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Constraints on egg discrimination and cuckoo–host co-evolution

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Abstract. To understand the co-existence of rejection and acceptance of cuckoo eggs within a host population, the mechanism of egg discrimination and the cost–benefit balance of rejection behaviour were investigated. At a study site in central Japan, rejection rate of cuckoo, *Cuculus canorus*, eggs by great reed warblers, *Acrocephalus arundinaceus*, was 61·5%. An analysis of host response to natural and experimental parasitism with real cuckoo eggs, cuckoo egg models and painted host eggs indicated that: (1) hosts are more likely to reject eggs that look different from their own; (2) almost all individuals (94%) can reject highly non-mimetic eggs, suggesting that there are few, if any, true accepter genotypes in the host population; (3) hosts usually reject by egg ejection; (4) during the host-laying period, the day of parasitism does not affect host response; (5) egg types that were rejected at lower rates also took longer to be rejected; (6) acceptance was more likely to occur among mid-season breeders which consist of a higher proportion of younger females in the host population. Two experiments indicated that previous exposure of a host to its own eggs affects its rejection behaviour, suggesting that a learning mechanism (an imprinting-like process) is involved. Parasitized nests from which the cuckoo egg was experimentally removed, or ejected by hosts, fledged more host young than nests in which the cuckoo egg was accepted. Hosts that deserted parasitized nests were likely to re-nest, and the success of re-nests was high. Costs due to breakage of host eggs occurred in only 3·5% of successful cuckoo egg ejections. A cost–benefit model of egg rejection suggests that under some circumstances, the cost of recognition errors may exceed that of parasitism. Egg variability within a clutch was higher among younger females. Some hosts rejected painted eggs and conspecific eggs based on differences that may occur naturally within variable clutches of other individuals. It is suggested that host egg variability is a major constraint on the learning mechanism of egg recognition. Accordingly, the cost of mistakenly rejecting an odd egg from the nest selects for greater tolerance towards divergent eggs in young breeders, and justifies a prolonged learning mechanism in which a host can learn to recognize the variation range of its own eggs. The co-existence of rejection and acceptance within the host population can therefore be explained as a compromise between the cost of parasitism and the cost of recognition errors, rather than as an evolutionary lag. This explanation is particularly pertinent where the cuckoo has evolved mimetic eggs and where the parasitism rate is low.

Avian brood parasites reduce the reproductive success of their hosts and thus select for the development of host defence mechanisms (Rothstein 1975a, b, 1990; Payne 1977). Host defences, like egg discrimination and aggressive behaviour towards the parasite, select for counter-adaptations in the parasite, such as egg mimicry and rapid laying behaviour (Davies & de L. Brooke 1988, 1989a; Rothstein 1990). Numerous experimental studies have recently shown the existence of co-evolved adaptations in parasitic birds and their hosts, and have demonstrated the usefulness of brood parasitism as a model system for the study of co-evolution (reviewed by Rothstein 1990). However, it is not yet clear whether parasitic birds and their hosts are continuously co-evolving in an ‘arms race’, or whether they have reached an evolutionary equilibrium. According to the ‘arms race’ hypothesis, the acceptance of parasitic eggs or nestlings is a maladaptive result of an evolutionary lag in the development of counter-adaptations by the host (Rothstein 1975a, 1982a; Dawkins & Krebs 1979; Davies & de L. Brooke 1988, 1989b; Moksnes et al. 1990). The equilibrium hypothesis, on the other hand, predicts that acceptance is a result of

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an adaptive balance between rejection costs and benefits (Zahavi 1979; Rohwer & Spaw 1988; Brooker & Brooker 1990; Petit 1991; Lotem et al. 1992; Lotem & Nakamura, in press).

The common cuckoo, *Cuculus canorus*, parasitizes a variety of passerine hosts from western Europe through eastern Asia (Cramp 1985). Because hosts that accept an egg laid by the common cuckoo are unlikely to fledge their own offspring, rejection should be adaptive (Wyllie 1981; Davies & de L. Brooke 1988). However, most cuckoo host species demonstrate only intermediate rates of rejection, and a considerable number of cuckoo eggs are still accepted (Davies & de L. Brooke 1988, 1989a; Moksnes et al. 1990, 1991). The co-existence of rejection and acceptance of cuckoo eggs within a host population has been commonly explained by the arms race model (Dawkins & Krebs 1979; Kelly 1987; Davies & de L. Brooke 1989b; Moksnes et al. 1990). Accordingly, the intermediate rejection rate may represent a dimorphic population in which rejection has not yet reached fixation (Kelly 1987; Davies & de L. Brooke 1989b), or a monomorphic population in which rejection is not sufficiently developed (Davies & de L. Brooke 1989b). The alternative hypothesis of evolutionary equilibrium was previously considered but rejected in the absence of supporting evidence (Davies & de L. Brooke 1988, 1989b; Rothstein 1990; but see Moksnes et al. 1993).

It has been suggested that some birds learn to recognize their eggs by an imprinting-like process during their first breeding attempt (Victoria 1972; Rothstein 1974, 1978). Accordingly, during their learning period, hosts should tolerate a range of egg types, and learn to recognize as their own the egg types they see in their nests. Based on this experience, hosts should then narrow their range of tolerance and reject any unfamiliar egg type. The learning hypothesis predicts, therefore, that acceptance of cuckoo eggs will be more common among naive breeders (Davies & de L. Brooke 1988).

In a recent paper (Lotem et al. 1992), we showed that the acceptance of cuckoo eggs by female great reed warblers, *Acrocephalus arundinaceus*, occurs mainly among the younger breeders in the host population. Based on these results we suggested an evolutionary equilibrium model to explain host response to cuckoo eggs. Our model suggests 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. The model is based on the idea that intra-clutch variation in hosts may cause inexperienced hosts to make recognition errors if they attempt egg rejection. Accordingly, the risk of such errors justifies a prolonged learning mechanism in which a host learns to recognize the range of variation of its own eggs. Our equilibrium model makes the following three predictions: (1) the mechanism of egg recognition should involve learning; (2) the cost of recognition errors can outweigh the benefit of rejection behaviour; and (3) host intra-clutch variation should be high enough to yield recognition errors.

To test these three predictions we conducted a study in a population of great reed warblers parasitized by the common cuckoo. The first part of the paper deals with the mechanisms of rejection behaviour. We analyse host response to natural and experimental parasitism with real cuckoo eggs, cuckoo egg models and painted host eggs, and describe experiments testing the role of learning in host egg discrimination (prediction 1). In the second part of the paper we report on the costs and benefits of rejection behaviour based on the outcomes of host rejection behaviour, experimental removal of cuckoo eggs from parasitized nests, and artificially induced nest desertions. These data are essential for testing the idea that the cost of recognition errors can outweigh the benefit of rejection behaviour (prediction 2). In the third part of the paper we analyse host egg variability and consider whether it can cause inexperienced breeders to make recognition errors (prediction 3). The paper is concluded with a general discussion of the evolutionary equilibrium model and its possible implications for cuckoo–host co-evolution.

GENERAL METHODS

Study Site and Natural History

We worked at Nagano prefecture, central Japan, during May–July 1989–1991. The study site was east of Nagano city, on the Chikuma river banks, and was composed of reed beds and willow bushes. The reed beds provide habitat and nesting sites for a dense population of great reed warblers which are occasionally parasitized by common cuckoos (10–20%; Nakamura 1990). Cuckoo females lay a single egg in a host nest. The egg hatches after 12 days of incubation. Usually, the cuckoo also removes one of the host eggs from a parasitized nest (Wyllie 1981). Soon after hatching, the cuckoo nestling ejects all host eggs or nestlings from the nest and it leaves the host nest after about 15–20 days (Wyllie 1981; de L. Brooke & Davies 1989). The biology of the great reed warbler has been studied in this area (Haneda & Teranishi 1968a, b) and in other areas in Japan (Ezaki 1981, 1987, 1988; Urano 1985, 1990, 1992). Nest building and incubation are carried out by the female. Males can be polygynous with one to three females in their territory. Males defend the territory, help to feed nestlings and may help the female in the last stages of nest building. Females lay three to six eggs in a clutch (96% of clutches incubated in our study (N=502) were of five eggs (N=358) or four eggs (N=123)). Incubation takes 13 days and nestlings fledge when they are 10–13 days old. Cuckoos were not observed in the study area 30 years ago (Haneda & Teranishi 1968b; Nakamura 1990). It is very unlikely, however, that the great reed warblers in our study were able to evolve their high rejection rate of cuckoo eggs (61·5%) within the 30 years of the recent interaction. In several other areas in Japan great reed warblers have lived in sympatry with the common cuckoo for a long period of time (Nakamura 1990), and in Europe it is one of the major hosts of the common cuckoo (Molnar 1944; de L. Brooke & Davies 1988). It is more likely, therefore, that some level of rejection already existed in the population due to genetic flow from other areas or a retention of rejection behaviour from a past interaction with cuckoos. Nakamura (1990) and Nakamura et al. (in press) suggested that the cuckoos that have recently colonized the study area shifted from a former host, the Siberian meadow bunting, *Emberiza cioides*, and currently parasitize several host species in central Japan. Cuckoo egg pigmentation and egg markings are variable (see Fig. 1) and appear to be in transition between mimicking the former host egg (dark lines on a white background) and the great reed warbler egg (dark dots and spots on a pale background).

Monitoring Host Nests

Host nests were found by searching through the reeds, using a stick to part the vegetation. Most of the nests (510 of 572) were found during nest building or egg laying and very few nests were over water. We checked nests at least every alternate day during egg laying, and on the day of clutch completion. Naturally or experimentally parasitized nests were checked daily during the first 6 days after parasitism or until rejection took place. Accepter nests were checked another three to five times during incubation to detect possible late rejections.

Measuring the Benefits of Cuckoo Egg Rejection

To measure the benefits of cuckoo egg ejection, we monitored host breeding success during the 1989 breeding season and compared the following groups: (1) parasitized nests in which the cuckoo egg was accepted; (2) parasitized nests from which the cuckoo egg was ejected by the host (including two cases of egg burial); (3) parasitized nests from which we experimentally removed the cuckoo egg; (4) unparasitized nests from which we experimentally removed a single host egg (a test for an egg removal effect); and (5) unparasitized nests that were not involved in any experimental procedure (a control group).

To measure the benefits of rejection through nest desertion we monitored the probability of re-nesting and re-nesting success. Re-nests of individually marked females (N=51) were built at a distance of 2–15 m from the first nest, and the first egg in the re-nest was laid 4–7 days after incubation in the first nest was interrupted. We identified 27 additional nests as known re-nests on the basis of their location, time of egg laying (see above), and similarity in egg pigmentation (see results of the analysis of host egg variability).

