NEST DEFENCE STRATEGIES IN THE FIELDFARE *TURDUS PILARIS*: THE RESPONSES ON AN AVIAN AND A MAMMALIAN PREDATOR

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The Fieldfare *Turdus pilaris*, a medium-sized passerine, is aggressive in nest defence and its use of faeces may be detrimental to avian but not to mammalian predators. The birds breed either solitarily or in colonies, the nesting pattern in subalpine forests is apparently dependent on the abundance of small rodents. In the crash year following a year with high density of small rodents, the staple food of several mammals, mustelids as Stoats *Mustela erminea* are forced to find alternative prey as eggs and nestlings. The year 2003 was such a small rodent crash year in subalpine birch forests in the middle of Norway. The Fieldfares then bred solitarily and behaved more inconspicuous towards a human observer compared to the previous year. The majority of the pairs studied, left the nest silently when a life-like Stoat was mounted 10 m from the nest tree, whilst most pairs attacked a Hooded Crow *Corvus corone cornix* mounted at the same place. When these dummies were placed 1 m from the nest tree, the Fieldfares attacked both dummy models intensely. The birds return to the nest after the dummy was removed, was later for the Stoat than for the Hooded Crow dummy. These results suggest that the Fieldfare responds specifically to nest predators: trying to avoid disclosing the nest containing eggs or nestlings for an olfactory oriented mammal, the Stoat that is scarcely deterred by the birds defecation, but attacking the Hooded Crow with use of ejected faeces that may be detrimental for the avian nest predator. When the predator is close to the nest, however, the best strategy may be to distract the predator away from the nest. The late return to the nest after the Stoat exposure, may be explained by the Fieldfares' behaviour towards a predator that is a lethal threat to the breeding bird.

Keywords: *Turdus pilaris* – nest defence – *Corvus corone cornix* – *Mustela erminea*

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INTRODUCTION

Nest predation strongly reduces the reproductive success of birds (e.g. Nilsson 1984; Martin 1988a), and about 60% of all losses of the eggs and nestlings of temperate-zone passerines are due to predation (Ricklefs 1969). Nest predation thus represents a very strong selective factor, and birds have evolved various anti-predator strategies which may reduce nest losses. In a mountain birch forest in Budal, central Norway, breeding passerines have been studied each year since 1966 (Hogstad 2000). In this area, the Fieldfare *Turdus pilaris*, a northern and subalpine species, suffers high rates of nest predation (Hogstad 1983, 1995). More than half of the pairs studied, annually lost their eggs or nestlings, mostly due to predation (Hogstad 1983). In some years, every nest found in the birch forest was abandoned. The majority of the nests which had been preyed upon revealed no

traces of the predator. However, in a few cases the lining of the nest cup was disturbed, indicating that the nest content had been taken by a mammalian predator. Teeth marks on destroyed eggs consistent with Stoats *Mustela erminea* (Hogstad 1996) strengthens this suggestion. Other nest predators in the area were Ravens *Corvus corax* (one pair), Hooded Crows *Corvus corone cornix* (one or two breeding pairs), Pine Martens *Martes martes* and Least Weasels *Mustela nivalis*.

The Fieldfares nest either in colonies or solitary. Since the nest predation rate in Fieldfares is density dependent (Wiklund 1982; Hogstad 1995), and since their use of ejected faeces in communal defence may be detrimental to avian but not mammalian nest predators (e.g. Bezzel 1975; Mester 1976; Weatherhead & Sommerer 2001), it has been suggested that a high density of mammalian predators (e.g. mustelids) results in selection for solitary breeding, whilst a dominance of avian predation risk selects for colonial breeding (Hogstad 1995). In Fennoscandian subalpine birch forests, the population densities of Stoats and Least Weasels follow the changes in small rodent populations. The densities of weasels track changes in vole densities with a six to 12 months lag, and in years when small rodents crash, Stoats shift to alternative prey, among which small passerine birds and their nest contents are important (e.g. Wiklund 1982; Järvinen 1985; Korpimäki *et al*. 1991; Hogstad 1995, 2000). In such small mammal crash years, nests of Fieldfares were subjects to increased nest predation (Hogstad 1995).

