

## Rejection of common cuckoo *Cuculus canorus* eggs in relation to female age in the bluethroat *Luscinia svecica*

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The evolutionary equilibrium hypothesis explains the existence of both acceptors and rejecters of brood parasite eggs within a host population as resulting from a balance between the costs of acceptance and the costs of recognition errors. In such equilibria conditional responses may play an important role. One such response that has been demonstrated in one common cuckoo *Cuculus canorus* host species is that first year, naive breeders accept parasitic eggs at a higher frequency than older and more experienced birds do. In the present study we tested whether this is the response in the bluethroat *Luscinia svecica*. We did not find any difference in rejection behaviour between first-year breeders and older birds. This finding is discussed in relation to recognition costs, cuckoo egg mimicry and the bluethroat's present status as a host. We conclude that the results are best explained by the evolutionary lag hypothesis.

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Interactions between avian brood parasites and their hosts have received much attention as model systems for coevolution in the last three decades (Rothstein 1990, Rothstein and Robinson 1998, Davies 1999, 2000). Interspecific brood parasites lay their eggs in the nests of other bird species and leave incubation and subsequent parental care to the foster parents. In the common cuckoo *Cuculus canorus*, which parasitises small passerines, different strains or gentes have evolved. These gentes have become specialised on different host species whose eggs they typically mimic (Chance 1940, Baker 1942, Moksnes and Røskaft 1995). After hatching, the cuckoo chick evicts all the eggs or young of the host and is raised by the foster parents. The consequence of such parasitism is a selection pressure on hosts for recognition and rejection of cuckoo eggs. Rejection of parasitic eggs that match those of the host poorly will in turn select for better egg mimicry in the cuckoo. These interactions are hypothesised to result in an arms race between host and parasite, and may ultimately lead to the evolution of specialised gentes, as described by Davies and Brooke (1989a). The arms race hypothesis has been experimen-

tally supported by Davies and Brooke (1989b) and Moksnes et al. (1990).

Even if it is beneficial for hosts to reject cuckoo eggs, in many host species a proportion of the individuals accepts parasitic eggs. In fact, there is a mixture of rejecters and acceptors within many species (see e.g. Rothstein 1990). The causes of such variation in rejection behaviour have been much debated. Two main hypotheses explain why some species have intermediate rejection rates: (1) the evolutionary lag hypothesis (Rothstein 1975a, Dawkins and Krebs 1979, Davies and Brooke 1989a, Moksnes et al. 1990), and (2) the evolutionary equilibrium hypothesis (Zahavi 1979, Rohwer and Spaw 1988, Brooker and Brooker 1990, Petit 1991, Lotem et al. 1992, Lotem and Nakamura 1998).

The evolutionary lag hypothesis states that it is always adaptive to reject parasitic eggs, but such behaviour may still not have appeared (no rejection) or spread to fixation in a host population (Rothstein 1975b). According to the evolutionary equilibrium hypothesis, the response towards the parasitic egg is determined by a compromise between the costs of acceptance and the costs of recognition errors.

Different types of evolutionary equilibria may exist. One central suggestion is of a mixed strategy where conditional responses play an important role (Lotem and Nakamura 1998). The first demonstration of such responses in cuckoo hosts was made by Lotem et al. (1992). They showed that among great reed warblers *Acrocephalus arundinaceus* parasitic eggs were normally accepted by first-year, naive breeders, whereas older and more experienced birds were rejecters. Lotem et al. (1995) argued that this was because the appearance of an individual's own eggs needs to be learned during the first breeding, to allow correct discrimination between own and parasitic eggs (Rothstein 1978).

To the best of our knowledge, the results of Lotem et al. (1992, 1995) are the only published records of conditional responses towards parasitic eggs dependent on host age. In the present study, we investigate whether such responses exist in the bluethroat *Luscinia svecica*. If they do, the results will provide further support for the existence of conditional responses towards parasitic eggs, which may set the stage for evolutionary equilibria to operate. The bluethroat is a suitable species for such a study because it is a cuckoo host with intermediate rejection rates (53–63%, Moksnes et al. 1990, Moksnes and Røskaft 1992) and because one-year-old and older birds can easily be separated in the hand (Svensson 1992). It is a selective ejector (Moksnes et al. 1991), which means that the parasitic egg is grasped with the bill and carried unbroken out of the nest, usually without damaging other eggs in the nest. In this study we investigate the rejection behaviour of young and old bluethroats by experimentally parasitising them with model cuckoo eggs.

