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AN EXPERIMENTAL STUDY OF CO-EVOLUTION BETWEEN
THE CUCKOO, *CUCULUS CANORUS*, AND ITS HOSTS.
II. HOST EGG MARKINGS, CHICK DISCRIMINATION
AND GENERAL DISCUSSION

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SUMMARY

(1) There was no difference in the distinctiveness of egg markings between species that have interacted strongly with cuckoos and species that have not, nor in intra-clutch variation, nor in inter-clutch variation within a species. In Iceland, where they are isolated from cuckoos, the eggs of meadow pipits and pied/white wagtails showed no differences in intra-clutch variation, nor inter-clutch variation, from those in parasitized populations in Britain. Thus there was no evidence that host egg patterns evolve in response to cuckoos.

(2) None of the four species tested discriminated against an odd chick (another species) in their nest (chaffinch, reed warbler, reed bunting, dunnock). Hosts therefore evolve discrimination against odd eggs but not against odd chicks.

(3) The variation in rejection of unlike eggs among different species of suitable cuckoo hosts is not related to the current costs or benefits of rejecting cuckoo eggs. We suggest that the variation represents snap shots in evolutionary time of different stages of a continuing arms race between the cuckoo and its hosts.

INTRODUCTION

We now consider the second two host responses suggested in the introduction to paper I (Davies & Brooke 1989), namely changes in host egg markings and chick discrimination. We then discuss the results of both papers and suggest a sequence of stages for the interaction between the cuckoo *Cuculus canorus* L. and its hosts.

DO HOST EGGS CHANGE IN RESPONSE TO PARASITISM?

If markings on hosts' eggs represented signatures that made their eggs more distinct and difficult for the cuckoo to match, then we would make the following three predictions.

(i) Species with a history of interaction with cuckoos will have more distinctly marked eggs. In theory, past interactions with brood parasites could have created much of the diversity found today among passerine birds' eggs (Swynnerton 1918).

(ii) There should be less intra-clutch variation in species exploited by cuckoos, to make it easier for the host to spot the cuckoo egg among its own eggs.

(iii) There may be more inter-clutch variation within species exploited by cuckoos, with each female having eggs distinct from other females. This would make it more difficult for the cuckoo to evolve a good matching egg for the host (Swynnerton 1918; Victoria 1972).

TABLE 1. Rank order of intra-clutch and inter-clutch variation in egg colour and markings (see text) for twelve species of passerine birds

Species	Rank order, least (1) to most (12)	
	Intra-clutch variation	Inter-clutch variation
(a) Suitable as hosts		
Reed warbler	12	12
Meadow pipit	4=	10
Pied wagtail	1	1
Spotted flycatcher	11	9
Reed bunting	8=	7
Chaffinch	10	5
Blackbird	3	6
(b) Unsuitable as hosts		
Linnet	2	4
Greenfinch	8=	3
Bullfinch	7	2
Great tit	4=	11
Swallow	6	8

*Methods and results**Distinctiveness of markings*

There are no striking differences between the markings on eggs of unsuitable species (bottom row, Fig. 1 of paper I), which have presumably not been affected by cuckoos, and suitable hosts which show strong rejection (> 50%) of unlike eggs, indicative of a history of interaction with cuckoos according to our analysis in paper I. Of the unsuitable hosts, three of the five hole-nesting species have immaculate blue eggs (pied flycatcher, wheatear, starling) which is typical for many hole nesters. Of the remaining six species, four have more or less diffuse fine markings on their eggs (blue and great tits, linnet, greenfinch) and two have more distinctive markings in the form of larger spots or scribbles (swallow, bullfinch). Of the suitable, strongly rejecting species, a similar proportion have these distinctive markings (three out of eight: reed bunting, chaffinch, song thrush) and the remaining five species have more diffuse markings.

