How to Design Experiments in Animal Behaviour*

14. Cuckoos Lay Their Eggs in Others' Nests, But Why Do the Hosts Get Fooled?

Raghavendra Gadagkar

That the cuckoo lays its eggs in the nests of other species and does not build its own nest or raise its own offspring, is one of the oldest known facts about Natural History and has been abundantly and eloquently immortalised in myths and stories, art and literature, music and poetry, philosophy and morals. Attempts to understand this curious phenomenon in any rational way began just about 100 years ago. With a landmark study consisting of a few simple and elegant experiments that needed no laboratory or funding, Nick Davies and Michael Brooke at Cambridge University in the UK ushered in its modern scientific study as recently as 1988. In this article, I will describe their experiments and their results and conclusions, accompanied by a running commentary relating their work to the theme of this series and end with some more general reflections on the pursuit of the science of animal behaviour.

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Exploring examples of simple, clever and inexpensive experiments in animal behaviour in this series, we have been encountering diverse animal taxa and at the same time, understanding fundamental principles in the proximate and ultimate causation of behaviour. Not surprisingly, evolution by natural selection has been a recurring theme. Because natural selection promotes the survival of the fittest, here and now, we often see the unexpected. We saw in the previous two articles [1, 2] that natural selection can promote cheating if that's what it takes to survive, and since those cheated are also subject to natural selection, we witness

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arms races between the cheaters and the cheated that can reach a variety of outcomes. The ongoing arms races make it appear to us as if evolution has perfected neither party, and that is how it should be if both parties are to co-exist. In the 12th [1] article, we saw that male frogs sing to attract mates but cannot do their best because of lurking predators that eavesdrop. And we saw in the 13th article [2] that while non-venomous snakes mimic venomous neighbours to escape predation, their likeness to their models is only as much as is necessary for their survival and not more. Considering only one of the interacting parties shows the limitations of natural selection but considering all parties, including others in the environment, can help us make more sense of the patterns observed in nature.

The Cuckoo

Having studied fishes, frogs and snakes in the previous three articles, here we will study some excellent examples from among the many elegant experiments done on birds. Birds are arguably the best-known animals to scientists and amateurs alike. Birds have provided endless opportunities for people of all walks of life to observe, study and experiment, to shoot, cage and eat, to admire, eulogise and write poetry on. Their flight, nests, eggs, family life, pair-bonding, songs and migrations capture the imagination of young and old alike. Their occasional departures from what we might consider an honest and harmonious family life are also equally well known. Perhaps the foremost example of the latter is the cuckoo's habit of laying its eggs in the nests of other species and avoiding the chores of building a nest and caring for its young, a fact that has been known at least since the time of Aristotle and has given us the word cuckold in the English language. Cuckoos belong to the family Cuculidae along with koels, malkohas, coucals and anis. Only some species of cuckoos are brood parasites while the rest rear their own young. This is convenient because it allows us to understand the gradual evolution of brood parasitism derived from closely related nest building and brood rearing species (*Figure* 1).

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Figure 1. Common cuckoo, *Cuculus canorus*, adult female, photographed at Bhondsi, near Gurugram, Haryana, India, by Satyajit Ganguly. Reproduced with permission.

The cuckoo has had a very prominent place in the mythology, art and literature of many human cultures including Greek, Indian and Japanese, but this is not so much on account of the 'aberrant' behaviour of the female cuckoo. Rather, it is on account of the real and imagined nature of the male cuckoo, not the least of which is his song. The cuckoo has been depicted as the symbol of love and desire and as the harbinger of spring. But for the evolutionary biologist, it is the 'cheating' female cuckoo that is of greater interest. The female cuckoo's unusual behaviour of laying all her eggs in the nest of other species and never bothering to build her own nests and exercise her own maternal instincts, is a striking evolutionary curiosity and one that did not escape Darwin's notice (*Figure* 2). The cuckoo not only attracted Darwin's notice but also drew out of him his speculation of the evolutionary sequence by which such a behaviour could evolve and be perfected. And yet, the proximate and ultimate causation of the cuckoo's unusual behaviour were not really understood until the 1980s. This is all the more surprising because what it finally took to bring about this understanding was no more than a set of simple, low-cost experiments of the kind we have been celebrating in this series.

The female cuckoo's unusual behaviour of laying all her eggs in the nest of other species and never bothering to build her own nests and exercise her own maternal instincts, is a striking evolutionary curiosity.

Figure 2. **Top**: Three reed warbler eggs and one cuckoo egg (slightly larger) in a reed warbler nest. **Bottom**: A 14-day old cuckoo chick in a reed warbler nest. Notice that the cuckoo chick has managed to evict all host eggs and/or chicks and occupy the whole nest for itself, into which it barely fits; its most conspicuous and most important part is the open gape designed to receive food and to induce the host to feed and to receive food. Photos courtesy: Nick Davies. Reproduced with permission.

Brood Parasitism

The habit of laying eggs in the nests of other birds is not restricted to the cuckoo. It is practiced by many species, some laying their eggs in the nests of other members of their own species (conspecific brood parasitism) while others laying some or all their eggs in the nests of other species (interspecific brood parasitism). Conspecific brood parasitism has been observed in over 250 species while interspecific brood parasitism is practised by over 100 species of birds. This means that there are over 350 species offering us opportunities to investigate this fascinating 'aberrant' behaviour. Although there is now a growing literature on the ecology, behaviour, evolution and coevolution of avian brood parasitism, very few species have been studied in much detail (reviewed in [3]), and unfortunately, almost none in India so far. This is in embarrassing contrast to the fact that the complete genomes of more than 100 species of birds have been sequenced, annotated and published, suggesting to my mind that while scientists who have access to expensive laboratories and large funds have been busy fulfilling their responsibilities, those of us who need relatively few facilities and modest budgets for our research, have come up somewhat short. This is the irony that I hope to mitigate with this series on the charms of low-cost research in animal behaviour. There are many interesting species and many more passionate bird watchers, and there is much to be learned by simple field experiments preceded, and followed, by careful observations. Although some of the pioneering work on brood parasitism by cuckoos was done by the Englishman Stuart Baker in India [4, 5], almost nothing has been published from India barring one recent report by another Englishman Gaston [6]. There is, fortunately, some new work emerging from Bangladesh on the Asian cuckoos [7] and the Asian Koel [8], and also on the common cuckoo from China [9].

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The perfect exemplar for our exploration of what we can learn about brood parasitism from simple experiments is the classic study of the common cuckoo *Cuculus canorus* parasitizing the reed warbler *Acrocephalus scirpaceus* in Cambridge, England by Nick Davies and Mike Brooke, in the 1980s [10] (*Figure* 3). Nicholas Barry Davies, now Professor of Behavioural Ecology at the University of Cambridge, and Fellow of Pembroke College, and Michael Brooke, now Strickland Curator of Ornithology, University Museum of Zoology, University of Cambridge, then recent PhD-buddies from Oxford, and both stricken by a passion for birds, teamed up to study cuckoos and reed warblers in Wicken Fen, a patch of old fenland 15 Km from Cambridge city.

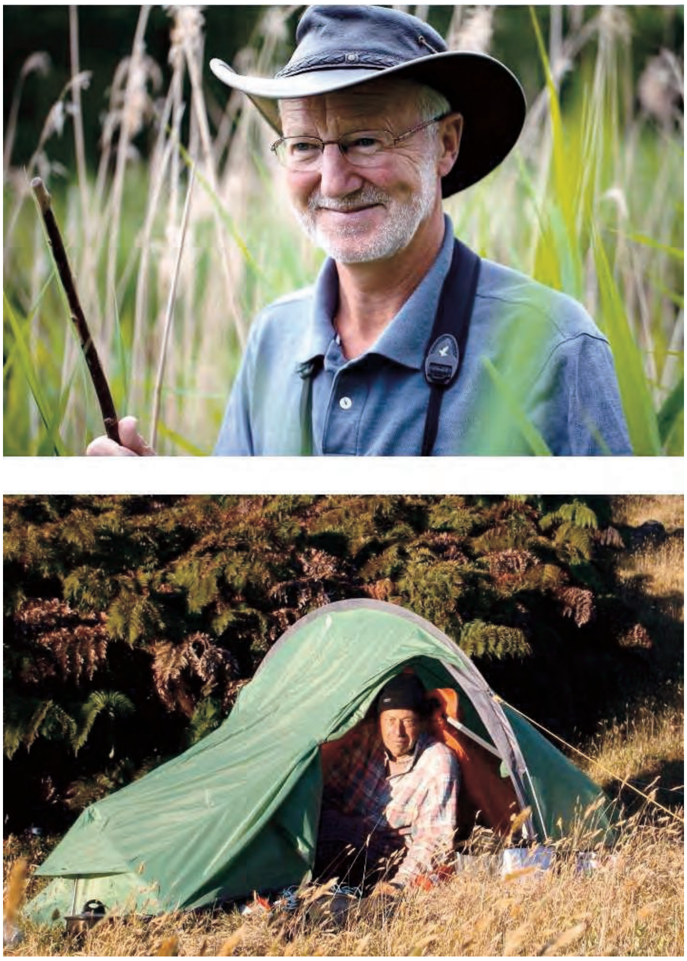

Figure 3. **Top:** Nicholas Barry Davies, now Professor of Behavioural Ecology at the University of Cambridge, and Fellow of Pembroke College. **Bottom:** Michael Brooke, now Strickland Curator of Ornithology, University Museum of Zoology, University of Cambridge Photo copyright Michael Brooke.

