 1993). In this case the cost of misimprinting reaches the maximum possible value. The question of why cuckoo chicks cannot be rejected on the basis of the host's innate knowledge is still an open problem (see also Lotem 1993).

Discussion

Optimal Behavior and the Limitations of the Model

Rejection Rules. We have already stated that it should not be assumed that host females calculate the conditional probabilities that their clutches have been parasitized. What we would claim is that natural selection should shape the decision rule of host species in such a way that they behave approximately in agreement with inequality (3). Such decision rules need not be utterly complicated. When the average clutch pigmentation is plotted versus the pigmentation of the darkest egg of the clutch for each female, one can normally see that the points corresponding to females who did or did not reject the darkest egg segregate in space (M. A. Rodríguez-Gironés, unpublished data). This implies that, instead of calculating the conditional probabilities that there is, or there is not, a cuckoo egg in the clutch, a simple relationship between the average clutch pigmentation and the pigmentation of the darkest egg in the clutch may be sufficient indication that the darkest egg should be rejected.

The Constraints of the Model. The model describes optimal learning strategies within the given constraints. However, the constraints themselves may be subjected to natural selection and, as they evolve, new and more efficient strategies may be developed. The frequency distribution of egg pigmentations is the main constraint of the model that can evolve (Kelly 1987; Davies and Brooke 1989*b*; Rothstein 1990). In that sense, the best strategy for the host would be to evolve distinct individual eggs with a low level of intraclutch variation (Davies and Brooke 1989*b*).

Although we have assumed, for simplicity, that variance in egg pigmentation was the same for all females, in our simulations, females did not use this information to decide whether to accept or reject eggs. It could be argued that using this additional information might allow females to behave optimally without having to learn their average pigmentation. This is, indeed, the case for a wide range of parameter values. But in many natural populations, individual variability in egg morphology is not constant (see, e.g., Lotem et al. 1995) and cannot be used to make

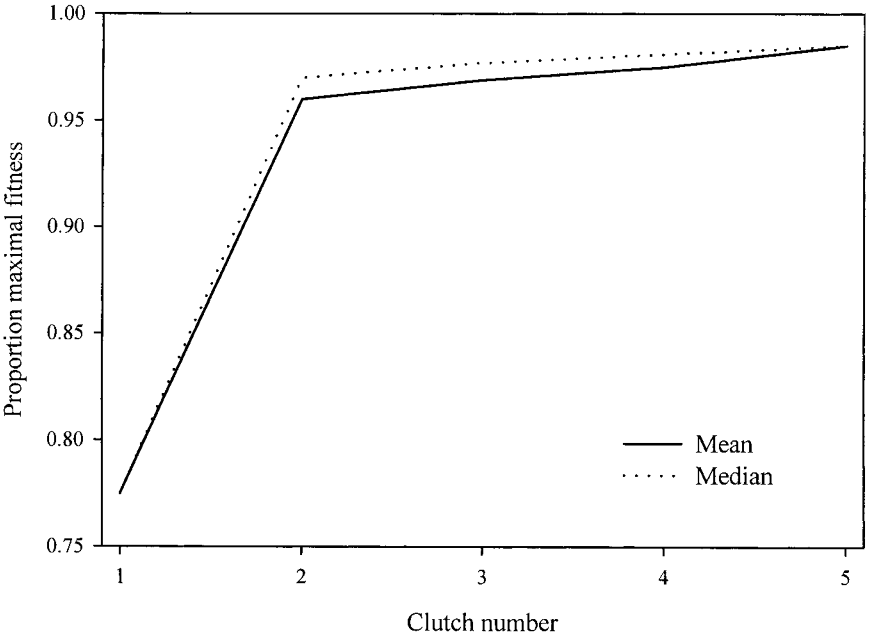

Figure 7: Expected payoff per brood relative to the payoff to an omniscient female (calculated as the average over 10,000 simulated females) as a function of breeding attempt (1 represents naive females) when following the standard (*solid line* = mean) and modified (*dotted line* = median) Bayesian algorithm. Parasitism rate was 40%, $c = 0$, individual variance $\sigma^2 = 1$, and population variance $\omega^2 = 16$.

decisions before learning. Our results should be taken as an approximation to the natural situation and not as an optimal solution for a hypothetical population where variability in egg morphology was constant among individual females.

