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# Host responses against natural and experimental conspecific brood parasitism in the Starling *Sturnus vulgaris*

Arne Moksnes* & Per-Anders Elvertø

*Moksnes, A., Department of Biology, Norwegian University of Science and Technology, NTNU, Realfagbygget, N-7491 Trondheim, Norway. arne.moksnes@bio.ntnu.no (* Corresponding author)*
*Elvertrø, P.-A., Regulatory Affairs Department, Sandoz/HEXAL, Jernbaneveien 4, N-1400 Ski, Norway. per-anders.elvertro@hexal.no*

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Intraspecific brood parasitism in the Starling *Sturnus vulgaris* was studied in Central Norway. Before clutch initiation, Starlings recognise and remove parasitic conspecific eggs but are usually not able to do so after they have started to lay eggs themselves. The frequency of natural parasitism was 10%. Since ejection of the whole clutch has been observed after parasitism in this and other populations, the hypothesis that Starlings can react against parasitism by a conditional response was tested experimentally. The nests in two experimental groups received a foreign conspecific egg into their nests, and in one of these groups a stuffed conspecific female (assumed to function as a conditional stimulus) was placed in the nestbox aperture. For the hypothesis to be supported hosts that observed the conspecific dummy at their nests should eject their clutch more often than those that did not see the foreign female dummy. No such ejection of the clutch was observed. Even with the sight of a conspecific parasite at their nest, and despite their aggressive behaviour against it, the hosts never removed any eggs. These results do therefore not support the hypothesis of a conditional response against parasitism.

## 1. Introduction

Conspecific brood parasitism (CBP) occurs when a female lays some of her eggs in the nest of a conspecific, thereby exploiting the parental care of other individuals. If the host accepts the parasitic egg, this will increase the host's cost of parental care and normally decrease its reproductive success (Brown 1984, Pinxten *et al.* 1993). Laying parasites may also themselves actively remove host eggs (Lombardo *et al.* 1989, Pinxten *et al.* 1991a). When the pressure from CBP is sufficiently high, there would be a selection for counter-adaptations by hosts, defending their reproduction against parasitism. Many species have thus evolved an ability to recognise and reject foreign conspecific eggs in their nest (e.g. Victoria 1972, Emlen & Wrege 1986, Stouffer *et al.* 1987, Brown & Brown 1989, Moksnes 1992, Grendstad *et al.* 1999, Peer & Sealy 2000, Avilés 2004).

Studies on interspecific brood parasitism have shown that several conditional responses may play an important role in determining host rejection behaviour (see e.g. Brooke *et al.* 1998). An example of such a conditional response is that Reed Warblers *Acrocephalus scirpaceus* and Meadow Pipits *Anthus pratensis* reject Common Cuckoo *Cuculus canorus* eggs more often when the hosts have observed a female Cuckoo near their nests (Davies & Brooke 1988, Moksnes *et al.* 1993). In this study, we investigate if such conditional responses against conspecific brood parasitism exist among Starlings *Sturnus vulgaris*.

Conspecific brood parasitism has been reported in several populations of Starlings (Yom-Tow *et al.* 1974, Evans 1988, Pinxten & Eens 1990, Romagnano *et al.* 1990, Smith *et al.* 1996, Sandell & Diemer 1999), and the frequency of parasitism has been highly variable from year to year (Pinxten *et al.* 1991a). In many cases, parasitic Starlings may remove one of the host s eggs during the time the host is laying (Lombardo *et al.* (1989, Pinxten *et al.* 1991a). Starlings are able to recognise and remove all conspecific parasitic eggs laid before their clutch initiation, but are generally not able to recognise such eggs after they have started to lay themselves (Stouffer *et al.* 1987, Pinxten *et al.* 1991b). However, we have observed that in a naturally parasitised Starling clutch where one host egg was removed and exchanged by a conspecific parasitic egg, all eggs were soon after ejected from the nest and were found on the ground under the nest box (A. Moksnes, unpubl. data). Such reactions have also been described by Stouffer *et al.* (1987). One probable explanation for such behaviour could be that the host had recognised some cue of parasitism, but had not been able to separate the parasitic egg from the rest of the clutch. Faced with this situation, a host may decide to get rid of the parasitic egg by ejecting all eggs and start a new clutch. A central question in such cases is therefore how a host may recognise brood parasitism. One possible explanation could be that, in cases where the entire clutch is ejected, the host has observed a foreign female at the nest. If so, such rejection behaviour could be classified as a conditional response.