The densities of small rodents, especially of Norway Lemmings *Lemmus lemmus*, were high in mid Norway in 2002. During the late summer and autumn, however, the populations of small rodents crashed. Thus, despite daily observations of small rodents in the Budal area in 2002, I did not observe any in the following winter and in the spring 2003. It was therefore predicted 1) that Fieldfares breeding in the study area, in attempt to reduce the nest predation by mammals, should nest solitarily in 2003. Fieldfares mob avian predators, but have less ability to defend nests from mammals. If Fieldfares have the ability to evaluate threats from potential predators, the birds should behave different in the presence of a visually oriented Hooded Crow (the most serious predator of eggs and nestlings of thrushes in Norway; Haftorn 1971), and an olfactory oriented mammal, the Stoat that moreover is a threat to the breeding bird (Lübcke & Furrer 1985). Thus, I predicted 2) that Fieldfares, in order to avoid disclosing their nest site, should be inconspicuous and behave in a more sneaky manner towards an approaching Stoat than towards a Hooded Crow. However, when the predator is close and apparently has discovered the nest, I also predicted 3) that Fieldfares should increase their nest defence towards the Hooded Crow in order to distract the predator away from the nest, whilst they should behave more carefully towards the Stoat. Because the Stoat represents a lethal risk to the breeding Fieldfare, I predicted 4) that the birds' return to the nest, after the dummy was removed, should be later to the small and slipping Stoat than for the larger and far more visible Hooded Crow. As a part of a yearly program on the breeding ecology of the Fieldfare, also the response against a human predator (the observer) was made (see Hogstad 1993). If most pairs nest solitarily in 2003 and moreover behave in an inconspicuous way, I also predicted 5) that the nest defence intensity against the observer should be relatively low (fewer attacks in 2003 compared to the preceding year).

METHODS

The Fieldfare study, a part of a passerine community study started in 1966, was carried out during the breeding season 2003 in a homogeneous, subalpine, heath birch *Betula pubescens* ssp. *czerepanovii* forest in Budal (*c*. 63 °N), central Norway. The forest extends from 750 to 900 m a.s.l., and the general tree height is 3-6 m. The Fieldfare is a medium-sized passerine (mean body weight females 111 g, males 114 g; unpubl. data) that builds open, cup-shaped and conspicuous nests in trees. The majority of the nests are placed in a fork between the trunk and a branch, 1.5-5 m above ground. They are well visible and probably easy to detect for predators, and has an easy access for mammalian as well as avian predators. The Field-

fare has shown great annual variation in breeding density in the study area (1966-2003: 3–63 pairs per km^2; mean 24.1 ± 15.2 SD). The species nests either solitary or in colonies (colony size in the study area is 2-6 pairs; Hogstad 1995). The nest dispersal is correlated with predator abundance. Thus, there is a relationship between the yearly small rodent density and the number of Fieldfare colonies in the area (r_S = 0.77, P < 0.001, n = 24). Furthermore, the proportion of Fieldfares breeding in colonies is correlated with the rodent density (r_S = 0.46, P = 0.03, n = 22; unpubl. data). The clutch size is 5-6 eggs (4-8), incubation period 12-13 days and nestling period 13-14 days (Haftorn 1971). Only the females build the nest, incubate the eggs and brood the young.

The presence of Stoats in the area was disclosed by their characteristic droppings, a headless Yellow Wagtail *Motacilla flava* stored in a birch tree, and in addition to occasional observations of the species, an observation of one animal climbing in a birch tree containing a Fieldfare nest.

The field experiments were made when the Fieldfares were in their second week of incubation or during hatching. A few females sat tightly, but left the nest when the observer knocked against the trunk of the nest tree. Then the defence reaction of the parents towards the observer was noted when the observer stayed by the tree for about one minute. Shortly afterwards, a dummy Hooded Crow or a Stoat was placed on a one meter high pole about 10 m from the nest tree. The response of the parents, most often the female, on the dummy was recorded from a distance of 20-25 m. Subsequently the dummy was placed 1 m from the nest tree. The two dummy models were exposed in a random order at each nest, and the two models were separated by a pause of 1-2 hours. The dummy was placed for a 10-min interval at each given distance. After the dummy was removed, the time when the Fieldfare returned to the nest was noted. Each experiment was conducted on a different nest, in total 16. In addition to these pairs, the Fieldfares' defence reaction towards an observer (see above) was noted for 18 other pairs (in total 34 pairs).
The reaction of the birds was recorded according to the following predetermined scale: 1) leaving the nest area silently, but giving alarm calls whilst staying more than 40 m away from the nest; 2) leaving the nest area silently, but calling persistently whilst remaining more than 15 m away from the nest; 3) attacking the predator, frequently also by defecating.

The effects of multiple trials on Fieldfares have previously been tested, showing that the nest defence behaviour was not influenced by the number of repeated experiments (Hogstad 1991; Meilvang *et al*. 1997).

All tests are two-tailed, and were performed using SPSS 11.0 for Windows. Means are presented ± 1 SD.

RESULTS

The Fieldfares nested solitary, i.e. nested more than 100 m from the nest of their nearest neighbour. The only colony found in the area (consisting of six pairs, maximum distance from their nearest neighbour was 35 m), was abandoned during the egg laying period or in the beginning of the incubating period as a consequence of nest predation. When the birds still were active in the colony, their response towards the observer approaching their nests was relatively aggressive, and most birds called persistently and remained close to their nests or attacked the observer.

