J Ethol (2004) 22:175–180
DOI 10.1007/s10164-004-0119-1

ARTICLE

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Are blackcaps current winners in the evolutionary struggle against the common cuckoo?

Received: October 31, 2003 / Accepted: March 30, 2004 / Published online: June 5, 2004

Abstract Blackcaps *Sylvia atricapilla* reject artificial cuckoo eggs, and their eggs vary little in appearance within clutches, whereas among clutches eggs vary considerably. Low variation within clutches facilitates discrimination of parasitic eggs, whereas high variation among clutches makes it harder for the cuckoo to mimic the eggs of a certain host species. These traits have most probably evolved as counteradaptations against brood parasitism by the common cuckoo *Cuculus canorus*, even though blackcaps are not regularly parasitised today. In this study, we investigated how fine-tuned the rejection of parasitic eggs is in this species by introducing three types of eggs into their nests: a real non-mimetic egg the approximate size of a cuckoo egg, an artificial mimetic egg the size of a cuckoo egg and a real conspecific egg. As the rejection frequency of both mimetic and non-mimetic artificial cuckoo eggs has been shown to be high in previous studies, the variation in rejection behaviour between individuals is low, indicating that most individuals within the population are able to reject parasitic eggs. Thus, we predict that (1) the intraclutch variation in egg appearance should be generally low in all individuals, and that (2) regarding conspecific eggs, rejection decisions should be highly dependent on the degree of mimicry between parasitic and host eggs. We found support for these predictions, which indicates that due to their highly sophisticated countermeasures against brood parasitism, blackcaps can probably be regarded as current winners of the arms race with the common cuckoo. Furthermore, the high and consistent rejection frequency of cuckoo eggs found throughout Europe for this species supports the spatial habitat structure hypothesis, which claims that woodland-nesting species breeding near trees, like blackcaps, presumably experienced a high level of parasitism throughout their range in the past and, therefore, their rejection behaviour, once evolved, spread rapidly to all populations.

Key words Blackcap · Brood parasitism · Cuckoo · *Cuculus canorus* · Egg discrimination · Egg recognition · *Sylvia atricapilla* · Spatial habitat structure

Introduction

The common cuckoo *Cuculus canorus* is an obligate brood parasite that lays its eggs mainly in nests of smaller passerines. Even though at least 125 species of passerines have been utilised as cuckoo hosts, individual cuckoo females are more or less host specific. Thus, there are at least 16 cuckoo tribes or gentes, which mimic the eggs of particular host species (Moksnes and Røskaft 1995; Davies 2000). These host-specific races represent genetically isolated female lineages (Gibbs et al. 2000).

Due to severe costs of parasitism, hosts of the cuckoo may evolve a lower intraclutch variation and a higher interclutch variation in egg appearance than species that are not utilised by the cuckoo (Øien et al. 1995; Soler and Møller 1996; Stokke et al. 2002a). This is believed to counter the evolution of mimetic eggs by the brood parasite, as described in the coevolutionary arms race hypothesis (Dawkins and Krebs 1979). A lack of "proper" counteradaptations in hosts can be due to a lag in the origin or spread of such traits (the evolutionary lag hypothesis; Rothstein 1990; Davies 2000), or due to a balance between opposing selection pressures (the evolutionary equilibrium hypothesis; Lotem et al. 1992; Davies 2000). One possible equilibrium scenario may exist when there are costs connected to recognition or rejection of foreign eggs (e.g., Davies et al. 1996; Røskaft and Moksnes 1998). The most recent explanation for why some species vary in host defences towards

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brood parasites has been developed by Røskaft et al. (2002a, b). They used the spatial structure of habitats to argue that species that more or less always nest among trees have more highly developed and more sophisticated anti-parasite behaviour than species breeding among trees and in open areas. This is because brood parasites need vantage points to search for host nests and, therefore, hosts that breed in the open are parasitised less frequently. Gene-flow from non-parasitised populations can therefore delay or stall the evolution or spread of rejection at a frequency that matches the level of parasitism in parasitised populations.