Intra-clutch variation

We considered the species listed in Table 3 of paper I for which we did more than five experiments with unlike models, omitting the five species with immaculate eggs where all eggs within a clutch looked identical (dunnock, redstart, pied flycatcher, wheatear, starling). Of the remaining species, there were two pairs of congeners and we omitted one of each pair (song thrush, blue tit). This left twelve species—seven suitable hosts which showed strong rejection of unlike eggs and five unsuitable hosts which showed little, if any, rejection (Table 1). From the results in paper I, we believe that the first group has had an evolutionary battle with cuckoos and that the second group has not. For each of these twelve species we photographed twenty clutches of eggs, using Kodachrome 64 film and natural daylight. Most of the photographs were of clutches taken at various sites in Britain, in the collection of the British Museum, Tring. For two species, meadow pipits

and reed warblers, we took photographs at nests in the field in Derbyshire and Cambridgeshire, respectively. Each photograph was of a different female's clutch laid out on a Kodak gray card. Fifteen colleagues were each given one photograph per species, chosen at random from the set of twenty, and asked to rank the twelve photographs in order from the one showing the least intra-clutch variation in colour and markings to the one showing the most.

There was significant agreement in the ranking of the twelve species by the fifteen colleagues (Friedman two-way analysis of variance, $\chi^2 = 19.789$, 11 d.f., $P < 0.05$). Table 1 (column 1) shows the rank order of the mean ranks of the twelve species. There was no difference between the ranks of suitable and unsuitable hosts (Mann-Whitney *U*-test, two-tailed, $P = 0.530$) and no significant correlation between degree of intra-clutch variation and proportion of unlike eggs rejected (from Table 3 in paper I; Spearman rank correlation = 0.245, N.S.). There was thus no evidence that a history of interaction with cuckoos influenced intra-clutch variation or that the variation influenced degree of rejection.

We took similar photographs of twenty clutches of meadow pipits and twenty clutches of white wagtails in Iceland. Fifteen colleagues were given five randomly chosen photographs of British clutches and five of Icelandic clutches and asked to rank them from the least to the most variable. For the pipits, ten of the fifteen colleagues gave the British clutches a higher average rank (binomial test, two-tailed, $P = 0.302$), and for the wagtails eleven of the fifteen gave the British clutches a higher average rank ($P = 0.118$). Thus, there was a tendency in both species for the parasitized population in Britain to show more intra-clutch variation than the unparasitized population in Iceland, the opposite trend to our predictions.

Inter-clutch variation

We used the photographs to assess variation between clutches within a species. Fifteen colleagues were each given five photographs per species, chosen at random from the sets of twenty, and asked to rank the twelve species from those showing the least variation between clutches to those showing the most variation.

There was significant agreement in the ranking of the twelve species by the fifteen colleagues (Friedman two-way analysis of variance, $\chi^2 = 59.292$, 11 d.f., $P < 0.001$). The rank order of the mean ranks (Table 1, column 2) did not differ significantly between suitable and unsuitable hosts (Mann-Whitney *U*-test, two-tailed, $P = 0.530$) and did not correlate significantly with the proportion of unlike eggs rejected ($r_s = 0.239$, N.S.). Thus there was no indication that a history of interaction with cuckoos was related to variation between clutches, or that increased variation resulted in higher rejection. There was no significant correlation between the degree of intra- and inter-clutch variation across the twelve species (Table 1; $r_s = 0.385$, N.S.).

Fifteen colleagues were also shown, for both meadow pipits and pied/white wagtails, a set of ten photographs of British clutches and a set of ten photographs of Icelandic clutches. For the pipits eleven of the fifteen colleagues scored the Icelandic population as having more variation between clutches ($P = 0.118$), and for the wagtails seven out of fifteen scored more variation in the Icelandic population. As for the comparison between suitable and unsuitable hosts, therefore, there was no support for our predictions.

In conclusion, this analysis provides no evidence that host egg markings evolve in response to parasitism by cuckoos.

HOST DISCRIMINATION OF CHICKS

We tested for discrimination against chicks unlike their own in four species, three which showed rejection of unlike eggs (chaffinch, reed warbler and reed bunting) and one which did not (dunnock; see paper I).

