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Can Skylarks *Alauda arvensis* discriminate a parasite nestling? Possible case of nestling Cuckoo *Cuculus canorus* ejection by its host parents

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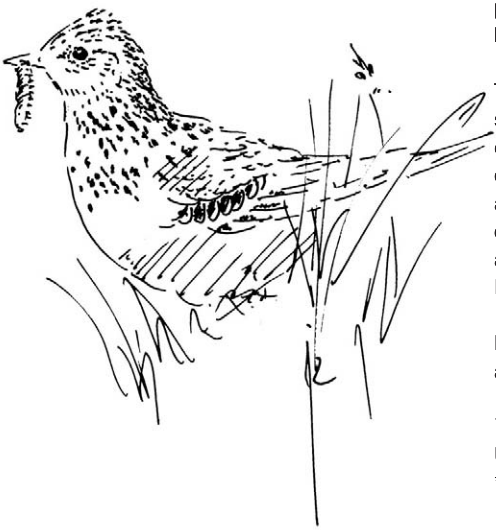

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The Common Cuckoo *Cuculus canorus* is an obligate brood parasite and many studies have dealt with egg rejection by host species. However, evidence for ejection of Cuckoo nestlings by host parents has not been reported. Here we describe an observation of a Skylark *Alauda arvensis* pair that probably ejected a young Cuckoo and subsequently raised their own offspring. This was the only case we detected Cuckoo parasitism among 348 Skylark nests in our study area in the northern Netherlands, while we found about 21% of 43 Meadow Pipit *Anthus pratensis* nests being parasitized by Cuckoos.

Key words: avian brood parasites, brood parasitism, evolutionary host–parasite arms races, nestling discrimination, nestling ejection, parasitizing

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The Common Cuckoo *Cuculus canorus* (hereafter, Cuckoo) is an obligate brood parasite which breeds across Eurasia (Glutz von Blotzheim & Bauer 1985, Davies 2000). More than 125 bird species are known as hosts, but only less than 20 are commonly used (Wyllie 1981, Moksnes & Roskaft 1995, Davies 2000). Many studies have dealt with egg rejection by host species (e.g. Moksnes & Roskaft 1989, Moksnes et al. 1991a, b, Honza & Moskat 2008, Vikan *et al.* 2010), but evidence for nestling rejection is very scare. There are several hypotheses to explain the lack of nestling discrimination (reviewed by Davies 2000, Grim 2006). The basic idea is that parents need to learn in their first breeding year how their own eggs and chicks look like, to be able to discriminate between own and foreign eggs/young. If parasitized in the first year, parents learn that their eggs are more variable (including the cuckoo egg), and in future years may not eject cuckoo eggs. In contrast, if they would imprint during the chick phase to find out how their own chicks look, a parasitized parent in the first breeding attempt would not accept its own young in future attempts, because cuckoo chicks eject host eggs and chicks (Lotem 1993). Chick discrimination therefore is more difficult and costly to evolve than egg discrimination, especially if parents need to learn the appearance of their own chicks. However, across the different avian host–parasite systems around the world, three ways that lead to nestling rejection have been identified. The nestling 'discrimination without recognition' hypothesis is based on tentative support that Eurasian Reed Warblers *Acrocephalus scirpaceus* might be able to discriminate own vs. parasite nestlings by the length of the feeding period, i.e. Cuckoo nestlings need to be fed for a longer period than own offspring. As the time span of parental care seems to be pre-programmed parents reduce or even stop feeding Cuckoo nestlings at their late nest stage (Grim *et al.* 2003, Grim 2007). However, experimental tests on other species found no evidence for discrimination against a nestling of a different species in their nest (Davies & Brooke 1989). Rejection of nestling parasites by deserting the nest in an early feeding stage has been rarely described for other parasite–host systems (see Grim 2006 and references therein). Direct nestling ejection (the physical removal of a live parasite nestling) has only recently been described for one host–parasite system. In Australia, two species of Gerygone *Gerygone laevigaster* and *G. magnirostris* regularly eject young of the Little Bronze-Cuckoo *Chalcites minutillus* (Sato *et al.* 2010, Tokue & Ueda 2010).