The main aim of the present study is to investigate if conditional responses are involved when Starlings discriminate against conspecific parasitic eggs. We tested the hypothesis that Starlings are capable to discriminate against parasitic eggs through a conditional response. In this context, the sight of a foreign female at the host s nest could be an important stimulus. We predict that individuals which face a conspecific egg experimentally introduced into their nest and at the same time observe a foreign female at their nest, will reject parasitic eggs by removing the whole clutch (including parasitic eggs) more often than individuals that do not observe a foreign female, but are still experimentally parasitised.

In the breeding season of 1998, we tested this hypothesis by experimentally parasitising Starling nests with a conspecific egg, and exposing some of the Starlings to a stuffed dummy of a foreign conspecific female.

## 2. Material and methods

### 2.1. Study area and field work

The field experiments were conducted during the 1998 breeding season. The study area, situated in Stjørdal in Central Norway (63 27’N, 10 55’E), comprised six small Starling colonies in an agricultural landscape situated from five to 30 meters above sea level. Here the term colony is defined as an assemblage of breeding pairs with a distance between neighbours not exceeding 20 m. One of the colonies was established prior to the 1998 breeding season. This colony consisted of 12 nestboxes in 1991–1996 and 14 in 1997 and 1998. The Starlings occupied several of these boxes each breeding season since 1991. The occurrence of conspecific brood parasitism had been recorded in this colony for every year prior to 1998 (A. Moksnes, pers. obs.). The number of active nests and parasitism events in this colony were also recorded in the years 1999–2002 (14 nestboxes in 1999 and 13 in 2000–2002). To establish new colonies, 100 additional nestboxes were put up after the breeding season in 1997. Each colony consisted of at least 15 boxes and were established on buildings at five different farms in the study area.

In the periods 1991–1997 and 1999–2002 the frequency of occupied nestboxes varied between 36 and 75%, with a mean of 53% (total n = 139). In 1998, 43 of 110 nestboxes (39%) were occupied. We recorded all breeding events in the nestboxes. To detect the occurrence of CBP, we recorded cases of two eggs being laid in the same nest per day during the laying period. Parasitism was also indicated by the occurrence of eggs laid before the onset of the host’s laying period, and after it had finished (for the applicability of this method see Yom-Tow 1980, Rohwer & Freeman 1989, Romagnano *et al.* 1989, Ringsby *et al.* 1993).

Clutch initiation was recorded by direct observation, and the nests were kept under observation from the beginning of the breeding season until hatching. In all nests, eggs were marked in sequence as laid with waterproof ink. Egg disappearance and natural CBP could then be recorded. The daily nest visits started about 11.00 a.m. when the egg-laying of the day usually was accomplished (Ringsby *et al.* 1993).

## 2.2. Experimental procedure

### *2.2.1. Egg experiments*

We performed the experimental parasitism by introducing a single foreign conspecific egg into the host's nest. Because the majority of parasitic Starlings do not remove host eggs during laying (34% removed eggs in the study of Lombardo *et al.* 1989), we did not remove any of the host's eggs. The colour contrast between the parasitic egg and the host eggs was subjectively classified into three categories (Moksnes 1992): Low; the parasitic egg could not be distinguished from the host eggs. Medium; the parasitic egg could be distinguished, but the difference was moderate. High; there was a marked contrast between the parasitic egg and the host eggs. Both the parasitic egg and the host eggs were marked with waterproof ink in sequence as laid. As a standard, the experimental parasitism as well as the dummy experiments were carried out on the third day during the hosts laying period, i. e. when the nests contained three host eggs. The experimental eggs used for these manipulations were collected, and chosen at random from other Starling nests in the study area. To ensure synchronous hatching, all experimental eggs were taken from nests that were at the same developmental stage as those of the host clutch into which they were introduced. The nests which were used to provide experimental eggs were not used for any other purposes. The artificially parasitised nests were controlled once a day during the first six days after the experiment. We considered introduced parasitic eggs to be accepted if they were still incubated at the end of this period (Moksnes *et al.* 1990). If the parasitic eggs had been ejected (together with the whole clutch) within six days after the experiment, this incident was recorded as a rejection of the parasitic egg.