Wicken Fen is a 250-hectare nature reserve protected as a wetland site of international importance and yet open to the public, not to mention young naturalists, year-round. By all accounts, Davies and Brooke had great fun, two old friends, riding their bicycles to locate and monitor nests of reed warblers and, as we shall soon see, playing cuckoo, by parasitizing reed warbler nests with artificial cuckoo eggs and watching the fun. The title of their paper 'Cuckoos versus reed warblers: adaptations and counteradaptations' promises a thriller.

The Behaviour of Cuckoos and Their Hosts

Like so many before them, Nick Davies and Michael Brooke were struck by the contradictions in the host's behaviour (reed warblers, in this case). On the one hand, the reed warblers seemed so well adapted to their lifestyle, navigating by stars from Europe to sub-Saharan Africa in the winter and returning to their own specific territories in spring, building exquisite nests and foraging with care and diligence to feed their chicks. And yet, they seemed utterly stupid to be fooled into blindly feeding a grotesquely large cuckoo chick (five times their own size) if their nest happened to be parasitized. How could this be? There were some clues. The cuckoos did not always succeed. Of the 142 reed warbler nests they monitored in 1985, only 32 were parasitized by cuckoos; and in 1986 only 12 out of 132 nests were parasitized. Of these 44 parasitized nests, two were destroyed by predation, and of the remaining 42, the reed warblers rejected the cuckoo eggs in eight nests, either by deserting the nest or by ejecting the cuckoo egg. So, the reed warblers were doing something right and/or the cuckoos were doing something wrong. Successful detective work required that they carefully study the behaviour of both parties.

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There are some striking features in the way cuckoos lay their eggs in the nests of their hosts. There are several genetically distinct "races" of the common cuckoo, each specializing on different hosts such as reed warblers, pied wagtails, redstarts and meadow pipits. Now each host lays somewhat different looking eggs; for example, redstarts lay plain blue eggs, meadow pipits lay brown eggs with spots while reed warblers lay greenish eggs with spots. Each race of cuckoos produce eggs that closely mimic the eggs of their hosts in their colour and markings. Davies and Brooke studied the race of the common cuckoo that specializes on reed warblers and lay eggs that mimic reed warbler eggs. The common cuckoo lays eggs that are very small for a cuckoo, as compared to non-parasitic cuckoos, for example. Not only are the eggs thus well adapted in the service of parasitism, but so is the egg-laying behaviour of the cuckoos. Cuckoos appear to patiently and deliberately plan their egg-laying, marking out particular nests for

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their use and waiting until the hosts themselves have begun to lay their own clutch of eggs. The common cuckoo lays just one egg in each host nest, and before doing so, she removes and promptly eats one of the host's eggs. While the hosts do their egg- laying in the mornings, the cuckoo does so in the afternoons. Perhaps most striking of all, the cuckoo accomplishes her clandestine act of parasitism so quickly and stealthily that there was previously a long-standing debate about how the cuckoo eggs ever came to be in the host nests. Finally, the cuckoo hatchlings eject, from their foster nests, any remaining host eggs or chicks by a complex set of manoeuvres [11, 12].

Speculation versus Proof

Based on what we have seen of the behaviour of the reed warblers and the cuckoos and of the rates and outcome of brood parasitism, we can make a reasonable argument that the reed warblers and cuckoos are locked in an evolutionary arms race, making it difficult for either party to declare total victory.

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Figure 4. **Left:** Reed warbler nest with one of its eggs replaced with a mimetic model cuckoo egg. **Centre:** Reed warbler nest with one of its eggs replaced with a non-mimetic model egg. **Right:** several model eggs ready to be sneaked into reed warbler nests; the large model egg at the bottom is about the size that a non-parasitic cuckoo of the same body size is expected to lay. Photo courtesy: Nick Davies. Reproduced with permission.

on my desk. Now I am ready to become a cuckoo myself." And "The model eggs looked realistic to our eyes, and they warmed up when the warblers sat on them, just like real eggs. We were delighted when our friend Bruce Campbell, one of Britain's most experienced ornithologists at the time, came across one of our experimental nests and noted it as parasitised by a real cuckoo." Armed with these model cuckoo eggs and a spirit of adventure, Davies and Brooke asked a series of questions about the adaptive significance of the cuckoos' behaviour. They located a number of reed warbler nests at the appropriate stage in their egg-laying and, in each, replaced one of the host's eggs with one of their model eggs (*Figure* 4).

Question 1. Why are cuckoo eggs mimetic?

Cuckoos lay eggs that mimic the eggs of their hosts, and different races of cuckoos specialize in mimicking the eggs of the particular hosts that they specialize in parasitizing; all this has been known since the 19th century. Yes, it is obvious that the egg mimicry is meant to fool the hosts into accepting the cuckoo eggs, but nothing that is merely obvious should be accepted as a proven fact. Thus, Davies and Brooke "parasitized" 83 reed warbler nests with model eggs bearing varying degrees of resemblance to real eggs laid by cuckoos in reed warbler nests. In 16 reed warbler nests they replaced a host egg with a pied wagtail type cuckoo

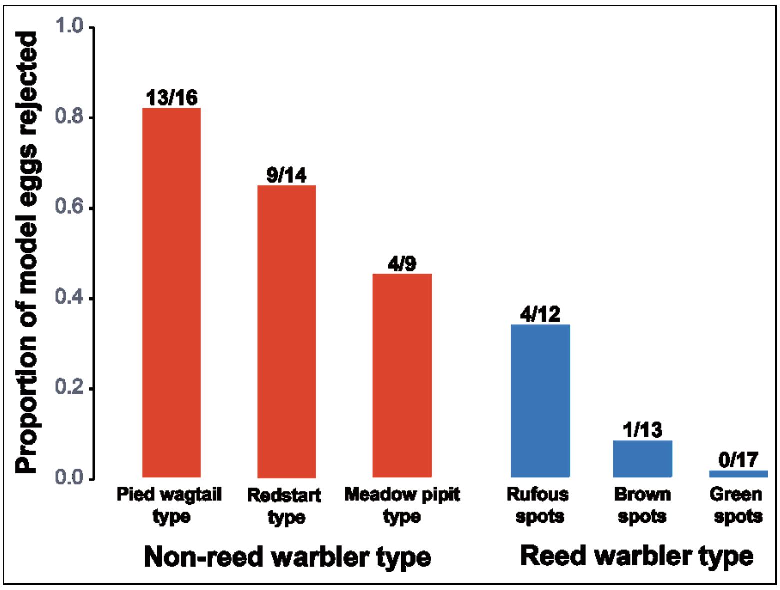

Figure 5. Responses of reed warblers to the different type of model eggs sneaked in by Davies and Brooke, shown as number rejected/total number introduced. There was a significant difference in the rates at which the reed warblers rejected the six types of model eggs ($\chi^2 = 32.32, df = 5, P < 0.001$). Within the reed warbler type models, green spots were more likely to be accepted than rufous spots or brown spots. Only the most mimetic eggs, those of the type that cuckoos themselves lay in reed warbler nests, were accepted in all trials (17/17). [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0].

model egg (i.e., models resembling eggs laid by cuckoos parasitizing pied wagtail nests), in 14 nests they introduced redstart type cuckoo eggs and in nine nests they introduced meadow pipit type cuckoo eggs. These were all non-reed warbler type models, i.e., the models resembled eggs laid by cuckoos parasitizing species other than reed warblers. They also used reed warbler type eggs, but some of them were painted differently. In 12 nests they placed reed warbler type models eggs but painted with rufous spots, in 13 nests they placed model eggs painted with brown spots, and in 17 nests they placed model eggs painted with the "correct" green spots.

Their results were clear-cut. Acceptance or rejection of the model cuckoo eggs depended significantly on the appearance of the egg. The non-reed warbler type of model cuckoo eggs were rejected more often than the reed warbler type model cuckoo eggs and even among the reed warbler type, eggs that more closely mimicked real cuckoo eggs laid by cuckoos in reed warbler nests (i.e., with the correct green spots) were significantly more likely to be accepted (17 out of 17 cases, in this experiment) (*Figure* 5).

That 17 out of 17 model eggs resembling the eggs laid by cuckoos in reed warbler nest were accepted, is not however adequate to argue that the acceptance is due to egg mimicry. The model eggs may simply have been accepted because the reed warbler considered them as harmless objects. It is the combined facts that model eggs resembling those laid by cuckoos in reed warbler nests were accepted, and that model eggs deviating from the 'correct' patterns were rejected, that is much more convincing. The model eggs of the non-reed warbler type and the reed warbler types that were painted differently, acted as controls to strengthen the conclusion to be drawn from the acceptance of the mimicking eggs. It is also a way of ruling out other possible explanations for the observed result of 100% acceptance rate of the mimicking eggs.