Measuring Host Egg Variability

During the 1991 breeding season, we photographed 202 hosts clutches; of which 44 were known to be re-nests. We photographed each clutch in the field, near the nest, on the day of clutch completion. The eggs were laid out on a Kodak grey card, and were photographed using a 100 ASA film and an electronic flash.

Analysis of the photographs focused on the eggs' general shade, determined by ground colour and overall brown pigmentation. We chose to analyse this characteristic of eggs because we found that great reed warblers use it as a discrimination criterion (host eggs painted half transparent light brown, without obscuring egg markings, were ejected at a high rate), and because host eggs may be variable with respect to their general shade (see Results).

For the analysis, we asked four observers that were inexperienced with great reed warbler eggs to classify the clutches according to 'shade variability' (the difference between the darkest egg in the clutch and the brightest one). Four other observers were asked to classify the clutches according to 'shade' (based on the darkest egg in the clutch). Each observer was given the photographs in random order and was not informed about the purpose of the analysis. To help classify the photographs more consistently, we first asked each observer to create a 5-point scale by ranking five pre-chosen representative photographs (that represent different degrees of shade or shade variability). There was significant agreement in the ranking of the representative photographs by the different observers (Kendall's coefficient of concordance: $W=0{\cdot}96$, $\chi^2=15{\cdot}4$, $df=4$, $P<0{\cdot}005$, for both shade and shade variability ranking). We then asked the observers to match each of the 202 photographs to a particular rank on the scale. There was also significant agreement among observers in the ranking of all the photographs with respect to shade and shade variability (Kendall's coefficient of concordance: $W=0{\cdot}73$, $\chi^2=590{\cdot}1$, $df=201$, $P<0{\cdot}001$; $W=0{\cdot}59$, $\chi^2=475{\cdot}2$, $df=201$, $P<0{\cdot}001$, respectively). For each clutch, we used the average rank for shade and shade variability in our analyses.

Estimating Host Age

We captured breeding females in mist nets near their nests, colour-ringed them, and aged them according to the presence or absence of juvenile tail feathers (Nisbet & Medway 1972; Lotem et al. 1992). This method involved some level of error because not all yearlings retain juvenile tail feathers (H. Nakamura, unpublished data) and because some adult females retain old tail feathers that make them look like yearlings (3 out of 16 individually marked females recaptured in our study). In a previous paper (Lotem et al. 1992), we showed that there is a significant difference between the distribution of breeding dates of females with juvenile tail feathers and without them, suggesting that mid-season breeding females (7–27 June) are younger on average than early-season breeding females (17 May–6 June). Additional data from 1991 also showed that juvenile tail feathers were more common among mid-season breeders than among early-season breeders (23 of 38 versus 2 of 29; $G_{adj}=22{\cdot}42$, $df=1$, $P<0{\cdot}0005$), and this trend was highly significant when data of all three breeding seasons were pooled together (62 of 96 versus 10 of 87; $G_{adj}=57{\cdot}94$, $df=1$, $P<0{\cdot}0005$). Using time of breeding as an index of female age was also supported by recaptures of individually marked females during 1990 and 1991: the proportion of individually marked females that were known to have bred in a previous year was higher among early breeders (14 of 75) than among mid-season breeding females (2 of 67; $G_{adj}=9{\cdot}498$, $df=1$, $P<0{\cdot}005$). Because recaptures were relatively few, we could not determine which of the two criteria, plumage or time of breeding, is a more reliable indicator of host age. It should be noted, however, that errors in estimating host age could only reduce the significance of age-related differences but not vice versa. In all our analyses, the two different age criteria give qualitatively similar results. However, there are greater potential biases when using plumage because capture rates of rejecter and accepter females differed in some experiments. We use time of breeding as an index to female age in all our analyses because it could be determined without bias for all females in the study.

Experimental Parasitism

Following the method developed by Rothstein (1975a), and used extensively by others (Alvarez et al. 1976; Davies & de L. Brooke 1988, 1989a; Higuchi 1989; Moksnes et al. 1990, 1991), we experimentally tested host response to real cuckoo eggs, cuckoo egg models and painted host eggs. Nests were chosen randomly for the different experimental groups and no nest was tested more than once. When the same breeders were tested again during their second brood in a season, the results were analysed separately. Model cuckoo eggs were made of synthetic clay, poured into a plaster mold and smoothed with sandpaper. The models' dimensions ($23{\cdot}8$–$24{\cdot}5 \times 17{\cdot}3$–$17{\cdot}9$ mm) and mass ($3{\cdot}5$–$4{\cdot}1$ g) were within the range of size and mass of real cuckoo eggs measured in the study area, but slightly larger than the average

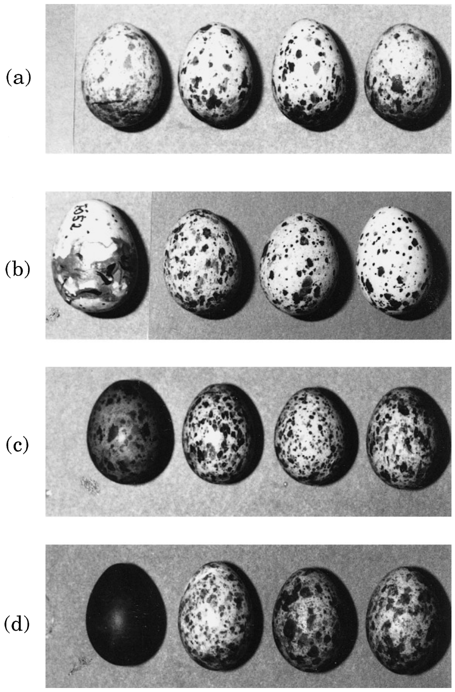

Figure 1. Real cuckoo egg (a, far left), cuckoo egg model (b, far left), host egg painted light brown (c, far left), and a host egg painted dark brown (d, far left), compared with great reed warbler eggs (the three eggs on the right of each row).

(length: 21·5–24·65 mm, $\bar{X}=22{\cdot}9\pm0{\cdot}83$, $N=34$; width: 16·3–18·4 mm, $\bar{X}=17{\cdot}46\pm0{\cdot}38$, $N=34$; mass: 3·4–4·4 g, $\bar{X}=3{\cdot}84\pm0{\cdot}25$, $N=18$). The models were painted to match the colour and pattern of a typical cuckoo egg in the study area. It should be noted, however, that it was our impression that real cuckoo eggs were usually better mimics of host eggs than our models (see also Fig. 1). To test host response to cuckoo eggs we replaced a host egg with a model or with a real cuckoo egg in the afternoon during the host-laying period. The experiments with model cuckoo eggs and most experimental parasitism with real cuckoo eggs (12 of 14 cases) were conducted in 1989.

Experimental Test of the Learning Hypothesis

To test the role of learning in host egg recognition we conducted two experiments using painted great reed warbler eggs. These eggs were collected in the field and were painted dark brown or light brown with raw umber Liquitex acrylic paint. The light brown painting (diluted paint) was half transparent, creating eggs with light brown ground colour (see Fig. 1), similar to, or somewhat darker than, the darkest great reed warbler eggs shown in Fig. 5. The experiments with painted host eggs were conducted in 1990 and 1991.

In the first experiment (the ‘egg replacement experiment’) we used host eggs painted dark brown. The experimental procedure was as follows: in one group of nests, we let hosts lay their eggs normally, but replaced one of the host eggs with a brown one on the fifth morning of egg laying, which is usually the morning of clutch completion. In a second group of nests, we minimized the amount of exposure a host had towards its own eggs by replacing each egg soon after it was laid (0530–0730 hours) with a brown egg. We replaced the eggs each morning until a clutch of four brown eggs was formed (additional eggs, if any were laid, were removed). In both groups, if hosts were willing to incubate brown eggs for 3 days after clutch completion, we returned one of their original eggs to their nests. Our aim in doing so was to provide the birds of the second group with a reference for comparison, and to test whether they reject their own egg after accepting a full clutch of brown eggs. A final response to the replacement experiment was scored as acceptance only if the host continued to incubate brown eggs for 4 additional days after the original egg was returned. We conducted the experiment on both early-season breeders (which are more likely to be experienced breeders) and mid-season breeders (which are more likely to be naive ones).

The second experiment (the ‘re-nesting’ experiment) was designed to test whether the exposure of a host to its eggs during the first nesting of the season affected its rejection behaviour in a later nesting attempt. The eggs used in this experiment were host eggs painted light brown (see above). To test host response to the experimental eggs, we replaced a single host egg with a painted one on the fifth morning of egg laying. We scored painted eggs as accepted if they remained in the active nest for at least 6 days. There were two experimental groups. The birds of the first group were tested with an experimental egg during their first nesting attempt. The birds of the second group (the controls) were not tested at that stage, but were allowed to incubate four of their own eggs and thus to experience them during the first nesting attempt. To create a second nesting attempt, we removed the eggs from the first nests (artificial predation) so the females had to re-nest. We found re-nests for most of the artificially predated nests (51 of 62). In all of the re-nests, we tested host response to the experimental egg. Most of the re-nesting females (41 of 51) were captured and colour-ringed before we removed their eggs, so the re-nest identification was certain. The other 10 re-nests were within a few metres of the first nest, started laying 4–7 days after the artificial predation, and resembled first clutches in their egg pigmentation. The re-nesting experiment was also conducted on both early- and mid-season breeders. Eggs were removed from early breeders' nests after 10 days of incubation to create re-nesting at mid-season. This timing also allowed us to test whether the time of breeding per se effects rejection. We removed eggs from mid-season breeders' nests after only 6 days of incubation to increase the probability that females would re-nest (females may be less likely to re-nest if it is too late in the season).

Analysis of Data on Host Response

For the basic analysis of host rejection behaviour, we used data from natural parasitism ($N=64$), experimental parasitism with real cuckoo eggs ($N=14$) and experimental parasitism with model cuckoo eggs ($N=35$). We also included in this analysis some results of the 'egg replacement' experiment and the 're-nesting' experiment (see above) in which we replaced a single host egg with a dark brown egg ($N=33$) or a light brown egg ($N=70$) on the fifth morning of egg laying (usually the morning of clutch completion). These data included only experiments conducted on females during their first brood of the season.