As predicted, the Fieldfares responded differently towards the Hooded Crow and the Stoat. Within one-two minutes of the first alarm calls, the majority of the Fieldfares (mostly the female) began to mob the crow, that was mounted 10 m from the nest tree, by swooping attacks, while they attacked the Stoat, mounted at the same place, less frequently (Table 1). Thirteen of the 16 Fieldfares (81%) attacked the Hooded Crow, while only five (31%) attacked the Stoat. The remaining 11 Fieldfares tested stayed more than 40 m away from the nest when the Stoat was exposed, apparently behaving in a way not to disclose the nest. The response patterns (attack versus no attack = defence reactions 1 and 2 pooled) towards the two predator models differed significantly (χ^2 = 6.22, df = 1, P = 0.01).

Table 1. The reaction of 16 Fieldfare pairs, during their second week of incubation or during hatching, on a stuffed Hooded Crow or a Stoat placed on a pole 10 m and 1 m, respectively, from the nest tree. Figures denote number of parents. Defence reaction of the birds: 1 = leaving the nest area silently, giving alarm calls whilst staying more than 40 m away from the nest; 2 = leaving the nest area silently, calling persistently whilst remaining more than 15 m away from the nest; 3 = attacking the predator, frequently also by defecating.

	10 m Defence reaction			1 m Defence reaction		
Predator	1	2	3	1	2	3
Hooded Crow	0	3	13	0	0	16
Stoat	11	0	5	2	2	12

The responses of the Fieldfares to the Hooded Crow and the Stoat placed only 1 m from the nest tree, however, showed no difference ($\chi^2 = 2.57$, $df = 1$, $P = 0.11$). Thus, while the anti-predator behaviour of the Fieldfares were similar whether the Hooded Crow was 10 m or 1 m from the nest ($\chi^2 = 1.47$, $df = 1$, $P = 0.23$), the reaction pattern on the Stoat differed ($\chi^2 = 4.52$, $df = 1$, $P < 0.05$). As expected, the Fieldfares behaved very aggressively when the Hooded Crow was close to the nest. Unexpectedly however, also the response on the Stoat was strong, and 75% of the Fieldfare pairs tested attacked the mammal mounted 1 m from the nest tree.

The return time to the nest, after the dummy was removed, was significantly longer for the Stoat (3-10 minutes, mean 5.5 ± 2.3) than for the Hooded Crow (1-4 minutes, mean 2.3 ± 0.9; Mann-Whitney *U* -test, $z = -4.17$, $P < 0.001$, $n = 15$).

The response towards the observer was as expected: most pairs behaved inconspicuously and only 3 of 34 pairs (9%) attacked the observer whilst 8 of 26 (31%) did so the preceding year ($\chi^2 = 3.39$, $df = 1$, $P = 0.06$). Among 18 pairs that were followed up whether they got fledglings, 15 did not attack the observer, whilst three did. Of these 15 pairs, 9 succeeded and 6 were robbed, while all 3 pairs that attacked the observer were robbed. Although the sample size is small, there is a tendency for Fieldfares behaving inconspicuously to be less predated than those who attacked the observer and apparently disclosed their nest site.

DISCUSSION

The Fieldfares suffer high rates of nest predation (Hohlt 1957; Furrer 1980; Wiklund & Andersson 1980; Hogstad 1983), probably because of their large and conspicuous nests which are easy to detect, and by their generally noisy behaviour near their nest sites. The patterns of nest spacing and difference in defence behaviour towards the avian and the mammalian predator found in the present study, may be explained as an adaptation to the local predation pressure. Communal defence by colonial breeding Fieldfares that use ejected faeces as an additional deterrent, may pose a lethal threat to the Hooded Crow because the faeces soil the plumage and destroy its insulating properties (Bezzel 1975; Furrer 1975; Mester 1976), but are less likely to deter the fur of the Stoat (e.g. Mester 1976; Weatherhead & Sommerer 2001). The Stoat is an efficient climber, and has been observed systematically climbing every tree in the wood searching for food (Norman 1994). Moreover, mustelids are active mainly during night when Fieldfares cannot employ such method of attack. Fieldfares therefore may reduce nest predation by nesting solitary because a clumped distribution of nests may increase the possibility of nest detection and total loss to mustelids that are not deterred by colonial defence. In accordance with the suggestion that the predation rate in the Fieldfare is positively related to the bird density in small rodent crash years (Hogstad 1995), all nests in the only colony found in the study area in 2003, were robbed. The distribution and density of Fieldfare nests, may therefore be a response of mustelids that are forced to find alternative food (see also Schmidt & Whelan 1999). Predators that find nests with eggs or young, may intensify their search for other similar nests, and a clumped distribution of nests therefore increase the risk of being predated (Martin 1988b; Hogstad 1995). Earlier studies in the Budal area have shown that colonies are frequent-

ly totally destroyed when discovered by predators (Hogstad 1983). The suggestion that nest predation is a major factor in determining the dispersion pattern in the Fieldfare, is strengthened by the fact that the fluctuation in small rodent density explained about 60 % of the variation in the number of Fieldfare colonies during 24 consecutive years (unpubl. data). Thus, predation events may create selective advantages to disperse.