It has recently been shown that the rejection frequency of parasitic eggs in a population of reed warblers *Acrocephalus scirpaceus* is significantly related to the variation in appearance of eggs within clutches (Stokke et al. 1999). Individuals that rejected parasitic eggs had a statistically significantly lower intraclutch variation than those that accepted the eggs. Interestingly, only 56.3% of the individuals rejected artificial non-mimetic cuckoo eggs in this population. Reed warblers typically nest both near and far from trees and, therefore, the moderate level of rejection could be explained by the spatial habitat structure hypothesis. However, for species where the overall rejection frequency of parasitic eggs is high the situation may be different. It should be expected that in such species the intraclutch variation will be generally low in all individuals and that there will be no relationship between rejection and intraclutch variation. Therefore, only the contrast (i.e. mimicry in colour, spotting pattern and egg size) between host eggs and parasitic eggs should influence rejection. To examine this scenario in more detail we studied the blackcap *Sylvia atricapilla*, which rejects both mimetic and non-mimetic model cuckoo eggs at high frequencies (Moksnes and Røskaft 1992; Moksnes et al. 1994; Soler et al. 2002). As stated previously, rejection behaviour may vary between different populations of the same species (e.g., Davies and Brooke 1989; Briskie et al. 1992; Soler et al. 1998, 1999; Lindholm and Thomas 2000; Moskát et al. 2002). However, according to the spatial habitat structure hypothesis (Røskaft et al. 2002a, b), a species like the blackcap should show little variation in rejection behaviour between populations because it more or less always nests among trees and therefore has developed very sophisticated anti-parasite defences.

Data on rejection frequencies obtained in previous studies on blackcaps were collected in Norway and Spain (Moksnes and Røskaft 1992; Soler et al. 2002; Martín-Vivaldi, personal communication); sites other than where the present study was conducted. For this reason, we wanted to first confirm that the level of rejection in the present study area was the same as that reported in these previous studies. We therefore conducted experiments with both non-mimetic eggs and eggs that resembled or mimicked cuckoo eggs to confirm that the rejection behaviour was similar to the previous studies. Furthermore, due to the high rejection frequency of artificial cuckoo eggs, which yields almost no variation in rejection behaviour, we designed a more finely tuned experiment in which we parasitised all clutches with an arbitrarily chosen conspecific egg. Blackcaps have a low intraclutch variation and a high interclutch variation in egg appearance (Øien et al. 1995). Therefore, the contrast between the parasitic and host eggs in this study varied from low to high from one clutch to the next.

We predicted that because most individuals in the population reject cuckoo eggs, there should be no relationship between rejection of conspecific eggs and intraclutch variation. In other words, intraclutch variation should be generally low in all individuals. Furthermore, we predicted that rejection behaviour should depend highly on the contrast between the foreign conspecific egg and host eggs: low-contrast eggs should be difficult to detect and therefore should be accepted, whereas high-contrast eggs should be easily detected and thus rejected.

Materials and methods

The study was carried out in deciduous woodland (85 ha) near the village of Dolní Bojanovice in the southeastern part of the Czech Republic (48°52′N, 17°00′E) in 1999, 2000 and 2003. The host and cuckoo population co-occur and although most nests were checked daily during laying and early incubation, no cases of interspecific or intraspecific parasitism were recorded in the study area. Furthermore, intraspecific brood parasitism has not been documented in blackcaps anywhere (Yom-Tov 2001). Altogether 74 experiments were carried out (Table 1); 16 with mimetic model cuckoo eggs, 23 with real non-mimetic eggs of cuckoo size and 35 with real blackcap eggs. The model cuckoo eggs, similar in size and mass to real cuckoo eggs, were made of hard plastic (see Moksnes and Røskaft 1989). The mimetic egg type was painted to resemble eggs laid by the blackcap. Real yellowhammer *Emberiza citrinella*, house sparrow *Passer domesticus*, cockatiel *Nymphicus hollandicus* and Bourke's parrot *Neophema bourkii* eggs represented non-mimetic eggs. These eggs were painted light blue to resemble the eggs of the redstart *Phoenicurus phoenicurus* cuckoo gens found in the Czech Republic (Čapek 1910). Even though the size of these eggs differed somewhat and it is known that size may be a cue in egg recognition (Marchetti 2000), the response of blackcaps to all types of real non-mimetic eggs was the same. We therefore pooled the real blue eggs of all four species into one category for our anal-