Based on previous studies (Rothstein 1975a; Davies & de L. Brooke 1988, 1989a), we scored host response as rejection if: (1) the cuckoo egg or the experimental egg disappeared from the nest but other eggs were still incubated (rejection by egg ejection); (2) the cuckoo or the experimental egg was buried under nest material (egg burial); (3) the nest was deserted after parasitism (desertion). Cases of nest desertion are likely to represent rejection because hosts rarely desert unparasitized nests during incubation (2 of 67; Lotem 1992). The day of rejection was recorded as the day on which we noted the rejection, although rejection may have taken place on the previous day. We scored cuckoo eggs or egg models as accepted if they remained in the nest until hatching time. When nest predation occurred before hatching ($N=7$), cuckoo eggs or egg models were scored as accepted only if they remained in the active nest for at least 6 days. Ninety per cent ($N=48$) of cuckoo egg rejections and 96% ($N=26$) of rejections of model cuckoo eggs occurred within this period. We scored painted eggs as accepted if they remained in the nest for at least 6 days. In all experiments, we excluded from the analysis all nests that were predated before the sixth day after parasitism. We found no differences between the response to natural cuckoo parasitism and experimental (human) parasitism with real cuckoo eggs (Lotem et al. 1992). We therefore combined the two groups to test for the responses to real cuckoo eggs. For statistical G-tests with one degree of freedom, we used 'G_{adj}' with William's correction. We used Fisher's exact tests with one degree of freedom when the expected frequency in one of the cells was smaller than 5.

RESULTS AND DISCUSSION

The Mechanism of Rejection Behaviour

Rejection rates

Great reed warblers in the study area exhibited high rejection rates of cuckoo eggs, model cuckoo eggs and painted eggs (Table I). The high rejection rate of painted eggs supports the view that hosts reject any different egg type, not only that of the parasite (Rothstein 1982a, b). We found significant differences among rejection rates of the different egg types (Table I; $G=15{\cdot}55$, $df=3$, $P<0{\cdot}005$). Hosts were more likely to reject egg types that looked different from their own (compare Fig. 1 and Table I). This tendency has been indicated by several previous studies (Rothstein 1982b; de L. Brooke & Davies 1988; Davies & de L. Brooke 1988; Higuchi 1989) and was suggested to be the factor selecting for mimicry in eggs of the parasite (Baker 1942; Payne 1977; de L. Brooke & Davies 1988).

The rejection rate of dark brown eggs (94%) appears unusually high for a common cuckoo host. In previous studies (Davies & de L. Brooke 1989a; Moksnes et al. 1990), common cuckoo

Table I. Responses of great reed warblers to real cuckoo eggs, cuckoo egg models and painted host eggs

	Number of nests					
		Rejected				
Egg type	Accepted	By ejection	By desertion*	By egg burial	Rejected/total	% Rejected
Cuckoo	30	37	9	2	48/78	61·5
Cuckoo model	9	20	6	—	26/35	74·2
Painted light brown	15	55	—	—	55/70	78·5
Painted dark brown	2	31	—	—	31/33	94

*Including ejection attempts in which egg breakage led to nest desertion ($N=7$).

hosts rejected non-mimetic eggs at lower rates. Such lower rejection rates could be explained, therefore, as representing a dimorphic host population in which rejection has not yet reached fixation (see Kelly 1987; Davies & de L. Brooke 1989b). Our results, on the other hand, show that almost all individuals (94%) can reject when tested with highly non-mimetic eggs. Hence, there are few, if any, pure accepter genotypes in the host population; instead, each individual host apparently has a certain discrimination threshold. Eggs with a higher degree of mimicry were accepted more frequently, simply because they fell below the discrimination threshold of many more individual hosts. We suggest that the lower rejection rates found in previous studies might be explained in a similar manner. The dark brown eggs used in our experiments (Fig. 1) appeared less mimetic than most of the 'non-mimetic' cuckoo egg models used by Davies & de L. Brooke (1989a, their Figure 1) and by Moksnes et al. (1990). It is therefore plausible that host species that were tested in these studies might show higher rejection rates, should they be tested again with highly non-mimetic eggs.

Methods of rejection

Hosts used three different rejection methods: egg ejection, nest desertion and egg burial with nest material (Table I). Hosts rejected painted eggs solely by egg ejection (86 of 86), that is, significantly more often than they ejected real cuckoo eggs and cuckoo egg models (57 of 74; $G_{adj}=27{\cdot}76$, $df=1$, $P<0{\cdot}0005$). Observations and video-recording (H. Nakamura, unpublished data) demonstrate that great reed warblers eject cuckoo eggs by puncturing the egg, drinking some of its content and removing it, while holding in the punctured area of the egg shell (see also cover illustration of Lotem et al. 1992). Hosts could not puncture the egg models that were made of clay, but several models were pecked by the host before they were ejected (as was indicated by pecking holes on the model surface). It seems that hosts were able to grasp the egg models and to eject them from the nest, probably by using pecking holes to improve their handling. Breakage of host or cuckoo eggs occurred in five (12%) attempts by hosts to eject cuckoo eggs, and in two (9%) attempts by hosts to eject cuckoo egg models. All these cases led to nest desertion. In two additional cases, a single host egg disappeared along with the cuckoo egg or the egg model, and was presumably cracked and removed by the host (see Davies & de L. Brooke 1988). There was no evidence of egg breakage in all 86 ejections of painted eggs. Painted host eggs were probably easier to eject because they were smaller in width than the cuckoo eggs (Lotem 1992) or, perhaps, easier to puncture.

Egg ejection might be difficult for hosts with small bills, causing them to reject parasitic eggs by nest desertion or by egg burial (Rothstein 1976; Clark & Robertson 1981; Rohwer & Spaw 1988; Davies & de L. Brooke 1989a; Moksnes et al. 1991). While in some cases nest desertion is an inevitable result of egg breakage during egg ejection (Rothstein 1976), in other cases it is initially chosen as an alternative rejection method (e.g. Davies & de L. Brooke 1988; Moksnes et al. 1991). Our results provide evidence that individual hosts alter their rejection method according to circumstances: when parasitized with cuckoo eggs or with cuckoo egg models, some individuals (10 of 74) chose an alternative rejection method even before egg breakage occurred. On the other hand, when parasitized with painted host eggs, which were easier to eject (see above) and easier to recognize (i.e. rejected at a higher rate), all individuals ($N=86$) rejected them by egg ejection (86 of 86 versus 64 of 74; $G_{\mathrm{adj}}=15{\cdot}42$, $df=1$, $P<0{\cdot}001$).

Table II. Stage of cuckoo parasitism

Days of host egg laying	Number of nests parasitized*	Cumulative number of nests parasitized†
2 days before	2	2
1 day before	6	8
1st day	13	23
2nd day	16	52
3rd day	7	67
4th day	3	75
5th day	4	84
After clutch completion	2	86
Total	53	86

*Cases for which the exact day of parasitism was unknown were excluded.

†Cases for which the exact day of parasitism was unknown but for which parasitism was known to have occurred before a certain day, were included.

Stage of parasitism and host response

Cuckoos in the study area laid their eggs mostly during the host laying stage (89%) and especially during the first 3 days of egg laying (Table II). Most cuckoo eggs that were laid before the host started laying were rejected (7 of 8; Table III). Previous studies also suggest that birds are likely to reject eggs introduced to their nests before commencement of egg laying (Vehrencamp 1977; Mumme et al. 1983; Emlen & Wrege 1986; Davies & de L. Brooke 1988). However, the rejection rate in our study was also high in response to cuckoo eggs and cuckoo egg models put in the nest during egg laying (54 of 81). Overall, there was no significant difference between the distribution of rejections and acceptances in relation to the stage of parasitism (Table III; Kolmogorov–Smirnov two-sample test: $D=0{\cdot}1142$). There were also no such differences observed when the data of mid-season breeders were analysed separately. The results suggest that at least during the host laying period, the day of parasitism does not affect host response. There are no indications therefore that great reed warblers improve discrimination ability immediately after seeing their first egg, as suggested for some cowbird hosts (Rothstein 1974).

Time to rejection

In many cases rejection did not occur immediately after parasitism, but only a day or several days later (Table IV). This delay in rejection is known from several studies on cowbird and cuckoo hosts (Rothstein 1975a; Alvarez et al. 1976; Davies & de L. Brooke 1989a). Our data suggest that the greater the difference between the introduced egg and the host eggs, the shorter the delay in rejection. Dark brown eggs, which were markedly different from the host eggs (see Fig. 1), were rejected sooner than light brown eggs, which were relatively more mimetic (Table IV; Mann–Whitney U-test: two-tailed $P<0{\cdot}05$). Cuckoo egg models, which were not as good mimics as real cuckoo eggs (see General Methods), were rejected sooner than real cuckoo eggs (Table IV; Mann–Whitney U-test: two-tailed $P<0{\cdot}05$). In general, egg types that were rejected at lower rates also took longer to be rejected (see Table IV). These results suggest that, like the rate of rejection, the time to rejection also may reflect discrimination ability.

Rejection, time of breeding and female age

In a previous paper (Lotem et al. 1992) we showed that cuckoo eggs were more likely to be accepted by mid-season breeders, which were younger on average than early-season breeders (see also General Methods). Our data (Lotem et al. 1992) were based on host response to real cuckoo eggs in 1989 and 1990. In Table V, we add the data of 1991, and that of host response to cuckoo egg models and to painted eggs. The results are consistent with our previous finding. In each data set, early breeders exhibited higher rejection rates than mid-season breeders (Wilcoxon matched-pairs signed-ranks test: $N_1=N_2=6$, $P<0{\cdot}05$). Rejection of cuckoo eggs appears to be common again at the end of the breeding season when most active nests are likely to be re-nests (after nest failure) or early breeders' second broods.

Females that accepted cuckoo eggs, cuckoo egg models, or painted host eggs, were more likely to

Table III. Responses of great reed warblers to real cuckoo eggs and cuckoo egg models in relation to the stage of parasitism

Stage of parasitism relative to host egg laying	Cuckoo eggs*		Cuckoo egg models		Total	
	Rejected	Accepted	Rejected	Accepted	Rejected	Accepted
2 days before	1	1	—	—	1	1
1 day before	6	—	—	—	6	—
1st day	8	5	13	4	21	9
2nd day	13	9	8	3	21	12
3rd day	1	2	4	2	5	4
4th day	3	1	1	—	4	1
5th day	3	1	—	—	3	1
After clutch completion	—	1	—	—	—	1
Total	35	20	26	9	61	29

*Including only cases for which both the day of parasitism and the host response were known.

Table IV. Time taken for great reed warblers to reject cuckoo eggs, model cuckoo eggs and painted host eggs

Time taken to rejection	Number of nests			
	Rejected cuckoo eggs	Rejected cuckoo egg models	Rejected host eggs	
			Painted light brown	Painted dark brown
1 day	6	6	26	22
2 days	7	8	10	6
3 days	11	4	10	1
4 days	8	3	5	1
5 days	8	4	3	1
6 days	4	—	1	—
More than 6 days	4	1	—	—
Total rejected	48	26	55	31
Average number of days to rejection	3·69 ± 1·78	2·81 ± 1·63	2·13 ± 1·35	1·48 ± 0·96
% Rejection	61·5	74·2	78·5	94

have juvenile tail feathers (25 of 46) than females that rejected those eggs (24 of 80; $G_{\text{adj}}=7{\cdot}14$, $df=1$, $P<0{\cdot}025$). In summary, our data show that low rejection rates were associated with mid-season breeding and with younger age. Based on the results of the experiments described below, we will attempt to assess whether rejection is affected by the time of breeding per se, or by host age or experience.

