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Fieldfare (*Turdus pilaris*) Breeding Success in Relation to Colony Size, Nest Position and Association with Merlins (*Falco columbarius*)

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Summary. Clutch size, nestling production and breeding success were studied in colonial Fieldfares (*Turdus pilaris*) in a subalpine birch forest during ten breeding seasons. Reproductive success was highest for central pairs in large colonies; such pairs benefited most from communal defence against nest predators. Fieldfares and Merlins (*Falco columbarius*) usually bred in association. Fieldfares breeding away from Merlins had lower breeding success than pairs associated with Merlins, which also benefited by reduced nest predation. Fieldfares apparently chose to nest near Merlins, which had already laid eggs when the thrushes started nest-building.

Introduction

Colonial breeding occurs in many bird species. Some of the selective forces suggested to favour coloniality are increased foraging efficiency (Horn 1968; Ward and Zahavi 1973; Krebs 1978) and reduced nest predation resulting from communal defence (Kruuk 1964; Patterson 1965; Andersson and Wiklund 1978; Wiklund and Andersson 1980) or 'predator swamping' (Kruuk 1964; Robertson 1973). Shortage of suitable nest sites may also force otherwise solitary birds to nest in colonies (Lack 1968).

Several studies have shown that individuals at the edge of a colony produce fewer offspring than those in the centre (reviews in Krebs 1978 and Burger 1981). For some group-nesting species there is experimental evidence for reduced nest predation as an advantage of colonial breeding (Kruuk 1964; Veen 1977; Andersson and Wiklund 1978). Successful mobbing of predators has been demonstrated in the Black-headed Gull (*Larus ridibundus*) (Kruuk 1964) and in the Bank Swallow (*Riparia riparia*) (Hoogland and Sherman 1976).

Breeding associations between two or more species have been described where at least one species regularly nests in colonies. In some cases one of the associated species is a potential predator of the other (Hagen 1947; Cade 1960; Wiklund 1979). Efficient nest defence by one of the associated species may improve the breeding success of the weaker one (Bengtsson 1972; Fuchs 1977; Clark and Robertson 1979). It is not always clear why the stronger species accepts the association. The weaker species could increase the detectability of the nest area and consequently the risk of predation because predators are often attracted by clumped prey (Curio 1976).

The Fieldfare, which nests in trees, presents an exception to many other passerines since it breeds both in colonies and solitarily, and sometimes is associated with predatory birds (e.g. Hagen 1947; Hohlt 1957a; Wiklund 1979). It is therefore well suited for studies of the adaptive value of coloniality and breeding associations between species. In this report, I examine Fieldfare breeding success in relation to colony size, nest position in the colony and association with nesting Merlins (*Falco columbarius*).

Materials and Methods

The study was carried out at Staloluokta, Padjelanta National Park (67° 18′ N, 16° 43′ E), N Sweden. During 1971–1975 fieldwork was conducted from the beginning of June to about July 15. During 1976–1980, it was prolonged to the end of July. The study area usually contained about six Fieldfare colonies before 1976, when it was enlarged. Afterwards it included about two more Fieldfare colonies.

The isolated birch forest of 18 km^2 at Staloluokta is about 40 km from the nearest forested region. The habitat is heterogenous and includes lakes, marshes, heaths, willow (*Salix sp.*) areas and birch groves. In some groves the ground vegetation

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is of heath character, whereas in others tall herbaceous plants predominate at the end of the breeding season. The birches (*Betula sp.*) rarely reach a height of more than 10–12 m and have a rich branch structure that starts some feet above the ground.

Clutch size, hatching success and fledgling production were recorded in Fieldfares, Merlins and in the main nest predator, the Hooded Crow (*Corvus cornix*).

Partial nest losses due to predation were rare, being recorded in 7 of all 640 nests found. Furthermore, these nests were always abandoned by the adults and therefore were easy to classify. Since the adults removed dead nestlings from the nest and the nesting area, disappearances of single nestlings have been attributed to nestling mortality due to starvation. This occurred in 200 nests. Nests from which the adults disappeared (10 nests) have been omitted from the calculations.

During 1977–1979, clutch size, nestling production, nestling mortality due to starvation, fledgling production, nest survival and the number of nests with unhatched eggs were studied in central and peripheral Fieldfare pairs.