Chaffinch and dunnock

At seven pairs of nests (one nest of each species per pair) where the young hatched on the same day, one 2–3-day-old chick of each species was exchanged between nests. The chicks were weighed on the day of exchange and then 1 day and 3 days later before being returned to their own nests. Chaffinch nestlings have pale purple gapes, cream gape flanges and no tongue spots. Dunnock nestlings are strikingly different, with bright orange gapes, yellow gape flanges and two black tongue spots.

All seven dunnock chicks grew well in the chaffinch nests and their weight increase (mean after 1 day = 2.2 g; 3 days = 6.3 g) was not significantly different from the average weight increase of their siblings back in the home nest, fed by their own parents (mean after 1 day = 2.4 g; after 3 days = 7.2 g; Wilcoxon matched pairs tests, two-tailed for 1 and 3 days, both N.S.).

Of the seven chaffinch nestlings placed in dunnock nests, one had disappeared by day 1 and two more by day 3. Of the six surviving chicks on day 1 after the exchange, all six had put on less weight (mean 1.0 g) than the average of their siblings back home, fed by their own parents (mean 2.2 g; $P=0.05$). By day 3, one transferred chick had put on more weight than the average of its siblings at home and three had put on less weight, but all four chicks were healthy when returned to their rightful nests. It is very unlikely that the three disappearing chaffinch chicks demonstrate discrimination by the adult dunnocks. In two cases the chaffinch chick, on transfer, was the lightest of a brood of three in the dunnock nest and in one case it was the second lightest of a brood of four. The four surviving chaffinch chicks were all the heaviest chicks in the dunnock nest on the day of transfer. It is not unusual for the lightest chicks to starve to death in dunnock broods (Davies 1986), and it seems likely that the disappearance of the nestlings in this experiment reflected starvation (dunnocks remove small dead chicks from their nests).

Reed warbler and reed bunting

We used the same procedure to exchange one chick between two pairs of nests (one nest of each species per pair). Reed warbler nestlings have naked black skin, a yellow gape flange and two dark tongue spots. Reed bunting nestlings, by contrast, have pink skin covered in down, a pale purple gape, a creamy yellow gape flange and no tongue spots. Both reed bunting chicks grew well in the reed warbler nests and both reed warblers grew well in the reed bunting nests. In another experiment we showed that reed warblers accepted a dunnock chick at six out of six nests (Davies & Brooke 1988).

There was thus no evidence of chick discrimination in any of the four species tested.

GENERAL DISCUSSION

*Host responses to parasitism by *Cuculus canorus**

We found no evidence for two of the three host responses proposed in the introduction to paper I (Davies & Brooke 1989). Although hosts do sometimes evolve chick discrimination in response to brood parasitism, this apparently does not occur in hosts exploited by *Cuculus canorus* (see Davies & Brooke 1988 for discussion). The idea that egg

colour and patterns in passerine birds have evolved as signatures, in response to brood parasitism, is appealing but was also not supported by our analysis. The most likely hypothesis is that egg markings enhance crypsis, and variation within and, to a lesser extent, between species may arise simply because there is no one best pattern for concealment. In some species, females make good use of the variation between individuals to recognize their own eggs and discriminate against parasitic eggs laid by both conspecifics and cuckoos (Victoria 1972). However, our comparative data show that species that have not engaged in an arms race with cuckoos have just as much inter-clutch variation as those that have been exploited by cuckoos. This suggests that, in response to parasitism, a species simply makes use of the existing variation and evolves the ability to discriminate eggs. Two results support the idea that better egg discrimination evolves in response to cuckoo parasitism; suitable hosts show stronger discrimination than unsuitable hosts and, within two species of suitable hosts, parasitized populations showed stronger discrimination than populations isolated from cuckoos.