Experimental test of the learning hypothesis

In the first stage of the 'egg replacement' experiment, before we returned an original egg to accepter females (see General Methods), most early- and mid-season breeders of the first experimental group rejected dark brown eggs introduced to their nests at the end of egg laying (18 of 19 and 11 of 13, respectively). However, among females of the second experimental group (all eggs replaced with painted ones), four early-season breeders (21%) and eight mid-season breeders (47%) were willing to incubate the brown eggs for 3 days ($G_{\text{adj}}=2{\cdot}635$, $df=1$, NS). When we returned an original egg to those females, all of them accepted their original eggs. However, three out of the four early breeding females, ejected all four brown eggs within 36 h of the return of the

Table V. Rejection rate of cuckoo eggs, cuckoo egg models and painted host eggs by early- (17 May–6 June), mid- (7–27 June) and late- (28 June–17 July) season breeders

Egg type	Year	Rejected/total Early	 Mid	 Late
Cuckoo eggs	1989	13/14	8/18	6/6
	1990	8/10	2/15	2/2
	1991	6/8	2/4	1/1
Cuckoo egg models	1989	13/15	12/16	1/4
Host eggs painted light brown	1991	33/38	22/32	—
Host eggs painted dark brown	1990–1991	19/19	12/13	0/1
Sub-total cuckoo eggs		27/32	12/37	9/9
Sub-total egg models and painted eggs		65/72	46/71	1/5
Total		92/104	58/98	10/14

The breeding season was divided into three distinct parts based on the different distribution of rejectors and acceptors (see Lotem et al. 1992).

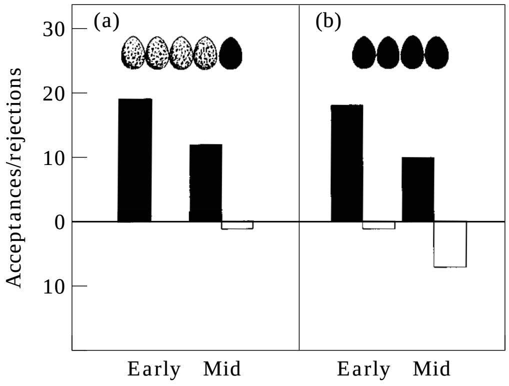

Figure 2. Number of rejections (■) and acceptances (□) of dark brown eggs by early- and mid-season breeders in response to: (a) replacement of a single host egg with a dark brown one on the fifth morning of egg laying and (b) replacement of all host eggs, soon after they were laid, with dark brown eggs.

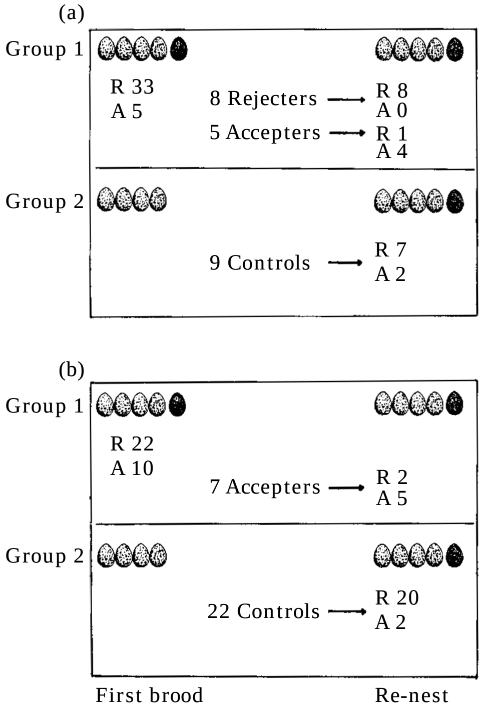

Figure 3. A scheme of the re-nesting experiment results, conducted on (a) early- and (b) mid-season breeding females. Clutches with a darker egg on the right are clutches for which hosts were tested with an experimental egg (host egg painted light brown). R: Rejected; A: accepted.

original egg. Interestingly, under the same circumstances, only one out of the eight mid-season breeding females ejected the brown eggs, and did so only after 72 h had elapsed since the return of the original egg. The final results of the ‘egg replacement’ experiment (after returning an original egg to accepter females) are described in Fig. 2. Both early- and mid-season breeders rejected dark brown eggs introduced to their nests at the end of egg laying (19 of 19 and 12 of 13, respectively). However, when we minimized the amount of exposure a host had towards its own eggs (by replacing all host eggs with painted ones), the rejection rate shown by mid-season breeders was significantly lower than that shown by early-season breeders (10 of 17 versus 18 of 19; Fisher’s exact-test: $P<0{\cdot}025$) and by

Table VI. Breeding success of early- (17 May–6 June), mid- (7–27 June) and late- (28 June–17 July) season breeders in parasitized nests, parasitized nests from which the cuckoo egg was removed and control nests (see text for further details)

		Time of breeding			
		Early	Mid	Late	Total
Group a	Success/total*	0/1	0/10	—	0/11
Parasitized: accepted cuckoo egg	No. fledged†	—	—	—	—
Group b	Success/total	3/4	1/2	3/3	7/9
Parasitized: ejected cuckoo egg	No. fledged	4·3 ± 0·6	3·0	2·3 ± 1·5	3·3 ± 1·4
Group c	Success/total	3/7	4/5	—	7/12
Parasitized: cuckoo egg removed	No. fledged	2·3 ± 1·2	3·0 ± 1·4	—	2·7 ± 1·3
Group d	Success/total	4/5	1/4	—	5/9
Unparasitized: host egg removed	No. fledged	3·0 ± 1·4	3·0	—	3·0 ± 1·2
Group e	Success/total	14/29	4/11	2/4	20/44
Unparasitized: control	No. fledged	3·7 ± 1·5	4·5 ± 0·6	4·0	3·9 ± 1·3

*Successful nests fledged at least one host nestling.
†Number of nestlings fledged in successful nests.

mid-season breeders in the first experimental group (10 of 17 versus 12 of 13; Fisher's exact test: $P<0{\cdot}05$). When rejecting a clutch of brown eggs, hosts almost always (26 of 28) ejected the brown eggs one by one, and deserted the nest only after it became empty (or remained with a single original host egg).

The results of the 're-nesting' experiment are shown in Fig. 3. All eight early breeding females that rejected painted eggs during their first nesting, rejected them again when tested during the re-nest (at mid-season). Also, among early breeding females, there was no difference in rejection rate between the two experimental groups (33 of 38 versus 7 of 9; Fisher's exact test: $P=0{\cdot}404$). These results support the hypothesis that the change in the time of breeding per se does not affect rejection. Another aspect suggested by this evidence is that early breeding females do not improve their rejection ability between the first and the second nesting of the season. In contrast to early breeding females, mid-season breeding females improved their rejection ability in the second nesting, after experiencing their own eggs during the first nesting (Fig. 3; 22 of 32 versus 20 of 22; Fisher's exact test: $P=0{\cdot}05$). However, not all the females of the second group rejected the experimental eggs when tested during their re-nest, despite the fact that they had the opportunity to experience their own eggs during the first nesting. Most females that accepted experimental eggs during the first breeding, also accepted them when tested during the re-nest (9 of 12), but three of these females rejected the experimental egg when tested again in the re-nest.

The two experiments described above provide evidence to support the learning hypothesis. The egg replacement experiment showed that mid-season breeders were more likely to accept dark brown eggs when we minimized exposure to their own eggs. The fact that such treatment did not affect early season breeders (which are older on average) suggests that acceptance was due to a lack of experience, rather than an artefact of replacing the entire clutch with brown eggs. The egg replacement experiment also provides another interesting piece of evidence in support of the learning hypothesis. The return of an original egg to females that were incubating brown eggs stimulated early breeders to reject the brown eggs, but had almost no effect on mid-season breeders. We suggest that early breeding females, which are likely to be experienced breeders, could associate the appearance of the original egg with the egg types they had experienced a year before, and used it as a reference for the correct egg type.

The finding that older females rejected a full clutch of brown eggs supports previous evidence showing that hosts know their own eggs, rather than reject any egg type that is in the minority (Rothstein 1975c). It is interesting to note that the birds did not anticipate that desertion would be inevitable, and failed to save time by deserting directly. Instead, they first ejected the eggs, as they

Table VII. Re-nesting success of early- (17 May–6 June) and mid- (7–27 June) season breeders

		Re-nests of early-season breeders	Re-nests of mid-season breeders	Total
Re-nest after nest desertion	Success/total*	2/5	1/2	3/7
	No. fledged†	4·00 ± 1·40	2·0	3·30 ± 1·50
Re-nest after nest predation	Success/total	7/10	3/8	10/18
	No. fledged	3·14 ± 1·34	3·30 ± 0·57	3·20 ± 1·13
Total	Success/total	9/15	4/10	13/25
	No. fledged	3·33 ± 1·32	3·00 ± 0·82	3·23 ± 1·17

*Successful nests fledged at least one host nestling.
†Number of nestlings fledged in successful nests.

usually reject cuckoo eggs, and deserted only when facing an empty nest, as they usually do after nest predation. Hosts were not able to react more efficiently, probably because they are never exposed to such a situation in nature. Replacement of an entire clutch with foreign eggs is not a natural phenomenon for great reed warblers.

The re-nesting experiment suggests that young females improve their rejection ability in the second nesting, after experiencing their own eggs during the first nesting. This result is consistent with the learning hypothesis, but could also be due to a maturational process occurring between the first and the second clutch. Nevertheless, a maturational process cannot explain the results of the egg-replacement experiment in which a significant difference was found between the mid-season breeders of the two experimental groups. In that case, all birds were at the same stage of maturation (the same age, and the first clutch of the season).

In its simplest form, the learning hypothesis predicts that young females that experience only brown eggs, should learn to recognize them as their own and should reject their own eggs in the future. Such behaviour, had it occurred, would have provided the strongest evidence for imprinting. However, in our experiment we failed to observe this result. Young females that incubated brown eggs also accepted their own eggs when those were returned to their nests. This 'negative result' provides no support for the learning hypothesis, but does not contradict it either. If egg recognition is indeed learned, this result can be explained in two ways. The first explanation stems from the experimental procedure; during our experiment, we tried to minimize host exposure towards its own eggs, but under field conditions we could not prevent a female from seeing its eggs immediately after laying and before we replaced the eggs. This exposure may have been sufficient for a female to imprint on her own eggs as well as on the brown eggs. The second possibility is that, like in other imprinting processes (Bateson 1979), females have some innate preference to learn egg types similar to their own, and that even in a late stage of their 'sensitive period' they are less likely to reject novel objects if they are sufficiently similar to the innate template.