To our best knowledge, there is no record of a live nestling Common Cuckoo being ejected by its host parents (Davies 2000, see also Grim *et al.* 2003, Grim 2006). Here, we describe an observation of a Eurasian Skylark *Alauda arvensis* pair that most likely ejected a young Cuckoo and subsequently raised their own offspring.

Study population

In 2006–2009 we studied a breeding population of Skylarks in the "Aekingerzand", part of the National Park Drents-Friese Wold in the northern Netherlands (52°55'N, 6°18'E). The area is a mixture of open sand, groups of trees, heath- and grasslands on nutrient-poor soil and surrounded by a thin belt of forests. Beside 80–100 pairs of Skylarks and about 50 pairs of Meadow Pipit *Anthus pratensis*, several other passerine species (including Woodlark *Lullula arborea*, European Stonechat *Saxicola rubicola* and Tree Pipit *Anthus trivialis*) breed in the area. Every breeding season several male and female Cuckoos are present in the area.

Figure 1. Clutch of four Skylark eggs and one Cuckoo egg (based on coloration and size supposedly middle left). Picture taken by Rob Voesten, 27 May 2009.

Rate of parasitism in our study area

We found in four successive breeding seasons 2006–09 a total of 348 Skylark nests (163 were found during egg stage, but 62 failed before hatching; 184 were found when already in the nestling stage). We detected parasitism by a Cuckoo only once (0.3%), the case described here. Since Skylarks do not seem to reject foreign eggs (Antonov *et al.* 2010), it is unlikely that we missed parasitation events due to eggs being rejected before we found the nest. In the study area the Meadow Pipit is a common breeding bird and we checked some nests in 2008 and 2009. We found a total of 43 nests of which nine were parasitized by Cuckoos (20.9%). Of the 34 unparasitized nests we found 12 with eggs of which six failed before hatching and 22 nests contained nestlings when found. Of the nine nests that were parasitized five contained at the moment of finding eggs (of which three hatched, and two were depredated), and four a young Cuckoo.

Observation of nestling Cuckoo rejection

On 27 May 2009 we discovered an incubated Skylark nest with 5 eggs (Fig. 1). On 3 June (around noon) three young Skylarks had hatched (day 0); two eggs were still remaining, and we did not realise at that time that one was a Cuckoo egg. We did not visit the nest on 4 and 5 June. At 5:45 on 6 June, we found a young Cuckoo in the nest, and two of the four Skylarks chicks (age of all day 3) were out of the nests, probably ejected by the Cuckoo chick. The two young out of the nest were dead, the two inside still alive (Fig. 2). At around 14:00 the young Cuckoo was found about 30 cm out of the nest, being still alive as were the two nestling Skylarks in the nest. We returned the young Cuckoo into the nest. At 19:50 all three nestlings were still alive in the nest. At 6:30 next morning the female Skylark was brooding one nestling Skylark. The other nestling and the Cuckoo were found dead about 10 cm out of the nest. Both carcasses were already cold, but had very fresh and thus probably post-mortem injuries likely caused by a rodent. Small bites were visible on the back of one and the belly of the other bird. We ringed the remaining young Skylark on 10 June and it left the nest on 13 June 2009.

Discussion

We interpret the observation that the young Cuckoo was twice found outside the nest as an ejection (physical removal) by the host parents. The first time we moved it back to see if it got ejected again, and indeed the next day we found it outside the nest for the second time. It was probably ejected from the nest in the early morning of that day after it presumably managed to eject one more Skylark nestling.

Two alternative explanations why the young Cuckoo was outside the nest seem very unlikely to us. (1) The young Cuckoo fell out of the nest while trying to eject a nestling Skylark. Such cases have rarely been described for Reed Warbler nests (Wyllie 1981), but seem unlikely for a ground nest in a shallow depression. (2) A predator took the Cuckoo nestling out of the nest. Predators would not leave nestlings next to the nest without eating any. Furthermore, during our study we never observed any similar cases of nestlings being dead or alive just outside the nests. We therefore believe that both alternative hypotheses are unlikely and instead postulate an active physical ejection of the live parasite nestling by one of the parent Skylarks.