Implications for Cuckoo-Host Coevolution

As mentioned above, it would appear that the best strategy for the host would be to minimize the overlap with the cuckoo PDF and to reduce intraclutch variation, while maintaining a high interindividual variability. However, besides the possibility that this process is limited by physiological constraints or still in an evolutionary lag (Davies and Brooke 1989*b*; Lotem et al. 1995; Øien et al. 1995; Soler and Møller 1996), our model suggests some additional complications. As shown by figure 3*B*, when the level of cuckoo egg mimicry becomes especially high, hosts are selected to be more conservative and, eventually, rejection may stall completely. Because the benefit from evolving a new egg pigmentation, or from reducing intraclutch variation, can be achieved only through increasing efficiency of egg rejection, hosts may be trapped in a situation in which rejection is already too weak to benefit from slight changes in pigmentation. In the most extreme case, a host with a high degree of intraclutch variation may be trapped as a complete accepter species without being able to evolve rejection. When the parasitism rate is low and intraclutch variation is high, the relative cost of recognition errors when not parasitized can make rejection maladaptive. Any "hopeful" mutation that reduces intraclutch variation cannot be adaptive without rejection behavior evolving first, and rejection cannot become adaptive before intraclutch variation is reduced.

Cowbird versus Cuckoo Hosts

While cowbird hosts appear to learn their eggs quickly from the first egg, cuckoo hosts, like the GRW, have a prolonged learning period in which they learn the whole clutch (Rothstein 1974, 1978; Lotem et al. 1995). These differences have been explained by the fact that cowbird hosts are parasitized with nonmimetic eggs and in higher rates, which makes the cost of recognition errors considerably smaller than in cuckoo hosts (Lotem et al. 1992; Lotem and Nakamura 1998). Our model suggest a second explanation. As indicated by figure 6, when one egg is sufficiently reliable to indicate the typical egg pigmentation (and this is likely to be the case when mimicry is poor and the host can, therefore, afford a wide range of tolerance around the mean), the best thing a female can do is to learn from her first egg, making sure that she learns before being parasitized. Accordingly, the cost of misimprinting provides another good reason for a quick learning strategy among cowbird hosts. Because parasitism rates among cowbird hosts are high, and being parasitized with two or three cowbird eggs is also common, the cost of misimprinting at the egg stage may be much higher than among cuckoo hosts.

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APPENDIX A

Basic Model

The probability that event A occurs given that event B has been observed, known as the conditional probability of A given B and denoted by $\Pr(A|B)$, is given by Bayes's formula (DeGroot 1986):

$$\Pr(A|B) = \frac{\Pr(A \cap B)}{\Pr(B)}, \qquad \text{(A1)}$$

where $\Pr(A \cap B)$ denotes the probability that events A and B are both verified.

Unparasitized Nest

Let A stand for "the nest has not been parasitized" and B stand for "the L eggs of the clutch have pigmentation $\boldsymbol{x}_L = (x_1, x_2, \ldots, \boldsymbol{x}_L)$" (where L can be either N or $N-1$, as required). Then $\Pr(A \cap B)$ can be calculated as the product of the probability that a nest is not parasitized $(1-\alpha)$ times the probability that a GRW female lays a clutch $\boldsymbol{x}_L$, $\Pr(\boldsymbol{x}_L|u)$. This later is simply

$$\Pr(\boldsymbol{x}_L|u) = \prod_{i=1}^{L} \rho_{rw}(x_i), \qquad \text{(A2)}$$

and, therefore,

$$\Pr(u \cap \boldsymbol{x}_L) = (1-\alpha) \times \prod_{i=1}^{L} \rho_{rw}(x_i). \qquad \text{(A3)}$$

