



Egg rejection in a passerine bird: size does matter

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Avian brood parasites reduce the reproductive success of their hosts, selecting for the evolution of egg discrimination by the host, and potentially creating a coevolutionary arms race between host and parasite. Host egg discrimination ability is crucial in determining whether the arms race results in extinction (of the parasite on a particular host) or stable coevolutionary equilibrium of the host–parasite pair. I examined egg discrimination behaviour in the yellow-browed leaf warbler, *Phylloscopus humei*, a presumed former host of parasitic cuckoos, to show how discrimination ability has become very strong. Field experiments using model eggs demonstrate that rejection decisions are based on the relative size of eggs in the clutch. Individuals do not learn the particular size of their own eggs, but will accept both large and small eggs as long as all eggs in the clutch are of similar size. Host rejection decisions are continuously modified based on assessment of variation in egg sizes currently in the clutch, making it a difficult strategy for a cuckoo to defeat.

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Avian brood parasites such as cuckoos, *Cuculus* spp., lay their eggs in the nests of passerine birds. Among cuckoos, successfully parasitized hosts often raise only the cuckoo young and have zero reproductive success. This results in strong selection for host discrimination of cuckoo eggs in order to eject them from the nest. Better host discrimination, in turn, selects for improved egg mimicry by the cuckoo, creating a coevolutionary arms race between host and parasite (Payne 1977; Dawkins & Krebs 1979; Mason & Rothstein 1986; Brooke & Davies 1988; Davies & Brooke 1988, 1989a, b; Rothstein 1990). Recent studies demonstrating successive adaptations and counteradaptations by avian brood parasites and their hosts provide some of the best examples of direct coevolution observed in nature (reviewed by Rothstein 1990).

Both continuous coevolution and evolutionary equilibrium are plausible outcomes of coevolutionary arms races between brood parasites and their hosts. If the arms race is continuous, then the outcome may be unstable with either host or parasite becoming extinct (Dawkins & Krebs 1979; Rothstein 1982; Davies & Brooke 1988, 1989a; Moksnes et al. 1990). For example, if the host evolves near-perfect discrimination of unlike eggs, the parasite is likely to be forced to switch to a different, less discriminating host (Davies & Brooke 1989b; Marchetti 1992). Alternatively, a balance may exist between the costs and benefits of host defences, such that single species of parasite and host reach a stable equilibrium

(Zahavi 1979; Rohwer & Spaw 1988; Brooker & Brooker 1990; Petit 1991; Lotem et al. 1992, 1995; Lotem & Nakamura 1998). Although the benefits to rejection are obvious, the costs are usually thought to be mistaken rejection of own eggs. For example, if discrimination errors lead to occasional own-egg rejections, and parasitism rates are sufficiently low, the costs of rejection may outweigh the benefits (Davies et al. 1996). This should result in some level of acceptance in the host population, and may result in stable coexistence of a parasite and its host (Lotem et al. 1995).

Whenever there are costs, a stable equilibrium can theoretically be achieved, but this depends critically on the mechanism of host discrimination. Hosts may evolve mechanisms of discrimination that always lead to rejection of cuckoo eggs, causing the cuckoo to become extinct (i.e. shift to a different, less discriminating host). One way to show that hosts are capable of evolving the near-perfect discrimination required to win a continuous coevolutionary arms race is to examine mechanisms underlying discrimination ability in a system where discrimination is so strong that the cuckoo egg is always rejected.

I examined mechanisms of egg recognition in the Hume's yellow-browed leaf warbler, *Phylloscopus humei*, a presumed former host of parasitic cuckoos that has extremely strong discrimination abilities and is not currently successfully parasitized (Marchetti 1992). Unlike most systems, in which coloration is of primary importance in egg rejection (Brooke & Davies 1988; Davies & Brooke 1989b; Lotem et al. 1992), in *P. humei* size is a

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stronger cue for rejection than either colour or spotting pattern (see also Marchetti 1992). Here I demonstrate that while discrimination ability appears to be innate, rejection decisions depend on the characteristics of eggs currently in the clutch. Rather than an absolute size threshold for rejection, the size of rejected eggs varies depending on the degree to which a given egg differs from other eggs in the clutch: an individual will reject or accept a given egg depending on its relative deviation from the other eggs. In addition, rejection rate increases with the number of natural eggs laid, suggesting that some females may wait until the clutch is complete and make a rejection decision by comparing eggs in the nest. This mechanism of egg recognition has resulted in strong discrimination that is unlikely to be defeated by the cuckoo.