That the reed warblers might have accepted the mimicking model eggs because they considered them harmless, is not the only alternative explanation that needs to be ruled out. Alfred Russel Wallace, the co-discoverer of the principle of natural selection, had long suggested that egg mimicry by cuckoos may be selected because by achieving the same level of camouflage as the host eggs they might escape the attention of predators. Davies and Brooke had seen avian predators such as crows, magpies and jays and mammalian predators such as the mink. They were able to distinguish such predation from egg rejection by the reed warblers most of the time because predation usually resulted in the loss of the whole clutch or in the whole nest being damaged. Moreover, egg rejection by the reed warblers often accompanied pecking at the model eggs and in the discovery of the rejected model eggs nearby. Is egg mimicry favoured by natural selection because it fools the hosts or because it fools the predators? It is possible to distinguish between these two possibilities and test Wallace's hypothesis. Davies and Brooke examined Wallace's hypothesis in three different ways. First, they looked for heterogeneity in the probability of being lost to predation among the nests receiving the different types of model eggs and found none (*Figure* 6). Second, they compared predation rates between nests receiving non-mimetic model eggs and mimetic model eggs and found no significant difference (*Figure* 7, upper panel). Third, they com-

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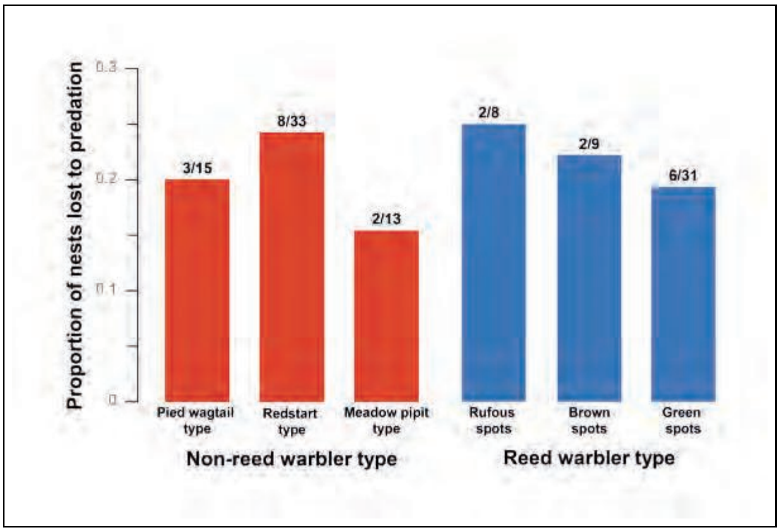

Figure 6. Reed warbler nests receiving different types of model eggs did not differ significantly in their probability of being lost to predation. [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0]].

pared daily rates of predation between nests with mimetic and non-mimetic eggs and found no significant difference (*Figure* 7, lower panel). Thus they were able to rule out Wallace's hypothesis.

We can see that there is a successive refinement of the analysis going from *Figure* 6, to *Figure* 7 upper panel and finally to *Figure* 7 lower panel. The analysis in figure 6 merely tells us that the kind of model egg contained in the nest does not influence its probability of predation. But this could simply be because of a high level of variation in predation rates. The analysis in Figure 7 upper panel makes a more specific comparison of the nest with mimetic and non-mimetic eggs. This answers a more direct question and also benefits from the sample sizes obtained by pooling all nests with different kinds of non-mimetic eggs and similarly pooling all nests with different kinds of mimetic eggs. Moreover, considering only the reed warbler type eggs painted with brown spots and green spots as mimetic and leaving out the reed warbler type eggs painted with rufous spots should increase the probability of detection of any existing difference in predation rates on account of the type of eggs. This is because the reed warbler type eggs painted with rufous spots appeared to be intermediate in their level of resemblance to the reed warbler's own eggs; reed warblers rejected them more often than the reed warbler type models eggs painted with brown or green spots but less often than model eggs resembling the non-reed warbler type eggs. And yet, they found no effect of egg type on nest predation.

Finally, comparing daily rates of predation (in *Figure* 7 lower panel) is even more powerful because in the previous two kinds of analyses predation rates of nests containing non-mimetic eggs may have been underestimated, making it less likely to detect a difference between nests bearing mimetic and non-mimetic eggs. This is because reed warblers harbouring non-mimetic eggs are more likely to reject those eggs, thus giving less time for predators to find and destroy the nests on account of being given away by the non-mimetic eggs. The analysis of daily rates of predation corrects for this bias by only considering the days when the model egg was present in the nest. And yet, no effect of egg type on predation rates was seen. All this makes the conclusion more robust that egg mimicry is unlikely to be selected by the ability of predators to detect nests with non-mimetic eggs, as proposed by Wallace and, by implication, more likely to have been selected because of the ability of the reed warblers to detect non-mimetic eggs.

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Field experiments of the kind described here are very tedious to perform and involve considerable disturbance to the animals involved, making it prudent to limit the total number of experiments, and squeeze as much juice out of the data as possible by clever and imaginative data analysis of the kind witnessed here. Field biologists have to sharpen their skills at planning and executing clever, well-designed experiments and imaginative data analysis for they seldom have the luxury of growing more experimental animals in the lab and repeating their experiments again and again, or simply performing new experiments for answering each question. They must perfect the art of combining rigour with economy, but that's the charm of field ethology. It's time to recall the words "attention, patience and heightened awareness" in the definition of ethology given by Peter and Jean Medawar [13].

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Yet another hypothesis Davies and Brooke considered is that egg

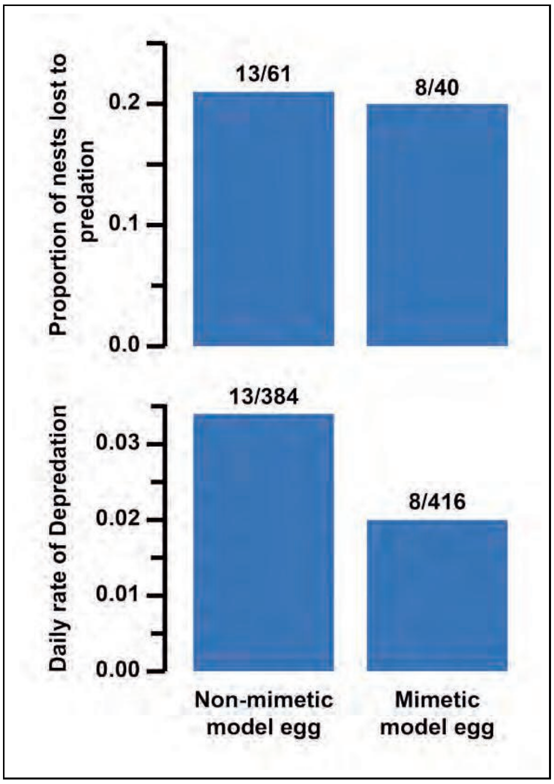

Figure 7. No effect of model egg type on rates of predation. **Upper panel:** No significant difference in predation probability between nests receiving non-mimetic versus mimetic model eggs ($\chi^2 = 0.008$, $df = 1$, NS). The pied wagtail, redstart and meadow pipit type model cuckoo eggs are taken as non-mimetic and the reed warbler type cuckoo model eggs with brown and green spots are considered as mimetic; the reed warbler type painted with rufous spots are ignored in the calculations because they are intermediate. **Lower panel:** No significant difference when daily rates of predation, either ($\chi^2 = 1.205, df = 1$, NS). 13 nests receiving the non-mimetic eggs and 8 nests receiving the mimetic eggs were lost to predation. In the upper panel these predation events are compared by dividing each number by the total number of nests receiving the non-mimetic and mimetic eggs respectively, while in the lower panel, the same numbers are compared by dividing by the numbers of days for which the model eggs remained in the nests and hence are available for predation. [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0].

mimicry is favoured because it protects a mimetic egg from discovery by a second cuckoo who might try to lay her egg in an already parasitized reed warbler nest. Cuckoos are known to do so; of the 142 reed warbler nests monitored by Davies and Brooke in 1985, 32 were parasitized by cuckoos and six of these were subsequently parasitized by a second cuckoo. Since cuckoos always remove one existing egg before they lay their one and since only one cuckoo chick can survive in one reed warbler nest, it would make sense for the second cuckoo to remove any pre-existing cuckoo egg rather than a host egg before laying her own. So, the hypothesis that egg mimicry may reduce the chances of the second cuckoo removing the egg of the first cuckoo is plausible. However, they found little evidence in support of this hypothesis; second cuckoos were not significantly more likely to remove a non-mimetic model egg than a mimetic one. In fact, they seemed to remove one egg more or less randomly; even if there was a slight preference for removing the cuckoo egg, it was not statistically significant. The inability of the cuckoos to remove a non-mimetic egg selectively is somewhat surprising—if the reed warblers can do it why not the cuckoo? Davies offers an interesting explanation. Cuckoos lay their eggs quickly and stealthily (see below) and fly away without looking back. And since they never build a nest and incubate their eggs, they have probably never seen a cuckoo egg! In any case, the data here are scanty and one cannot be sure that they do not preferentially remove the previous cuckoo's egg; we can only say that there is no conclusive evidence that they do preferentially remove cuckoo eggs rather than reed warbler eggs. Moreover, as Davies and Brooke point out, even if they do discriminate and remove cuckoo eggs, the selection pressure from host discrimination is likely to be much greater than from discrimination by the second cuckoo.

