Ornis Fennica 80:86–91. 2003

Brief report

Egg rejection in European Blackbirds (*Turdus merula*): the effect of mimicry

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Received 23 December 2002, accepted 16 May 2003

1. Introduction

Earlier studies revealed that European Blackbirds (hereafter 'Blackbird', *Turdus merula*) evolved egg recognition and rejection abilities (Davies & Brooke 1989a, Grim & Honza 2001, Moksnes *et al.* 1990). However, there could be different reasons that might be responsible for the development of egg rejection in bird species. One of these possibilities is interspecific parasitism (e.g. Davies & Brooke 1988, 1989b, Moksnes *et al.* 1990), but there are only a few cases of parasitism of this potential host species by the European Cuckoo (hereafter 'Cuckoo', *Cuculus canorus*) (e.g. Makatsch 1955, Wyllie 1981, Moksnes & Røskaft 1995). In Hungary, this species also rarely was found to be parasitised (e.g. out of 694 Cuckoo eggs found in the nests of 15 species in a montane habitat in Hungary where Blackbirds were common, only one egg was reported from a Blackbird clutch; Varga 1994). Grendstad *et al.* (1999) and Grim and Honza (2001) suggested that intraspecific parasitism and the benefit of rejecting eggs of unrelated parasites could be the selective force for the evolution of egg rejection in thrushes. Sometimes nest cleaning behaviour might also contribute to egg rejections (Moskát *et al.* 2003). Even birds in populations that have never been parasitised by any brood parasite may identify the parasitic egg as a foreign object.

Several studies revealed the importance of mimicry of the parasitic eggs in egg discrimination of different bird species (e.g. Brooke & Davies 1988, Davies & Brooke 1988, 1989a,b, Moksnes & Røskaft 1992, 1993, Moskát & Fuisz 1999, Bártol *et al.* 2002, Moskát & Honza 2002, Rutila *et al.* 2002). Rejection in a host population may depend on the level of parasitism (Davies *et al.* 1996), e.g. below the threshold 19%–41% parasitism, Reed Warblers (*Acrocephalus scirpaceus*) should accept the mimetic parasitic egg because the costs of rejection outweigh the benefits. On the other hand presently unparasitised populations may retain some egg rejection ability from former parasitism (e.g. Davies & Brooke 1989b).

In the present study we wanted to reveal how mimicry of the foreign eggs affect egg rejection in Blackbirds. For this reason we monitored the responses of Blackbirds to experimental brood parasitism using mimetic and non-mimetic artificial Cuckoo eggs, as well as conspecific eggs. We hypothesised that rejection level depends on mimicry. We predict the highest rejection against the non-mimetic eggs, but a lower rejection rate towards the mimetic eggs and the conspecific eggs. We also hypothesised that method of rejection depends on mimicry. We predict more ejections than desertions against the non-mimetic eggs. Alternatively, we predict more desertions than ejections towards the mimetic eggs.

2. Study area and methods

We studied Blackbird populations in the extensive woodlands of the Buda Hills (300–500 m a.s.l.), in the surroundings of the village of Budakeszi (47°01′N, 19°00′E), ca. 1–5 km from the western edge of the city of Budapest. The forest is mainly composed of two oak species *Quercus petraea, Q. cerris*, and generally has a well-developed shrub layer. We also studied Blackbirds in three similar urban parks in Budapest: Vérmező Park (13 ha), Margaret Island (66.5 ha) and Városliget Park (81.5 ha). These parks have a great variety of broad-leaved and evergreen bushes and trees, containing many pathways and lawn areas. The closest distance to the Budakeszi Forest was 3.8 km. Two of the city parks are surrounded by blocks of flats, but the Margaret Island is surrounded by the River Danube. Cuckoos avoid closely built urban areas (Cramp 1985). We did not observe any Cuckoos in these city parks, although 10–35 ha urban parks would contain most of the bird species breed in towns (Fernández-Juricic & Jokimäki 2001).

The Blackbird is one of the commonest bird species in Budapest (Sasvári 1984): in the Vérmező Park the density of breeding pairs was estimated as 57.7 pairs/10 ha (Ludvig *et al.* 1995). In the Buda Hills its population density was much lower, ca. 6.0 pairs/10 ha (Moskát *et al.* 1988).

