

MECHANISMS OF AVIAN EGG RECOGNITION: POSSIBLE LEARNED AND INNATE FACTORS

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THE belief that at least some passerine birds reject nonmimetic eggs placed in their nests was confirmed long ago by the experiments of Swynerton (1916, 1918) and Rensch (1924). The latter worker (Rensch 1925) went on to question whether such birds actually recognize their own eggs (rejection by true egg recognition) or whether they simply reject any egg that differs from the majority (rejection by discordancy). Rensch was interested in egg recognition because he believed it to be vital to the evolutionary interactions between brood parasites and their hosts. Whether birds rejected eggs on the basis of true recognition or discordancy, the behavior would still function as an efficient antiparasite adaptation because brood parasites generally deposit only one egg in each host nest. Although Rensch's (1925) experiments have been widely interpreted as demonstrating rejection by discordancy (e.g. Welty 1963), the bulk of his results actually indicate true egg recognition (Rothstein 1970). Numerous recent experiments and a literature review suggest that most or all passerines that reject foreign eggs practice true egg recognition (Rothstein 1974).

Nearly all these recent experiments, though, were conducted on birds that had completed their clutch. The fact that birds that reject foreign eggs practice true egg recognition after completing their clutch prompts two significant questions: (1) Is this recognition as highly developed at earlier stages of the breeding cycle? (2) Which components of rejection by true egg recognition are primarily learned and which are primarily innate? This paper reports on experiments that were designed to deal with these two questions.

The new experiments reported here were done on naturally breeding Gray Catbirds (*Dumetella carolinensis*). Previous experiments showed that catbirds are extremely intolerant of foreign eggs placed in their nests. Single artificial or real cowbird eggs experimentally added to 30 catbird nests in eastern North America (Connecticut, Maryland, and Michigan) were all removed by the catbirds. Catbirds in western North America (Manitoba and Nebraska) may be slightly more tolerant, with 22 of 25 nests yielding ejections of single cowbird eggs. In 17 additional catbird nests (from Connecticut and Maryland), where experiments resulted in clutches consisting of only cowbird eggs or of only one catbird egg and two or more cowbird or other type of foreign eggs, the catbirds ejected the foreign eggs in every instance (see Rothstein 1974 for details).

Friedmann (1963) has stated that while such intolerance of foreign eggs serves as an efficient host defense it is probably not evolved in response to brood parasitism. I suggest this intolerance can be explained only in terms of an adaptation that evolved because it protects birds from brood parasites. This is the most parsimonious explanation, as rejecting foreign eggs does not seem to have any adaptive value in most birds, other than in the context of brood parasitism (Rothstein 1970, MS).

Although catbird and cowbird eggs differ little in size (averaging 23.3×17.5 mm and 21.45×16.42 mm, respectively, according to Bent 1948, 1958), they are strikingly different in coloration and thus provide a valuable pair for experimentation. Catbird eggs are immaculate with a blue-green ground color whereas cowbird eggs usually have a whitish ground color and are heavily mottled with brown and gray spots.

Previous work by Tschanz (1959) has shown that in a nonpasserine, the Common Murre (*Uria aalge*), egg recognition is realized through a learning process. In the case of a passerine, the Village Weaverbird (*Ploceus cucullatus*), it has been suggested that egg recognition is also learned (Victoria 1972). Given the variable nature of murre and weaverbird eggs these findings might not be unexpected. The eggs of most songbirds, the catbird included, show little variation and egg recognition through largely innate means might not be difficult to evolve. Nevertheless the hypothesis of egg recognition by learning will be supported by a demonstration of greater tolerance toward a foreign egg type in the early stages of the breeding cycle than in later stages. If egg recognition has a learning component, greater tolerance in the early stages of the nesting cycle would be expected whether the birds learn the appearance of their eggs anew with each breeding attempt, or whether the learning occurs only in completely naive individuals during the first nesting attempt of their lives. In the latter case though, increased acceptance early in the cycle would occur only at those nests tended by naive birds. Unfortunately it is impossible to determine whether the catbirds tested in the experiments reported here were naive or experienced; but given the high mortality of passerines it is reasonable to assume that within any series of nests experimented upon in the field some will be tended by naive and others by experienced individuals.