In the re-nesting experiment, some females in the second experimental group (4 of 31) accepted painted eggs during the re-nest although they experienced their own eggs during the first clutch. We cannot exclude the possibility that these individuals lack rejection ability completely. However, because most females (94%) were able to reject dark brown eggs, it is quite possible that these individuals are simply less sensitive than others (i.e. have different discrimination thresholds). In another paper (Lotem & Nakamura, in press) we have suggested that when host response is determined phenotypically (according to experience and circumstances), we can expect to find genotypic variability in the adjustment of the phenotypic response.

Rejection Costs and Benefits

The benefit of cuckoo egg ejection

Parasitized nests in which the cuckoo egg was accepted did not fledge any host young

Table VIII. Parasitism rate (parasitized/total) of early- (17 May–6 June), mid- (7–27 June) and late- (28 June–17 July) season breeders in 1989, 1990 and 1991 breeding seasons

Year	Time of breeding			Total	Total %
	Early	Mid	Late		
1989	14/70	17/62	2/19	33/151	21·8
1990	9/62	10/45	3/10	22/117	18·8
1991	10/106	6/111	4/25	20/242	8·3
Total	33/238	33/218	9/54	75/510	
Total %	13·8	15·1	16·6		14·7

Data from nests found during nest building or egg laying.

(Table VI). It appears that this is the case in general (Wyllie 1981), excluding rare occasions in which cuckoo eggs fail to hatch (1 of 30 in our study; see also Moksnes et al. 1993). To test the possibility that the lower rejection rate of mid-season breeders (Lotem et al. 1992) is associated with a lower benefit of cuckoo egg ejection, the results were analysed separately for early-, mid- and late-season breeders. There was no evidence that the potential benefit of egg ejection was lower for mid-season breeders which would explain their acceptance behaviour. Parasitized nests of mid-season breeders from which we removed the cuckoo egg, succeeded in four of five cases and fledged 3·0 nestlings on average (see Table VI). There was also no evidence that cuckoos re-visit parasitized nests and prey upon the host eggs or nestlings when the cuckoo egg has been removed (as suggested by Zahavi 1979). The proportion of successful nests (those that fledge at least one host nestling) among parasitized nests from which the cuckoo egg had been removed (experimentally or by the host) was higher (but not significantly so) than the proportion among control tests (Table VI; 14 of 21 versus 20 of 44; $G_{\mathrm{adj}}=2{\cdot}534$, $df=1$, $P>0{\cdot}1$). The number of nestlings fledged from these parasitized nests after the cuckoo egg had been removed ($3 \pm 1{\cdot}3$, $N=14$), was slightly lower than the number fledged from the control nests ($3{\cdot}9 \pm 1{\cdot}3$, $N=20$), and similar to the number fledged from unparasitized nests from which we removed a single host egg ($3 \pm 1{\cdot}2$, $N=5$). The results therefore support the assumption of Kelly (1987) that the benefit of cuckoo egg ejection is equal to the value of an unparasitized nest, reduced by the loss of one host egg that was removed by the cuckoo.

The benefit of nest desertion

The benefit of deserting a parasitized nest is determined by the host's ability to re-nest and by its re-nesting success. During the 1989 breeding season, we found re-nests for eight of 14 females that had deserted in response to natural or artificial parasitism. From six additional nests of individually marked females, we removed the eggs to induce re-nesting. After an extensive search, all six re-nests were found. As part of the experiments during 1991, we removed the eggs from 63 nests, and found re-nests for 52 of them. There was no indication that mid-season breeders were less likely to re-nest, because we found re-nests for 30 of 32 mid-season breeders. These results suggest that in most cases (at least 80%, 66 of 83), great reed warblers re-nest if preyed upon. We believe that the frequency of re-nesting is actually greater than 80% because we probably failed to find all of the re-nests.

Re-nesting success was monitored during 1989. The proportion of successful nests among re-nests (Table VII; 13 of 25) was similar to that among control nests (Table VI; 20 of 44; $G_{\mathrm{adj}}=0{\cdot}267$, $df=1$, NS). However, the number of nestlings that fledged from successful re-nests was slightly lower than that from the control (unmanipulated) nests ($3{\cdot}2 \pm 1{\cdot}2$ versus $3{\cdot}9 \pm 1{\cdot}3$). This difference was mainly due to a reduced clutch size ($4{\cdot}3 \pm 0{\cdot}7$ versus $4{\cdot}8 \pm 0{\cdot}5$; Wilcoxon matched-pairs signed-ranks test (excluding cases in which clutch size of one of the broods was unknown): $N_1=N_2=21$, $P<0{\cdot}01$). The re-nesting success of mid-season breeders was similar to that of early-season breeders (Table VII). However, including data on clutch size of re-nests from 1991, reductions in clutch size were more common among re-nests of mid-season breeders than among those of early-season breeders (23 of 36 versus 13 of 37; $G_{adj} = 5{\cdot}998$, $df = 1$, $P < 0{\cdot}025$).

The results presented in Tables VI and VII suggest that the benefit of nest desertion is similar to the benefit of cuckoo egg ejection (the value of an unparasitized nest, reduced by the loss of one host egg). However, the actual benefit of nest desertion might be lower because the effort needed to re-nest may reduce future host reproductive success, and because nestlings that fledge later in the season may have lower survival rates than those that fledge earlier (Newton 1989). Time and energy costs of re-nesting may also explain why great reed warblers prefer to reject by egg ejection (see Table I).

Ejection costs

In most cases (7 of 9), egg breakage during ejection attempts led to nest desertion, the consequences of which were discussed above. Accordingly, the major cost of ejection is an increase in the frequency of rejections by nest desertion. Out of 57 ejections of cuckoo eggs or cuckoo models, only in two cases (3·5%) did a host egg disappear along with the cuckoo egg or model. Presumably, these eggs were cracked by the host while ejecting the cuckoo egg, and then removed, resulting in an ejection cost (Davies & de L. Brooke 1988).

Recognition costs

Parasitized hosts may mistakenly eject one of their own eggs instead of ejecting the cuckoo egg (Molnar 1944; Davies & de L. Brooke 1988). In such cases the nest is still parasitized and likely to produce no host young. Such an error was observed in our study only once (less than 1%), where a single host egg disappeared from a nest experimentally parasitized with a light brown egg. The frequency of these errors in our study was lower than in similar studies (Molnar 1944; Davies & de L. Brooke 1988), possibly because cuckoo egg mimicry in our study area is not fully developed (see General Methods), and thus the cuckoo egg seems to be the oddest egg in a parasitized clutch.

Unparasitized hosts may mistakenly suspect that one of their eggs is a cuckoo egg, and as a result may eject it from the nest or desert the nest (Davies & de L. Brooke 1988; Marchetti 1992). A mistaken desertion is costly because of the loss of time and energy and because re-nests tend to have smaller clutches (see above). The cost of mistaken ejection is the loss of an egg from the clutch. Our data (Table VI) confirm that this is indeed a cost because removal of one egg from the clutch reduces the number of fledglings. The number of nestlings fledged from nests from which a host egg was removed (experimentally or by the cuckoo; Table VI: groups b, c and d) was less than in control nests ($3{\cdot}0 \pm 1{\cdot}2$ versus $3{\cdot}9 \pm 1{\cdot}3$; Mann–Whitney *U*-test: two-tailed $P < 0{\cdot}05$).

Evidence for recognition errors in unparasitized nests was rare. During our study we found one nest in which a host egg was buried with nest materials, in the same way hosts reject some of the cuckoo eggs. The buried egg was slightly darker than the other eggs, but was very similar to them in shape and egg markings. Another such case was observed previously by Nakamura in 1987 (unpublished data). Because most rejections in our study were by egg ejection or by nest desertion (see Table I), it is also likely that most mistakes are expressed in these ways. On the other hand, because not every egg disappearance or nest desertion is a result of a recognition error, an estimation of the frequency of possible errors can only serve as an upper limit. An analysis of the frequency of egg disappearance in unparasitized nests, and of the frequency of nest desertion by unparasitized hosts, suggests that the frequency of mistaken ejections is lower than 14%, and that the frequency of mistaken desertions is lower than 5% (Lotem 1992). However, the frequency of recognition errors made by ‘rejector’ individuals (mostly early-season breeders) may not indicate the frequency of errors that mid-season breeders (which are younger on average) might experience, if they tried to discriminate between egg types. Unfortunately, we found no way to experimentally stimulate young females to express their probability of making errors. Later in this paper, we try to assess this probability indirectly.

Probability of being parasitized

In cases where rejection behaviour entails costs to unparasitized hosts (i.e. recognition errors), parasitism rate has an important effect on the cost–benefit balance of egg rejection (May &

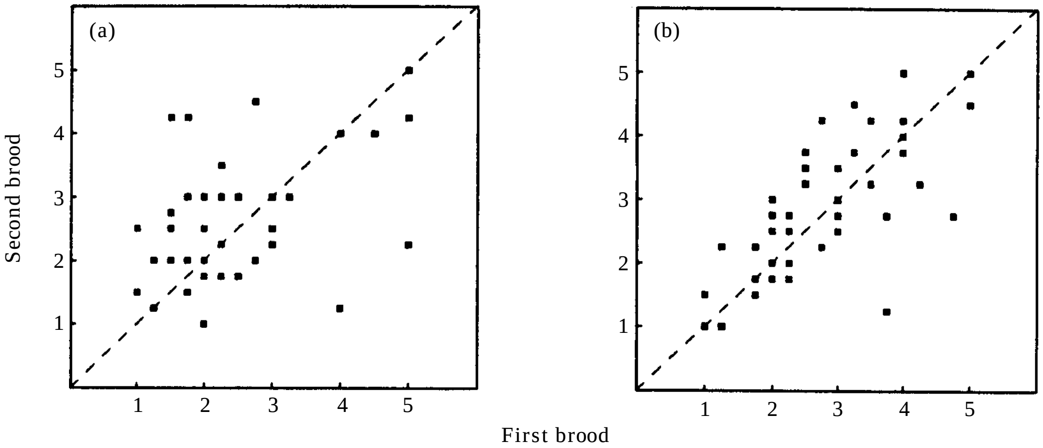

Figure 4. The similarity of (a) shade variability rank and of (b) shade rank of second versus first clutches of individual females. The diagonal line represents the line of perfect similarity of each.