Such behaviour is not only astonishing because we know of no published case of Cuckoo nestling ejection by host parents, but also because Antonov *et al.* (2010) showed in an experimental study a complete lack of egg recognition abilities in Skylarks and suggested that anti-parasite defences never evolved in this species. Skylarks are only rarely reported as host for Cuckoos (Glutz von Blotzheim & Bauer 1985, Moksnes & Roskaft 1995, Davies 2000) and the few known cases have been attributed to Cuckoo females that were unable to find a suitable nest of the preferred Meadow Pipit (Davies 2000). The 'spatial habitat structure hypothesis' suggests that Skylarks are usually breeding too far away from trees to be a potential Cuckoo host (Roskaft *et al.* 2002, Antonov *et al.* 2010). In our study area Skylarks and Meadow Pipits share the same meadows for breeding, both equally close to single trees, hence the chances for a female Cuckoo finding nests should be similar for these species. However, Meadow Pipits were commonly parasitized in our study, whereas we discovered only a single case of Cuckoo parasitism among 348 Skylark nests over four years. Meadow Pipits are one of the most common Cuckoo hosts in Europe (Glutz von Blotzheim & Bauer 1985, Moksnes & Roskaft 1989, Davies 2000). We also noted that Meadow Pipits strongly reacted to the presence of an adult Cuckoo and expressed intensive antagonist and alarming behaviour, while we never observed a similar reaction in Skylarks.

Why then the egg was laid into a Skylark nest in the first place remains speculative. Individual Cuckoo females usually specialize in parasitizing one particular host species (Lack 1968, Davies 2000, Honza *et al.* 2001) or a group of species that have similar eggs and nests (Moksnes & Roskaft 1988). Laying in a nest of a species that is not commonly parasitized but that has similar nests and eggs in the same habitat has been suggested when a nest of the preferred host species is unavailable (Davies 2000). For the case described here, we suggest the same mechanism. A suitable Meadow Pipit nest was unavailable at the moment of laying and thus the female Cuckoo chose for a Skylark nest.

Our observation is anecdotal, and it remains to be tested experimentally if Skylarks have a more general ability to reject Cuckoo nestlings from their nest. This would be spectacular, because current models of evolutionary host–parasite arms races are to a large extent based on the idea that egg discrimination evolves more easily than chick discrimination (Lotem 1993). If egg discrimination can evolve more easily it might also explain why species that are recently not parasitized show advanced egg recognition abilities. These species probably have a history of Cuckoo parasitism that led to the evolution of egg discrimination (Schulze-Hagen *et al.* 2009). However, there may be (few) species that have evolved chick discrimination rather than egg discrimination as a viable anti-parasitism strategy. This may not be through discrimination of own offspring against a young parasite, but rather by rejecting nestlings that eject

Figure 2. Two young Skylarks and one young Cuckoo. Same nest as in Fig. 1. Picture taken by Rob Voesten, 6 June 2009.

other offspring from the nest. In this light, it is interesting that in our case the Cuckoo nestling hatched not first as it is usually the case (Davies 2000), but later than some of the Skylark nestlings. It is remarkable that the incubation period of Skylark and Cuckoo eggs is similar with 11–12 days (Wyllie 1981, Glutz von Blotzheim & Bauer 1985), and thus the head start Cuckoo eggs usually have because of the internal incubation (Birkhead *et al.* 2011) is not bringing any advantage in Skylark nests. As a result, the Cuckoo chick hatched later than the first Skylark nestlings, and at this moment the host parents were more likely to discriminate against the Cuckoo chick that started to eject the other nestlings from the brood.

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Samenvatting

Er is veel onderzoek gedaan naar de wijze waarop waardvogels een ei van de Koekoek *Cuculus canorus* in hun nest onderscheiden en vervolgens verwijderen. Zodra een Koekoeksjong uit het nest gekropen is lijkt het risico van herkenning geweken en er is nooit vastgesteld dat waardvogels een Koekoeksjong uit hun nest werken. Dit artikel betreft een waarneming van een paartje Veldleeuwerik *Alauda arvensis* dat waarschijnlijk een jonge Koekoek uit het nest verwijderde, waarna ze hun eigen jong grootbrachten. Dit was het enige geval van parasitisme door de Koekoek bij 348 nesten van de Veldleeuwerik die in het onderzoeksgebied Aekingerzand (onderdeel van het Nationale Park Drents-Friese Wold) werden gevonden. Graspiepers *Anthus pratensis* in hetzelfde gebied werden daarentegen wel veel geparasiteerd (21% van 43 nesten). (JP)

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