Table 1. Host responses towards eggs experimentally introduced into blackcap nests. *n* Number of nests, % Percent of nests

Fate of nests							
Treatment	Accepted		Deserted		Ejected		Total (*n*)
	n	(%)	*n*	(%)	*n*	(%)	
Control	33[a]	89.2	4	10.8	0	0.0	37
Model mimetic	2	12.5	4	25.0	10	62.5	16
Conspecific	22	62.9	2	5.7	11	31.4	35
Real non-mimetic	1	4.3	0	0.0	22	95.7	23

[a] Acceptance here means that the nests remained active for the 6-day period without any desertion due to our nest visits

yses. Finally, 37 clutches were inspected and the eggs handled in the same way as the experimental nests, except that no parasitic egg was added.

Blackcap clutches were artificially parasitised during laying or the first days of incubation and the nests were inspected every day for the next 6 days. If the parasitic egg had not been removed or damaged (selective ejection), or the nest was not abandoned within this period, it was considered accepted. If the clutch was depredated or otherwise failed within this time it was excluded from the analyses. Each nest was tested only once.

In the experiments with the conspecific egg, the whole clutch including the parasitic egg was photographed at the same time that the parasitic egg was added. The eggs were removed and photographed in a standardised manner (grey background card with colour scale), using a Canon EOS 100 camera with an ML 3 flashlight and Fujicolor 200 ASA film. The intraclutch variation in egg appearance (ground colour and spotting pattern) and the contrast between the parasitic egg and the host eggs were later judged based on the photos by three persons unaware of the fate of the introduced eggs.

The intraclutch variation was measured on the following scale from one to five (Øien et al. 1995; Stokke et al. 1999): (1) no variation, all eggs were similar, (2) at least one egg differed slightly from the others, (3) at least one egg showed marked differences from the other eggs, (4) at least one egg differed dramatically from the others, and (5) all eggs were different from one another. The contrast between the parasitic and host eggs was scored on the following scale from one to three (Braa et al. 1992; Moksnes 1992): (1) no contrast between host and parasitic eggs, i.e. the foreign egg was indistinguishable from the host eggs, (2) medium contrast between host and parasitic eggs, i.e. the foreign egg could be distinguished from the host eggs, but the difference was only moderate, and (3) high contrast between host and parasitic eggs, i.e. the foreign egg could be easily distinguished from the host eggs.

The mean of the assessments of test persons was used for both intraclutch variation and contrast. This was justified by the fact that the test persons were highly consistent in their assessments, as measured by calculation of repeatability (Lessells and Boag 1987). The repeatability of scores for intraclutch variation was 0.52 ($F_{34,104} = 4.26$, $P < 0.001$), and the repeatability of scores for contrast was 0.83 ($F_{34,104} = 15.87$, $P < 0.001$).

The data were analysed using SPSS 10.0 for Windows (SPSS, Chicago, Ill.). All tests are two-tailed.

Results

Rejection frequencies

The host responses against the introduced eggs and the fate of the control nests are summarised in Table 1. The rejection frequency in the experimental treatments combined was significantly higher than in the control treatment (Fisher's exact test, $P < 0.0001$), clearly indicating that rejection was a response to artificial parasitism. In addition, even the lowest rejection frequency in the experimental procedure (conspecific treatment) was significantly higher than the desertion frequency in the control nests (Fisher's exact test, $P = 0.012$). There was no significant difference in rejection of real non-mimetic and model mimetic cuckoo-sized eggs (Fisher's exact test, $P = 0.557$), which shows that blackcaps reject both egg-types at a high frequency (87.5 vs 95.7%, respectively). However, there was a significant difference in rejection frequency between cuckoo-sized eggs and conspecific eggs (Fisher's exact test, $P < 0.0001$, 92.3 vs 37.1% respectively).

