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# Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium

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Because hosts that accept a parasitic egg laid by the common cuckoo, *Cuculus canorus*, are unlikely to fledge their own offspring, rejection should be an adaptive response. Evidence that cuckoo host species attain only intermediate rates of rejection are commonly interpreted as resulting from an evolutionary lag. Yet, we found that the acceptance of cuckoo eggs by female great reed warblers, *Acrocephalus arundinaceus*, occurs mainly among the younger breeders in the host population. We suggest that some level of acceptance can arise in the host population as a result of the need of naive breeders to learn to reliably recognize their own eggs rather than representing evolutionary lag. [*Behav Ecol* 3:128–132 (1992)]

Behavioral ecologists attempt to interpret the behavior of animals in terms of the contribution it makes to the animal's fitness in the framework of optimization theory (Krebs and Davies, 1987; Maynard Smith, 1978). This approach is based largely on the assumption that natural selection is a major force in evolution and that there has been sufficient time for evolution to operate. Yet, in the case of avian brood parasitism, the acceptance of parasitic eggs or nestlings by hosts seems to be maladaptive and nonoptimal. This has led some researchers to reject the possibility of an evolutionary equilibrium in brood parasitism and to endorse evolutionary lag and the arms race theory as a more likely explanation (Brooke and Davies, 1988; Davies and Brooke, 1989b; Dawkins and Krebs, 1979; Rothstein, 1982, 1990). It has been suggested that evolutionary lag is a legitimate, tentative explanation after all other reasonable adaptive explanations have been tested and rejected (Rothstein, 1982). However, it has also been claimed that not all the possibilities for the existence of an evolutionary equilibrium have been sufficiently investigated (Rohwer and Spaw, 1988; Zahavi, 1979).

The common cuckoo, *Cuculus canorus*, parasitizes a large variety of passerine hosts from western Europe through Japan (Cramp, 1985; Nakamura, 1990). During the host's laying period, the cuckoo lays a single egg, which mimics to varying degrees the eggs of its particular host (Brooke and Davies, 1988). After hatching, the cuckoo's nestling ejects all host eggs or nestlings from the nest and thus reduces

host reproductive success to zero (Wyllie, 1981). Recent studies suggest that rejection of poorly matching eggs by hosts is indeed an evolutionary response to brood parasitism (Brown et al., 1990; Davies and Brooke, 1989a; Soler and Møller, 1990). However, most cuckoos' host species demonstrate only intermediate rates of rejection, and a considerable number of cuckoo eggs are still accepted (Davies and Brooke, 1988, 1989a; Moksnes and Røskaft, 1989; Soler and Møller, 1990). The coexistence of rejection and acceptance of cuckoo eggs within a host population is commonly interpreted as resulting from an evolutionary lag in the host's response during a continuing evolutionary arms race between the cuckoo and its host (Davies and Brooke, 1989b; Dawkins and Krebs, 1979). Alternatively, such coexistence may be interpreted as an equilibrium among selective pressures. The evolutionary lag model requires a dimorphic population in which rejection has not yet reached fixation (Kelly, 1987). Evolutionary equilibrium, on the other hand, may develop either in a dimorphic population, when acceptor and rejecter genotypes are equally adapted (May and Robinson, 1985), or as a result of phenotypic plasticity in the host response.

To determine which of these mechanisms the cuckoo–host relationship is based on, we studied a population of great reed warblers parasitized by the common cuckoo. In this paper we investigate the distribution of rejections and acceptances of cuckoo eggs by the host. We expected that if the host response is determined phenotypically, the occurrence of

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each strategy (reject or accept) would not be random and would follow some adaptive rules.

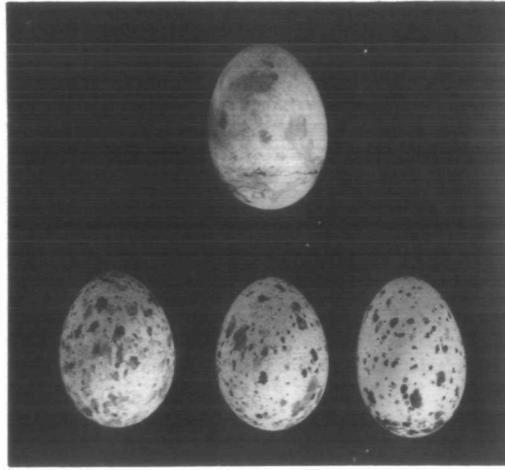
## METHODS

We conducted the study at Nagano, central Japan, where it formed a part of an ongoing cuckoo study (Nakamura, 1990). The study site was located east of Nagano city, on the Chikuma river banks, and was composed of reed beds, willow bushes, and acacia trees. The reed beds provide a habitat and nesting sites for a dense population of great reed warblers.