What might the 'evolution of better egg discrimination' entail? One possibility is that there is no difference in perceptual abilities between species which accept *v.* reject odd eggs from their nests; what evolves in response to cuckoo parasitism may simply be the decision to reject odd eggs. Given that rejection entails costs, both of recognition and ejection (Davies & Brooke 1988), we would expect species to accept odd eggs unless there is some benefit of rejection, as would arise if there was a chance of there being a cuckoo egg in the nest. Victoria (1972) and Rothstein (1982) have both shown, however, that species that reject foreign eggs (those of conspecifics or brood parasites) do not simply use the rule 'reject the odd egg', but are able to recognize their own eggs and reject foreign eggs whether they are in the minority or form the majority of the clutch. By contrast, in both our experiments and those of Rothstein, species that showed no rejection accepted even whole clutches of foreign eggs unlike their own. This suggests that what evolves in response to brood parasitism is not simply a decision to reject odd eggs, but also the ability to recognize one's own eggs, probably by learning. Further work with individually recognizable birds is needed to test whether the species with intermediate levels of rejection of unlike eggs (values greater than 0% but less than 100% in Table 3 of paper I) are dimorphic, with some individuals being 'accepters' and others 'rejecters', or whether all individuals have only a certain probability of rejection.

The sight of a cuckoo on a host's nest stimulates greater rejection of cuckoo eggs by both reed warblers (Davies & Brooke 1988) and meadow pipits (Moksnes & Røskoft 1989). This raises the possibility that differences between species and between populations in response to cuckoo eggs may simply reflect differences in individuals' experience of contact with cuckoos. Against this is the fact that one accepter species, the dunnoek, showed no rejection even after mobbing a stuffed cuckoo on its nest. Furthermore, given the large differences between accepter and rejecter species in response to gross clutch manipulations (Rothstein 1982), it seems more likely that the evolution of a response to cuckoo eggs involves genetic change, as shown for response to predators in some species of fish, where genetic differences underlie population variation in recognition and response to predators (Seghers 1974; Giles & Huntingford 1984).

Species differences in egg discrimination among suitable hosts

The fact that species unsuitable as hosts, which have never interacted with cuckoos, show largely no discrimination against unlike eggs suggests that the various degrees of

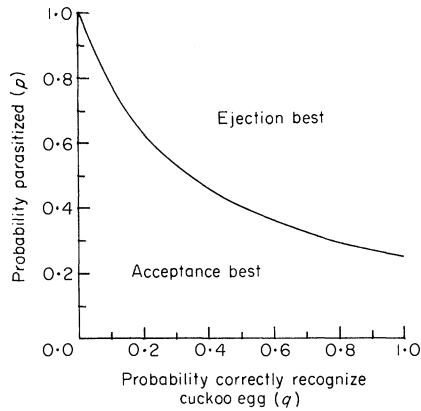


FIG. 1. A model, described in the text, predicts that it will pay hosts to reject odd eggs from their nest only if both the probability of being parasitized and the probability of correctly recognizing the cuckoo egg are sufficiently high (above the curve). Below the curve, hosts do better to accept odd eggs.

discrimination shown by suitable hosts have evolved in response to cuckoo parasitism. What, then, accounts for the variation in degrees of rejection among different species of suitable hosts? We consider three hypotheses.

(1) *Differences in the current costs and benefits of rejecting eggs*

Species differences could reflect differences in the optimum degree of discrimination set by the costs and benefits of rejection. On this view, there is stabilizing selection for the various degrees of discrimination now shown with, for example, it being best for dunnocks to accept cuckoo eggs and reed buntings to reject them.