METHODS

The study was conducted at the Manali Wildlife Sanctuary, Himachal Pradesh, North India during May–July 1994–1997. The study site is located in the Western Himalaya, at an elevation of 3000–4000 m. *Phylloscopus humei* (formerly *P. inornatus*, but recently elevated to species status; see Irwin et al., in press) is a small (approximately 6 g) ground nesting passerine that lays a single clutch (three to five eggs) in the breeding season; replacement clutches are laid if the first clutch fails. *Phylloscopus humei* is common; its nests are relatively easy to find and appear to be accessible to cuckoos. Most nests were found while females were building and monitored at least every other day.

To determine the mechanisms underlying egg discrimination and rejection, I conducted a series of experiments by artificially parasitizing *P. humei* nests using model eggs made of Plasticine. As Plasticine does not completely harden, it is possible to determine whether artificial eggs that were not ejected from the nest had been attacked by the host (see Fig. 1). Artificial eggs that were found in the nest, but that had obviously been pecked, were counted as rejections. Because egg size is the primary cue for rejection in *P. humei* (Marchetti 1992), I varied the size, but not the colour, of model eggs introduced into nests. The colour of model eggs was similar to the off-white background, but lacked the reddish-brown speckling of natural *P. humei* eggs. I define mean egg size as length \times (breadth)², which is highly correlated with true egg volume (e.g. van Noordwijk et al. 1981). Individual nests were used only once in the experiments. Nests were chosen haphazardly for one of four different experimental treatments (Table 1), and checked for rejection the following day. Similar to most studies (cf. Davies & Brooke 1989a; Moksnes et al. 1990; Lotem et al. 1992; Marchetti 1992), rejections occurred within 24 h after artificial parasitism with a few exceptions.

Experiment 1: Controls

I conducted two control experiments. First, I introduced natural *P. humei* eggs that were taken from a different individual's nest (in 1996, $N=11$). This allowed

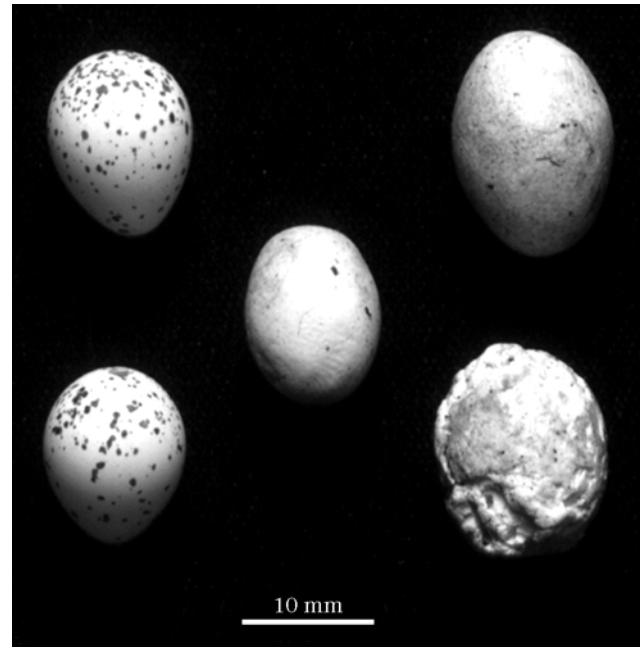


Figure 1. Photograph of natural *P. humei* eggs and artificial eggs used in the different experiments. Natural *P. humei* eggs (left top and bottom); small artificial egg (centre); example of large artificial egg (top right); large artificial egg that has been rejected and attacked by the host, note the beak mark on the lower left of the egg (bottom right).

me to determine whether rejection occurred in response to intraspecific brood parasitism rather than parasitism by cuckoos (see also Marchetti 1992). Second, I introduced control artificial eggs, similar in size to natural *P. humei* eggs (in 1996, $N=8$). This allowed me to determine whether rejection was in response to some characteristic of the artificial eggs themselves (see also Marchetti 1992).