During the breeding seasons of 1989 and 1990, we monitored host response to real cuckoo eggs (Figure 1) in 51 cases of natural parasitism and 14 cases of experimental parasitism. To detect natural parasitism, we monitored host nests during the nest-building and egg-laying periods. We checked nests at least every alternate day and at the day of clutch completion. Because 18.5% ( $N = 38$ ) of rejections of cuckoo eggs were found to occur within 2 days after the cuckoo egg was laid, it is possible that some cuckoo eggs were rejected before we noted them.

We performed experimental parasitism by replacing a host egg with a real cuckoo egg in the afternoon during the host laying period (four replacements at the first, nine at the second, and one at the fourth day of host egg laying). Rejection rate of experimental parasitism appeared higher than that of natural parasitism (12/14 versus 27/51,  $\chi^2 = 3.6452$ ,  $df = 1$ ,  $p = .053$ ). However, this might be due to the fact that we performed only four cases of experimental parasitism in mid-season, when breeders are more likely to be accepters (Figure 2). Moreover, adding the data on experimental parasitism yielded a more conservative result in the case of host response versus time of breeding (Figure 2) and an equally significant result in the case of host response versus female plumage (Figure 3). We therefore chose to pool the data on natural and experimental parasitism. We scored cuckoo eggs as accepted if they remained in the nest until hatching time. If nest predation occurred before hatching, eggs were scored as accepted only if they remained in the active nest for at least 6 days [89% ( $N = 37$ ) of rejections of cuckoo eggs known to occur within this period].

We captured breeding females by using mist nets near their nests, color ringed them, and checked their plumage. Great reed warbler yearlings are often distinguishable from older birds because they tend to retain juvenile tail feathers (Nisbet and Medway, 1972). Retention of juvenile feathers was indicated by one to four ragged central tail feathers. This aging



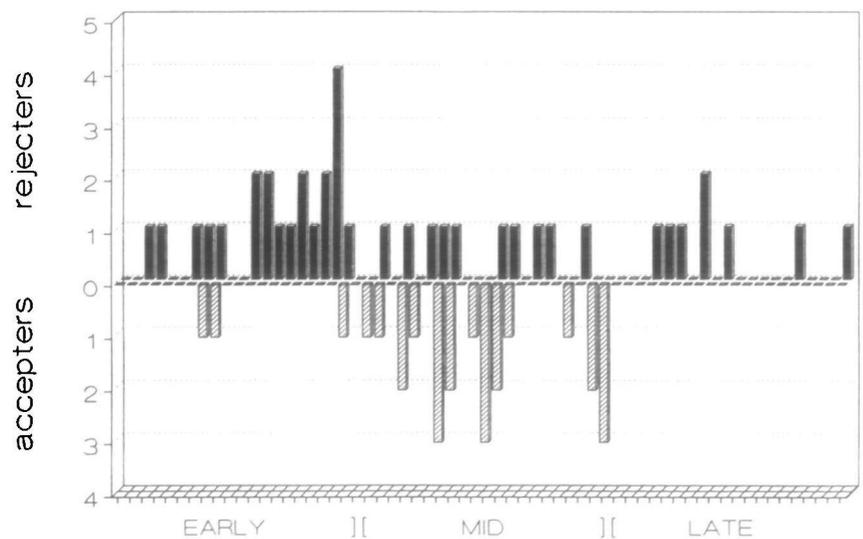
**Figure 1**  
A cuckoo egg (top) and great reed warbler eggs (bottom) from the study area. Chikuma River, Nagano, Japan.

method enabled us to test the possible association between age and rejection (Davies and Brooke, 1988; Rothstein, 1974, 1978). The female's age is particularly relevant, as only females incubate in this species. It should be noted, however, that it is possible that not all yearlings retain juvenile tail feathers and that a few older females might have ragged central tail feathers (Lotem A, unpublished data).