The Fieldfares discriminated between the avian and the mammalian dummies. Although there was a between-pair variation in the ability to defend their nest against these predators, the majority of the Fieldfares followed a similar pattern. The responses to the Hooded Crow were strong both when the dummy was placed 10 m from the nest and when it was closer to the nest, whilst the response to the Stoat was strong only when it was placed 1 m from the nest tree. The experiments supported the prediction that the best strategies for parents are to be inconspicuous in presence of the olfactory oriented Stoat, but attack the approaching Hooded Crow and use ejected faeces that may soil the plumage of the bird predator. A strong response to the Stoat being close to the nest tree, however, may have a confusing effect and also distract the attention of the predator onto themselves. After the predator models were removed, the Fieldfare females had to decide how long to wait before returning to the nest. The longer return time facing the Stoat compared to that of the Hooded Crow may be explained by their different element of risk. Because the small and rather cryptic Stoat, in addition to be a nest predator, also represents a deadly danger to the breeding Fieldfare, the birds have to make sure that the mammal has left the nest site. Whether the large Hooded Crow is still near the nest or not, is easy to detect.

The tendency found for inconspicuous Fieldfares to be less predated than those that defended their nest vigorously, may be related to their physical condition (Hogstad 1993) as well as the effect of reduced risk for disclosing their nest site. However, earlier studies have revealed no relationship between the intensity of nest defence behaviour of Fieldfares and their breeding success (Meilvang *et al*. 1997; Hogstad unpubl. data).

To conclude, the results suggest that predation events may create a selective advantage to disperse. The Fieldfares discriminate between nest predators and respond differently towards them, depending on the threats involved.

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SAMENVATTING

Nestpredatie is een belangrijk gegeven voor veel vogelsoorten. Afhankelijk van de predator bestaan er verschillende mogelijkheden om predatie te minimaliseren. Kramsvogels *Turdus pilaris* in Noorwegen hebben te maken met grondpredatoren als Hermelijnen en Wezels. Deze roofdiertjes eten in knaagdierrijke jaren vooral lemmingen en nemen in zulke jaren in aantal toe. Na het instorten van de knaagdierpopulatie vormen de roofdiertjes een belangrijk gevaar voor de nesten van vogels. Daarnaast hebben nesten van Kramsvogels te lijden van predatie door kraaiachtigen. Verschillen tussen deze predatoren zijn dat de kleine marters vooral op de geur jagen en ook een gevaar voor de broedende ouders vormen, terwijl kraaien vooral zichtjagers zijn die mogelijk te verjagen zijn door een gericht poepbombardement van de Kramsvogels. Daarom is gesuggereerd dat in jaren met weinig predatie door kleine marters, de Kramsvogels in kolonies zouden moeten broeden, die gezamenlijk verdedigd kunnen worden tegen kraaien. In jaren met een hoge predatie door kleine marters zouden de vogels vooral solitair moeten broeden. Kramsvogels bleken inderdaad meer in kolonies te broeden in jaren met veel lemmingen (dus weinig vogelpredatie door de twee roofdiertjes) en meer solitair in jaren met weinig lemmingen (dus veel predatie door deze roofdiertjes). In 2003, een jaar met weinig lemmingen en solitair broedende Kramsvogels, is een aantal experimenten uitgevoerd om de reacties van Kramsvogels op de predatoren te onderzoeken. De reacties op een opgezette Hermelijn en Bonte Kraai Corvus cornix verschilden sterk. Kraaien werden van nabij aangevallen, terwijl voor Hermelijnen op een grote afstand van de predator werd gealarmeerd. Nadat het opgezette dier was verwijderd, duurde het bij de Hermelijn veel langer dan bij de Bonte Kraai voordat de Kramsvogels naar het nest terugkeerden (waarschijnlijk omdat Hermelijnen minder zichtbaar zijn en ook voor de ouders een groter gevaar vormen dan kraaien). De verschillende reacties op predatoren zullen, samen met de keuze voor het al of niet in koloniaal verband broeden, de predatiekans van een nest minimaliseren. (CB)

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