Experiment 2: Introduction of Single Large Artificial Eggs

In these experiments I introduced large artificial eggs that were nonmimetic in size to natural *P. humei* eggs. *Phylloscopus humei* sometimes break their own eggs when rejecting very large artificial eggs. Thus artificial eggs used in these experiments were ca. 75% larger than natural *P. humei* eggs, but smaller than the eggs of *Cuculus poliocephalus*, which is the most abundant cuckoo in the study area (measurements from Ali & Ripley 1983). In some nests, artificial eggs were introduced after clutch completion and within the first few days of incubation (in 1995 and 1997, $N=28$). This allowed me to determine whether all individuals in the population are capable of discriminating and rejecting nonmimetic eggs, or whether the population is polymorphic and consists of both rejectors and acceptors. In other nests, I introduced artificial eggs during the laying stage, prior to clutch completion (in 1994 and 1997, $N=11$, 13 and 6 artificial eggs introduced into clutches that were incomplete after one, two and three eggs were laid, respectively). This allowed me to

Table 1. Summary of experiments and results

Artificial egg type	Number of rejections of introduced egg(s)	Sample size (total nests)
Natural <i>P. humei</i> (from different nest)	0 (0%)	11
Control artificial egg (mimetic in size to <i>P. humei</i>)	0 (0%)	8
Artificial nonmimetic large (introduced after clutch completion)	28 (100%)	28
Artificial nonmimetic large* (introduced during laying)	9 (30%)	30
Full clutch artificial small*	3 (38%)	8
Full clutch artificial uniform large*	0 (0%)	7

*See text for full results of experiment.

determine whether individuals eject nonmimetic eggs at any time during laying, or whether they require experience with a complete clutch in order to make a rejection decision.

Experiment 3: Introduction of Full Clutches of Small Artificial Eggs

In these experiments I introduced full clutches of small artificial eggs (ca. 30% smaller than natural *P. humei* eggs; $N=8$). At all nests, I removed each natural egg as it was laid and replaced it with a small artificial egg, until the entire clutch consisted of artificial eggs. Females' experience with their own eggs was thus minimized, and instead they were exposed to eggs considerably smaller than their own. I allowed the females to incubate the clutch of small eggs for 2 days after clutch completion, and then I removed one of the model eggs and replaced it with one of the female's own natural eggs. This allowed me to determine whether females have a size threshold for rejection (i.e. they accept both the small artificial eggs and their own egg because all eggs in the clutch are below a certain size), or whether rejection decisions are made based on the relative sizes of eggs in the clutch (i.e. the aberrant egg is rejected; in this case, the female should reject her natural egg when introduced into a clutch consisting of relatively small artificial eggs).

Experiment 4: Introduction of Full Clutches of Large Artificial Eggs

In this experiment I replaced the entire natural clutch with a full clutch of large artificial eggs of uniform size (in 1997, $N=7$; artificial eggs were ca. 80% larger than natural eggs from the clutches used in the experiment). Because entire clutches of natural eggs were replaced within 1–3 days after the start of incubation, females already had experience with their own eggs. Females were exposed to the clutch of large uniform artificial eggs for 1–2 days, and then the artificial eggs were removed and again replaced by the female's entire natural clutch. After re-exposure of the female to her own clutch for 24 h, one artificial egg that the female had previously incubated was reintroduced into the nest along with her natural

eggs. This experiment was designed to address three questions. First, is discrimination ability malleable after exposure to one's own clutch? For example, if females concretely learn their eggs after laying them, they would be expected to reject the clutch of large artificial eggs. Second, is there some threshold egg size above which females always reject? Third, is egg size per se, or variation in egg size, the most important cue for rejection?