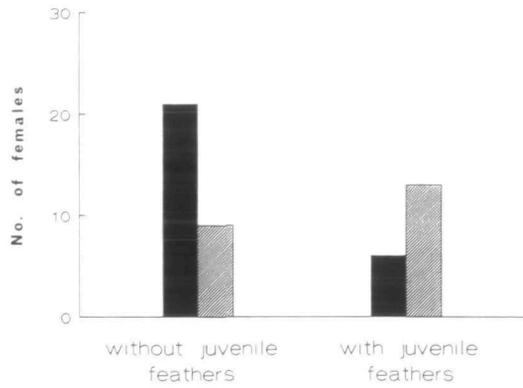
## RESULTS AND DISCUSSION

During the breeding seasons of 1989 and 1990, parasitism rates were 20% ( $N = 188$ ) and 21% ( $N = 133$ ), respectively. Cuckoo eggs were accepted in 26 cases (40%) and rejected in 39 (60%). Cuckoo eggs were rejected by ejection ( $N = 29$ ), desertion ( $N = 8$ ), or by egg burial with nest material ( $N = 2$ ). The distribution of rejecters through the breeding season differed significantly from the distribution of accepters (Figure 2;  $D = 0.436$ ,  $p < .01$ , Kolmogorov-Smirnov two-sample test), forming three distinct periods within the

**Figure 2**  
Distribution of rejecter ( $N = 39$ ) and acceptor ( $N = 26$ ) nests through the breeding season. The breeding date of a nest was determined by the first day of laying. Each column represents a single day. There is no repeated observation of the same individual within a breeding season. One ringed female that was parasitized in 1989 was parasitized again in 1990. It ejected the cuckoo egg in both cases. According to the different distribution of rejecters and accepters (see text), the host breeding period, from the earliest onset of egg laying to the latest one, may be divided into three distinct parts: early (17 May–6 June), mid (7–27 June), and late (28 June–17 July).



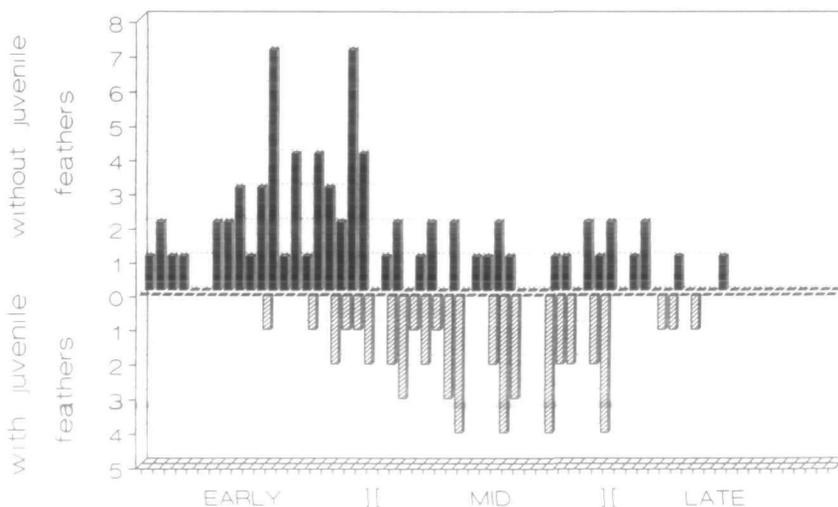
**Figure 3**  
Number of rejecters (solid bars) and accepters (hatched bars) of cuckoo eggs among females with and without juvenile tail feathers.



breeding season: early season (17 May–6 June), with a high proportion of rejecters (87%,  $N = 24$ ); mid-season (7–27 June), with a low rejecter proportion (30%,  $N = 33$ ); and late season (28 June–17 July), where rejecters appear to be abundant again (100%,  $N = 8$ ). This pattern was clearly indicated also for each breeding season separately. During the 1989 breeding season, the proportion of rejecters was 13/14 for early breeders, 8/18 for mid-season breeders, and 6/6 for late breeders. Similarly, during the 1990 breeding season, the proportion of rejecters changed from 8/10 among early breeders to 2/15 among mid-season breeders and was 2/2 among late breeders. The different distribution of rejecters and accepters is hard to explain by a model of evolutionary lag.

Because yearling passerines are known to breed later in the season than older birds (Klomp, 1970; Lack, 1966), we postulated that the seasonal changes in rejection rate were due to differences in age and experience. It has been previously suggested that egg recognition is attained by learning (Victoria, 1972). There are indications that some hosts of the cowbird, *Molothrus ater*, learn to recognize their own eggs by an imprinting-like

**Figure 4**  
Distribution of breeding females with juvenile tail feathers ( $N = 50$ ) and without them ( $N = 74$ ) through the breeding season (see legend to Figure 2). The two distributions differ significantly ( $D = 0.542$ ,  $p < .001$ , Kolmogorov-Smirnov two-sample test).



process during their first breeding attempt (Rothstein, 1974, 1978). Davies and Brooke (1988) considered the possibility that the acceptance of nonmimetic eggs by a cuckoo host (the reed warbler, *Acrocephalus scirpaceus*) occurs mainly among naive breeders. Although they pointed out that the presence of an experienced female is likely to lead to rejection (three out of three cases), they did not strongly support this hypothesis because when they added their data on the age of the males there was no clear relation between age and rejection.