Robinson 1985; Davies & de L. Brooke 1989b; Lotem & Nakamura, in press). The rate of parasitism in our studied population during 1989, 1990 and 1991 breeding seasons was 20% ($N=188$), 21% ($N=133$) and 8% ($N=251$), respectively. Because it is possible that some cuckoo eggs were ejected before we found the nest, the analysis of parasitism rate (Table VIII) was based only on nests we found during nest building or egg laying. These nests were checked at least every other day and at the day of clutch completion. Because 27% of rejections of cuckoo eggs occurred within 2 days after the cuckoo egg was laid (Table IV), it is possible that some cuckoo eggs were ejected before we noted them. Parasitism rate did not differ between early-, mid- and late-season breeders (Table IX; $G=0{\cdot}328$, $df=2$, NS). There is no evidence therefore, that cuckoos chose to parasitize mid-season breeders, which were more likely to accept their eggs, or that the acceptance behaviour of mid-season breeders is associated with a lower risk of parasitism. There was, however, a significant difference in parasitism rate among years (Table VIII; $G=16{\cdot}23$, $df=2$, $P<0{\cdot}001$).

Owing to fluctuations in parasitism rate between years and between different areas, the parasitism rate, which selects for rejection behaviour, might be difficult to measure. Among cuckoo hosts in Europe and Britain, local parasitism rates can be as high as 20% (Wyllie 1981; Cramp 1985; Davies & de L. Brooke 1988; Rothstein 1990), while the overall parasitism rate for a given species, as shown by the British nest record system, is only 1–6% (Davies & de L. Brooke 1989b). In a similar manner, the overall parasitism rate of great reed warblers in Japan might be much lower than in our study area. In some other areas in Japan, cuckoo parasitism on great reed warblers is absent (Y. Ezaki, personal communication) or rare (Urano 1985).

Host Egg Variability

Similarity between successive clutches

Successive clutches of a particular female were similar in shade variability and in shade rank (Fig. 4; Spearman rank correlation: $r_S=0{\cdot}38$, $t=2{\cdot}66$, $df=42$, $P<0{\cdot}01$; $r_S=0{\cdot}76$, $t=7{\cdot}6$, $df=42$, $P<0{\cdot}001$, respectively). To assess the similarity between successive clutches more accurately, we created a second set of photographs in the following way. Clutches that were taken from nests as part of a re-nesting experiment were kept in a refrigerator. After we found the re-nest, we took the first clutch to the field and photographed the two clutches (38 pairs) side by side in the same frame (laid out on a grey background in natural daylight). For comparison, first clutches were also photographed side by side with three other clutches of neighbouring females. We were able to compile 23 groups of four photographs. In each group, only one picture showed the first clutch with a second clutch from

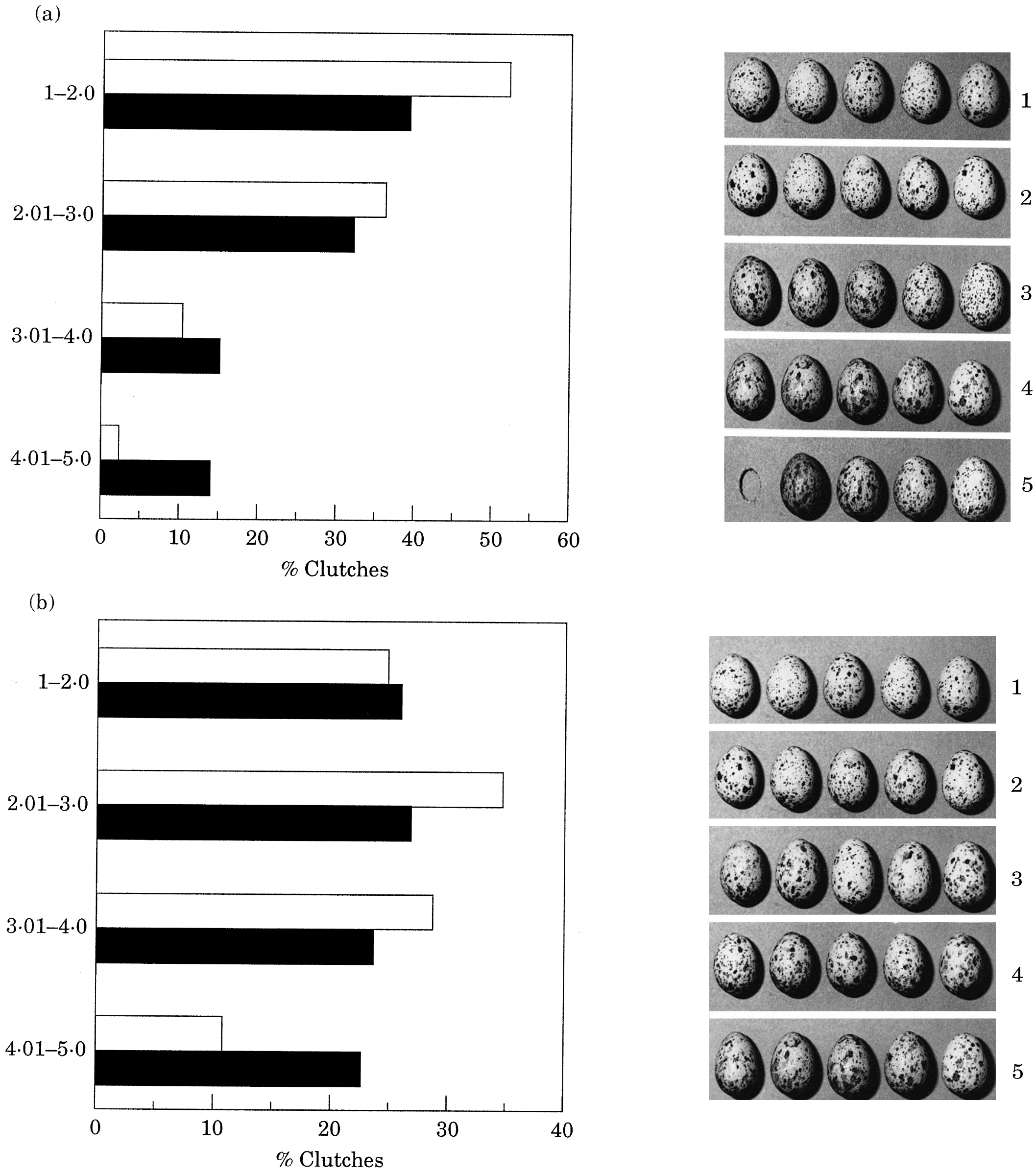

Figure 5. (a) Shade variability rank and (b) shade rank of clutches of early- (□; *N*=92) and mid- (■; *N*=66) season breeders (see text for further details).

the same marked female. We asked four independent observers to rank the pairs in each group according to the similarity between the two clutches. All four observers gave the real pair a higher similarity rank than expected by chance (G=23·1, 16·3, 23·1, df=3, P<0·001; G=12·6, df=3, P<0·01), suggesting that the similarity between two successive clutches of a particular female is greater than the similarity between any two clutches in the population. This pattern has been observed in several bird species (Thomas et al. 1989), and is important for learned egg recognition to be a successful strategy (see also Lotem et al. 1992).

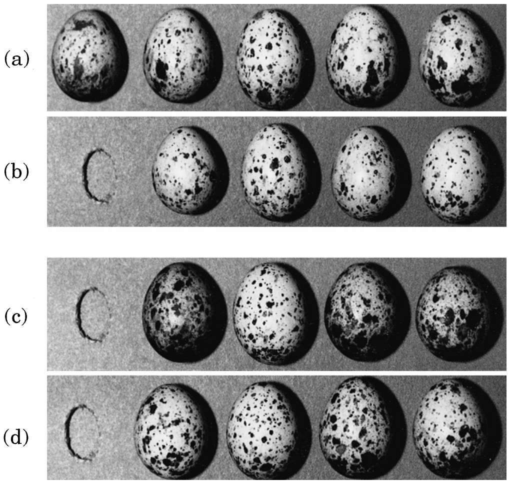

Figure 6. Differences in pigmentation between the first (a) and the second (b) clutch of female RRON, and between the first (c) and the second (d) clutch of female YBWN.

Table IX. Shade and shade variability of clutches of mid-season breeders that rejected or accepted a host egg painted light brown

Rank	Rejectors	Accepters
Shade variability		
1–2	7	5
2–3	5	5
3–4	4	—
4–5	5	—
Shade		
1–2	5	6
2–3	3	3
3–4	4	—
4–5	9	1

Egg variability within a clutch

Nineteen per cent of host clutches scored a variability rank higher than 3 (Fig. 5a). The frequency of variable clutches among mid-season breeders was higher than that among early-season breeders ($G=9\cdot90$, $df=3$, $P<0\cdot025$). Mid-season breeders were also more likely to have clutches with darker eggs (shade rank >4) than early-season breeders (Fig. 5b; $G_{\mathrm{adj}}=3\cdot92$, $df=1$, $P<0\cdot05$). Shade and shade variability were positively correlated (Spearman rank correlation coefficient: $r_S=0\cdot71$, $t=14\cdot4$, $df=200$, $P<0\cdot0001$). When considering that mid-season breeders are younger on average than early-season breeders (see General Methods), the probability of a female laying a variable clutch (a mixture of dark and bright eggs) decreases slightly with age. This trend is also supported when using female plumage as an age criteria; clutches that ranked higher than 3 in shade variability and shade were more common among females with juvenile tail feathers than among females without juvenile tail feathers (10 of 24 versus 7 of 40; $G_{\mathrm{adj}}=4\cdot24$, $df=1$, $P<0\cdot05$; and 14 of 24 versus 12 of 40; $G_{\mathrm{adj}}=4\cdot86$, $df=1$, $P<0\cdot05$, respectively).

Because we showed that successive clutches within a season tend to be similar in their shade and shade variability (Fig. 4), the reduction in clutch variability and pigmentation with age is more likely to occur between years than within a season. In only two of 38 photographs in which first and second clutches were photographed together (see above) was there clear reduction in clutch variability and pigmentation in the second clutch (Fig. 6). Although not common, these examples demonstrate that shade and shade variability of clutches may vary within a female's lifetime. Contrary to other studies (Davies & de L. Brooke 1988; Verbeek 1990), there was no clear relationship between laying order within a clutch and egg pigmentation; first eggs were sometimes lighter and sometimes darker than the rest of the clutch. Conspecific nest parasitism (Yom-Tov 1980; Petrie & Møller 1991) cannot explain the frequency of variable clutches observed in our study; in 510 nests that were monitored at least twice (and often daily) during egg laying, there was never a case of two eggs being laid on the same day. If parasitic great reed warbler females had removed eggs of their hosts, we would have noted such cases in the egg replacement experiment, or when we marked host eggs daily in 12 other nests (Lotem 1992). Moreover, eggs that differed in shade were often very similar to the rest of the clutch in shape, size and egg markings (see Fig. 6, two bottom rows). A long-term study on egg pigmentation of individually marked females would be most valuable.