This study was conducted in 2000–2002, from mid-March to early May. (An extraordinarily early clutch with four incubated eggs was found on 18 February 2002). We experimentally parasitised Blackbird nests by adding a Cuckoo-type experimental egg to the clutch on the day when the fourth host egg was laid, because the modal clutch size was 4. Artificial Cuckoo eggs were made of plastic (synthetic clay), and painted with acrylic paints. Size and weight of an artificial egg were similar to that of a real Cuckoo egg. Two types of artificial Cuckoo eggs were used (we refer to PANTONE 2001 codes when describing colours): (1) non-mimetic egg: ground colour was extra light sepia (code: 614 C), with dark brown (462 C) and sepia (457 C) spots; (2) mimetic egg: ground colour is greenish (code: 563 C), with dark brown spots and lines (code: 462 C). The non-mimetic eggs were similar to a poorly mimetic Cuckoo egg found in a Great Reed Warbler (*Acrocephalus arundinaceus*) nest in Hungary. The mimetic eggs were painted to be similar to Blackbird eggs.

In another experiment we exchanged the fourth egg in clutch on the day when it was laid with a conspecific egg from another experimental clutch or with an egg collected from an abandoned nest to study intraspecific parasitism experimentally. Each artificial or conspecific egg was used in only one experiment, and each nest was used for experimentation only once. A control group of nests was also used to estimate the natural level of nest desertion.

We monitored nests daily for six days after manipulation. We regarded Blackbirds' responses to parasitism as acceptance, if the experimental egg was in the nest on the sixth day after the clutch manipulation. Two types of rejection were observed: ejection, if the foreign egg was missing from the nest within six days, or desertion, if the clutch was abandoned within the six day observation period. We found no year effect on the reactions against the two types of the artificial eggs in any of the rural and the urban study sites (Fisher's exact tests, $P > 0.05$). As reactions of Blackbirds did not differ among the city parks, we treated them together ($\chi^2_2 = 2.67$, $P = 0.263$, and $\chi^2_2 = 1.36$, $P = 0.507$ for the non-mimetic and the mimetic eggs, respectively). Conspecific eggs were used for the experiment in 2002.

All statistical tests were two-tailed, and were carried out by Statistica. Fisher's exact test was applied instead of the chi-square test when frequencies were lower than five.

3. Results

Altogether we conducted experiments at 136 Blackbird nests and observed 30 control nests that were not predated during the observation period (Table 1). Blackbirds in the Budakeszi Forest rejected all non-mimetic artificial Cuckoo eggs, but rejected a significantly lower proportion of mimetic parasitic eggs ($\chi^2_1 = 15.17$, $P < 0.001$). In the city parks, Blackbirds rejected a greater proportion of non-mimetic eggs versus mimetic eggs ($\chi^2_1 = 5.01$, $P = 0.025$). Ejections dominated over desertions for both egg types in both habitats (Table 1), so there was no significant difference between the use of rejection methods against the two egg types (Fischer's exact test, 2-tailed: $P = 0.228$ and $P = 0.368$, for the rural and urban habitats, respectively). Ejection cost was low: we observed only three cases (two in the city parks and one in the woodland), when two times one, and one time two host eggs were missing after a successful ejection of the non-mimetic parasitic egg. We did not observe any case of recognition error, i.e. the loss of host eggs when the parasitic egg remained in the nest.

Our study did not reveal any statistical difference in rejection rates between the urban and rural Blackbird populations in response to mimetic artificial Cuckoo eggs ($\chi^2_1 = 0.24$, $P = 0.623$), but the two populations showed a significant difference in response to non-mimetic eggs ($\chi^2_1 = 4.55$, $P = 0.033$).

We have two evidences for natural intraspecific parasitism (two eggs laid on the same day, one looking different from the rest of the clutch) in the parks. Experimental intraspecific parasitism using real conspecific eggs resulted in almost no rejection (Table 1). Desertion rate in the control group within 6 days after clutch completion was similar to desertion rate in the conspecific egg group (Fisher's exact test: $P = 0.541$). No ejection of the conspecific egg was observed. The rejection rate for the mimetic artificial Cuckoo eggs was almost ten times higher than the rejection rate for the conspecific eggs (Fisher's exact test: $P < 0.001$).

