

Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts

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THE picture of a tiny passerine host feeding a huge cuckoo nestling challenges evolutionary biologists who explain animal behaviour as adaptive¹⁻⁴. Cuckoo eggs sometimes resemble the eggs of the host, but nestlings of the common cuckoo, *Cuculus canorus*, look very different from the young of the host. The inability of the host to discriminate against such divergent nestlings is especially puzzling as some cuckoo hosts show a finely tuned discrimination ability between eggs⁵⁻⁸. Here I present a simple model to explain this paradox. The model shows that although learning to recognize eggs is adaptive, learning to recognize nestlings might not be. The mechanism of learned recognition, previously shown to maintain egg recognition, is unlikely to be adaptive for hosts like those of the common cuckoo, in which only the parasitic nestling remains in the nest. The reason that discrimination against parasite nestlings is not adaptive is that the cost of misimprinting (learning to recognize the parasite nestling as the parents' own) exceeds the benefit of correct learning. The model also explains why nestling discrimination is mostly found in host-parasite systems in which the parasite and the hosts' young are reared together¹.

Recent studies indicate that cuckoos and their hosts may have evolved several adaptations and counter adaptations to each other^{1,5,9,10}. Egg recognition is the common host defence against cuckoo parasitism, but some level of acceptance of cuckoo eggs by hosts is also common^{6,8,9}. Mimicry in cuckoo eggs and the cost of errors in egg recognition may prevent the parasitized host from always rejecting the cuckoo eggs⁷. But because cuckoo nestlings look different from the hosts' young, nestling discrimination should be easy. Soon after hatching, the cuckoo's nestling ejects all host eggs or nestlings from the nest. Although it is thus too late for the host to save its young, by deserting the cuckoo nestling a host can save about 30 days of parental care which might be used for re-nesting. It is therefore surprising that hosts have not developed nestling recognition by the same mechanism used for recognizing eggs.

Several studies suggest that egg recognition in birds is learned by an imprinting-like process^{7,11-13}. Accordingly, hosts imprint on their own egg type during their first breeding attempt and later will reject any different egg type. Given this ability, a host should be able to learn the appearance of its nestlings when it first breeds, and use this knowledge to discriminate against parasitic nestlings in future breeding attempts. But, as I show below, learning to recognize nestlings is maladaptive for hosts like those of the common cuckoo, for which only the parasitic nestling survives in parasitized nests. Such hosts, if parasitized during their first breeding attempt, will face only a parasitic nestling during their learning period, and consequently will reject their own young in any future breeding attempt. In other words, the learning mechanism may incur a cost, termed here the 'misimprinting cost', which is the result of learning to recognize the wrong type of egg or nestling as 'own'. The following model explores the effect of the misimprinting cost on the evolution of egg recognition (Fig. 1) and nestling recognition (Fig. 2) in a typical host of the common cuckoo (such as the great reed warbler, *Acrocephalus arundinaceus*).

Each arrow in the model is labelled with its probability of

occurrence, and a payoff is listed at the end of each path. A rejection strategy is adaptive if its overall payoff is greater than that of an acceptance strategy. In either case (egg or nestling recognition), if an acceptor is parasitized by a common cuckoo (a probability of P), its reproductive success is usually zero^{14,15}, and if it is not parasitized (probability of $1 - P$), its reproductive success is on average equal to x ($x > 0$). As an acceptor, by definition, does not learn to discriminate, its payoff does not change between its first breeding and the later breeding, and is constantly equal to $P0 + (1 - P)x$, which is $(1 - P)x$. In general, the payoff of an acceptor will be $n(1 - P)x$, where n is the number of breeding cycles during a host lifetime.