Time elapsing from experimental parasitism until rejection

There was no significant difference in the number of days that elapsed before rejection between the two experimental groups receiving a cuckoo-sized egg (model mimetic; $\bar{x} = 1.17 + 0.39$ (SD), $n = 12$ vs real non-mimetic; $\bar{x} = 1.05 + 0.21$ (SD), $n = 22$, respectively, Mann-Whitney U-test; $U = 116$, $n_1 = 22$, $n_2 = 12$, $P = 0.58$; Table 2). However, when comparing the day of rejection between the experiments with the conspecific egg and the two other egg-types combined we found a significant difference (conspecific; $\bar{x} = 2.77 + 1.64$ (SD), $n = 13$ vs cuckoo-sized; $\bar{x} = 1.09 + 0.29$ (SD), $n = 34$, respectively, Mann-Whitney U-test; $U = 77$, $n_1 = 34$, $n_2 = 13$, $P < 0.0001$; Table 2). Thus, more time elapsed between parasitism and rejection of conspecific eggs compared to cuckoo-sized eggs.

Influence of contrast and intraclutch variation on rejection of conspecific eggs

The mean contrast between parasitic and host eggs (Table 3) differed significantly between acceptors and rejecters ($\bar{x} = 1.67 + 0.48$ (SD), $n = 22$ vs $\bar{x} = 2.26 + 0.60$ (SD), $n = 13$, respectively, Mann-Whitney U-test: $U = 62$, $n_1 = 22$, $n_2 = 13$, $P = 0.005$). However, the mean intraclutch variation in egg appearance did not differ significantly between acceptors and rejecters ($\bar{x} = 1.65 + 0.62$ (SD), $n = 22$ vs $\bar{x} = 1.54 + 0.40$ (SD), $n = 13$, respectively, Mann-Whitney U-test: $U = 139$, $n_1 = 22$, $n_2 = 13$, $P = 0.88$). We also investigated possible differences in intraclutch variation in egg appearance in individuals that accepted versus those that rejected a moderately mimetic parasitic egg to control

Table 2. Time elapsing from experimental parasitism in blackcap nests until rejection of the parasitic egg. The figures show the distribution of nests according to the day of rejection in each experimental treatment. In the group of model mimetic eggs there were two cases where the exact date of rejection was unknown

Experiment	Day of rejection						Total
	1	2	3	4	5	6	
Model mimetic	10	2	–	–	–	–	12
Conspecific	4	2	3	2	1	1	13
Real non-mimetic	21	1	–	–	–	–	22

Table 3. Mean intraclutch variation (±*SD*) and contrast in egg appearance between alien and host eggs among acceptors and rejecters of conspecific eggs in blackcaps

	Intraclutch variation			Contrast		
	Mean	SD	*n*	Mean	SD	*n*
Acceptors	1.65	0.62	22	1.66	0.48	22
Rejectors	1.53	0.39	13	2.25	0.59	13

Table 4. Relationship between contrast between host and parasitic eggs (recoded, see text), and rejection behaviour in blackcaps

Contrast	Fate of nests				
	Accepted		Rejected		Total (*n*)
	n	(%)	*n*	(%)	
1	7	87.5	1	12.5	8
2	14	63.6	8	36.4	22
3	1	20.0	4	80.0	5

for the effect of contrast on rejection behaviour. We recoded the mean contrast into a class variable (1 = 1–1.44, 2 = 1.45–2.44, 3 = 2.45–3; Table 4) to make these analyses, and selected the cases where contrast was moderate (i.e. = 2). The mean intraclutch variation in egg appearance did not differ significantly between acceptors and rejecters ($\bar{x} = 1.62 + 0.65$ (SD), $n = 15$ vs $\bar{x} = 1.71 + 0.30$ (SD), $n = 7$, respectively, Mann-Whitney *U*-test: $U = 37$, $n_1 = 15$, $n_2 = 7$, $P = 0.26$). We carried out a binary logistic regression analysis to determine the combined effect of contrast and intraclutch variation (independent variables) on rejection behaviour (dependent variable). Rejection behaviour was significantly affected by the contrast between parasitic and host eggs (Wald $\chi^2_1 = 6.10$, $P = 0.01$); as the contrast between parasitic and host eggs increased, so did the rejection frequency of the parasitic egg [$B = 2.46 \pm 1.00$ (SD)]. However, the intraclutch variation in egg appearance had no effect on rejection behaviour (Wald $\chi^2_1 = 1.04$, $P = 0.31$).