## Methods

### Study area and general procedures

The field work was carried out in June 1993 in Øvre Heimdalen, southern Norway (61° 25'N, 8° 52'E). The study area is situated at an elevation of about 1100 m and consists of subalpine birch forest and heaths dominated by dwarf birch *Betula nana*, willow thickets *Salix* spp. and juniper *Juniperus communis*. Bluethroat nests were found by watching the birds during nest building or by flushing incubating females off the nest. The nests were thus found during the building, laying and early incubation stages. The total study area was around 5 km<sup>2</sup> and the density of the bluethroat population was about 30 pairs/km<sup>2</sup>. Egg-laying takes place in June, and typical clutch size ranges from 5 to 7 eggs (modal clutch size is 6 in most years, including the year of study) (Smiseth et al. 1998). Cuckoos belonging to the "meadow pipit *Anthus pratensis* gens" (Moksnes and Røskaft 1987, 1995) were present in the area, occasionally parasitising bluethroat nests with eggs resembling

the brown spotted eggs of the meadow pipit, which contrast with the blue-green bluethroat eggs (Brobakken 1995, A. Johnsen and J. T. Lifjeld unpubl. data).

Bluethroats were mist-netted and marked with colour rings to facilitate visual identification. The age of breeding birds was determined from the coloration and wear of the greater wing coverts (Svensson 1992). This method allowed the identification of one-year-old birds – hereafter called young birds – and birds that were two or more years old – old birds. All, except three breeding males, were aged.

### Experimental procedure

There are no reports of a cuckoo gens mimicking bluethroat eggs (Moksnes and Røskaft 1992, 1995) and the few records of parasitism on bluethroats in the study area were of the meadow pipit gens. We therefore used artificial cuckoo eggs that mimicked eggs of meadow pipits (see Moksnes and Røskaft 1989) (N = 15) or eggs of willow warblers *Phylloscopus trochilus* (white with red-brown spots; Moksnes and Røskaft 1992) (N = 6). The model eggs were made of hard plastic (Moksnes and Røskaft 1989). Both kinds were non-mimetic in relation to bluethroat eggs. There was no difference in rejection behaviour towards the two kinds of model egg used.

During egg-laying, bluethroat eggs were numbered with a felt-tip marker to indicate their position in the laying sequence. If a nest was found before the fourth egg was laid, the third host egg was exchanged with a model cuckoo egg. Otherwise an arbitrary bluethroat egg was exchanged with an artificial egg. To imitate the cuckoo's egg-laying behaviour (see Davies 2000) all egg exchanges were done in the afternoon. In six nests that were found during the incubation period, the eggs were floated to determine how long they had been incubated (Hays and Lecroy 1971). The laying dates were also estimated from observed hatching dates. In accordance with the procedure of Moksnes et al. (1990), all experiments were made during egg-laying or the three first days of incubation. During this period, the rejection of parasitic eggs by both bluethroats and meadow pipits occurs at a higher frequency than later on during incubation (Moksnes et al. 1990, 1993).

After eggs were exchanged, the nests were visited daily to record the occurrence and eventual timing of rejection of the parasitic egg. If no rejection had occurred by day 6 after experimental parasitism, the model cuckoo egg was considered accepted. If the host had ejected the model egg or damaged some of its own eggs, the event was defined as an ejection (Moksnes et al. 1990). No nests were deserted after they were experimentally parasitised. If no rejection occurred, the parasitic egg was removed shortly after hatching.

Table 1. Responses of bluethroats to experimental cuckoo parasitism during or shortly after egg-laying, in relation to age (N = 21 nests).

Sex	Age	Nests parasitised	Acceptance	Rejection	% rejection
Female	Young	8	0	8	100
	Old	13	2	11	84.6
Male	Young	4	0	4	100
	Old	14	2	12	85.7
	Unknown	3	0	3	100

Statistical tests were made using Statview 4.02. Non-parametric statistics were used throughout because the data were generally not normally distributed. All tests are two-tailed.