In order to calculate the conditional probability that the clutch contains no parasitic eggs, given $\boldsymbol{x}_L$, we must now calculate the probability that the clutch has pigmentation $\boldsymbol{x}_L$, or $\Pr(B)$. In order to calculate this probability, we first notice that it must be the sum of two terms: the probability that the clutch is unparasitized and has pigmentation $\boldsymbol{x}_L$, which we have just calculated, and the probability that the clutch is parasitized and has pigmentation $\boldsymbol{x}_L$, $\Pr(p \cap \boldsymbol{x}_L)$:

$$\Pr(B) = \Pr(\boldsymbol{x}_L) = \Pr(u \cap \boldsymbol{x}_L) + \Pr(p \cap \boldsymbol{x}_L). \qquad \text{(A4)}$$

We proceed to calculate the latter. $\Pr(p \cap \boldsymbol{x}_L)$ is again the product of two terms. It is the probability that the clutch is parasitized, α, times the probability that a parasitized clutch has pigmentation $\boldsymbol{x}_L$, $\Pr(\boldsymbol{x}_L|p)$. In order to calculate this, we will make the simplifying assumption that parasitized clutches always contain one parasitic egg (this is a good approximation for the GRW versus cuckoo system but not so good for some other systems, particularly ones involving cowbirds; the calculations for these systems are straightforward but tedious).

The probability that a clutch has host eggs with pigmentation $\boldsymbol{x}_{L-1}$ and a parasitic egg with pigmentation $\boldsymbol{x}_L$ is

$$\rho_c(\boldsymbol{x}_L) \times \prod_{i=1}^{L-1} \rho_{rw}(x_i). \qquad \text{(A5)}$$

But in a clutch $\boldsymbol{x}_L$, the parasitic egg might be any one of the eggs. Hence, if we denote by $\boldsymbol{x}_{L-i}$, the set of pigmentation of the clutch when the ith egg is excluded,

$$\boldsymbol{x}_{L-i} = (x_1, \ldots, x_{i-1}, x_{i+1}, \ldots, \boldsymbol{x}_L), \qquad \text{(A6)}$$

we have that

$$\begin{aligned} \Pr(\boldsymbol{x}_L|p) &= \frac{1}{L} \times \sum_{j=1}^{L} \rho_c(x_j) \times \Pr(\boldsymbol{x}_{L-i}|u) \\ &= \frac{1}{L} \times \sum_{j=1}^{L} \rho_c(x_j) \times \prod_{i \neq j} \rho_{rw}(x_i). \qquad \text{(A7)} \end{aligned}$$

Therefore,

$$\Pr(p \cap \boldsymbol{x}_L) = \alpha \times \frac{1}{L} \times \sum_{j=1}^{L} \rho_c(x_j) \times \prod_{i \neq j} \rho_{rw}(x_i) \qquad \text{(A8)}$$

and, from equations (A1) and (A4),

$$\Pr(u|\boldsymbol{x}_L) = \frac{\Pr(u \cap \boldsymbol{x}_L)}{\Pr(u \cap \boldsymbol{x}_L) + \Pr(p \cap \boldsymbol{x}_L)}, \tag{A9}$$

where $\Pr(u \cap \boldsymbol{x}_L)$ and $\Pr(p \cap \boldsymbol{x}_L)$ are given by equations (A3) and (A8), respectively.

Parasitized Nest

A very similar calculation shows that

$$\Pr(p|\boldsymbol{x}_L) = \frac{\Pr(p \cap \boldsymbol{x}_L)}{\Pr(u \cap \boldsymbol{x}_L) + \Pr(p \cap \boldsymbol{x}_L)}, \tag{A10}$$

where $\Pr(u \cap \boldsymbol{x}_L)$ and $\Pr(p \cap \boldsymbol{x}_L)$ are given by equations (A3) and (A8), respectively.