Consider the following simple model, where a host lays a clutch of four eggs and has a probability p of being parasitized by a cuckoo. Acceptor individuals with the rule 'accept everything' have zero reproductive success when they are parasitized (because the cuckoo chick, on hatching, ejects their own eggs from the nest) and the reproductive success resulting from four eggs when they are not parasitized. Their payoff is thus: $p \cdot 0 + (1 - p) \cdot 4$. Rejecter individuals which adopt the rule 'eject the most extreme egg' would, on the occasions they are parasitized, lose one egg to the female cuckoo (who removes a host egg when she lays) and then eject the cuckoo egg (assuming, for the moment, that the cuckoo egg is always the most extreme). On the occasions they are not parasitized, they eject the most extreme of their own eggs. Their payoff is thus $p \cdot 3 + (1 - p) \cdot 3$. The rule 'eject the most extreme egg' results in greater host reproductive success only if $p > 0.25$. If the cuckoo egg is mimetic then it may not always be the most extreme egg in the clutch and the host may make recognition errors (Davies & Brooke 1988). If q is the probability that the cuckoo egg is the most extreme (i.e. that it is correctly recognized) then the payoff to rejecters is $qp \cdot 3 + (1 - q)p \cdot 0 + (1 - p) \cdot 3$. It then pays to reject only if $3qp > 1 - p$. Figure 1 shows that the threshold value of p , above which it pays to eject $[1/(3q + 1)]$, becomes greater the lower the probability of correctly recognizing the cuckoo egg.

In this model, cost of rejection has been represented as recognition cost but other costs could also be involved such as costs of ejection or increased attraction of predators to the nest while the host was inspecting eggs. The main point is that if there are costs of

rejection, then it may pay hosts to accept cuckoo eggs if the costs of rejection are high or if the benefits of rejection, measured by probability of being parasitized, are low.

Is there any evidence that among suitable cuckoo hosts species more likely to accept unlike model eggs have either greater costs of rejection or fewer benefits? Desertion is a more costly method of rejecting a cuckoo egg than ejection because the host loses its current clutch if it deserts. We showed in paper I that smaller-billed hosts were more likely to reject by desertion and, furthermore, smaller-billed species were more likely to suffer the costs of cracking their own eggs whenever they tried to reject by ejection. However, there is no indication that these greater rejection costs for smaller-billed species have resulted in them being less discriminating against cuckoo eggs. Species with a more costly method of rejection (as measured by the percentage of rejection by desertion) were not more likely to accept model eggs, and there was no correlation among suitable hosts between bill length (which influences costs of rejection) and proportion of unlike eggs rejected (paper I).

There is also no evidence that differences in current benefits of rejection explain differences in discrimination shown among suitable cuckoo hosts, because the more regularly parasitized species are not the most highly discriminating. There is no significant correlation between the percentage of nests parasitized, measured by the nest record scheme of the British Trust for Ornithology (Table 2), and the rejection frequency of unlike model eggs (Table 3 of paper I; $r_s = -0.056$, for thirteen species of suitable hosts). Among the regular hosts, the dunnoek, which shows virtually no rejection, suffers a similar rate of parasitism to the meadow pipit and a much greater rate than the pied wagtail, two species which show strong rejection (Table 3 of paper I). It could be objected that the nest record scheme records only cases where cuckoo eggs have been accepted by hosts, not the proportion of nests initially parasitized. To consider this objection we have estimated the rates of parasitism for each species making the assumption that the cuckoo lays a mimetic egg for pied wagtails, meadow pipits and reed warblers (Brooke & Davies 1988) and unlike eggs for the other species, and that the proportion of eggs rejected (and therefore unrecorded by the nest record scheme) is as in Table 3 of paper I. This gives an upper estimate of the parasitism rate by cuckoos (Table 2). Even under these extreme assumptions, there is no correlation between frequency of parasitism and rejection rate ($r_s = 0.279$, $N = 13$, N.S.). Indeed, contrary to the prediction of this hypothesis, several of the most strongly rejecting species suffer the least parasitism by cuckoos.

The only evidence we can find that could be regarded as support for this hypothesis is the fact that the two species in Europe for which the cuckoo lays the best mimetic eggs have both been reported as suffering locally the highest recorded rates of parasitism, namely 43.5% for redstarts in southern Finland (430 nests studied by Lagerström 1983) and 50% for great reed warblers *Acrocephalus arundinaceus* in Hungary (374 nests studied by Molnar 1944). These high levels of parasitism would provide exceptionally strong selection for rejection which, in turn, would select for unusually good mimicry by the cuckoo. High levels of parasitism have also been reported for the robin in eastern Europe (37% of 1285 nests studied by Varga 1977), where the degree of mimicry by the cuckoo is decidedly closer than in England (Baker 1942). However, experiments need to be done to test whether these populations of hosts are more discriminating than where parasitism levels are lower. In fact, experiments by von Haartman (1976, 1981) and Järvinen (1984) suggest that the frequency of rejection of unlike eggs (those of other species) by redstarts in Finland is only 30%, about the same rejection frequency we found in Britain (Table 3 of paper I) where the redstart is a very rare host (Table 2).