Ethical Note

I conducted a pilot study of egg rejection in 1989 at my former study site in Kashmir, India (see Marchetti 1992). Nonmimetic artificial eggs used in the pilot study were the size of natural cuckoo eggs (ca. $2.5 \times$ larger than *P. humei* eggs; Ali & Ripley 1983), and a total of four out of 15 females unexpectedly damaged their own eggs when rejecting these very large artificial eggs. While most females can reject even large eggs without damaging their own, the larger the eggs the more disruptive they are. To reduce both prolonged disruption to the females, and the chances that females would damage their own eggs when rejecting artificial eggs, subsequent to the pilot study I altered the experimental design in two ways. First, at all except four nests, artificial eggs were removed within 24 h of experimental parasitism. Second, artificial eggs were sufficiently small such that females did not damage their own eggs when rejecting them. In some of the experiments described here, I removed natural *P. humei* eggs during incubation. Eggs that were removed from the nest were carefully placed in a small box lined with cotton and kept safely in my tent for the duration of the experiment. No eggs were broken as a result of removal. All eggs that were removed during incubation later hatched, despite not having been kept in an incubator. *Phylloscopus humei* is one of the earliest species to lay in the study area, and has adapted accordingly. For example, during a storm (it sometimes snows until mid-June), incubating females leave their nests and spend the duration of the storm at lower elevations. When they return they resume incubation (some after digging through snow to get to their nests), and the eggs hatch a few days later than they would had the female not left the nest.

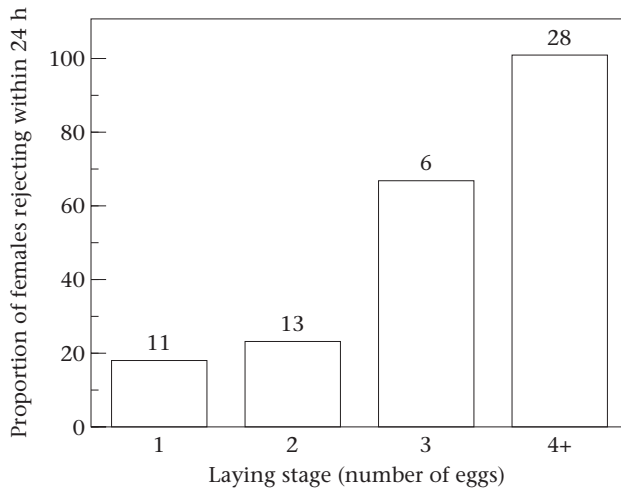


Figure 2. The proportion of female *P. humei* that rejected non-mimetic artificial eggs during different stages of laying and after clutch completion (four or more eggs). Numbers above bars indicate sample size. Unrejected artificial eggs were usually removed after 24 h. At the four nests in which unrejected artificial eggs were not removed, females rejected them at the start of incubation.

RESULTS

All of the females accepted natural eggs that were introduced into their nests from other *P. humei* nests (Table 1), demonstrating that rejection was not in response to conspecific egg dumping. Increasing clutch size by one egg did not provide a stimulus to reject. Control artificial eggs, mimetic to natural *P. humei* eggs in size, were always accepted (Table 1), demonstrating that females were not using cues such as artificiality in making a rejection decision (see also Marchetti 1992).

Introduction of Single Large Artificial Eggs

Natural and large nonmimetic artificial eggs differed in size. The mean \pm SD size of natural *P. humei* eggs was $1722.94 \pm 151.14 \text{ mm}^3$ ($N=55$ eggs collected from 16 nests), and that of a representative sample of 12 artificial eggs used in the experiments was $3020.88 \pm 164.54 \text{ mm}^3$. All of the females rejected larger artificial eggs that were introduced into the nest after clutch completion (Table 1, Fig. 2). All rejections occurred within 24 h after introduction of the artificial egg (five females attacked the artificial egg by pecking large holes in it, but the egg remained in the nest; 23 females ejected the artificial egg from the nest). These experiments demonstrate that all females in the population are capable of discriminating and rejecting nonmimetic eggs regardless of age or prior breeding experience, which may be a factor in discrimination ability (Lotem et al. 1995).

I was unable to determine directly the age of females used in these experiments, and some females may have had experience with their own eggs in prior breeding attempts. However, less than 30% of females return to the study area to breed in a subsequent season (personal observation), making it likely that many females were naïve breeders. While naïve breeders may require more

experience with their own eggs than older breeders in order to reject (Lotem et al. 1995), these experiments demonstrate that, if this is the case in *P. humei*, the learning period is brief, requiring no more than experience with one's own eggs during the breeding attempt.