Discussion

The high rejection frequencies of both mimetic and non-mimetic cuckoo-sized eggs by blackcaps in the present study correspond closely with previous reports (Moksnes and Røskaft 1992; Moksnes et al. 1994; Soler et al. 2002). However, the response towards foreign eggs is intriguing. Although it is distributed widely and is one of the most numerous passerines in Europe (Berthold and Solenen 1997), the blackcap is currently parasitised only rarely (Makatsch 1955; Malchevsky 1987). As mentioned above we did not detect any cases of intraspecific brood parasitism (see also Yom-Tov 2001). The high rejection frequency of foreign eggs has therefore most likely evolved as a consequence of previous parasitism by common cuckoos. The high rejection frequencies of cuckoo eggs found in this and other studies strongly support the spatial habitat structure hypothesis (Røskaft et al. 2002a, b). Because the blackcap (similar to other woodland-nesting species) has always bred near trees, it presumably experienced a high level of parasitism throughout its range and therefore the rejection behaviour, once evolved, would have spread rapidly to all populations. In support of this view is that in a large-scale study of cuckoo egg collections at European museums, Moksnes and Røskaft (1995) found 180 parasitised clutches of blackcaps. Altogether, 117 (65%) of the parasitic eggs among blackcaps belonged to the corresponding cuckoo egg morph (*Sylvia*). Most of these clutches were collected about a century ago and indicate that the species was more or less regularly parasitised. In addition, in some cases, there is extraordinarily good mimicry of some cuckoo eggs found in blackcap nests (Lucanus 1921; Moksnes and Røskaft 1995).

There also exist other data on former cuckoo parasitism of blackcaps (Čapek 1910; Lucanus 1921; Makatsch 1937; Géroudet 1950; Moltoni 1951; Malchevsky 1958). Another indication that *Sylvia* warblers may have been common cuckoo hosts for a long time can be found in an ancient ornithological work from the Bohemian territory. In Master Claretus' *Ortulus phisologie*, a collection of didactic poems dating before 1366, the cuckoo is said to have laid her eggs in nests of *canapellus*. The Latin name (in accordance with the old Czech name *penyczye*) refers to an unspecified *Sylvia* species (Flajšhans 1928). Additional support for a previous interaction between cuckoos and these passerines is the fact that blackcaps respond very aggressively towards dummy cuckoos near their nests (Moksnes et al. 1990; Røskaft et al. 2002b), and obviously look upon the parasite as a threat. Glue and Murray (1984) found that 3 out of 1,696 (0.17%) blackcap nests in Britain were parasitised by the cuckoo, indicating that this species might still be parasitised in other parts of Europe.

According to investigations on common whitethroats *S. communis* (Procházka and Honza 2003), lesser whitethroats *S. curruca* and barred warblers *S. nisoria* (P. Procházka and M. Honza, unpublished results), warblers of the genus *Sylvia* in general seem to be able to discriminate between their own eggs and eggs unlike their own. Honza et al. (2001) found that the *Sylvia* egg morph is the most common in the Czech Republic and that it has been found in at least 20 species. The garden warbler *S. borin*, which is also a good rejecter of foreign eggs (Moksnes et al. 1990), was parasitised by its corresponding egg morph in 68.4% of the cases, but only 7.7% of the *Sylvia* cuckoo eggs were found in this species. Such eggs in other *Sylvia* warblers were very rare, and in blackcaps only two eggs were found. Interestingly, 86.3% of cuckoo eggs found in reed warblers in the Czech Republic belonged to the *Sylvia* egg morph. Therefore, it seems very likely that cuckoos have switched from *Sylvia* hosts to more tolerant species like reed warblers, as suggested by the high rejection frequencies found in the former species.