Our examination of females, whose response to the cuckoo egg was known, indicated that 13 (68.5%) out of 19 females with juvenile feathers accepted the cuckoo egg, whereas among females without juvenile feathers only 9 (30.0%) out of 30 accepted the cuckoo egg (Figure 3;  $\chi^2 = 5.47$ ,  $df = 1$ ,  $p < .025$ ). The argument that naive breeders are more likely to accept cuckoo eggs is also supported by the similarity between the distributions of accepters (Figure 2) versus that of females with juvenile feathers (Figure 4;  $D = 0.134$ ,  $p > .3$ , Kolmogorov-Smirnov two-sample test) and by the similarity between the distributions of rejecters (Figure 2) versus that of females without juvenile feathers (Figure 4;  $D = 0.178$ ,  $p > .3$ , Kolmogorov-Smirnov two-sample test). If acceptance is mainly found in naive breeders, its rarity among late-season breeders (Figure 2) is a logical consequence because the latest nests of the season are likely to be renests or second broods.

The relation between host age and rejection suggests a possibility of an evolutionary equilibrium in which the cuckoo can successfully parasitize a population of rejecters by exploiting naive breeders: A cuckoo egg that mimics the host egg may fall within or near the range of egg variation of the host species. But because the variation among eggs of a particular female is usually lower than the variation range in the whole population (Thomas et al., 1989), some of the cuckoo eggs might differ from those of a particular female. Consequently, by learning to recognize its own eggs during the first breeding, a female might be able to reject at least some of the cuckoo eggs. Because of intraclutch variation, learning to recognize only the first egg in the clutch may yield mistaken rejections of slightly divergent eggs. The risk of such errors justifies learning to recognize the whole range of variation within a clutch. However, if a naive breeder is parasitized, this prolonged learning process increases the probability of the cuckoo's egg being accepted and, possibly, even increases the probability of accepting such cuckoo eggs for the host's entire lifetime.

The adaptiveness of such a prolonged learn-

ing strategy should be influenced by the parasitism rate. When the parasitism rate is high (20%–70%), the risk of a mistaken rejection may be smaller as compared to the risk of parasitism. But when parasitism rate is low (0.1%–20%), as in most cuckoos' hosts (Brooke and Davies, 1987; Moksnes and Røskaft, 1987), the relative risk from mistaken rejections (in nonparasitized nests) may exceed the risk of accepting a cuckoo egg laid during the host's learning period. In the latter situation, prolonged learning is more likely to be favored by selection.

Many hosts of the parasitic cowbird attain rejection rates of 80%–100%, which are considerably higher than those of many cuckoo hosts (Rothstein, 1990). There are indications that some cowbird hosts learn to recognize their eggs right from the first egg of laying, and therefore even a yearling can reject parasitic eggs (Rothstein, 1974, 1978). This may be possible because, in contrast to cuckoo eggs, cowbird eggs usually differ greatly from the eggs of their hosts (Rothstein, 1975b), and parasitism rates among cowbird hosts are usually higher (Davies and Brooke, 1989b; Rothstein, 1975a). Discrimination is therefore easy, and the risk of error is relatively low. Under these conditions, even one host egg can enable an individual to learn to distinguish reliably between egg types.

The idea that host rejection behavior should be adjusted according to the risk of making mistakes is also supported by a previous finding about the phenotypic plasticity of host response. Davies and Brooke (1988) and Moksnes and Røskaft (1989) have found that in some cuckoo hosts, rejection rate of cuckoo eggs and of mimetic models is usually less than 20%. But when the host has a better indication of being parasitized (if the host sees a cuckoo near its nest), the rejection rate increases to about 50%.

Our proposed view of an equilibrium in cuckoo–host coevolution does not imply that an evolutionary lag cannot exist. Where a cuckoo–host interaction is relatively recent (cf. Nakamura, 1990; Soler and Møller, 1990), an evolutionary lag in host response is likely to occur. But, with time, the coevolving egg discrimination ability in the host and egg mimicry in the cuckoo will reach a state of equilibrium. It might be possible that some cuckoo–host interactions will terminate before an equilibrium is achieved. However, cuckoo–host systems that reach equilibrium would last longer and provide the stable niche for the cuckoo population.

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