Much of what follows is relevant only to the catbird and to other species that I have termed "rejecters." Experiments with cowbird eggs have shown little intraspecific variation in response to artificial cowbird parasitism. A minority of North American species reject cowbird eggs at nearly 100% rates. These are the rejecters. Most species accept the eggs at nearly 100% rates and are termed "accepters." Rejecter and

accepter species have presumably responded and not responded, respectively, in a major way to the evolutionary pressures of brood parasites (Rothstein 1970). As accepter species demonstrate little or no egg recognition (except under special circumstances (Rothstein 1970, MS)), questions on their acquisition of this behavior have reduced relevancy.

METHODS AND CONTROLS FOR ARTIFICIAL EGGS

The artificial eggs used in most experiments were cast in plaster of paris and painted with artist's paints of the acrylic polymer type. Artificial cowbird and catbird eggs were also shellacked. I have elsewhere (Rothstein 1970, 1974) described the production and properties of these eggs in greater detail. Suitable controls for artificiality of the eggs have been performed. For example, at four nests all four of the catbirds' own eggs were replaced with one artificial catbird egg plus three artificial cowbird eggs. In all four cases the cowbird eggs were ejected while the artificial catbird egg was left in the nest. At another five nests a single artificial catbird egg added to a nest with two or more real catbird eggs was accepted, whereas a single real or artificial cowbird egg was rejected under similar conditions at 52 of 55 nests from five localities in North America. These different acceptance rates (5-0 vs. 3-52) are significant at $P < 0.005$ (Fisher Exact Probability Test, Siegel 1956). Throughout this paper data on which statistical tests have been performed will be reported as in the preceding sentence. The entire two-by-two contingency table can be constructed from the information given (e.g. 5-0 vs. 3-52).

To determine whether catbirds possess true egg recognition at an early stage in their breeding cycle and whether any recognition that occurs is learned, the following manipulation (experiment I) was performed: The first egg laid in 11 catbird nests was replaced with an artificial cowbird egg. The time interval between egg laying and initiation of the experiment is unknown, but it could have ranged from a few minutes to 4½ h. The nests were checked later the same day and then the next morning. In some cases additional egg manipulations were conducted. Of the 11 nests studied 10 were in New Haven County, Connecticut during May and June 1969 and 1970; the 11th nest, number 72-215, was in Anne Arundel County, Maryland in May 1972.

RESULTS FROM PRIMARY EXPERIMENTS

Results of experiment I are summarized in Table 1. At three nests, the cowbird egg was missing by the same afternoon of the day it had been inserted. At another three, it was missing and a second catbird egg was in its place the next morning. The catbirds at these six nests clearly recognized their own egg type even at the earliest stages of clutch initiation. At the three nests where the cowbird egg was ejected by the same afternoon, it was ejected in the absence of any cues or information that one or more catbird eggs might have supplied. It cannot be determined whether the cowbird eggs in the other three nests were ejected before or after the second catbird egg was laid. But it is of course certain that they were not the minority type egg at the time of their ejection. It could be argued that the missing cowbird eggs in these six nests were removed

TABLE 1
RESPONSES OF CATBIRDS TO ARTIFICIAL COWBIRD EGGS PLACED IN THEIR NESTS¹

Experimental procedure and location	Status of cowbird egg after 1 day		Status of cowbird egg after 2 days	
	Accepted	Ejected	Accepted	Ejected
I First catbird egg laid replaced with an artificial cowbird egg (experiment done within 4½ h after the first egg was laid); Connecticut, Maryland	5	6	4	7
II One artificial cowbird egg added to clutch when there were at least two catbird eggs present; Connecticut, Maryland, Michigan	4	25	2	27

¹ A catbird egg was removed at the time the cowbird egg was added in 23 of the 29 experiment II nests. Whether or not a catbird egg is removed at the time of experimentation has no effect on response (Rothstein 1970). At one experiment II nest a real cowbird egg was used rather than an artificial one. It was ejected within a day.

by predators rather than by the catbirds, but 20 other catbird nests subjected to different experimental procedures during the same years and in the same study areas as the experiment I nests can serve as a control for nest predation. Only one of these nests suffered nest predation (all the eggs were missing) within 1 day after the experiment was initiated, and this is significantly ($P \leq 0.01$) less than the proportion of experiment I nests at which the cowbird egg disappeared within 1 day (19-1 vs. 5-6).