The payoff for a rejecter is more complex and will be considered first for the case of egg recognition (Fig. 1). If a naive rejecter is parasitized during its first breeding, there is a risk not only that its payoff will be reduced to zero, but that it may also learn to recognize the cuckoo egg, as well as the other eggs in the clutch, as its own. Such an individual, if parasitized during later breeding attempts, might accept the cuckoo egg as its own, and consequently its payoff will be the same as that of an acceptor. However, if a rejecter is not parasitized in its first breeding and does learn to recognize its own type of eggs correctly, and if it is parasitized in later breeding, it will gain the benefit of rejection, designated as b . The payoff of a rejecter is therefore $P0 + P(n - 1)(P0 + (1 - P)x) + (1 - P)x + (1 - P)(n - 1)(Pb + (1 - P)x)$, which reduces to $P(n - 1)((1 - P)x) + (1 - P)x + (1 - P)(n - 1)(Pb + (1 - P)x)$. According to the model, and assuming that the parasitism rate is never 100% ($P < 1.0$), a rejecter will do better than an acceptor as long as $P(n - 1)((1 - P)x) + (1 - P)x + (1 - P)(n - 1)(Pb + (1 - P)x) > n(1 - P)x$, which after solving, gives $Pb > 0$, or, put in words, rejection is favoured as long as the population is parasitized ($P > 0$) and that some benefits are gained by rejection ($b > 0$). Clearly, these are elementary conditions for the adaptiveness of rejection *per se*, no matter what the rejection mechanism is. Hence, despite the cost of misimprinting, the proposed learning mechanism of egg recognition is adaptive.

The situation is different in the case of nestling recognition (Fig. 2). As in parasitized nests only the cuckoo nestling remains, a naive rejecter, if parasitized, may learn to recognize only the

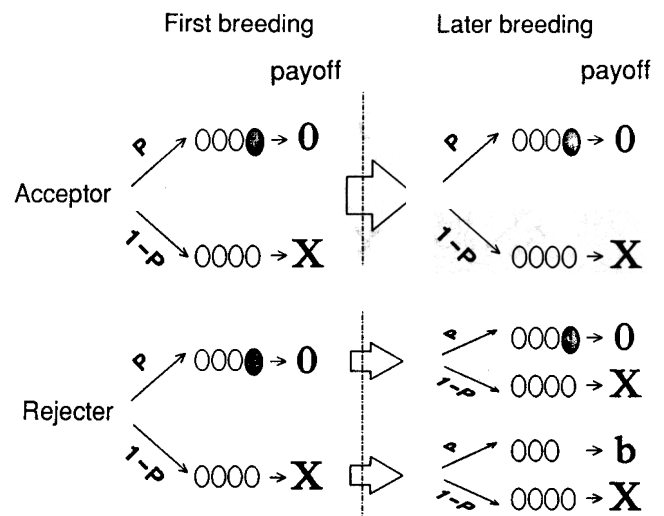


FIG. 1 The mechanism of learned egg recognition, for a typical host of a common cuckoo (see text for explanation). P , the host probability of being parasitized; X , the average reproductive success (number of fledglings) of a non-parasitized host; 0 , zero: the reproductive success from a parasitized nest; b , the benefit of egg rejection, which is the average reproduction success of a parasitized host that rejects the cuckoo egg.

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cuckoo nestling as its own. Such an individual will always accept cuckoo nestlings when parasitized, but because it was not exposed to its own young during the learning period, it will reject them in later breeding attempts. Hence, the cost of misimprinting in this case is the loss of all future reproductive success. Considering that cost, the payoff of a rejecter will be $P0 + P(n-1)(P0 + (1-P)0) + (1-P)x + (1-P)(n-1)(Pb + (1-P)x)$, which reduces to $P(n-1) + (1-P)x + (1-P)(n-1)(Pb + (1-P)x)$. Assuming that $0 < P < 1$ and $x > 0$, rejecters will do better than acceptors only if $P(n-1) + (1-P)x + (1-P)(n-1)(Pb + (1-P)x) > n(1-P)x$, which after solving, gives $b > x$. Put in words, rejecters will do better than acceptors only if the benefit of nestling rejection (b) is greater than the reproductive value of unparasitized nests (x). A situation like this probably never occurs; when rejection is achieved by deserting the cuckoo nestling, the benefit of rejection is likely to be lower than the value of an unparasitized nest because re-nesting is not always possible, and even when it occurs, later nests tend to have smaller clutches¹⁶ and to lead to lower reproductive success¹⁷. The benefit of rejection might be higher if the host can discriminate and eject the cuckoo nestling immediately after it hatches, thus saving its own young. But even if the host can save all its young ($b = x$) rejection is no better than acceptance. Moreover, because the cuckoo usually removes one host egg when laying its own^{1,15}, the host still remains with fewer nestlings than if it had not been parasitized ($b < x$). In conclusion, the proposed learning mechanism cannot be adaptive when the cuckoo nestling remains alone in the nest.