As predicted there was no relationship between rejection behaviour of conspecific eggs and intraclutch variation in egg appearance in the present study, as would be expected if there was little variation in host defences within this host population (Øien et al. 1999; Stokke et al. 2004). The results therefore do not support the existence of an evolutionary equilibrium between rejecters and acceptors based on a learning process among first-year breeders. In some species, like the great reed warbler *Acrocephalus arundinaceus* in Japan, first-year breeders seem to need a prolonged period that enables them to learn the whole spectrum of variation among their own eggs (Lotem et al. 1992, 1995). However, this is not necessary for species with a low intraclutch variation, like blackcaps, due to the minor variation among their eggs within a clutch, making the probability of recognition errors negligible (Rodríguez-Gironés and Lotem 1999; Stokke et al. 2002b).

We also found as predicted that rejection of foreign eggs depended highly upon the degree of similarity between parasitic and host eggs. When there was a marked contrast between parasitic and host eggs, most individuals rejected the foreign egg (80%). However, as the degree of mimicry between host and parasitic eggs became better, fewer foreign eggs were rejected. The same results have been detected in the chaffinch, which also shows high rejection of both cuckoo eggs and non-mimetic conspecific eggs (Braa et al. 1992; Moksnes 1992; Stokke et al. 2004). We therefore assume that the failure to detect foreign eggs when they are too similar to an individual's own eggs is due to limitations of the cognitive system (e.g. McLean and Maloney 1998), and that there is a threshold regarding the visual system for detection and rejection of such eggs. Their low intraclutch variation makes it easier to detect even a relatively good mimetic parasitic egg. In addition, their high interclutch variation makes it very difficult for brood parasites to successfully parasitise these species (Øien et al. 1995; Soler and Møller 1996). Although the parasite lays a perfectly mimetic egg in one host nest, the high interclutch variation implies that the same egg type in another host nest would appear as non-mimetic. The differences in the time elapsing from experimental parasitism until rejection between the experiments with conspecific and cuckoo-sized eggs further support the view that blackcaps find it more difficult to recognise and reject conspecific eggs than cuckoo eggs. Cuckoo-sized eggs were rejected significantly sooner than conspecific eggs, which is not surprising because conspecific eggs were not only mimetic in ground colour and maculation, but also in size, making host discrimination more difficult.

In this study we tested for possible intraspecific differences in rejection behaviour related to intraclutch variation in egg appearance in a good rejecter species. As the intraclutch variation in blackcaps is generally low (Øien et al. 1995) and the species has good discrimination ability, we found no relationship between rejection behaviour and intraclutch variation. According to Rothstein (2001) host species may retain egg rejection even in the absence of the previous selection pressures presumably because they involve few costs for the hosts. The persistence of rejection behaviour also indicates that the blackcap experiences few recognition errors when rejecting parasitic eggs (Stokke et al. 2002b). In addition, the fact that rejection frequencies are high throughout the range of the species makes it very difficult for the cuckoo to start using this species again as a host. Species like the blackcap apparently have evolved advanced counteradaptations against the cuckoo. As they are presently not parasitised but still react to the cuckoo as a threat (Stokke et al. 2002b), these species can be regarded as current winners in their co-evolutionary arms race with the brood parasite.

Acknowledgements We thank Milica Požgayová and Tomáš Grim for their assistance in the field. Professor Jana Nechutová kindly provided a copy of the Latin text of Master Claretus' poem on the cuckoo. Two anonymous referees significantly improved a previous version of the manuscript. This study was supported by grants from the Grant Agency of the Czech Republic no. 206/00/P046, the Grant Agency of the Academy of Sciences no. A6093203 awarded to M.H., the Grant Agency of Charles University no. 124/2001-B-BIO awarded to P.P. and the Research Council of Norway, grant no. 125805/410 to B.G.S.

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