Events at the remaining five nests were variable. The cowbird egg in nest 69-228 was ejected after 2-2½ days. At nest 69-222 the cowbird egg remained in the nest for 2-2½ days while laying proceeded and the nest was then predated. The cowbird egg in nest 69-251 was accepted along with the three catbird eggs subsequently deposited. At nest 72-215 the cowbird egg and the second catbird egg were present the next morning. This second catbird egg was replaced by a cowbird egg but both cowbird eggs were missing that afternoon. The two catbird eggs were then returned to the nest and three catbird eggs were there the next morning.

The complicated events at the last nest (69-264) are worth reporting in detail: 28 May, first egg laid replaced with an artificial cowbird egg; 29 May, one catbird + one artificial cowbird egg, replaced the former with second artificial cowbird egg; 30 May, one catbird egg + one real (naturally deposited) cowbird egg + two artificial cowbird eggs, removed the catbird egg and added a third artificial cowbird egg; 31 May, one catbird egg + three artificial cowbird eggs, real cowbird egg is gone, replaced the catbird egg with a fourth artificial cowbird egg; 1, 2, 3, and 5 June, nest active, contents four artificial cowbird eggs; 7 June, same, added a real

catbird egg; 8 June, four artificial cowbird eggs + real catbird egg; 9 June, same; 11 June, four artificial cowbird eggs, real catbird egg is gone, added an artificial catbird egg; 13 June, four artificial cowbird eggs + one artificial catbird egg; 14 June, same; 15 June, last nest visit, same, nest still active. This history shows that the catbirds at nest 69-264 apparently accepted a clutch consisting only of artificial cowbird eggs. I suspect the catbirds removed both the real catbird egg, which I added on 7 June, and the real cowbird egg, which appeared on 30 May.

Thus while the experiment I series shows that some catbirds recognize their own eggs even in the initial stages of egg-laying, the situation is rather complex for other individuals. By contrast none of the 29 pairs of catbirds in eastern North America whose nests received experimental cowbird eggs when at least two catbird eggs were present (experiment II), showed comparable complexities. All ejected the cowbird egg within 3 days, although as shown in Table 1, two had not yet done so by the end of the first 2 days.

EVIDENCE THAT EGG RECOGNITION IS LEARNED

The results (Table 1) suggest that the catbird learns to recognize its eggs through an imprinting-like process on the first egg or eggs that a bird sees. The evidence is derived from several aspects. First, catbirds were relatively tolerant of cowbird eggs that replaced their first egg. The cowbird egg in four of the 11 nests in the experiment I series was still accepted after 2 days. This is opposed to only two of 29 for other experiments in eastern North America in which a cowbird egg was added when there were at least two host eggs in the nest (see experiment II, Table 1). The difference in 2-day acceptance rates (4-7 vs. 2-27) is significant at $P = 0.039$. If the criterion of a 1-day acceptance rate is applied, the difference (now 5-6 vs. 4-25) is also significant (at $P = 0.047$). It is possible that the longer acceptance time in the experiment I nests occurred because some of the birds in question had not yet fully learned their egg type when I removed their first egg. The presence of the cowbird egg alone, where previously only a catbird egg had been present, may have interfered with the egg recognition of some birds and either caused them to delay their rejection or to accept both egg types.

In contrast to learned egg recognition, two alternative interpretations can be offered to explain the differences between the results of experiments I and II. Birds at experiment I nests could have shown increased acceptance because their motivational state, as regards rejection, was lower than that of birds at experiment II nests. A number of records indicate that rejecter species show slightly greater tolerance towards foreign eggs

as their nesting cycle progresses (Rothstein 1970). This increased tolerance may occur because the later a cowbird egg appears in the host's nesting cycle the less chance it has of hatching and of resulting in harm to the host's own young. On this basis, experiment II rather than experiment I should have had the higher acceptance rate. Secondly, it could be argued that birds at experiment I nests showed greater acceptance than those at experiment II nests because they visited their nests less frequently. While catbirds were usually in close attendance to their nests on the first day of egg laying, my observations indicate that birds at experiment II nests were in more frequent contact with their nests, so the possible confounding factor of differential contact with the nest cannot be completely discounted. However, frequent nest inspections after egg-laying has begun are to be expected, as this would permit early detection of predation. In addition, while they have greater contact with their nest, incubating birds may see their eggs less frequently than do birds early in the egg-laying stage because they keep the eggs covered. Lastly, evidence presented below supports learned egg recognition, nearly all of it independent of the problem of differential contact with the nest.