4. Discussion

Our results revealed that Blackbirds have a moderate level of egg rejection ability. The rural population showed the highest rejection rate against the non-mimetic eggs, but in the urban population reactions towards the two artificial egg types proved to be more similar. Most acceptances occurred towards the highly mimetic conspecific eggs.

Although we found a low rejection rate against experimental conspecific eggs (6%), we found two natural cases of intraspecific parasitism in Blackbirds' nests. The risk of intraspecific parasitism is expected to be higher in the dense urban population than in the woodland habitat. Grim and Honza (2001) suggested that intraspecific parasitism may play a role in the development of egg rejection behaviour both in the Blackbird and the Song Thrush (*Turdus philomelos*). However, molecular techniques would be useful to paint a more exact picture on intraspecific parasitism in

Table 1. Responses of Blackbirds to experimental parasitism with artificial Cuckoo eggs and real conspecific eggs (number of acceptances, egg ejections and nest desertions) in rural and urban study sites in Hungary.

Experimental egg	Budakeszi Forest (natural woodland)			Budapest (city parks)		
	Acceptance	Ejection	Desertion	Acceptance	Ejection	Desertion
Non-mimetic egg	0	23 (88.5%)	3 (11.5%)	9 (20.9%)	23 (53.5%)	11 (25.6%)
Mimetic egg	8 (57.1%)	4 (28.6%)	2 (14.3%)	16 (44.4%)	16 (44.4%)	4 (11.2%)
Conspecific egg	–	–	–	16 (94.1%)	0	1 (5.9%)
Control nest	–	–	–	27 (90%)	0	3 (10%)

thrushes. Andersson and Åhlund (2001) found more frequent conspecific brood parasitism in Common Goldeneyes (*Bucephala clangula*) when using protein fingerprinting compared to traditional methods and Hauber (2000) recorded on a videotape that an intraspecifically parasitic Song Sparrow (*Melospiza melodia*) rejected a host egg.

Blackbirds rejected more non-mimetic eggs in the rural than the urban habitats, possibly caused by a conditional effect of the presence of Cuckoos in woodland (Øien *et al.* 1999), so this difference is not related to genetical components of isolated populations. Groom (1993) described a case when Blackbird populations in urban parklands did not maintain themselves as a consequence of increased predation, but probably sustained by immigration from woodland habitats. In Hungary ringing recoveries revealed some distinctness of the rural and urban Blackbird populations (Móra *et al.* 1998), but the closeness of the rural and urban breeding areas of Blackbirds in our study makes possible some gene flow between the two areas. However, the relationship between adjacent habitats is also affected by local features (Jokimäki 1999, Clergeau *et al.* 2001), which may affect gene flow.

An average Blackbird egg is much bigger than a Cuckoo egg (29 × 21 mm and 22 × 17 mm for the Blackbird and the Cuckoo eggs, respectively; Snow & Perrins 1998), and its weight is more than two times greater (7.7 g vs 3.4 g, Snow & Perrins 1998). Our artificial Cuckoo eggs had the same size and weight as a real Cuckoo egg. If the artificial egg was in the centre of the nest cup, the Blackbird eggs frequently covered a part of these small eggs. In deep nests the artificial egg rolled down into the central bottom of the nest cup, so the big Blackbird eggs might totally cover the artificial egg. Females might be unable to rotate these deeply placed artificial eggs properly. Such eggs can be regarded as egg-shaped foreign objects in the nest. In one category (non-mimetic eggs in the rural population) we found a 100% rejection rate, so Blackbirds were able to reject the deeply-placed, hardly-visible artificial eggs, too. Grim and Honza (2001) experimentally parasitised Blackbird clutches with blue painted quail eggs, which were similar in size to a Blackbird egg. They revealed a 67% rejection rate, which is somewhat less than our values on rejection towards the non-mimetic artificial Cuckoo eggs (79%–100%), but higher than our values against the mimetic eggs (43%–56%). Accordingly, we think that nest cleaning mechanisms (Moskát *et al.* 2003) may also play a role in our finding of high rates of Blackbirds' egg rejection, especially when the parasitic egg is much smaller than a Blackbird egg (like the artificial Cuckoo eggs applied in our experiments).