### *2.2.2. Dummy experiments*

A stuffed female Starling that was placed in the nestbox aperture with the upper part of the body facing outwards, was used as a dummy. This experiment was carried out at the same time as the introduction of the parasitic egg. The number of Starlings present was noted, as well as the behaviour of each individual. The dummy was removed when it was obvious that the hosts had seen it for at least five minutes. In accordance with Moksnes *et al.* (1990), the behaviour against the dummy was classified as 1) not aggressive: the host had detected the dummy, without any indication of aggression, 2) mobbing: the host mobbed the dummy, usually from a distance of 0.5–1.5 m and 3) attack: the host attacked the dummy physically. To accomplish the experiments, two stuffed female Starlings were used, alternating between consecutive experiments to counteract possible effects of pseudoreplications (Hurlbert 1984, Kroodsma 1990).

## 2.3. Experimental- and control groups

The present experimental study included altogether 83 active nests, of which 40 were from the 1991–1997 breeding seasons, and 43 were from the 1998 breeding season. In 1998, 30 nests were used for experiments and 13 served as sources for experimental parasitic eggs or were naturally parasitised. Each experimental nest was tested only once.

Control group. No egg manipulation was performed, but the eggs were handled, marked and controlled in the same way as those in the experimental groups. The control group consisted of 40 nests, all from the years 1991–1997.

Experimental group 1. A single foreign conspecific egg was experimentally introduced into 15 nests.

Experimental group 2. A single foreign conspecific egg was introduced at the same time as the stuffed dummy was placed in the nestbox aperture. This experiment was carried out in 15 nests.

Experiments were not carried out in nests that already were naturally parasitised but one nest became parasitised by a conspecific after it had been experimentally parasitised. Both parasitic eggs were accepted.

## 3. Results

### 3.1. Natural parasitism

The number of parasitised nests in the periods 1991–1997 and 1999–2002 varied between zero and two per year. The overall parasitism rate for these years was 11.0% (eight out of 73 nests). This was quite similar to the parasitism rate recorded in the study year 1998, which was 9.3% (four out of 43 nests). The overall parasitism rate for all years was thus 10%. All eggs in one nest in the laying stage (containing five eggs) were found ejected on the day after it had been parasitised. Such ejection also happened in three other nests where parasitism was not recorded. These ejections could possibly have been a respons to parasitism (which we did not detect) but since eggs also may be ejected for other reasons (see Pinxten *et al.* 1995, Smith *et al.* 1996), these nests were not counted as parasitised.

Four parasitic eggs appeared during the host's laying period, of which three were accepted and one ejected together with the whole clutch. Two parasitic eggs laid before the host's laying were ejected. After termination of the host's laying, six parasitic eggs appeared, of which five were accepted and one ejected. Removal of host eggs (one egg) by the parasitic female occurred only in two of the 12 (16.7%) incidences of natural parasitism.

### 3.2. Experimental parasitism

The conspecific parasitic eggs were accepted in all 15 nests in each of the experimental groups. The presentation of the dummy had therefore no effect on the host's reaction against parasitism. There was no difference between the experimental groups and the control group where no eggs disappeared from the 40 nests. In 11 of the 30 experiments (experimental groups one and two), the contrast between the parasitic egg and host eggs was scored as low, in 15 experiments as medium and in 4 experiments as high. The distribution was similar in the two groups. However, since all parasitic eggs were accepted, the contrast between the host's own and the parasitic egg was clearly not important.

Most hosts (in 14 / 15 nests) were aggressive and attacked the dummy physically. Only in one case there was no aggression against the dummy. In case of aggression, both parents were typically present (in 12 / 14 nests) and participated in the attack. However, in some cases where both parents were present, only one of them was aggressive. This was usually the female (in four out of five cases).

## 4. Discussion

### 4.1. Natural parasitism

The frequency of natural conspecific parasitism in the present'study is within the range reported in other studies (see e.g. Evans 1988, Romagnano *et al.* 1990, Pinxten 1991a). Egg removal by the parasite did occur in two of the 12 nests (16.7%) which were naturally parasitised. This finding is not'significantly different from the results of Lombardo *et al.* (1989) where egg removal by the parasite occurred in 12 out of 35 boxes (34%) (Fishers exact probabilities test, two-tailed, n.s.) (See also Pinxten *et al.* 1991a). Although the data on host ejection of conspecific parasitic eggs are very limited in the present'study, they seem to confirm the general patterns found in other studies, where ejection of parasitic eggs only occur before the host's clutch initiation (Stouffer *et al.* 1987, Pinxten *et al.* 1991b). However, Stouffer *et al.* (1987) found that in four (out of 26) nests which experimentally received a parasitic conspecific egg after clutch initiation, all eggs, including the host's own eggs, were ejected. This is a similar reaction as was observed in one naturally parasitised clutch in the present study. Removal of all eggs after parasitism, therefore, seems to be a reaction against parasitism, although not so often used. Removal of all eggs could be regarded as a desertion and may be a beneficial behaviour in an environment where suitable nesting sites (boxes) act as a limiting factor.