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Hence, we are moving closer to the conclusion that egg mimicry is an adaptation to avoid detection and rejection by the hosts. It is an impressive adaptation because the same species of cuckoos parasitize several host species whose eggs are quite different in appearance—one size doesn't fit all. The common cuckoo species consists of several races (called 'gentes' or 'gens' in singular) which specialize in producing eggs resembling the eggs of the targeted host species. Even if we were to imagine that such gradual perfection of mimicry can be brought about by natural selection over evolutionary time, there is the interesting problem that the different races of cuckoos should breed true at least in their egg types and in their preference for certain host species. How is this 'purity' of racial egg type and host preference maintained within a race? One possibility is that egg type, and host preference is genetically passed down only through the female line, from mother to daughter to granddaughter. This is possible in principle because in birds females are the heterogametic sex with ZW chromosomes and males with a ZZ configuration (mirror image of the more familiar XX females and XY males in humans and most other organisms). The other possibility is that the various races are indeed reproductively isolated, with females

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of one race mating only with males of that race. The answer to this question is not yet clear. Be that as it may, since reed warblers remove non-mimetic or imperfectly mimetic model eggs, such as eggs of the wrong race of cuckoos, it is clear that there is an on-going arms race between host and parasite. Even more suggestive of an ongoing process of adaptation and counter-adaptation (over evolutionary time, of course) is the observation that reed warblers reject some, but not all, non-mimetic eggs. Besides, egg mimicry is not the only weapon in the cuckoo's arsenal. There are several more, and Davies and Brooke test their efficiency too, as we will see below.

Question 2. Why are cuckoo eggs so small?

In order to masquerade their eggs as though they belong to the hosts themselves, cuckoos not only have to mimic host egg colour and pattern of spots but also have to make their eggs rather small in size. Parasitic cuckoos do lay eggs that are really small for a cuckoo.

In order to masquerade their eggs as though they belong to the hosts themselves, cuckoos not only have to mimic host egg colour and pattern of spots but also have to make their eggs rather small in size. Parasitic cuckoos do lay eggs that are really small for a cuckoo. Since there are many non-parasitic cuckoos, it is possible to make a comparison to what the size of their eggs might have been if they were not selected for a brood-parasitic way of life. Non-parasitic cuckoos of comparable adult body size lay eggs weighing about 10 g while the common cuckoo parasitizing reed warblers lays eggs that weigh a mere 3.4 g. And yet, their chicks are enormous compared to reed warbler chicks. The physiological and developmental processes that take part in orchestrating a phenotype that can stay in the (arms) race between host and parasite remain to be understood in detail. But does the reduction in egg size really help the cuckoo, and if so how? One possibility, and by no means the only one, is that, like the appearance of the egg, it helps fool the host into confusing the identity of the cuckoo egg and accepting it as its own, as first suggested by Darwin. This is the possibility that Davies and Brooke put to test. In addition to the model eggs mimicking the cuckoo eggs that in turn mimic reed warbler eggs, they used model 'giant' eggs that were about the size expected to be laid by non-parasitic cuckoos.

Their giant model eggs weighed between 9.3 and 10.1 g and were

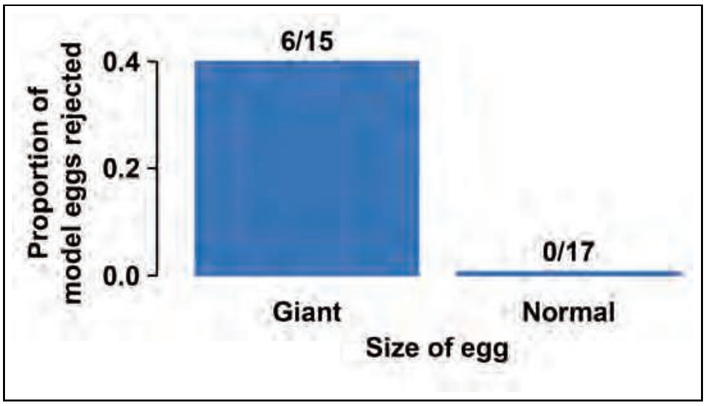

Figure 8. Reed warblers reject the giant model eggs about the size of eggs laid by non-parasitic cuckoos more often than the model eggs resembling common cuckoo eggs ($\chi^2 = 5.949, df = 1, P < 0.02$). [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0].

1.3 times the length and 2.8 times the weight of the eggs laid by the common cuckoo. As Darwin might have predicted, reed warblers rejected the large model eggs in six out of 15 nests, significantly more often than they rejected the normal cuckoo eggs (*Figure* 8). This suggests that one of the factors that select for small eggs laid by the common cuckoo is the ability of the reed warblers to detect and reject eggs that are oversized even though they may be similar to their own eggs in colour and pattern of spots. Notice that this experiment does not rule out other reasons that might also select for small eggs, such as Darwin's other suggestion that small eggs may be at an advantage because they may hatch within a shorter period of time. Nevertheless, the experiment does show that the small-sized egg is a second item in the cuckoo's bag of tricks. The fact that reed warblers rejected six giant model eggs and accepted 9, reminds us that neither party wins in the arms race. In addition to modifying their eggs to resemble those of their hosts in size and appearance, cuckoos employ a number of behavioural tricks to fool their hosts, and these can also be tested for their significance and efficiency in similar experiments.

Question 3. Why do cuckoos wait until the hosts start laying their own clutch?

A striking feature of the cuckoo's strategy is the timing of its parasitism. Male cuckoos have no role in facilitating brood parasitism by the females. While male cuckoos occupy and defend territories to keep out competition from other males, the female cuckoos occupy and defend territories to keep out competition from other females for access to reed warbler nests suitable for parasitism. They patrol the chosen reed warbler nests surreptitiously and bide their time. They have to not only avoid detection by the reed warbler parents but have to time their egg-laying such that they can sneak in one of their own eggs sometime after the reed warbler female has begun but not completed her egg-laying. Why do the female cuckoos have to time their act of parasitism in this way and indeed, how precisely do they have to time it? Does such timing increase the chance of the cuckoo egg being accepted by the host? Davies and Brooke set out to answer these questions by timing their own acts of parasitism either by being as precise as the cuckoo or less precise or more precise.

A striking feature of the cuckoo's strategy is the timing of its parasitism. Female cuckoos have to not only avoid detection by the reed warbler parents but have to time their egg-laying such that they can sneak in one of their own eggs sometime after the reed warbler female has begun but not completed her egg-laying.

In one experiment, they placed their mimetic model eggs (the kind that were accepted 17 out of 17 times) in six reed warbler nests even before the host had commenced its own egg laying. All six were rejected—a far cry from all 17 accepted, when they did what the cuckoos did! (*Figure* 9). So it certainly pays for the cuckoos to be precise. It is probably not surprising that the reed warbler is suspicious about a mysterious egg when she has not laid any of her own, which of course means that she is somehow 'aware' of whether or not she has begun egg laying. But how precise should the cuckoos be in their timing? Does it matter how many eggs the host has already laid? To answer this question, Davies and Brooke first examined the stage of host egg-laying at which the 17 accepted mimetic cuckoo eggs had been introduced; six when the hosts had laid one egg, six when the host had laid two eggs, one when the host had laid three eggs, and four when the hosts had laid four eggs. These numbers suggest that the stage of egg-laying does not matter as long as the host

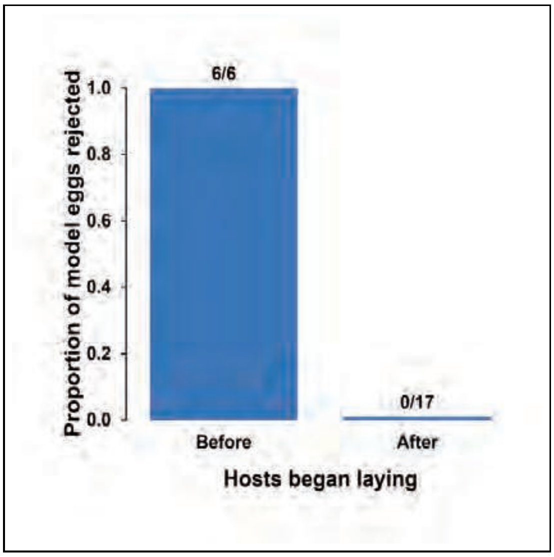

Figure 9. Six out of six model eggs are rejected if introduced before the hosts began laying their own clutch while 17 out of 17 model eggs are accepted when introduced after the hosts had begun egg laying. Although the sample sizes are small, these rejection rates are statistically significantly different ($\chi^2 = 18.106, df = 1, P < 0.001$). [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0].

has started laying. But it's not good enough to look only at the accepted cases. What about rejections? Are the rejections stage dependent? To answer this question, they also introduced non-mimetic eggs, both the pied wagtail type model cuckoo eggs as well as the reed warbler type non-mimetic eggs (i.e., painted with rufous spots or brown spots) at various stages during the host laying period. The results of these experiments also showed that rejection rates (when some model eggs were indeed rejected) did not depend on the number of eggs already laid by the host (*Figure* 10).