## Results

### Rejection of model cuckoo eggs

The model cuckoo egg was ejected from 19 of the 21 experimentally parasitised nests, and accepted in two nests. In 18 of the 19 nests where the model egg was ejected, the host's eggs were not visibly damaged, suggesting that bluethroats selectively eject model eggs by grasping them in the bill (Rohwer and Spaw 1988). Five of the 19 ejected eggs were found. The mean distance between the ejected eggs and the edge of the nest was 18 cm (range 3–35 cm).

In one case, bluethroat eggs were damaged. Five eggs in a clutch of six were ejected, of which at least three were punctured, and only the model cuckoo egg was left. The bluethroat egg that had been exchanged with the model cuckoo egg was then returned to the nest. By the next visit, the model egg had been ejected and the female incubated her recently re-introduced egg successfully.

Among the 21 pairs there were 13 old females and 8 young ones. All the young and 11 of the old females rejected the model cuckoo egg (Table 1). Thus, there was no statistically significant difference in rejection rate between old and young females (Fisher's exact test,  $N = 21$ ,  $P = 0.50$ ). There was neither any difference in rejection frequency between nests tended by old and young males (Table 1; Fisher's exact test,  $N = 18$ ,  $P = 1.0$ ). At the two nests where the model cuckoo egg was accepted, both pair members were old birds.

Though most pairs ejected the model cuckoo egg, considerable variation was found in the time that elapsed from experimental parasitism until ejection (range 0–6 days) (Fig. 1). There was no difference in time to rejection between young and old birds (females: young  $3.1 \pm 1.7$  days (mean  $\pm$  SD); old  $2.6 \pm 1.6$  days; Mann-Whitney U test:  $Z = -0.62$ ,  $N = 21$ ,  $P = 0.54$ ; males:  $Z = -0.67$ ,  $N = 18$ ,  $P = 0.50$ , data not shown).

Six of the nests were experimentally parasitised after egg-laying was completed. There was no significant

difference in the time to ejection between these (mean  $2.3 \pm 1.6$  days) and those parasitised during laying ( $3.1 \pm 1.7$  days) (Mann-Whitney U test,  $Z = -0.92$ ,  $N = 19$ ,  $P = 0.34$ ). The two cases of acceptance occurred in nests parasitised during laying.

## Discussion

### Responses in relation to age

Young and old bluethroats rejected non-mimetic cuckoo eggs with similar frequency and efficiency (time to ejection). In fact, all females except two old ones rejected the experimental cuckoo egg. Hence, our results do not support the idea of a conditional response towards parasitic eggs related to host age (Lotem et al. 1992, 1995). The fact that all young hosts in our study rejected the cuckoo egg suggests that learning is not essential for appropriate rejection behaviour. The similar ejection times in young and old hosts support the same conclusion. The delay in ejection shown by several pairs may still have been due to a learning process, although not related to age.

In contrast, Lotem et al. (1992, 1995) found that young female great reed warblers accepted cuckoo eggs at a higher frequency than did old females. However, for the reed warbler *Acrocephalus scirpaceus*, Davies and Brooke (1988) found that old birds were not more likely to reject than young ones. A similar lack of an age-related difference in rejection behaviour has been found in yellow warblers *Dendroica petechia* (Sealy

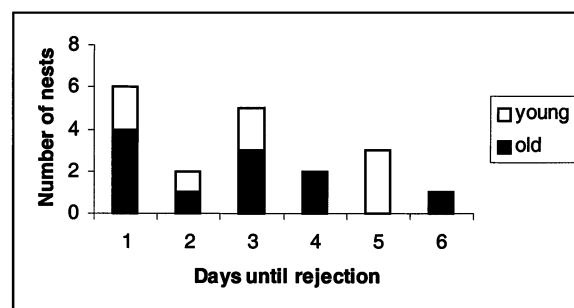


Fig. 1. Time from the introduction of an experimental cuckoo egg in a bluethroat nest until its ejection, related to age of the female host (young = one-year old, old = two years or older).

1995), parasitised by the brown-headed cowbird *Molothrus ater* in North America, and in chaffinches *Fringilla coelebs* (Stokke 2001). Taken together, age-related rejection behaviour has been demonstrated in only one species, while absence of age-related responses has now been reported in at least three species, of which two are parasitised by cuckoos. Hence the current evidence questions the general importance of age-related learning in host responses to cuckoo parasitism. It is noteworthy that brood parasites sometimes even show preferences for experienced hosts, as documented by Smith et al. (1984) for brown-headed cowbirds parasitising song sparrows *Melospiza melodia* and by Soler et al. (1995) for great spotted cuckoos *Clamator glandarius* parasitising magpies *Pica pica*.