In conclusion, our results agree with the hypothesis that Blackbirds reject the less mimetic foreign eggs more frequently than the more mimetic eggs, but our results did not support the second hypothesis, that method of rejection depends on mimicry. We showed that Blackbirds give preference to ejection over desertion against both egg types in both populations.

Acknowledgements: The authors are indebted to Eivin Røskaft for consultations during the study and Mark E. Hauber for his comments on the manuscript. Permission for the fieldwork was provided by the Duna-Ipoly National Park (No. 132/2/2001). The study was supported by the grant No. T35015 of the Hungarian Scientific Research Fund (OTKA) to C. M.

Selostus: **Mustarastaan kyky tunnistaa pesään ilmestyneet vieraat linnunmunat**

Aiemmat tutkimukset ovat osoittaneet, että mustarastaalle on kehittynyt kyky tunnistaa vieraat linnunmunat sekä taito hylätä ne. Vieraiden munien hylkäämiseen on monia syitä, joista yksi on muiden lintulajien mustarastaaseen kohdistaman loisinnan aiheuttamien haittojen välttäminen. Linnulle on hyödyllistä tunnistaa ja hylätä pesäänsä munittu vieras muna myös silloin, kun se on lajitoverin muna. Monissa tutkimuksissa on todettu vieraan munan ulkoasun olevan tärkeä hylkäämiseen vaikuttava tekijä. Artikkelin kirjoittajat tutkivat mustarastaiden käyttäytymisvastetta pesiin asetettuja keinotekoisia munia kohtaan. Vieraat munat muistuttivat joko käen munimaa mustarastaan tai rastaskerttusen munaa. Lisäksi tutkittiin, kuinka mustarastasyksilöt reagoivat muiden mustarastasnaaraiden munimiin muniin. Vieras muna sijoitettiin mustarastaan pesään, kun siinä oli neljä munaa. Mustarastaan reaktio vieraaseen munaan tarkistettiin kuuden päivän kuluttua. Tutkimuksessa oli mukana myös kontrollipesäryhmä, jonka avulla selvitettiin mustarastaan luonnollinen pesän hylkäämisprosentti. Tutkimus tehtiin Budapestin lähimetsissä ja kaupungin puistoissa. Mustarastas on yleinen pesimälintu etenkin Budapestin puistoissa. Käki sen sijaan puuttuu kaupungista. Mustarastas joko hyväksyi pesäänsä laitetun vieraan munan, hylkäsi pesänsä tai nosti vieraan munan pois pesästä. Kokeessa oli mukana kaikkiaan 136 pesää ja kontrolliryhmässä 30 pesää. Metsissä mustarastaat hylkäsivät kaikki pesiin asetetut rastaskerttusen munan kaltaiset käenmunat, sen sijaan mustarastaan munia muistuttavia käenmunia hylättiin harvemmin (43%). Myös Budapestin puistoissa mustarastaat hylkäsivät useammin rastaskerttusen munaa muistuttavan käenmunan (79%) kuin mustarastaan munaa muistuttavan käenmunan (55%). Sekä puistoissa että metsissä pesivät mustarastaat yleensä nostivat vieraan munan pois pesästä; pesän hylkäämisiä tapahtui harvemmin. Metsän ja kaupungin puistojen välillä ei havaittu eroja mustarastaan suhtautumisessa omia muniaan muistuttavia käenmunia kohtaan. Sen sijaan kaupungissa pesivät mustarastaat hyväksyivät metsissä pesiviä mustarastaita useammin rastaskerttusen munaa muistuttavan käenmunan. Mustarastas hylkäsi vain kerran (6%) pesäänsä asetetun oman lajinsa vieraan naaraan muniman munan. Kontrollipesien hylkäysaste oli niinikään 6%. Tutkimuksen yhteydessä havaittiin kaksi lajinsisäistä loisintatapausta, jotka molemmat tapahtuivat puistossa. Lajinsisäisen loisinnan riski yleensä kasvaa populaatiotiheyden kasvaessa. Budapestin puistojen mustarastastiheys oli suurempi (58 paria/10 ha) kuin kaupunkia ympäröivien metsien mustarastastiheys (6 paria/10 ha). Tutkimustulokset osoittavat, että mustarastas hyväksyy pesäänsä helpommin omaa munaansa muistuttavan vieraan munan kuin siitä suuresti poikkeavan munan.

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