Considering that all model eggs introduced before the commencement of egg-laying by the host were rejected, and that mimetic egg models were accepted at all stages, and non-mimetic model eggs were rejected at the same rates at all stages of egg-laying, we can conclude that the cuckoos need to be precise enough to time their egg-laying so as not to begin until the hosts have commenced egg-laying but need to be no more precise as to the number of eggs laid by the host at the time of parasitism. But there may be another reason for the cuckoos to lay their egg as soon after the host has started laying as possible. This is not because the hosts care any more about the stage of their own laying (as we

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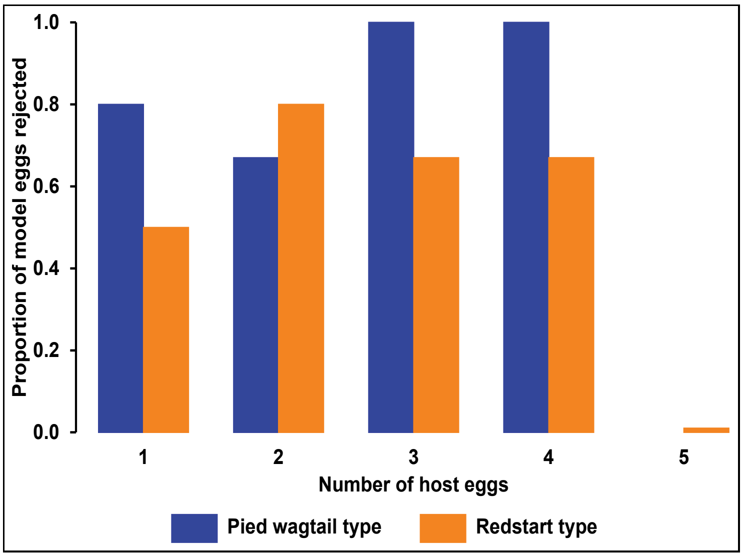

Figure 10. Rejection rate for non-mimetic eggs does not depend on the stage of egg laying by the host ($\chi^2 = 0.975, df = 3, P > 0.05$). [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0].

have seen) but because the sooner they lay their egg, the sooner it will hatch and get a head-start, ahead of the host chicks, for it will have to eject the host eggs and chicks and gain monopoly over the nest and the host parents' attention. But of course, the more mimetic the eggs, the better for acceptance, whenever they are laid. While cuckoos thus use a mixture of strategies to fool their hosts, the hosts use information about whether or not they have started laying eggs to augment their ability to detect foreign eggs. As we will see below, this is not merely because their ability to detect foreign eggs may be limited but because they cannot afford to be too finicky, lest they reject some of their own eggs that might look a little different by chance. Not only is there an arms race between host and parasite, but there are also trade-offs between different strategies used by each party. This is the kind of fascinating complexity we should expect when natural selection is simultaneously perfecting two or more parties attempting to undermine each other's survival. But there is more to come.

A passionate egg collector by the name of Edgar Chance (more about him later) had discovered through a considerable amount of detective work of his own in 1920, that cuckoos always lay their eggs in the afternoon, although most of their hosts are known to lay their eggs early in the morning.

Question 4. Why do cuckoos lay their eggs in the afternoon?

A passionate egg collector by the name of Edgar Chance (more about him later) had discovered through a considerable amount of

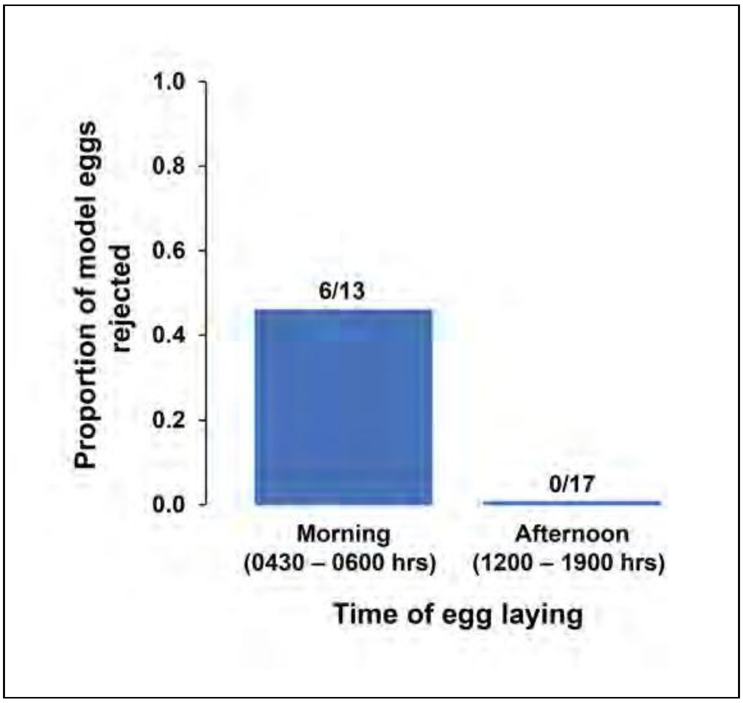

Figure 11. Model eggs introduced in the mornings (0430–0600) rather than in the afternoons (1200–1900) (as the cuckoos themselves do) were rejected by reed warblers significantly more often than when the model eggs were introduced in the afternoons ($\chi^2 = 7.135, df = 1, P < 0.01$). [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0].

detective work of his own in 1920, that cuckoos always lay their eggs in the afternoon, although most of their hosts are known to lay their eggs early in the morning. Is this timing adaptive, meaning does it increase the chance of acceptance of the cuckoo egg by the host? The answer seems to be yes. When Davies and Brooke place their model eggs in the morning, a significantly larger fraction was rejected (*Figure* 11). It turns out that we do not quite know why afternoon laying is better for acceptance. Are the hosts otherwise busy in the afternoons, do they only inspect the contents of their nests in the mornings, immediately after they lay their egg?

If any reader was beginning to get the feeling that Davies and Brooke have discovered everything that can be discovered, this is just one of the numerous examples of unanswered questions. There is much more for all of us to do, there will always be. It is usually the case that answering one question opens up at least one (usually more) unanswered question/s. It would not be so unreasonable, I think, to judge the success of a scientific investigation by how many additional questions it has opened up, instead of how many previously known questions it has answered.

Question 5. Why do cuckoos remove a host egg before laying their own?

Cuckoos always remove one (and rarely two) of the host eggs before laying their own single egg.

Cuckoos always remove one (and rarely two) of the host eggs before laying their own single egg. Why should they do so? Perhaps the host remembers how many eggs she has laid and will be suspicious of an additional egg. If this conjecture is correct, then model eggs introduced without removing a host egg should be rejected more often than when they were introduced after removing a host egg. But that is not what happened. Davies and Brooke found no significant difference between the rates of rejection of model eggs when they removed one or more host eggs, and when they did not (*Figure* 12). Then why do the cuckoos bother? Spending more time at the host nest to remove an egg might increase the cuckoo's risk of being detected and jeopardise its effort. Another possibility is that cuckoos may remove a host egg before laying one of their own because, if the host accepts the cuckoo egg and also lays her full clutch then there would be one egg too many in the nest and the incubation efforts of the little reed warbler may be inadequate to hatch all the eggs efficiently.

If there are two different genotypes of cuckoos, one producing a phenotype that removes a host egg before it lays its own and another that lays its eggs without removing a host egg, and if the eggs laid without removing a host egg have a lower probability of hatching, then the genotype which produces an egg-removing phenotype will have higher reproductive success and genes for removing a host egg may come to be disproportionately over-represented in future generations.