TABLE 2. Two estimates of current parasitism by cuckoos. The first gives the % nest record cards, submitted to the British Trust for Ornithology in the period 1939–82, recording cuckoo parasitism (derived in part from Glue & Murray 1984). The second estimate assumes that the nest record cards record only cuckoo eggs accepted by hosts and calculates the initial % nests parasitized assuming rejection rates as in Table 3 of paper I (see text)

Species	No. of nest record cards			Maximum estimate of nests initially parasitized (%)
	Total	With cuckoo	Observed (%)	
Reed warbler	6927	384	5.54	5.54
Meadow pipit	5331	142	2.66	3.11
Pied wagtail	4945	21	0.42	1.02
Dunnock	23352	453	1.94	2.06
Robin	12917	38	0.29	0.37
Sedge warbler	2685	9	0.33	0.42
Wren	9210	4	0.043	0.043
Redstart	2778	1	0.036	0.054
Spotted flycatcher	6589	8	0.12	1.09
Reed bunting	5753	9	0.16	3.13*
Chaffinch	13752	0	0	0
Blackbird	95135	6	0.0063	0.016
Song thrush	59052	0	0	0
Linnet	20278	23	0.11	0.11
Greenfinch	10334	6	0.058	0.058
Bullfinch	4239	2	0.047	0.047
Great tit	19339	0	0	0
Blue tit	31006	0	0	0
Pied flycatcher	10334	0	0	0
Wheatear	1591	0	0	0
Starling	8344	0	0	0
Swallow	24573	0	0	0

**Note.* Reed buntings rejected all unlike models (Table 3 of paper I); the maximum number of nests initially parasitized cannot be estimated assuming 100% rejection, so a figure of 95% rejection has been used to allow comparison with other species (see text).

(2) *Differences in genetic variation*

In similar experiments to test host responses to model cowbird eggs in North America, Rothstein (1975a) found that species could be divided into accepters (species which accepted most, if not all, cowbird eggs—even though in most cases they were different in coloration from their own eggs) and rejecters (species which rejected most, if not all, models). His results (cf. Rohwer & Spaw 1988) suggested that these differences were not obviously related to the current costs and benefits of rejecting cowbird eggs; for example, many accepter species suffered very high levels of parasitism. Rothstein (1975b, 1982) suggested that some species had, by chance, suitable mutations or recombinations which enabled rejection and these rapidly evolved to become rejecters under selection from cowbirds. Other species, he conjectured, have remained accepters because suitable genetic variation has not yet appeared.

We can reject this hypothesis for the variation observed among suitable hosts in Table 3 of paper I because ten of the thirteen species showed clear rejection responses (i.e. ejection) at least to some model eggs. This shows that rejection is, in principle, a possibility for these species.