For simplicity, the model assumes equal probability of facing a cuckoo nestling in the first and in later breeding attempts. But in cases in which experienced breeders are more likely to reject cuckoo eggs⁷, they are inevitably less likely to face cuckoo nestlings. Consequently, the probability of facing a cuckoo nestling as a naive breeder, and thereby paying the cost of misimprinting, is greater than the probability of facing it as an experienced breeder and then gaining the benefit of correct learning. The likelihood of learned recognition being adaptive is thus even less than that predicted by the model.

The cost of misimprinting is also relevant to cases where the parasite and the host nestling are reared together. If host nestlings frequently fail to compete for food with the parasite and

starve to death, the cost of misimprinting may outweigh the benefits of correct learning. On the other hand, if both host and parasite nestlings survive to fledging, learning to recognize nestlings should be adaptive. In agreement with this prediction, comparative evidence shows that nestling discrimination is mostly found in host-parasite systems in which the parasite is reared along with the host young¹ and causes little or no mortality among them^{9,18,19}. Although more comparative evidence of this kind can partially test the model, the mechanism of nestling discrimination needs to be studied directly. The learning hypothesis can be tested by experimentally replacing host nestlings with other nestling types during the host first breeding attempt. My model will be falsified if nestling discrimination is exhibited by hosts in which only the parasitic nestling remains in the nest, and if discrimination in this case is learned.

The model does not explain why hosts cannot recognize their nestlings innately. But it is doubtful whether the common forms of innate recognition could be sufficiently effective to reject a single cuckoo nestling. An innate response to key releasers is often stimulated by a broad range of stimuli that only slightly resemble the 'correct' one^{20,21}. Animals may prefer the stronger stimulus when faced with a simultaneous choice, but still respond to the weaker stimulus when it is the only one provided²¹. Such an innate preference may allow nestling discrimination where the parasite and the hosts' young are reared together, but not in common cuckoo hosts where the parasite remains alone. What is needed, but apparently does not exist, is a genetic programme that allows the hosts to ignore all other similar stimuli, and to desert only the single cuckoo nestling. The apparent lack of such a mechanism cannot serve as an explanation, but should stimulate further research into innate recognition and its limitations. □

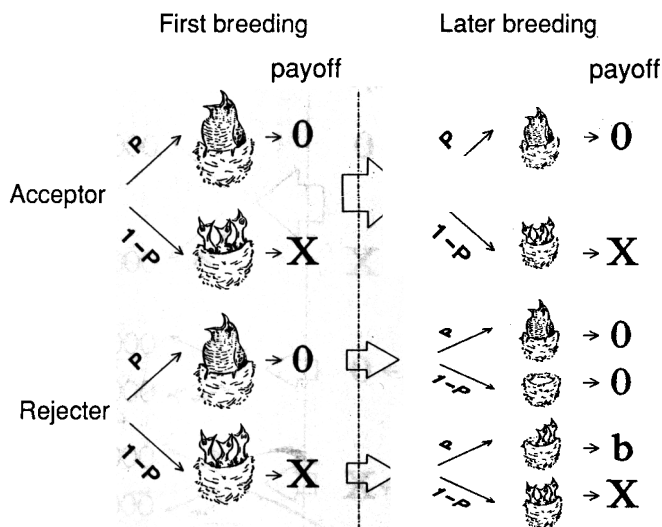


FIG. 2 Hypothetical mechanism of learned nestling recognition, for a typical host of a common cuckoo (see text for explanation). P , the host probability of being parasitized; X , the average reproductive success (number of fledglings) of a non-parasitized host; 0 , zero; the reproductive success from a parasitized nest; b , the benefit of nestling rejection, which is the average reproduction success of a parasitized host that rejects the cuckoo nestling.

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