The proportion of artificial eggs rejected when placed in the nest prior to clutch completion increased with the number of eggs laid (Fig. 2). Relatively few females rejected artificial eggs introduced in the nest after the first and second eggs had been laid, but rejection increased sharply when artificial eggs were introduced into nests after the third egg had been laid (Fig. 2). Because large artificial eggs may be disruptive to females, I usually removed nonrejected eggs when checking the nest the day following artificial parasitism. At four nests, I did not remove unrejected artificial eggs. In each case, the female rejected the artificial egg within the first few days after the start of incubation. These results suggest that females may often wait until the clutch is complete, and make a rejection decision by comparing eggs in the nest.

Introduction of Full Clutches of Small Artificial Eggs

Artificial eggs used in these experiments were about 30% smaller than natural *P. humei* eggs (the mean \pm SD of small artificial eggs was $1254.18 \pm 77.50 \text{ mm}^3$, $N=31$). Five of the eight individuals used in this experiment accepted and incubated the clutch of small artificial eggs. In each case, the female rejected her own, larger egg when it was reintroduced along with the clutch of small artificial eggs. However, when artificial eggs were again replaced by the clutch of natural eggs, females always accepted and incubated them. These results demonstrate that there is not a threshold egg size below which females always accept, nor do they concretely learn their own egg size. Instead, rejection decisions are based on the characteristics of eggs in the clutch, and egg variability (i.e. the presence of an aberrant egg) provides an important cue for rejection.

Introduction of Full Clutches of Large Artificial Eggs

In these experiments, I replaced complete clutches of natural eggs with large artificial eggs that were uniform in size. The mean \pm SD of artificial eggs used was $2973.31 \pm 82.28 \text{ mm}^3$ ($N=28$), and that of natural *P. humei* eggs from these clutches was $1649.72 \pm 139.52 \text{ mm}^3$ ($N=24$). Natural and artificial eggs differed in size, but not size variability (mean within-clutch standard errors of seven clutches of artificial and seven clutches of natural eggs, respectively, were 57.06 ± 11.05 and $62.41 \pm 14.47 \text{ mm}^3$, respectively; $t_{12}=0.29$, NS).

All females in this experiment accepted and incubated full clutches of large artificial eggs, despite the fact that their natural clutches were replaced after the start of incubation and the females already had experience with their own eggs. When the clutch of artificial eggs was

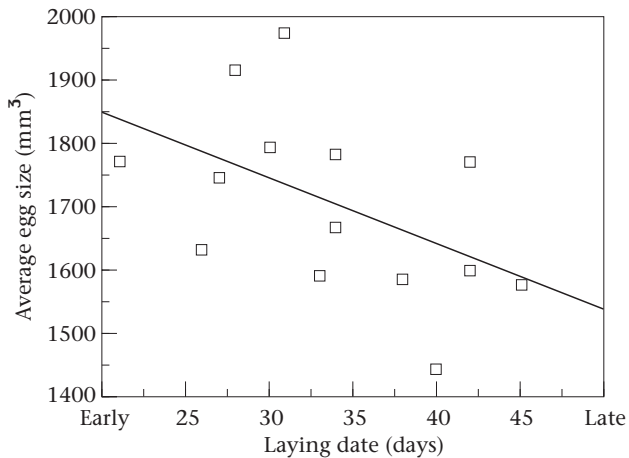


Figure 3. Regression of average egg size (mm^3) in the clutch on breeding date (days) for individual *P. humei*. Early breeding females on average tended to have larger eggs in their clutches than those that bred later ($r_{1,12} = -0.50$, $N = 14$ clutches, $P < 0.07$). There was no significant association of average egg size with clutch size ($r_{1,12} = 0.30$, $N = 14$, $P > 0.20$).

removed and replaced by the females' natural eggs, 100% accepted their own eggs. However, when one of the large artificial eggs that the female had previously incubated was introduced into the nest along with her natural eggs, all seven females rejected the (now aberrant) artificial egg. Females thus accepted large nonmimetic artificial eggs as their own as long as all eggs in the clutch were similar, but rejected them when they were the aberrant egg in the clutch. The result is similar to the previous experiment (experiment 3, above) in that it demonstrates the importance of egg size variability in making rejection decisions, and also that rejection decisions are modified based on the characteristics of eggs in the clutch.