Host discrimination threshold and the risk of errors

The existence of host intra-clutch variability increases the likelihood of recognition errors, but is not, in itself, sufficient to cause errors to occur. Recognition errors will occur only if hosts adjust their discrimination threshold erroneously within the range of variation of their own eggs. This might occur rarely if hosts adjust their discrimination threshold based on a prolonged learning period. As discussed earlier, we could not measure the risk of errors directly, because we could not manipulate the host learning strategy. Yet, indirect evidence for the risk of error can be demonstrated if some hosts reject eggs on the basis of differences that naturally occur within clutches of other individuals. Such evidence would suggest that hosts adjust their discrimination threshold near the edge of the variation range of their own eggs, and that each individual does it based on its own experience.

To test this hypothesis, we took five photographs of natural clutches with a shade variability rank of 5, and three photographs of clutches in which one of the eggs was a host egg painted light brown that had been ejected from that clutch by the host. We then asked eight independent observers to rank the eight photographs according to their shade variability. These three experimental clutches were ranked as no more variable than the natural ones (Mann–Whitney *U*-test: $N_1=24$, $N_2=40$, two-tailed $P>0{\cdot}5$). Thus, some hosts reject eggs on the basis of differences that naturally occur within clutches of other individuals. Additional evidence for the low discrimination threshold developed by great reed warblers is their ability to reject conspecific eggs. In three cases we introduced a dark-type egg to early breeders' nests containing light-type eggs. The introduced egg was ejected by the host in two of these three cases.

In conclusion, indirect evidence suggests that hosts would be likely to make mistakes if they tried to learn to recognize their eggs based only on the appearance of the first egg they laid. We discuss later (see General Discussion) the extent to which this qualitative evidence supports the equilibrium model.

Do mid-season breeders accept because they have variable clutches?

Because mid-season breeders were more likely to have variable clutches, one can argue that their acceptance behaviour was a direct result of their inability to spot a foreign egg in a variable clutch. To test this possibility we compared shade and shade variability in clutches of mid-season breeders that rejected or accepted host eggs painted light brown. Contrary to the prediction above, the shade and shade variability rank of accepter clutches were both lower than those of rejecter clutches (Table IX; Mann–Whitney *U*-test: two-tailed $P<0{\cdot}05$, for both shade and shade variability). Accordingly, neither high variability, nor dark pigmentation, induced young females to accept foreign eggs. The tendency of rejecter clutches to be more variable is puzzling and should be studied further.

Why does host egg variability exist?

It has been suggested that parasitism (conspecific or interspecific) would select for a reduction in host intra-clutch variation and for an increase in inter-clutch variation (Victoria 1972; Freeman 1988; Davies & de L. Brooke 1989b; Møller & Petrie 1990). Some comparative evidence regarding conspecific nest parasitism appears to support these predictions (Møller & Petrie 1990). However, common cuckoo hosts showed no such evolutionary response to cuckoo parasitism (Davies & de L. Brooke 1989b). This is also evident in the intra-clutch variability exhibited by great reed warblers in our study. The causes of host egg variability are not clear, because the process responsible for egg pigmentation is not fully understood (Solomon 1987; Burley & Vedehra). Some evidence suggests, however, that egg variability may simply represent physiological constraints. The production of egg pigmentation may decrease in old age (Solomon 1991) and under stress (Welty 1975; Solomon 1991). The first eggs laid by young captive quails, *Coturnix coturnix*, may vary in size, shape and pigmentation, but become more uniform in later layings (A. Bar, personal communication). This evidence, and our finding that clutch variability was more common among younger females, suggest that variation in egg pigmentation may occur under poor conditions, and that host egg variability is a phenotypic expression of physiological constraints during the process of egg production. Physiological constraints may not, however, explain the tendency of mid-season breeders to lay darker eggs.

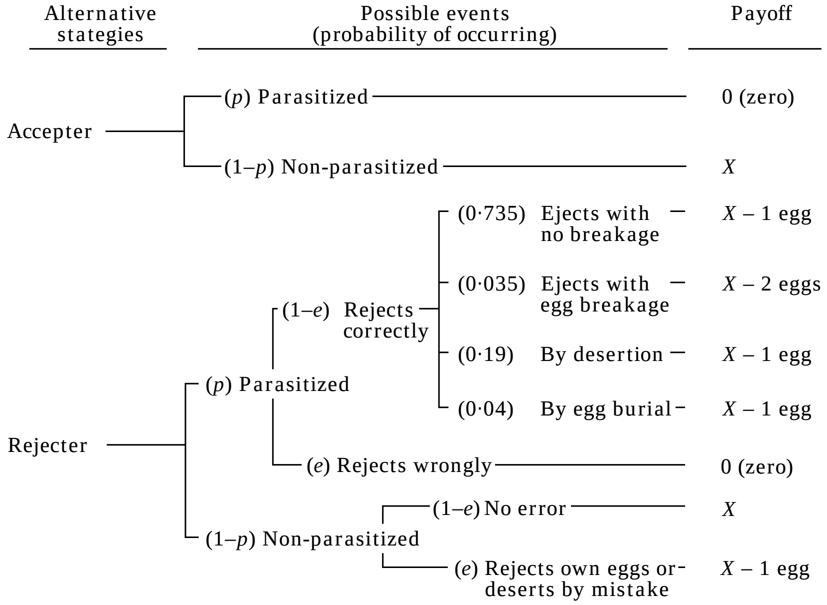

Figure 7. A cost–benefit model of cuckoo egg rejection by great reed warblers. The model compares two alternative strategies, an accepter and a rejecter. Each possible event has a probability of occurring (denoted in parentheses), and at the end of each course of events there is a payoff. The overall payoff of each strategy is the sum of all the payoffs, each multiplied by its probability of occurring. *p*: The probability of parasitism; *e*: the probability of making a recognition error; Rejects correctly: rejects the cuckoo egg; Rejects wrongly: rejects own egg instead of the cuckoo egg; *X*: the average reproductive success of a non-parasitized host, assuming no rejection costs.

GENERAL DISCUSSION

Can the Costs of Rejection Outweigh the Benefits?

Acceptance of cuckoo eggs by hosts may be explained as an evolutionary equilibrium if the costs of rejction outweigh the benefits. In another paper (Lotem & Nakamura, in press), we suggested a general model to explore the cost–benefit balance of egg rejection. We now incorporate the costs and benefits described in the results section into such a model, and examine under what conditions acceptance is adaptive. As we have mentioned before, two important parameters cannot be estimated directly from our data. The first is the frequency of recognition errors young females might make when trying to discriminate between egg types. The second is the parasitism rate that affects the evolution of rejection behaviour (a regional average of temporal and local variations in parasitism). However, using the other parameters provided by our data, the model can predict the frequency of recognition errors required to justify acceptance for a given rate of parasitism.

The model (Fig. 7) compares two strategies, an accepter and a rejecter. The overall payoff of each strategy is the sum of all the payoffs, each multiplied by its probability of occurring. The overall payoff of an accepter is therefore: $p*0+(1-p)X$, where p is the probability of parasitism, 0 (zero) is the reproductive success of parasitized hosts that accept a cuckoo egg (see Table VI), and X is the average payoff of an unparasitized nest, represented by clutch size. We chose to measure X by clutch size because predation rates did not differ significantly between groups (Tables VI, VII) and in order to simplify the model. An extended version of the model (A. Lotem, unpublished data) accounts for differential predation rate on parasitized versus unparasitized nests, showing that lower predation on parasitized nests favours rejection behaviour and vice versa. We also assumed that the frequency of recognition errors, designated e, is equal in parasitized and unparasitized nests. It is possible that error rates in

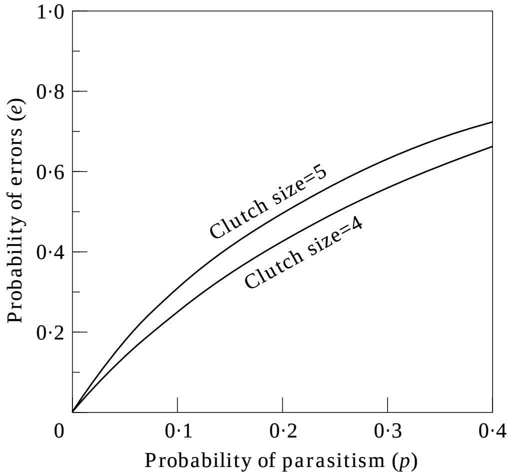

Figure 8. The probability of errors (e) required to justify acceptance for a given rate of parasitism (p), assuming clutch sizes of four and five eggs (see text for further details).

parasitized and unparasitized nests may be different, but it is hard to predict in which way. Some hosts may be less likely to make mistakes when not parasitized because without seeing a cuckoo near their nest they are less likely to reject any odd egg (Davies & de L. Brooke 1988; Moksnes et al. 1993). On the other hand, fewer errors may be expected if the cuckoo egg is the oddest egg in a parasitized nest.

Calculating the overall payoff of a rejecter is based on the following arguments. (1) Most cases of egg breakage during ejection attempts led to nest desertion and are accounted for in the frequency of nest desertions. The frequency of cases in which egg breakage reduced clutch size was negligible (3·5%). (2) Cuckoo egg burial is similar to ejection (a removal of the cuckoo egg from the clutch) and therefore its payoff is $X-1$ egg (see above). (3) We assume that the payoff of nest desertion is the same as that of cuckoo egg ejection, which is $X-1$ egg. As we suggested earlier, the benefit of nest desertion may actually be lower than that of egg ejection. However, the estimate we use, which maximizes the benefit of nest desertion, creates a conservative test for the hypothesis that acceptance is adaptive. The overall payoff of a rejecter is thus simplified to the sum of the following expressions: (a) parasitized and rejected correctly; $p(1-e)(X-1)$; (b) parasitized and rejected its own egg; $p*e*0$; (c) non-parasistized, no error; $(1-p)(1-e)X$; (d) non-parasitized and rejected its own egg; $(1-p)e(X-1)$. The payoff of an accepter will be equal to that of a rejecter when

$$(1-p)X = p(1-e)(X-1)+(1-p)(1-e)X+(1-p)e(X-1)$$

To describe the probability of errors required to justify acceptance, the equation above can be expressed as: $e=(p-pX)/(2p-pX-1)$, and illustrated by Fig. 8. The model shows that under a parasitism rate of 20%, the probability of errors required to justify acceptance should exceed 43% (when $X=4$) or 50% (when $X=5$). On the other hand, if the parasitism rate is around 1–5%, even an error probability of 3–14% (when $X=4$) or 4–18% (when $X=5$) can make acceptance be a better strategy than rejection.

The results of the model provide a range of conditions in which the cost of recognition errors can outweigh the benefit of rejection. In the following section we consider how likely it is that these conditions are met.