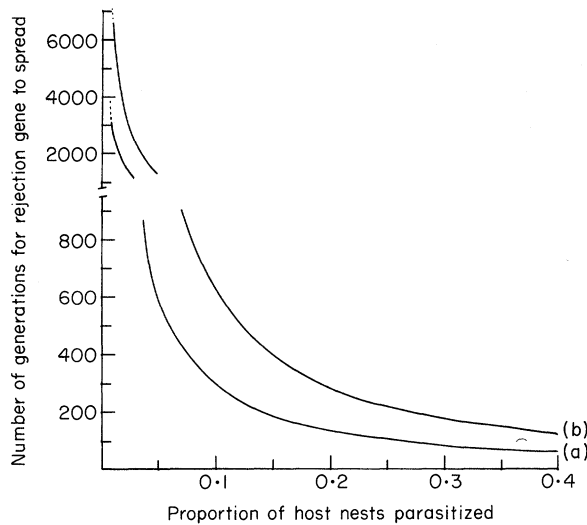


FIG. 2. The number of generations for a hypothetical dominant 'rejecter gene' to spread through the host population, calculated using Haldane's formula (Gale 1980), depends on the proportion of nests parasitized by cuckoos. With the low rates of parasitism experienced by most hosts in Britain (3% or less; Table 2), the spread is slow. Number of generations taken for the gene to increase from a frequency of 10^{-6} to 0.1 (curve a), and 0.9 (curve b).

(3) *Different stages of a continuing arms race with cuckoos*

The third possibility, and the one we favour, is that the various degrees of rejection shown by suitable hosts reflect different stages of a continuing arms race with cuckoos. The sequence of events may be as follows.

(a) Our data suggest that initially, before it becomes a victim of the cuckoo, the host species will show no rejection of unlike eggs.

(b) Once cuckoos begin to parasitize, selection will favour discrimination. The time taken for discrimination to spread through the host population will depend on the rate of parasitism (Fig. 2). With parasitism levels of less than 3%, typical for current hosts in Britain (Brooke & Davies 1987), rejection could take several thousand generations to spread because most of the host population never encounter cuckoos, so rejection has only a small selective advantage. With higher levels of parasitism, say 20% or more, rejection could spread much more rapidly, within a few hundred generations (see also Kelly 1987).

(c) Once hosts begin to reject unlike eggs, selection will favour a mimetic cuckoo egg. Mimicry is expected to spread through the cuckoo population faster than does rejection through the host population because whereas not all hosts encounter a cuckoo, every cuckoo encounters a host; thus selection is stronger on the cuckoo to deceive the host than on the host to spot the deception (Dawkins & Krebs 1979). There will be a stage, therefore, where the cuckoo lays a mimetic egg but not all hosts in the population reject unlike eggs (see Kelly 1987, who showed this result by simulation).

(d) If parasitism levels became high, then host populations could be driven to extinction before they had time to evolve rejection (May & Robinson 1985). If host and parasite populations coexisted stably for a sufficient length of time then we can imagine two outcomes of the arms race. (i) If there are other unexploited, naive acceptor species available, then as a host evolves rejection it may pay the cuckoo to turn to alternative

hosts. (ii) Once all suitable hosts have been exploited, and have evolved rejection of unlike eggs, then the only possibility open to the cuckoo is to evolve better mimicry of one host's eggs. The result would be several gentes of specialist cuckoos, each showing excellent mimicry of their respective host eggs. If the host population declines, or if the host evolves sufficiently strong rejection, then the cuckoo gens may be doomed to extinction if there are no alternative acceptor species to turn to.

(e) Once freed from parasitism, because its cuckoo gens had gone extinct or changed to exploit other species, the host would slowly revert back to become an acceptor of unlike eggs. The loss of rejection would be much slower than the initial spread of rejection under selection from cuckoos, because the only selection against rejection would be due to the small cost to the host of, for example, occasionally rejecting an aberrant egg of its own.

Our suggestion is that the least discriminating among the suitable hosts, dunnocks and robins for example, are at an early stage of an arms race with cuckoos ((b) above) and their acceptance of unlike eggs represents evolutionary lag to a recently changed environment; reed warblers, meadow pipits and pied wagtails are at stage (c) and chaffinches, spotted flycatchers, reed buntings, song thrushes and blackbirds at stage (e). This hypothesis gives a plausible explanation for why, on average, suitable but rarely used hosts are more discriminating against unlike eggs than current favourite hosts (paper I). We suggest that they were common hosts in the past and evolved such strong rejection that the cuckoo was forced to change to new hosts. Three other species, rarely used by cuckoos, have also been reported to show stronger rejection of cuckoo eggs than current favoured hosts (tree pipit *Anthus trivialis* L., Chance 1940, Baker 1942; wood warbler *Phylloscopus sibilatrix* Bechstein and chiffchaff *P. collybita* Vieillot, Gärtner 1982).