Within-individual Variation in Egg Size

The average egg size of *P. humei* varies among years (Marchetti 1992). In this population, egg size varied throughout the season, with later-breeding individuals (which are likely to be in poor condition; Marchetti 1998) having smaller eggs than earlier-breeding individuals (Fig. 3). Individuals laying 20 days apart had an average egg size difference of about 200 mm^3 (11%), indicating substantial interindividual variation in egg size within a single breeding season.

DISCUSSION

Few reasons other than parasitism by cuckoos or conspecifics have been suggested to explain the evolution of egg discrimination and rejection in birds. While some bird species reject broken eggs, this is most commonly observed in tree-nesting species in which eggs may be jostled and broken by movement of the nest (Kemal & Rothstein 1988), but not in ground nesters such as *P. humei*. Although it cannot be demonstrated directly, all available evidence indicates that egg discrimination

in *P. humei* has evolved in response to parasitism by cuckoos. First, adult *P. humei* display an extremely strong and highly specific behavioural reaction against cuckoos that has never been observed in response to any other natural or experimentally introduced predator (Marchetti 1992). It is unlikely that a specific defensive behaviour against cuckoos has evolved in the absence of cuckoo parasitism. Second, field experiments demonstrate that egg rejection has not evolved as a result of conspecific egg dumping: neither conspecific natural eggs from different nests, nor model eggs mimetic in size to natural *P. humei* eggs, were rejected by artificially parasitized hosts.

Although *P. humei* has extremely strong egg discrimination abilities which have most likely evolved in response to parasitism by cuckoos, the species is not currently parasitized (Marchetti 1992; this study). Eggs of the small cuckoo, *C. poliocephalus*, have never been found in approximately 800 *P. humei* nests found during this and previous studies, although they have been found in the nests of other *Phylloscopus* species in the area (cuckoo eggs or chicks were found in 2/22 *P. affinis* nests and 1/10 *P. reguloides* nests; Marchetti 1992, personal observation). *Cuculus poliocephalus* eggs apparently were found in *P. humei* nests in studies conducted in North India during the early 1900s (Ali & Ripley 1983, although the authenticity of the cited records is not clear), suggesting that the cuckoo may have shifted from *P. humei* to a less discriminating host. Finally, rejected artificial eggs are sometimes found outside the host nest (at least 15 artificially parasitized nests; the artificial egg was usually attacked by the host; Fig. 1). Similarly, if *P. humei* were currently parasitized rejected cuckoo eggs should occasionally be found outside of nests, but this has never been observed.

All individuals in the population were able to discriminate and reject relatively large unlike eggs, regardless of age or prior breeding experience. While rejection behaviour itself appears to be innate, rejection decisions are modified based on the characteristics of eggs currently in the nest. Individuals neither concretely learn their own egg size, nor is there a threshold criteria for rejection. The experiments using full clutches of artificial eggs that were smaller and larger than the size of natural eggs demonstrate that variation in egg size within the clutch, rather than size itself, is the most important cue for rejection. Even after exposure to their own eggs, female *P. humei* accepted and incubated full clutches of large, nonmimetic artificial eggs. However, when a single previously incubated artificial egg was reintroduced along with natural eggs, it was always rejected. Similarly, females that were incubating a clutch of small artificial eggs rejected their own natural egg when introduced along with them, but accepted a full clutch of their own eggs after removal of the artificial eggs.

Some studies suggest that egg recognition occurs through an imprinting-like process during the first breeding attempt (Victoria 1972; Rothstein 1974, 1978). During this period hosts should tolerate a range of egg types in order to learn to recognize the eggs they see in the nest as their own, only later narrowing their range of tolerance to reject unfamiliar eggs (Lotem et al. 1995). Under this mechanism, the need of naïve breeders to learn to

recognize their own eggs reliably can result in low levels of acceptance in the population, which could lead to stable equilibrium of host–parasite pairs (Lotem et al. 1995). One potential problem with this mechanism is that naïve breeders that are parasitized during the first breeding attempt may learn to recognize a range of egg types that includes the cuckoo egg. Accordingly, these individuals should accept cuckoo eggs in future breeding attempts.