In the present study, 90% of the parasitic eggs were ejected. This figure is considerably higher than the 53–63% reported previously for the same species (Moksnes et al. 1990, Moksnes and Røskaft 1992). However, previous tests were partly made well into incubation when rejection rates are lower than during and immediately after egg-laying. Actually, the rejection rate for non-mimetic eggs added during egg-laying in previous studies was quite similar, 83% (Moksnes et al. 1990) to what we found. Although some individuals accept parasitic eggs even when introduced during egg-laying and, in consequence, the species is strictly an intermediate rejector, the success rate of cuckoo eggs laid in bluethroat nests at the appropriate time (egg-laying) would be very low. That successful parasitism occurs is, however, evidenced by two known records of cuckoo chicks in bluethroat nests elsewhere in Norway (Kværne 1971, G. and P. Grimsby pers. comm.).

### Natural parasitism and rejection behaviour

There are few records of cuckoo parasitism in the bluethroat. Among 11 870 cuckoo eggs from European museum collections only nine (mostly of the meadow pipit gens) were found in bluethroat nests (Moksnes and Røskaft 1995). However, at Øvre Heimdalen where bluethroat nests were visited each day during the laying period, a parasitism rate of around 3% (3 out of 102 nests) was recorded (J. T. Lifjeld, A. Johnsen, P. T. Smiseth and T. Amundsen unpubl. data). In this area, therefore, the bluethroat can hardly be classified as a rare cuckoo host because this frequency is similar to that of many “commonly used” hosts (Glue and Murray 1984, Brooke and Davies 1987, Moksnes and Røskaft 1987). As pointed out by previous authors (Rothstein 1975a, Scott 1977, Sealy and Bazin 1995), the rate of parasitism of host species with strong rejection behaviour, like the bluethroat, may easily be underestimated.

Recognition errors are probably infrequent among bluethroats because all model eggs except one were selectively ejected without any damage to own eggs (probably by grasp ejection; see Moksnes et al. 1991). However, in one case where rejection of a natural cuckoo egg was observed, one host egg was punctured (P. T. Smiseth pers. comm.). Thus, bluethroats may sometimes incur rejection costs. This is also indicated by the fact that bluethroats typically accept experimental cuckoo eggs introduced late in the incubation period when the parasitic egg would not be expected to hatch (Moksnes et al. 1990, Røskaft and Moksnes 1998).

Real recognition costs (Lotem et al. 1992, Davies et al. 1996, Lindholm 1999, Rodríguez-Gironés and Lotem 1999) should mostly occur in unparasitised nests when own eggs are mistakenly rejected as parasitic eggs. Such costs are very difficult to measure (Røskaft et al. 2002) and are probably small or absent in the bluethroat, because egg disappearance occurs only infrequently in this species (T. Amundsen, J. T. Lifjeld, A. Johnsen and P. T. Smiseth unpubl. data).

### Evolutionary lag or equilibrium?

Our results do not support the existence of a conditional response towards parasitic eggs related to host age. Clearly, both young and old bluethroats have the ability to reject non-mimetic cuckoo eggs. According to the evolutionary lag hypothesis rejection is always adaptive. Moksnes et al. (1990) have argued that the evolutionary lag hypothesis predicts old (over evolutionary time) but rarely used hosts to show a highly developed rejection behaviour. This is the pattern found in the bluethroat. However, according to Lotem and co-workers (Lotem et al. 1995, Lotem and Nakamura 1998), this pattern may under certain circumstances also be consistent with the idea of an evolutionary equilibrium. The present data on bluethroats do not allow us to conclusively distinguish between the two hypotheses. Before the evolutionary equilibrium hypothesis can be further assessed for the bluethroat, the existence of recognition costs needs to be documented and quantified. In contrast, the evolutionary lag hypothesis does not rest on any untested assumptions. The rejection pattern of bluethroats in relation to age demonstrated in this study suggests that evolutionary lag is, so far, the most parsimonious explanation of host responses in bluethroats.

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