At several nests events occurring more than 2 days after experiment I was initiated also support the hypothesis of learned egg recognition. At nest 69-251 the cowbird egg was accepted for at least 8 days before the nest was destroyed. No other catbirds tested in eastern North America accepted a single cowbird egg for more than 3 days. Nest 69-228 is also relevant; here the cowbird egg placed in the nest on the first day of laying was accepted for 2-2½ days, after which the birds continued to incubate two eggs of their own. Nine days after laying was completed I removed both catbird eggs and added two artificial cowbird eggs, which the birds ejected within 6 h, indicating that they were then able to detect this egg type as foreign quickly whereas earlier they needed at least 2 days.

Learned egg recognition is most strongly supported by the results from nest 69-264. At this nest, the catbirds accepted a clutch containing only artificial cowbird eggs when these were deposited in such a manner that each cowbird egg replaced a catbird egg soon after the latter was laid. The best explanation for the results from this nest is that the catbird eggs were not in the nest long enough to allow the birds (or just the female) to learn this egg type as their own and that they learned the artificial cowbird egg as "their own type." That they still retained rejection behavior is indicated by the disappearance of both the naturally deposited cowbird egg and the real catbird egg that were added to the nest on days 2 and 10, respectively. It seems likely that both these eggs were removed because they were detectably different from the artificial cowbird eggs.

(Real cowbird eggs show great variation, whereas the artificial ones were identical mimics of an average cowbird egg.) A catbird nest at Delta, Manitoba in June 1970 yielded similar data. An artificial cowbird egg was added to the nest on the day the catbird laid its third or fourth egg. This cowbird egg was one of the few (three of 55) anywhere in North America that was accepted when added to a nest already containing more than one catbird egg; but a naturally deposited cowbird egg appearing 7 days later was ejected while the artificial cowbird egg was left in the nest. In this case the catbirds may have learned both the artificial cowbird egg and the catbird egg patterns as their own and rejected the real cowbird egg because it was sufficiently different from both these egg types.

The most reasonable interpretation of these results is that the tendency to reject eggs other than their own is largely innate in catbirds but that individuals normally learn the egg type responded to as their own from the first eggs that appear in their nest. Once the individual learns its egg type, it presumably ejects all other eggs that depart from this type to a sufficient degree (catbirds will accept some types of nonmimetic eggs (Rothstein 1970)). Possibly a genetic component in this learning process prevents catbirds learning any eggs whose features lie beyond a certain range of variables as their own.

An important question regarding the learning process is whether it occurs only once or with each nesting attempt. If the former is the case the variation in response to experiment I could be due to some of the birds being naive and some experienced. If the latter is the case the variation could be due to the length of time the birds were in contact with their first egg before I replaced it with a cowbird egg. Since naive and experienced birds could not be differentiated, my data do not permit resolving this question definitely. I tested the hypothesis that learning occurs only in naive birds by determining whether nests in experiment I that yielded acceptances had smaller eggs, smaller clutches, or were started later than those that resulted in rejections. Birds breeding for the first time often have smaller eggs (Romanoff and Romanoff 1949, Coulson et al. 1969) and often have smaller clutches and breed later (Klomp 1970) than older birds. These analyses failed to demonstrate a correlation between egg or clutch size or date of laying and response to experiment I, suggesting that the factor responsible for the variation in response to the experiment was related to how long the birds were in contact with their first egg before I started the experiment and not to whether the birds were naive or experienced. But as I found no correlation between response to experiment I and time of day I started the experiment, the length of time the birds were in contact with the first egg was also apparently unimportant. None

of these analyses provides a definite explanation for the variation in responses to experiment I, but I believe learning probably occurs primarily in naive birds, and each breeding attempt may further refine it.