In *P. humei* the mechanism of discrimination differs considerably from the imprinting-like process described above. There is no evidence for constraints on rejection, such as a prolonged learning period, that could result in some level of acceptance in the population. Rather than specifically learning the characteristics of their own eggs, individuals assess variability and distinguish any aberrant eggs. Rejection decisions thus depended on the characteristics of eggs in the clutch, even when these characters were experimentally altered within a single incubation period. There were few differences among individuals in their responses to the different artificial egg treatments, with the most apparent differences occurring when large artificial eggs were placed in the nest prior to clutch completion (Fig. 2). In these experiments, a greater proportion of individuals rejected the model eggs at later relative to earlier stages of laying. Although the sample size is small, females that did not reject artificial eggs prior to clutch completion did reject them after the start of incubation. These results suggest that females may often wait until the clutch is complete, or nearly complete, before making a rejection decision (see also Davies & Brooke 1988). Several eggs in the nest may be required in order to determine which egg to reject, or females may not notice aberrant eggs until they start incubation.

A mechanism of discrimination that is flexible, and based on assessment of eggs currently in the clutch, is an efficient method of defence against brood parasites. The main cost to discrimination is likely to be mistaken rejection of one's own eggs (e.g. Marchetti 1992; Lotem et al. 1995), and strong discrimination may have resulted in selection for reduced within-clutch relative to between-clutch variability in egg size in *P. humei* (Marchetti 1992). Individuals with variable clutches made rejection errors more often than those with relatively uniform clutches, and *P. humei* appears to have lower within-clutch variability in egg size relative to a closely related species that does not discriminate unlike eggs (Marchetti 1992). The combination of modifiable rejection decisions and reduced within-clutch variability in egg size should make it difficult for the cuckoo to defeat host defences: if discrimination is very strong, and individual hosts differ in their egg characteristics, the cuckoo will be unable to lay eggs mimetic to all individuals in the population.

A recent model shows that, under certain conditions, selection will favour host acceptance of unlike eggs and thereby lead to an equilibrium between host–parasite pairs (Lotem et al. 1995; Lotem & Nakamura 1998). The main conditions required are a low rate of parasitism ($\leq 6\%$) and recognition errors by rejector individuals (3–14% of individuals did not reject the cuckoo egg). The equilibrium arises because strong discrimination ability

causes some individuals to reject their own eggs mistakenly. *Phylloscopus humei* never made rejection errors when responding to nonmimetic artificial eggs placed in the nest, as long as the artificial eggs were sufficiently different from their own (about 20% larger; Marchetti 1992). However, unparasitized *P. humei* occasionally reject one of their own eggs, possibly in response to egg size variability within their own clutch. Marchetti (1992) showed that at least 10 out of 190 (5%) of *P. humei* individuals mistakenly reject one of their own eggs in the absence of parasitism. Under the parameters of the model (Lotem et al. 1995; Lotem & Nakamura 1998), a rate of parasitism lower than 1%, and the existence of individuals in the population that accept unlike eggs, would be required for equilibrium to be a favoured outcome in *P. humei*. Acceptor individuals have not been observed in natural *P. humei* populations.

As parasitism rates become very low and discrimination ability becomes extremely strong, the cuckoo should switch to a less discriminating host (e.g. a different species: Marchetti 1992; an allopatric population of the same species: Soler et al. 1998). Once the parasite has switched hosts, costs to host defences in the absence of parasitism should result in the loss of discrimination behaviour, ultimately allowing the parasite to re-exploit past hosts (Marchetti 1992; Soler et al. 1998). Although stable equilibrium of single host–parasite populations is theoretically possible, it may not often be realized in nature as long as there exist other available hosts that are less discriminating. Instead, a cycling mechanism of extinction and recolonization of the host by the parasite may provide a more likely mechanism to explain the continued persistence of brood parasites and their hosts over evolutionary time.

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