At first, it seems that evidence from the literature would argue against the view that the dunnock is a recent host. Reference to cuckoos parasitizing hedge sparrows (an alternative name for the dunnock) was made by both Gilbert White (1770) and Shakespeare (*King Lear*; Act I, scene IV; written *c.* 1605). There is an even more ancient reference in Chaucer's poem 'The Parlement of Foules' written in 1382, where the cuckoo is chastised as 'thou morderer of the heysugge on the braunche that broghte thee forth!' Heysugge is Old English for hedge sparrow, so we know that the dunnock has been a cuckoo host for at least 600 years. On an evolutionary time scale, however, the dunnock could still be a recent host because with a parasitism rate of only 2%, discrimination may take several thousand generations to spread (Fig. 2). Most of Britain was covered in primeval woodland 6000–8500 years ago. The dunnock is not common in extensive woodland (Tomialojc, Wesolowski & Walankiewicz 1984), and it is possible that it did not become a victim of the cuckoo until extensive forest clearance occurred 6500–2500 years ago (Rackham 1986), within the time which calculations suggest it would take discrimination to spread. This view must be expressed with some caution, however, because forest clearance may also have led to an increase in moorland species, such as the meadow pipit (Perrins 1983) which has had time to evolve discrimination and to select for a mimetic cuckoo egg.

Although we think that this hypothesis gives the best explanation of the data presented here, the only direct test, to repeat the model egg experiments in several hundred years time, is impossible for us to perform. Nevertheless, the idea that brood parasites may change their use of hosts with time is supported by observations of great spotted cuckoos *Clamator glandarius* L. in Spain (Arias de Reyna & Hidalgo 1982) and cuckoos *Cuculus canorus* L. in Japan (Yamagishi & Fujioka 1986), both of which have recently begun to parasitize a new host, the azure-winged magpie *Cyanopica cyana* Bonaparte. In Spain,

this new host shows much less rejection of unlike eggs than the common magpie *Pica pica* L., which is the regular and presumably much older host (Arias de Reyna & Hidalgo 1982).

This third hypothesis may also explain some of the variation in rejection of non-mimetic eggs shown by hosts of the brown-headed cowbird *Molothrus ater* Boddaert in North America. This brood parasite was originally a bird of the short-grass plains of central North America, but it has undergone a remarkable increase in range and abundance within the last 200 years as forested areas have been cleared and tall-grass prairies ploughed for agriculture. Several hosts have only recently come into contact with cowbirds, and may accept the parasite's eggs simply because rejection has not had time to spread through the population (Mayfield 1965). Rothstein (1975b) presents two arguments against this view. First, parasitism levels are so high for some acceptor species (40–60% of nests parasitized) that selection would be expected to change them to rejecters within 100 years or less. Second, many species of accepters appear to have had a long history of sympatry with cowbirds, for example in the open grasslands of central North America. Both arguments suggest rejection should have spread by now and for these reasons Rothstein prefers hypothesis (2).

The two alternative hypotheses cannot, however, be firmly rejected. First, some hosts with a long period of coexistence with cowbirds may accept parasitic eggs simply because acceptance is better than rejection (hypothesis (1) above; see Rohwer & Spaw 1988). Second, some of Rothstein's acceptor species showed low rates of rejection which suggests that they are not constrained to accept through lack of genetic variation (see, for example, Clark & Robertson 1981). Rejection, if advantageous, may spread more slowly than suggested by the calculations of Rothstein (1975b), first because rejection has costs, and second because parasitism levels over a large area may on average be lower than the very high rates observed in some local populations (Friedmann, Kiff & Rothstein 1977). For some acceptor species, therefore, evolutionary lag remains a possibility (hypothesis (3)). In conclusion, we suggest that for several hosts of both the cowbird and the cuckoo the varying degrees of rejection reflect different stages in a continuing arms race.

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