If egg recognition is learned, an individual of a rejecter species might accept a naturally deposited cowbird egg if this egg replaces its own first egg or is deposited before any of its own eggs. Probably this is a rare occurrence, but it seems to have taken place at a catbird nest in the same study area (New Haven County, Connecticut) and at the same time that I conducted most of the experiments reported here. On 21 May 1969 I found an unlined catbird nest. When next visited on 24 May, the completed nest contained one naturally deposited cowbird egg that a catbird was incubating. The bird behaved normally in that it scolded me while I was at the nest. I checked the nest once or twice daily until the morning of 31 May when it was empty. Until this last visit, the nest contained only the cowbird egg. On all nine visits from 25 May until 30 May (my penultimate visit) the cowbird egg showed signs of being incubated (it was warm), and a catbird scolded me. It is unlikely that incubation behavior by the catbird would have occurred in the absence of egg-laying, so the most likely interpretation of the events at this nest is that the cowbird egg appeared shortly before any catbird eggs or quickly replaced the first catbird egg (female cowbirds often remove a host egg (Friedmann 1963)). In either case, the catbird could have learned the cowbird egg as its own egg type. Then, shortly after laying each of its own eggs, it may have ejected them since they were unlike the egg it had learned as its own. The catbird continued to incubate the cowbird egg until it was removed, perhaps by a predator, between 30 and 31 May. This explanation accounts for the unique features of this nest—a cowbird egg was accepted and incubated, and only a cowbird egg, never a catbird egg, was seen in the nest.

Experiments with another egg type also suggest that egg recognition is learned. As indicated above, rejecter species generally show slightly greater tolerance towards foreign eggs as their nesting cycle progresses, but catbirds show the reverse tendency when parasitized with an egg that differs only slightly from their own. This egg, type Va, measures 23.32×17.91 mm and has a blue-white ground color with 16 symmetrically placed brown dots (each dot being 0.5 to 1 mm in diameter). Real catbird eggs differ little in size but are blue-green and unspotted. All four catbirds parasitized with egg type Va after they had completed their clutch rejected the egg whereas all five parasitized during the egg-laying period accepted it. This difference (0-4 vs. 5-0) is significant at $P \leq 0.025$ and is what one might expect if, as the nesting cycle progresses, learning

continues to refine an individual's recognition behavior so that it becomes easier for it to detect slight differences. Even if egg recognition is acquired primarily at a bird's first nest, the recognition may be sharpened temporarily during each successive nesting attempt through prolonged contact with the eggs. Thus, two conflicting tendencies may develop the longer a bird has contact with its eggs: The drive to reject foreign eggs decreases, but the ability to detect their presence increases.

Although several independent lines of evidence based on field studies are all easily explained by the single hypothesis that catbirds learn their own egg type, this should be confirmed with experiments on breeding birds of known ages. This could be done most easily in captivity, but unfortunately none of the North American species that have been found to reject nonmimetic eggs breed readily in captivity.

EVOLUTIONARY IMPLICATIONS OF LEARNED RECOGNITION

The likelihood that rejecter species learn their egg type and do not recognize it innately has important evolutionary implications for the interactions between brood parasites and their hosts. It is commonly accepted that brood parasites may evolve new egg types that mimic those of the host because this reduces the host's ability to distinguish between the parasitic eggs and its own. Some workers have stated that this evolutionary process will eventually end when the mimicry is perfect (Meise 1930 *in* Southern 1954) and result in "perfect or complete" evolution (Baker 1942: 3), but the possibility of selective pressures on the host's eggs has not been given sufficient consideration. It is unlikely that the egg-related aspects of the evolutionary interactions of a parasite and its host come to an end and are completed if the parasite's egg mimics the host's egg perfectly. Selection might favor changes in the host's eggs so that these diverge in appearance from a highly mimetic parasitic egg. Evolution could take two different pathways. The development of egg polymorphism in the host would make it difficult for the parasites to match their eggs to those of the host even if they had egg types identical to one or all of the host's morphs (Rothstein 1971, Victoria 1972). This matching difficulty would arise because brood parasites apparently commit themselves to host nests before any eggs appear (Chance 1940, Hann 1941) and thus have no way of predicting what egg morph a given nest will contain. Another strategy would be for the hosts to undergo directional selection and evolve a single new egg type as the parasite's mimicry of their old type becomes more highly developed. Swynnerton (1918) also suggested that brood parasitism might be a selective pressure that modified the appearance of host eggs. He stated (1918: 145) "that a

race may in some cases have taken place between the host's eggs and those of the overtaking Cuckoo"; of course, this race need never end.