Perhaps it is no longer necessary, but I will pause here to remind my readers that when we make statements of the kind I have just made, we are of course not pretending that the cuckoo makes any conscious decision about what is good for her eggs. We are merely using a convenient shorthand to replace the following more precise but extremely cumbersome language. If there are two different genotypes of cuckoos, one producing a phenotype that removes a host egg before it lays its own and another that lays its eggs without removing a host egg, and if the eggs laid without removing a host egg have a lower probability of hatching, then the genotype which produces an egg-removing phenotype will have higher reproductive success and genes for removing a host egg may come to be disproportionately over-represented in future

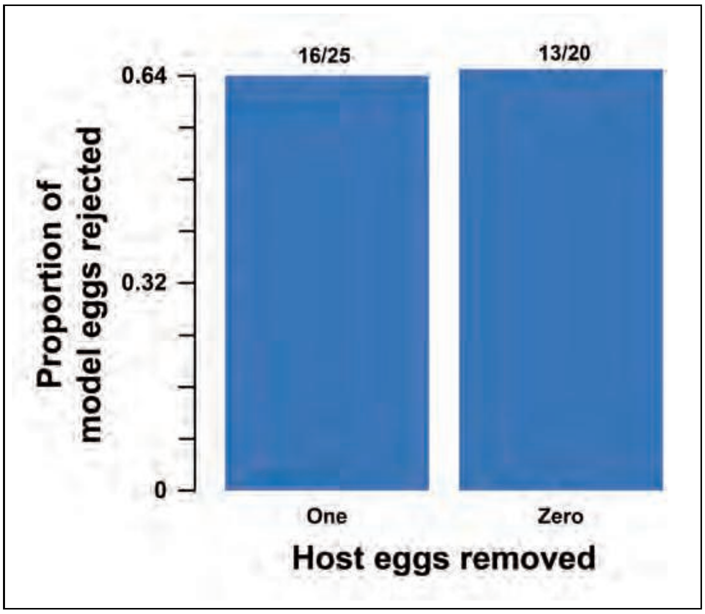

Figure 12. No difference in the rates of rejection of model eggs whether host eggs were removed or not removed before introducing the model egg ($\chi^2 = 0.059, df = 4, P > 0.05$). [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0].

generations, leading eventually to the situation where all or most cuckoos remove a host egg before laying their own.

Stated cumbersomely or not, the hypothesis is the very same one, and a very eminently testable one. Assuming that the detrimental effects of an extra egg for the host's incubation efforts will be evenly distributed across all eggs, host and cuckoo, Davies and Brooke performed three kinds of experiments to test this hypothesis. In one experiment, they removed a host egg before introducing the model cuckoo egg. In the second experiment, they again removed a host egg before introducing the model egg, but in this case, they replaced the removed egg back into the nest after the host had completed laying her clutch of eggs. In the third experiment, they introduced the cuckoo model egg without removing the host egg at all. If the above-mentioned hypothesis is valid, then the number of eggs that should hatch successfully at the end of the incubation period should be higher in experiment one where they removed a host egg as compared to experiment three where they did not remove the host egg. The second experiment, where they removed a host egg but replaced it later, serves as a control to see if the disturbance caused by the act of removing the egg itself affects incubation success rather than the number of eggs. It is very important, but not always easy, to imagine alternate explanations and introduce appropriate controls. This aspect of designing experiments, especially in animal behaviour, is, I would say, as much an art as science, depending much more on imagination than on knowledge. I am, therefore, always surprised at how little importance we give to encouraging imagination in our education. Worse, we actively curb the ability of students to imagine, imploring them to stick to facts. Even worse, this is what I have sometimes been told even by the reviewers of my papers.

Luckily, Davies and Brooke had apparently escaped such suppression of their imagination and performed all three experiments and were rewarded handsomely. The results of the three experiments combined did not support the hypothesis that removing an egg facilitates better incubation (*Figure* 13). If we look closely at the data in *Figure* 13, we get the impression that there are somewhat more nests with two or three unhatched eggs in the third experiment where no host eggs were removed. This seems to support the hypothesis being tested. However, such apparent trends can be misleading, and we should go only by the results of rigorous statistical tests. The statistical tests specifically check whether the observed trends could have been obtained by chance alone. Nevertheless, this is a tricky business, especially when we have a fondness for a particular hypothesis or expect it to be right or wrong based on previous knowledge. It is only human to have such expectations and biases, and it is not possible to sanitise ourselves completely from them because then we will hardly have the imagination to design good experiments. My solution to this conundrum is to neither accept them nor to ignore them totally but to pay close attention to non-statistically significant trends and use them to generate further hypotheses and design new experiments. So, in this case, at least for the time being, we have to look for another possible explanation for the cuckoos' behaviour of taking the trouble of removing a host egg before laying her own.

Let us look at the behaviour of the cuckoo more carefully. What

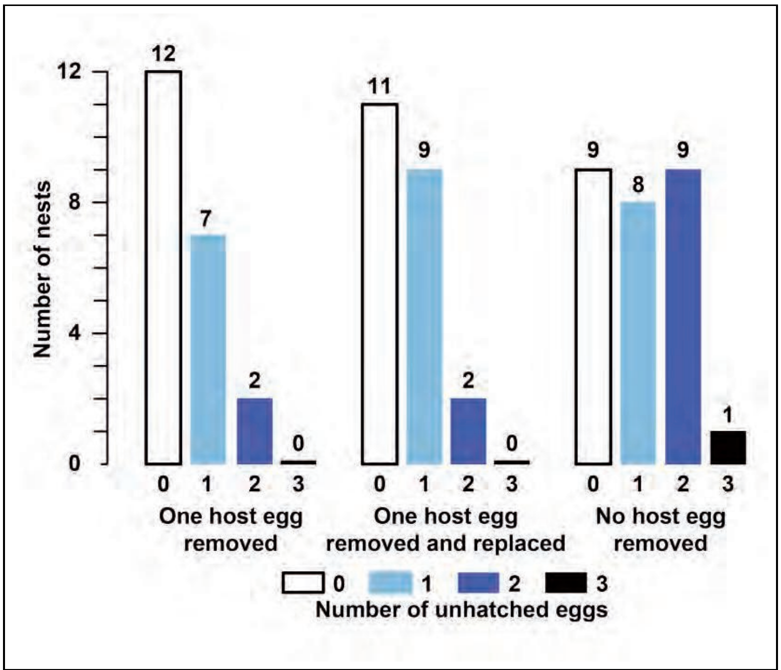

Figure 13. The numbers of nests with different numbers of unhatched eggs are not significantly different whether a host egg was removed, removed and replaced or not removed at all ($\chi^2 = 8.216, df = 4, P > 0.05$). [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0].

does she do with the egg she removes? Well, she eats it. It could of course be that she removes it for a different reason and, having removed it, why not eat it? Or, could she be removing it for the very purpose of eating it and getting much-needed nutrition and getting a head-start on producing her next egg to parasitize the next nest? It is not so easy to test this hypothesis directly, at any rate, not by the technique of introducing model eggs into host nests. It would require forcing some cuckoos not to eat the egg they have removed and following the future egg production by cuckoos who had the chance to eat the egg they have removed and those that were prevented from doing so. But even in the present situation, one can go at least a step further. If the purpose of removing the egg is to eat it, why do cuckoos remove just one, or at most two eggs, and not help themselves to even more? We have already seen that the hosts don't seem to count the number of eggs because they don't seem to care whether or not one of their eggs is removed before a cuckoo lays her egg. One conclusion from this line of reasoning is that eating may not be the primary

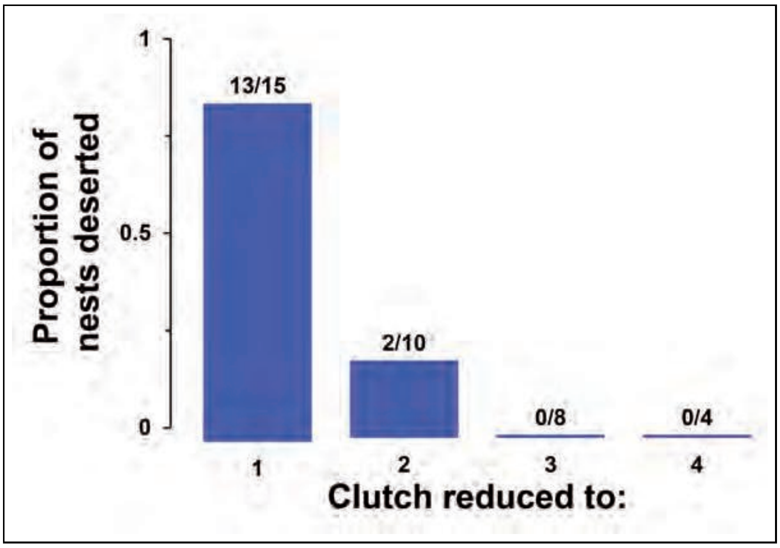

Figure 14. As more eggs are removed, the greater is the chance that reed warblers will desert their nests altogether. [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0].

purpose of removing a host egg but another possible conclusion is that while removing and eating one egg is okay, being too greedy and eating more eggs may somehow reduce the chances of success for their own eggs. This, last mentioned idea suggests a new kind of experiment within the paradigm of parasitizing reed warbler nests with model cuckoo eggs. As you might expect, this is what Davies and Brooke did next. They introduced model cuckoo eggs into reed warbler nests after removing different numbers of host eggs, reducing the remaining clutch size to one, two, three or four eggs. They found that the smaller the remaining clutch size, the greater was the chance that the hosts would abandon their nest altogether (*Figure* 14). Although not conclusive, especially in the absence of a rigorous statistical test, these data suggest a reason why cuckoos do not remove too many eggs. The implication is that the hypothesis that they remove the eggs in order to eat them may still be valid because the objection as to why they don't remove and eat more may not be valid. In summary, we do not quite know why the cuckoos remove an egg before laying their own, but it could well be to gain some nutrition without jeopardising the chances of success for the egg she has herself laid.