Acceptance of Cuckoo Eggs by Hosts: Adaptive or Maladaptive?

Our evolutionary equilibrium model (Lotem et al. 1992) suggests that the risk of recognition errors justifies a prolonged learning mechanism in which a host learns to recognize the range of variation of its own eggs. Our results are consistent with the three predictions of this model (see Introduction): experiments strongly suggest that the mechanism of egg recognition involves learning (prediction 1), a cost–benefit analysis shows that under some conditions the costs of recognition errors can outweigh the benefit of rejection behaviour (prediction 2), and data on host egg variability and host discrimination threshold suggest that host egg variability is high enough to yield recognition errors (prediction 3). Because we were not able to manipulate the host learning strategy, however, our data do not provide a direct experimental test of the hypothesis that a prolonged learning strategy is optimal.

An optimization approach can help to assess whether a prolonged learning strategy is the best solution under the system's constraints. In Fig. 9, we suggest an optimal strategy for learning to discriminate against mimetic cuckoo eggs. Based on the cost–benefit model described earlier,

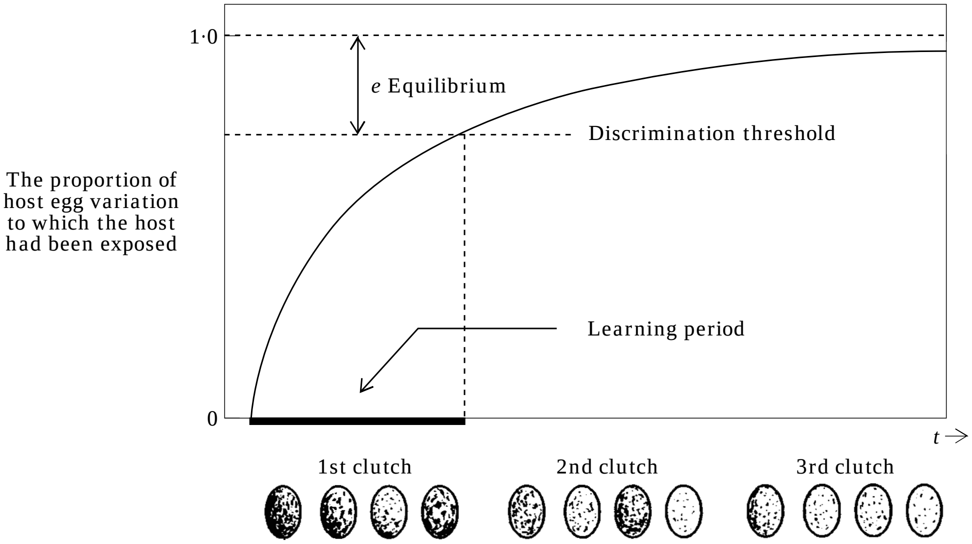

Figure 9. A model of an optimal learning strategy for discriminating against mimetic cuckoo eggs. The proportion of egg variation to which the host is exposed (on the *Y*-axis) increases with time (the *X*-axis) as more eggs are laid. The discrimination threshold is adjusted based on the egg types a host experiences during the learning period. The error probability *e* is determined by the proportion of host egg variation to which the host had not been exposed. The model predicts that hosts should prolong the learning period up to the point at which the error probability *e* is no longer greater than *e* equilibrium (the error probability, below which the rejecter strategy is better than the accepter strategy).

acceptance will be better than rejection beyond a critical error probability (*e* equilibrium). It is important to note that errors will occur if a host develops a discrimination threshold that is lower than the range of variation of its own eggs. We assume that a host adjusts its discrimination threshold according to the egg types it has experienced. Considering this, and because the proportion of egg variation to which the host is exposed increases with time (as more eggs are laid), the host should prolong the learning period up to the point at which the error probability *e*, is no longer greater than *e* equilibrium. The model suggests that the length of the optimal learning period is determined by *e* equilibrium, and by the curve of the proportion of egg variation to which the host had been exposed (see Fig. 9). In the absence of egg variability, this curve would reach a value of 1·0 immediately after the first egg laid, and a short learning period will be best.

Our data on egg variability in great reed warblers suggest that young females are more likely to have variable clutches (in 10–30% of cases), but that successive clutches tend to be similar. Accordingly, the curve of the proportion of egg variation to which the host had been exposed should be convex as illustrated in Fig. 9. The cost–benefit model of egg rejection, presented earlier, suggests that with a parasitism rate of 6%, an error probability of more than 0·2 can justify acceptance. Under these circumstances (see Fig. 9), a prolonged learning mechanism is expected to be adaptive, and acceptance of cuckoo eggs by young females is an inevitable result of this adaptive strategy. As we discussed earlier, it is likely that the regional parasitism rate in great reed warblers in Japan, and among other cuckoo hosts, is around 1–6% (see also Moksnes & Røskaft 1987; Davies & de L. Brooke 1989b). Because our data do not provide a quantitative test of whether this is really the case, we cannot determine whether host behaviour is optimal, and as a result of the temporal and spatial fluctuations in parasitism rate, host rejection behaviour (or learning strategy) may often be sub-optimal. We believe that the results of this study can best be explained by the view that the mechanism of egg discrimination represents a compromise between the cost of parasitism and the cost of recognition errors. However, this compromise may not have reached an optimal equilibrium in a particular population at a particular time.

Cuckoo–Host Co-evolution: an Evolutionary Equilibrium or an Evolutionary Lag?

Intermediate rates of rejection in cuckoo hosts have commonly been interpreted as resulting from an evolutionary lag in hosts' responses during a continuing evolutionary arms race between the cuckoo and its hosts (Dawkins & Krebs 1979; Kelly 1987; Davies & de L. Brooke 1989b; Moksnes et al. 1990). If so, the co-existence of rejecters and accepters represents a dimorphic population in which rejection has not yet reached fixation (Kelly 1987; Davies & de L. Brooke 1989b), or a monomorphic population in which rejection is not sufficiently developed (Davies & de L. Brooke 1989b). The first scenario seems less applicable to our study. Although we cannot rule out the possibility that some females (6%) are of an accepter genotype, most females (31 of 33) rejected highly non-mimetic eggs (painted dark brown), and the rejection rate of this egg type was 100% (19 of 19) among early-season breeders that were likely to be experienced females. It is more difficult to rule out the possibility that host rejection ability is not sufficiently developed and that it will be improved in the future. One can always suggest that further evolution may reduce host egg variability, or result in a discrimination mechanism that is not affected by egg variability. In other words, natural selection may change the constraints of the system. This suggestion is appropriate in general, and should be investigated whenever optimality is tested (see Stephens & Krebs 1986, page 181). Yet, the results of our study suggest that within the observed constraints, natural selection may favour acceptance behaviour. This evidence for a compromise between selection pressures supports an evolutionary equilibrium view, although it does not necessarily suggest that the system has reached an ultimate evolutionary equilibrium.

Under the lag view, the variation in rejection rates among different host species represents snapshots in evolutionary time of different stages of a continuing arms race between the cuckoo and its hosts (Davies & de L. Brooke 1989b; Moksnes et al. 1990; Soler & Møller 1990). In light of the results presented here, evolutionary time is only one factor, which is mostly relevant when cuckoo–host interaction is recent. In a later stage of cuckoo–host co-evolution, host rejection rates will reflect the host's rejection strategy, determined by the system's constraints. As suggested above (Fig. 9), these contraints are host egg variability and the cost–benefit balance of egg rejection (greatly affected by parasitism rate). An additional factor that influences host rejection strategy is the level of cuckoo egg mimicry. The model above deals with a situation in which cuckoo egg mimicry is well developed and discrimination should be refined. On the other hand, when mimicry is poor, rapid and less accurate learning may be favoured by selection (see Lotem et al. 1992). Even at evolutionary equilibrium, cuckoo egg mimicry may still not be perfect if the range of variation of egg types in the host population is much larger than that of a particular female (Rothstein 1990). Hence, rejection rates of cuckoo hosts may be determined by a combination of constraints acting on both cuckoo egg mimicry and on host discrimination.

Cuckoos were not observed in our study area 30 years ago, and cuckoo egg pigmentation appears as if in transition between mimicking the former host egg and the great reed warbler egg (see General Methods). It is unlikely, therefore, that the rejection strategy of great reed warblers in our study area is perfectly adapted to the current parasitism rate and to the present degree of cuckoo egg mimicry. On the other hand, it would be wrong to assert that great reed warblers accepted cuckoo eggs simply because they did not have sufficient time to evolve egg discrimination. Great reed warblers in our study show finely tuned discrimination ability between eggs, possibly due to genetic flow from other areas or a retention of rejection behaviour from a past interaction with cuckoos (see General Methods). The possible evolutionary lag in our system is in the adjustment of the host rejection strategy (learning strategy and discrimination threshold) to the current cost–benefit circumstances.

Based on the arms race theory, if sufficient time for evolution to operate is provided, hosts should evolve good discrimination ability, and cuckoos will be forced, therefore, to switch to a new, non-discriminating host (Davies & de L. Brooke 1989b; Rothstein 1990). Obviously, when choosing between hosts species of equal quality (in terms of food provisioning, nest availability and predation rates), cuckoos should prefer those hosts that reject their eggs at a lower rate. However, this is correct whether the differences in rejection rates represent different stages on an evolutionary time scale, or are determined by differences in the constraints acting on each host species. The evidence that current favourite hosts of the common cuckoo in Europe exhibit lower rejection rates than rarely used hosts (Davies & de L. Brooke 1989b; Moksnes et al. 1990) is therefore consistent with both the equilibrium and the lag hypotheses.

Implications for the Problem of Nestling Discrimination

The paradox that some cuckoo hosts exhibit a finely tuned ability to discriminate among eggs, but exhibit no discrimination among nestlings was explained by the arms race theory (Dawkins & Krebs 1979; Davies & de L. Brooke 1988). Dawkins & Krebs suggested that because of its higher selective value, egg discrimination can evolve faster than nestling discrimination. This is likely to be the case because cuckoo nestlings eject all host eggs or nestlings from the nest and as a result, it is too late for the host to save its young by rejecting the cuckoo nestling. If indeed egg discrimination evolves faster than nestling discrimination, then it might be predicted that where egg discrimination has not reached fixation, nestling discrimination would not have evolved. However, this explanation of the absence of nestling discrimination can hold only if intermediate rejection rates are due to a time lag in the fixation of the rejection genes in the host population. Our results make this possibility unlikely because rejection behaviour was common in the entire host population. Unless the benefit of rejecting a cuckoo chick is extremely low, great reed warblers should have had sufficient time to evolve at least some level of nestling discrimination. The results presented here are therefore inconsistent with an arms race explanation, and alternative models for the lack of nestling rejection (e.g. Lotem 1993) should be considered.

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