APPENDIX B

Imperfect Information, Inexperienced Female

The eggs of an individual female are distributed according to

$$\rho_{in}(x|\mu) = \frac{1}{\sqrt{2\pi}\sigma} \exp\left[-\frac{1}{2}\left(\frac{x-\mu}{\sigma}\right)^2\right], \tag{B1}$$

where the exact value of μ is not known. The only information known about μ is that

$$\mathrm{f}(\mu) = \frac{1}{\sqrt{2\pi}\Xi} \exp\left[-\frac{1}{2}\left(\frac{\mu-\upsilon}{\Xi}\right)^2\right]. \tag{B2}$$

Assuming a particular value of μ, the probabilities that the clutch is (or is not) parasitized can be calculated according to (A10) (or [A9]). This yields the values $\Pr(u\,|x_L, \mu)$ and $\Pr(p|\boldsymbol{x}_L,\mu)$. The overall probabilities are calculated as the expectation of these values. For instance,

$$\Pr(p|\boldsymbol{x}_L) = \int \mathrm{f}(\mu) \times \Pr(p|\boldsymbol{x}_L, \mu) \times \mathrm{d}\mu. \tag{B3}$$

Because $\Pr(\mu|\boldsymbol{x}_L, \mu)$ and $\Pr(p|\boldsymbol{x}_L, \mu)$ are given as the ratio of two probabilities, $\Pr(u|\,\boldsymbol{x}_L)$ and $\Pr(p|\,\boldsymbol{x}_L)$ cannot be given in closed form. We will, therefore, approximate $\Pr(u|\,\boldsymbol{x}_L)$ and $\Pr(p|\,\boldsymbol{x}_L)$ by computing (A9) and (A10) using in (A3) and (A8), for $\rho_{rw}(x)$, the overall distribution of pigmentations. This one can be calculated from (DeGroot 1986):

$$\begin{aligned}\rho_{rw}(x) &= \int f(\mu) \times \rho_{in}(x) \times d\mu. \\ &= \frac{1}{\sqrt{2\pi}\sqrt{\sigma^2 + L \times \Xi^2}} \\ &\quad \times \exp\left\{-\frac{1}{2}\left[\frac{(x-\upsilon)^2}{\sigma^2+\Xi^2}\right]\right\}.\end{aligned} \tag{B4}$$

For an inexperienced female, $\upsilon = \nu$ and $\Xi = \Sigma$.

APPENDIX C

Imperfect Information, Bayesian Learning

Suppose that a female has laid K eggs with pigmentation $x_1, x_2, \ldots, x_K$ and that (following the assumptions of model 3) the expected distribution of egg pigmentation before laying any egg (i.e., the prior distribution) was given by equation (B1) with

$$\mathrm{f}(\mu) = \frac{1}{\sqrt{2\pi}\,\Sigma} \exp\left[-\frac{1}{2}\left(\frac{\mu-\nu}{\Sigma}\right)^2\right]. \tag{C1}$$

It is a standard statistical result (DeGroot 1986) that the posterior distribution is again normal, with mean

$$\nu_{\text{post}} = \frac{\sigma^2 \times n + K \times \sum^2 \times \langle x\rangle}{\sigma^2 + K \times \sum^2} \tag{C2}$$

and variance

$$\Sigma^2_{\text{post}} = \frac{\sigma^2 \times \Sigma^2}{\sigma^2 + K \times \Sigma^2}, \tag{C3}$$

where

$$\langle x\rangle = \frac{1}{K} \times \sum_{i=1}^{K} x_i. \tag{C4}$$

Therefore, the optimal strategy for such a female would be to behave as if she laid eggs normally distributed with mean υ_{post} and variance $(\Sigma^2_{\text{post}} + \sigma^2)$. Within the approximation of appendix B, to calculate $\Pr(u|\,\boldsymbol{x}_L)$ and $\Pr(p|\,\boldsymbol{x}_L)$, we substitute in (A3) and (A8) the distribution (B4), where $\upsilon = \nu_{\text{post}}$, and $\Xi^2 = (\sum^2_{\text{post}} + \sigma^2)$.

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