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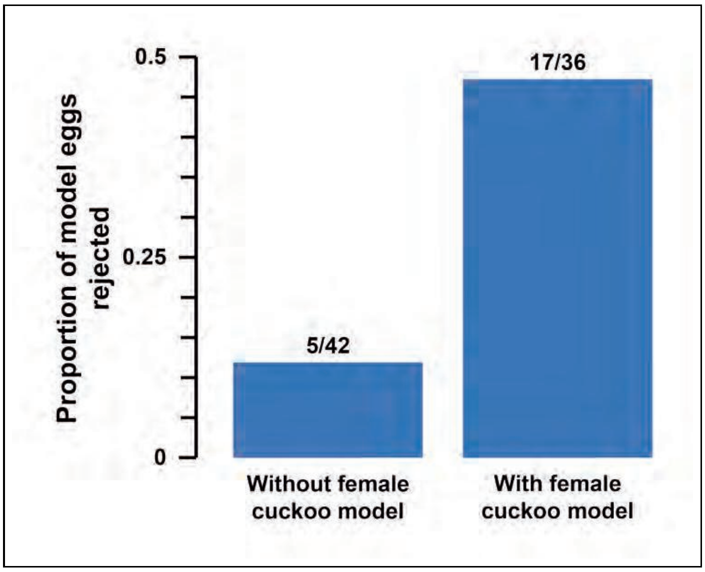

Figure 15. Rejection of model cuckoo eggs is significantly higher if a stuffed adult cuckoo is placed on the reed warbler nest before the model egg is introduced (G test: G = 12.04, $df = 1, P < 0.001$). [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0].

Question 6. Why do cuckoos lay their eggs so quickly and stealthily?

Another striking feature of the cuckoo's behaviour is that she lays her eggs ever so quickly and stealthily; cuckoos remove a host egg and lay their own, in an incredible, 10 seconds or less, as compared to about 20 minutes that other birds typically take to lay their eggs and that too without the additional task of having to remove any eggs! No wonder there is a long and interesting history about the mystery of how the cuckoo's egg ever got into the host nest. You can read an enchanting account of how Edgar Chance, Director of a glass manufacturing company and passionate egg collector finally discovered how the cuckoo lays its eggs, in the book *Cuckoo: Cheating by Nature* by Nick Davies [11], and if you are lucky to find them, in Edgar Chance's own words in his two books *The Cuckoo's Secret* [14] and The *Truth about the Cuckoo* [15], and with no need to depend on luck (just on YouTube), you can watch him in the act of discovering these thousand-year-old secrets in a charming black and white, silent film he made in 1921 [16].

Striking feature of the cuckoo's behaviour is that she lays her eggs ever so quickly and stealthily; cuckoos remove a host egg and lay their own, in an incredible, 10 seconds or less, as compared to about 20 minutes that other birds typically take to lay their eggs and that too without the additional task of having to remove any eggs!

How the cuckoo manages this incredible feat is a most interesting question, but here we are concerned with why she even bothers. Several obvious hypotheses suggested themselves. Maybe, she is trying to avoid drawing attention to the nest in which she lays her egg to other cuckoos or other predators. Maybe, she is worried about being attacked and chased by the hosts. Or perhaps she is actually increasing the chances of the host accepting her egg by this stealth. Apparently, there is not much evidence to support the first two hypotheses, but the third hypothesis is more interesting precisely because it is not so obvious. And this is the hypothesis that Davies and Brooke put to the test with an interesting twist to their strategy of playing cuckoo. Before introducing the model cuckoo egg, they placed a stuffed adult cuckoo on the nest of reed warbler and allowed the hosts to watch this for five minutes. The question they were asking is whether the sight of the adult cuckoo on their nest will increase the chances of their rejecting the cuckoo egg. And the answer is yes. Significantly more model eggs were rejected by reed warblers when a stuffed adult cuckoo was placed on the nest compared to when it was not (*Figure* 15). It appears that the reed warblers check much more carefully for possible cuckoo eggs if they have seen a cuckoo on their nest and are somewhat more relaxed if they have no *prima facie* reason to worry about a cuckoo having laid an egg in their nest.

Tug of War

Cuckoos employ a variety of strategies to maximize their chances of sneaking in one of their own eggs into reed warbler nests and minimize the chances that the host will detect and reject their egg.

In summary, cuckoos employ a variety of strategies to maximize their chances of sneaking in one of their own eggs into reed warbler nests and minimize the chances that the host will detect and reject their egg. They make their eggs resemble the host eggs as closely as possible in appearance and size; they wait until the hosts have started laying their own clutch, and then lay their single egg in the afternoon, after removing and eating one of the host eggs, and they do so incredibly quickly and stealthily in less than 10 seconds. The series of experiments described above demonstrate that each of these strategies of the cuckoo helps in maximising the acceptance of cuckoo eggs by the hosts. All of these strategies must have been favoured by natural selection because they maximize the cuckoo's reproductive success. But the cuckoos don't always succeed. It is easy to see why. Although they would not be expected to drive the hosts to extinction leaving no nests for them to parasitize, clearly there is room for them to be at least somewhat more successful than they seem to be. We have seen that in the study site where Davies and Brooke worked, cuckoos managed to parasitise only 44 out of 272 (16%) of the available nests. The reason for this, as we have mentioned before, is because natural selection is also acting on the reed warblers to minimize the chances of being parasitised and therefore maximize their own reproductive success. This is what leads to an arms race between the hosts and the parasites. Reed warblers have evolved their own counter-strategies. They reject the eggs that do not sufficiently mimic their own in appearance and size; they reject eggs laid before they have started laying any of their own; they reject eggs laid at the wrong time of the day, and they are more likely to reject eggs found in their nests if they have seen a cuckoo around their nests. Moreover, many reed warblers nest away from bushes from where the cuckoos can easily spy on them. It is also true that there are many fewer cuckoos than reed warblers; one reason for the low (and now further declining) populations of cuckoos, may be because they are not more successful at parasitizing host nests, but there may be other reasons as well, including more ecological reasons such as high mortality during migration.

Reed warblers have evolved their own counter-strategies. They reject the eggs that do not sufficiently mimic their own in appearance and size; they reject eggs laid before they have started laying any of their own; they reject eggs laid at the wrong time of the day, and they are more likely to reject eggs found in their nests if they have seen a cuckoo around their nests. Moreover, many reed warblers nest away from bushes from where the cuckoos can easily spy on them.

If the reed warblers prevent the cuckoos from doing much better at cheating, what prevents the reed warblers from doing much better at detection? It is not merely a push back from the cuckoos. There is a curious asymmetry in this arms race. The reed warblers, unlike the cuckoos, must face a push back also from themselves. If they become too finicky, they might end up rejecting their own eggs instead of the cuckoo eggs. If there is a cost to accepting cuckoo eggs, there is also the cost (danger) of rejecting their own eggs. Reed warblers must therefore balance these two costs; it might well be that accepting some cuckoo eggs may ultimately be better than losing their own eggs.

Question 7. Is there a cost that hosts pay when rejecting cuckoo eggs?

By observing how often and when reed warblers mistakenly reject their own eggs instead of the model cuckoo egg, Davies and Brooke have demonstrated that there indeed is a cost of rejection. It turns out that when the model egg is a perfect mimic, the reed warblers accept the model egg and never reject their own. But if the model egg is not a good mimic, then there is scope for confusion and the reed warblers will have to decide whether to reject the egg in their nest that looks the most alien. Interestingly, it is in this situation when the model egg is not a perfect make that reed warblers make mistakes and reject eggs of their own, significantly more often than when the model is a perfect mimic (*Figure* 16). If they accept, it may be a cuckoo egg, and if they reject it may be their own—it's a tough life for the reed warblers!

Reed warblers and other birds parasitized by cuckoos or other brood parasitic species seem to have managed to survive over many millions of years, occasionally rearing cuckoo chicks but usually their own.

But reed warblers and other birds parasitized by cuckoos or other brood parasitic species seem to have managed to survive over many millions of years, occasionally rearing cuckoo chicks but usually their own. What I find even more remarkable is the fact that parasitic cuckoos have managed to maintain their lifestyle as obligate brood parasites for millions of years, never failing to fool at least some hosts of some species in every generation—as good an illustration of the balance of nature as we can think of. Little wonder then that Richard Dawkins says "If I were asked to nominate my personal epitome of Darwinian adaptation, the *ne plus ultra* of natural selection in all its merciless glory, I might hesitate...But I think I'd finally come down on the side of a parasite manipulating the behaviour of its host—subverting it to the benefit of the parasite in ways that arouse admiration for the subtlety, and horror at the ruthlessness, in equal measure" [17].