### 4.2. Experimental parasitism

As expected, there was a complete lack of rejection behaviour among the Starlings whose brood was experimentally parasitised without being exposed to the dummy. This result is in accordance with results from earlier studies (Stouffer *et al.* 1987, Pinxten *et al.* 1991b, see also Eens & Pinxten 1999). However, the acceptance of all parasitic eggs in the second experimental group where the hosts were exposed to a stuffed female Starling, did not support the hypothesis of a conditional response against parasitism by ejecting the clutch. It has been confirmed in the present study and by Stouffer *et al.* (1987) that some individual Starlings are able to get rid of parasitic eggs during their own laying cycle by ejecting the whole clutch. Intuitively, this could be a response conditional upon perceiving a conspecific at the nest. It is therefore surprising that even with the sight of a foreign female, which should be a cue for parasitism, and also in spite of differences in contrast between host and parasitic eggs, no host ever ejected the clutch.

This result indicates that the Starlings in this population did not suspect that they were parasitised in spite of the presence of the female dummy against which they were very aggressive. However, aggression could be an adaptation against parasitism even if the parasitic egg was not recognised, because this behaviour could prevent the parasite from laying an egg in the nest (Power *et al.* 1981, Romagnano *et al.* 1990). On the other hand, such behaviour could also be considered as female–female aggression by the nestowner thereby counteracting her mate's opportunity to engage in extra-pair copulations with the foreign female (Sandell & Smith 1997). It is also possible that the Starling would have shown aggressive behaviour against any species placed in its nestbox aperture. Irrespective of the background, however, such aggression could indirectly serve as a protection against conspecific brood parasitism (see also Whittingham & Dunn 2001).

The results of the present study as well as results from several previous studies indicate that adaptations against conspecific parasitism is poorly developed in the Starling. Starlings are not able to recognise parasitic eggs after clutch initiation. The only response in case of suspected parasitism is to remove the whole clutch, including own eggs, which entails high costs of rejection. There is probably also a relatively low cost of being parasitised and, thus, the selective pressure for evolving anti-parasite responses would be small and not exceeding the costs of rejection and recognition errors.

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### Kokeellinen loismuninta ei johtanut kohonneeseen pesän hylkäämiseen hautovilla kottaraisilla

Kottaraisten pesäloisintaa tutkittiin Keski-Norjassa. Ennen kuin kottaraiset aloittavat muninnan, ne poistavat lajitoveriensa pesiinsä munimia loismunia. Aloitettuaan muninnan kottaraiset eivät yleensä enää kykene erottamaan loismunia omistaan. Tutkimuspopulaatiossa loismunia esiintyi 10 %:ssa pesistä. Kottaraisten on havaittu hylkäävän pesänsä loismuninnan jälkeen sekä tutkimusettä muissa populaatioissa. Tämä ilmiö mahdollisti ehdollisen hylkäämisreaktion tutkimisen tutkimuspopulaatiossamme. Kahdessa koeryhmässä oleviin pesiin laitettiin loismuna. Tämän lisäksi toisen loismunan saanen ryhmän pesien suuaukolle laitettiin täytetty kottaraisnaaras (ehdollinen ärsyke). Teorian mukaan pesällään vieraan naaraan nähneiden emojen tulisi hylätä pesänsä useammin kuin niiden, jotka eivät tätä ärsykettä koe. Edellä mainittua ilmiötä ei kuitenkaan havaittu. Vaikka naaraat näkivät täytetyn linnun pesällään ja käyttäytyivät aggressiivisesti sitä kohtaan, ne eivät hylänneet pesäänsä, eivätkä poistaneet pesästään yhtään munaa. Tulokset eivät tue teoriaa pesän ehdollisesta hylkäämisestä.

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