While these evolutionary responses by the host to the egg-related adaptations of the parasite are a logical expectation, they would have little chance of occurring if the hosts innately recognized their own egg type. When new egg variations appeared, the hosts would reject their own eggs, unless the genetic change producing the new egg type was accompanied by another genetic change permitting the individual to recognize innately the new egg type as its own. But, if the egg recognition is not rigidly determined by innate means and is learned, then the successful development of new, more adaptive host egg types would require only the genetic change that affects the egg's phenotype. Thus hosts with learned egg recognition should be able to evolve additional antiparasite adaptations much more rapidly than hosts with innate egg recognition.

Swynnerton (1918) and Victoria (1972) collected data that support the above arguments. Each worked on a different species of African weaver (Swynnerton probably *Hyphantornis jamesoni* and Victoria *Ploceus cucullatus*). Both species are cuckoo hosts, have highly variable eggs, and reject nonmimetic eggs. Even the eggs of other members of their own species are rejected if such eggs are of a sufficiently different type. The two authors thought it likely that the weavers evolved both rejection behavior and variable eggs in response to cuckoo parasitism. Certainly these apparent adaptations of the weavers could have evolved much more easily if their egg recognition was largely learned rather than innate. It should be indicated though, that like learned egg recognition, rejection of discordant eggs would facilitate evolutionary changes in host eggs. The hosts would always reject only the minority type egg and in nearly all cases the parasitic egg would be the minority type. But Swynnerton's evidence (1916: 559) suggests, and Victoria's (1972) proves, that the two weaver species involved actually recognize their own eggs.

If egg recognition via a primarily learned route proves to be the general mechanism among passerines, it is important from an evolutionary viewpoint to ask why it rather than a primarily innate mechanism evolved. As indicated above, learned recognition would provide advantages in the future because of its evolutionary flexibility, but it would be teleological to suggest that these future advantages would enhance the initial development of egg recognition by learning. I suggest that learned egg recognition was simply evolved more easily than innate recognition. Birds are relatively flexible in their behavior and perhaps even among accepter species older individuals become conditioned to the egg type they have seen in their many breeding attempts. If in some individuals this predilection

to conditioning were strengthened by genetic determinants, the species might then evolve into a rejecter species. Possibly even in the beginning of the evolution of rejection behavior, simultaneous selection for a new host egg type sometimes facilitates the discrimination between host and parasitic eggs. Such simultaneous selective pressures might result in the development of both rejection behavior and learned egg recognition.

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SUMMARY

Another paper in this series demonstrated that birds that reject foreign eggs practice true egg recognition after their own clutch is completed and do not simply reject any egg type that is in the minority. This paper attempts to answer the questions of whether this recognition is as highly developed when egg-laying starts and whether it has both learned and innate components. The first egg laid in 11 catbird nests was replaced with an artificial cowbird egg. At six nests the cowbird egg was rejected either before or shortly after the second catbird egg appeared. In the case of these nests the catbirds clearly knew their own egg type at the onset of laying. On an overall basis these 11 nests demonstrated significantly greater tolerance towards cowbird eggs than nests experimentally parasitized later in the breeding cycle. This suggests that a learning component to egg recognition exists. At one nest the catbirds' entire clutch was gradually replaced with artificial cowbird eggs. These were accepted, but a real catbird egg was then rejected, suggesting that the egg type responded to as the catbird's own is learned from the first eggs an individual sees in its nest and that the tendency to reject other eggs is innate. Data from additional experimental and nonexperimental nests also support this hypothesis, but none of the data allow a determination of whether the learning occurs only once in an individual's lifetime at its first nest or repeatedly with each nest. Egg recognition by learning has significant implications as regards the long range evolutionary interactions between brood parasites and their hosts. Hosts that learn their own egg type can evolve additional antiparasite adaptations much more easily than hosts that innately recognize their own egg.

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