Almost anyone can perform cutting- edge research and create significant new knowledge while also having a great deal of fun, even without access to any sophisticated laboratory or equipment and virtually no special funding.

Reflections

As will be familiar to readers by now, my aim in writing this series of articles is to show that almost anyone can perform cutting-edge research and create significant new knowledge while also having a great deal of fun, even without access to any sophisticated laboratory or equipment and virtually no special funding. The set of experiments by Davies and Brooke that I have described in this 14th article in the series, eminently illustrate every aspect of this theme. Luckily, we can hear confirmation from the horses' own mouth. Nick Davies recalls in his *Cuckoo: Cheating by Nature*: "When I was a student, one of my tutors warned me: 'The days when you can go out into the countryside with binoculars and notebook and discover something interesting are long gone.' By this he was implying that scientific progress often depends on new techniques. For example, since the 1980s new and powerful methods of DNA profiling have been developed which allow us to determine paternity and maternity in wild populations. These have revolutionised studies of animal mating systems, revealing that socially monogamous birds are not the models of fidelity that we had once assumed. But sometimes progress is made not through new techniques but through new ideas, or simply by asking new questions. Darwin's idea that cuckoos are exploiting the 'mistaken instincts' of their hosts immediately raises new questions. How do hosts recognise their own eggs and chicks? What is it about cuckoo eggs and chicks that leads to mistaken acceptance? Patient observations with binoculars and notebook can still provide a fresh look at the natural world and lead to new discoveries, provided that the new questions are interesting. I felt sure that cuckoo–host interactions would be a fascinating corner of Darwin's 'entangled bank', and one that could be untangled by simple field experiments." [11].

We have seen plenty of evidence that Davies and Brooke had a great deal of fun performing their experiments and needed no sophisticated laboratory or other facilities, and there is no evidence of any great deal of money that was required for this research. All they probably needed were bicycles, some resin, paint and brush, some rubber boots maybe, perhaps a pair of binoculars, a cuckoo egg and a stuffed cuckoo, both of which could be borrowed, and lots of passion. But what about creating significant new knowledge? In an appraisal of this 1988 paper 25 years later,

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Mary Stoddard and Rebecca Kilner [18] write: "With their landmark publication… Davies & Brooke ushered in a new era of research on avian brood parasitism. Building on centuries of rich natural history and detailed observation of common cuckoos,… [they] performed a set of simple but powerful experiments to understand the adaptive value of a female cuckoo's behaviour as she parasitizes a host nest. In this essay,… we evaluate four conceptual innovations made by [them] involving rejection costs, egg mimicry, frontline defences and chick discrimination, and we show how these advances have shaped research in the last 25 years. Davies & Brooke... paved the way for diverse and dynamic research on avian brood parasites...". Need I say more?

If this paper were sent for publication today, I can easily imagine some hypercritical reviewers complaining about the statistics, especially about the small and non-uniform sample sizes and the lack of statistically independent data sets. For example, they might complain that the same data set of 17 out of 17 mimetic model eggs being accepted, were used to compare with many other data sets to derive many different conclusions (see *Figures* 5, 8, 9, 11 and 16). Is this a valid criticism? Should Davies and Brooke have done, and should we do today, five different sets of experiments with mimetic eggs to compare with each data set where the model eggs were sometimes rejected, to understand why they were rejected? This is a complex question, and we have to have the wisdom to consider the requirements of rigorous statistics in context and decide what is possible, and indeed, what is desirable. The problem is especially acute and tricky in the context of field experiments with wild animals. Whether we like to admit it or not, every experiment, every intervention, might negatively impact the animals and their environment. Of course, the benefits of the knowledge gained may compensate for the small damage we cause, and may even help mitigate damage caused by humans while not in the pursuit of knowledge. Nevertheless, it is our moral imperative to gain the maximum possible knowledge with the minimum possible damage. Here is another interesting trade-off and one which we will have to negotiate on behalf of

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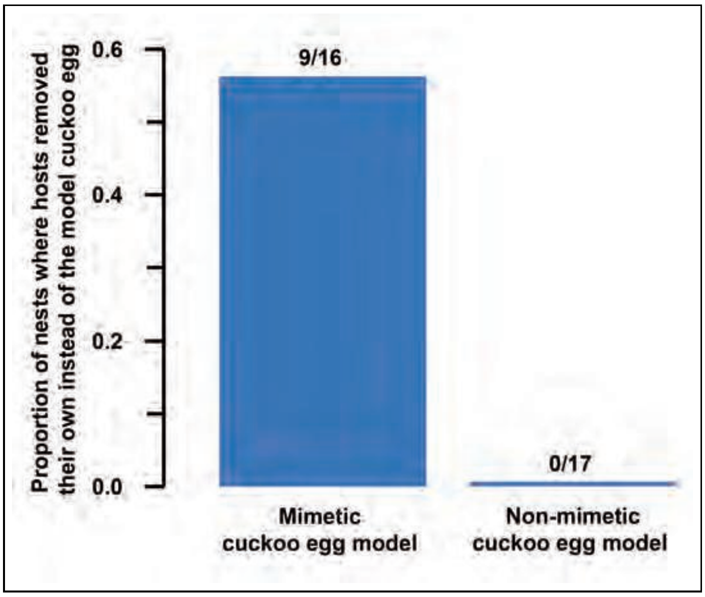

Figure 16. Reed warblers are significantly more likely to reject one of their own eggs instead of the model eggs when the model eggs were not perfect mimics of their own eggs ($\chi^2 = 4.369, df = 1, P < 0.05$). [Redrawn by the author based on data from N. B. Davies and M. de L. Brooke, Cuckoos versus reed warblers: Adaptations and counteradaptations, *Animal Behaviour*, Vol.36, No.1, pp.262–284, Feb. 1988, doi: 10.1016/S0003-3472(88)80269-0].

both parties, because the animals are merely silent spectators at best or mute sufferers at worst.

And the problem is not restricted to experiments in the natural environment alone. There is a growing realization of the need to minimise the use of animals even in laboratory experiments, even for experiments that may claim to test new drugs and vaccines and make a difference between life and death for humans. There is nothing wrong with some of us seeking knowledge for its own sake, but it behoves us to show even greater responsibility. You can easily get much expert advice on the ethical use of animals in research [19], in estimating the required sample sizes for a given experiment [20] and about how to reduce the number of animals used [21]. Some years ago I met Bernhard Voelkl of the Division of Animal Welfare at the University of Bern, in Switzerland, who told me about his fascinating work showing that while "Single-laboratory studies generally failed to predict effect size accurately, and larger sample sizes rendered effect size estimates even less accurate . . . multi-laboratory designs including as few as 2 to 4 laboratories increased coverage probability by up to 42 percentage points without a need for larger sample sizes." [22]. I

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think there are lessons to be learned here even for those of us who do field experiments. Surely, we would like to reduce the number of animals used in research and, in addition, if we can distribute even the small disturbance we might cause among different localities, that might be even better. For example, several educational institutions such as The Indian Institute(s) of Science Education and Research (IISER's) might coordinate their field projects for undergraduates and get their students to do the same experiment with small sample sizes each, at different localities and pool their data. They will have an excellent opportunity to produce publication quality research. The training and experience the students will get in collaborating, standardising methods, pooling data, maintaining uniform ethical and intellectual standards, co-publishing, agreeing on the order of authorship ... are not merely collateral benefits but, I would say, the essence of education and training.

Just as Davies' tutor told him in the 1980s that 'The days when you can go out into the countryside with binoculars and notebook and discover something interesting are long gone.', there will be plenty of tutors telling you the same thing today with renewed conviction. But, nothing could be further from the truth. Taking just the example of avian brood parasitism, decades of research have shown that there are so many species exhibiting brood parasitism, that species can be quite different from each other and that there is so much more to be discovered using simple natural history experiments, not to mention the inevitable discovery of more examples of conspecific and interspecific brood parasitism. Consider the claims of just a few recent papers: 'Learning to recognize nestlings is maladaptive for cuckoo hosts' [23], 'Constraints on egg discrimination and cuckoo–host co-evolution' [24], 'How to learn to recognize conspecific brood parasitic offspring' [25], 'Communal breeding: Clever defense against cheats' [26], 'Resistance is futile: Prohibitive costs of egg ejection in an obligate avian brood parasite host' [27], "... Isolated host nests are more vulnerable to cuckoo parasitism," [28], "egg recognition ability of chestnut thrushes was likely a retained anti-parasitic strategy because of being parasitized by cuckoos in the past" [29], "Son or daughter, it does not matter: brood parasites do not adjust offspring sex based on their own or host quality" [30], "... brood parasitism as a driver of phenotypic diversity in birds" [31], "Cuckoos use host egg number to choose host nests for parasitism" [9]. For modellers and the theoretically minded, there are rich opportunities to explore the evolution of animal recognition systems, more generally [32]. There is much to learn and it will cost very little—this topic is tailor-made, and will remain so for a long time, for cutting edge research at trifling cost.

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Suggested Reading

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