Since the study area was completely searched for nests about seven times during each field season, it is unlikely that any Fieldfare colony or nests of the Hooded Crow or Merlin were overlooked. On the other hand, some solitary Fieldfare nests may not have been found.

A distance of 75 m between a Fieldfare nest and its nearest conspecific was used to separate solitarily breeding pairs from those nesting in colonies (see Andersson and Wiklund 1978; Wiklund and Andersson 1980). The same distance was used to determine whether a Merlin pair was associated with a colony or not.

During 1971–1975 the last check of reproductive success was done when the chicks were ringed, usually 1–4 days before fledging. From 1976 to 1980 most nests of the three species were checked every second day until the chicks fledged.

Eighteen Fieldfare colonies were mapped and inter-nest distances measured in 1977–1979. A convex polygon was created by connecting the nests on the edge of each colony with a line. All nests inside the polygon were considered as central ones and those at the corners as edge nests.

The rodent population, which undergoes 4-year cycles in northern Scandinavia, crashed in May 1975. Since the population of the Hooded Crow also reached a peak this year, predation on Fieldfare nests was extreme. In addition, this was the coldest summer during the whole investigation period, and no chicks fledged from any fieldfare nest. As this year was exceptional, I have omitted data from 1975 in calculations of reproductive success and nest survival. In 1979, the next year with high predation rate, I protected one large colony against predation. Results from this colony were also omitted from the calculations.

Data from each year were initially tested separately and then the results for all years were weighted together. Unless otherwise stated, all tests are two-tailed Pitman tests (Mantel 1963; Bradley 1968).

Results

All Fieldfare nests were in birches, usually near the trunk and in the middle of the tree, 2.0–3.5 m above the ground. There was no apparent difference in nesting height between thrushes associated with a pair of Merlins and thrushes breeding away from Merlins. Centrally placed nests as well as nests on the fringe of the colony also seemed to be at similar levels above the ground (Wiklund, in preparation).

Availability of Nest Sites and Association with Merlins

Merlins arrive earlier than Fieldfares, often in late April. Their breeding cycle also starts earlier and the female is usually incubating when Fieldfares select nest sites.

To evaluate the supply of suitable nest sites I investigated the following predictions from Lack's nest-site limitation hypothesis (1968): if suitable nest sites are in short supply, areas well suited for breeding should be used regularly and the colony size should be correlated with the population size. Furthermore, only at extreme levels would population size influence the number of colonies. During 1971–1980 the number of breeding Fieldfares varied synchronously with the two rodent cycles, but the population peaks were displaced with 1 year relative to the rodent population peaks (Table 1). No correlation was found between colony size and Fieldfare population size ($P > 0.43$). The number of colonies, on the other hand, was positively correlated with the size of the breeding population ($P < 0.01$, Spearman r_s, Siegel 1956). The spatial distribution of colonies within the study area changed between years, independently of population size. Thus, colony sites used in earlier years could be empty during one or several breeding seasons. Furthermore, colonies only occupied a minor part of the fairly homogenous birch groves. In 1979, the year with the largest number of breeding Fieldfare pairs (Table 1), 5% of the forested area commonly used for breeding was occupied by colonies without a Merlin pair. Fieldfare colonies associated with Merlins occupied 10% of the forest. Two additional pairs of Merlins nested in the remaining 85% of the potential breeding habitat for both Fieldfares and Merlins.

Hagen (1947) proposed that Merlins occur in Fieldfare colonies simply because of similar habitat preferences. I examined this hypothesis in the following way: for each year, all Fieldfare colonies and Merlin nests were marked on maps of the study area. A grid of 500 × 500 m squares was superimposed on each map; the largest colony was 400 m in length. Thus no colony extended over more than one full square. On another map all breeding sites of Merlins and Fieldfares during 1971–1980 were summarized. Squares with birch forest where neither species had bred were excluded to reduce the possibility that some un-

Table 1. Fieldfare colony size and number of breeding pairs 1971–1980. $+M$ Fieldfares associated with Merlins; $-M$ Fieldfares not associated with Merlins

Year	Colony size (pairs)																									Total	% +M	% −M
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	19	20	21	22	24	27	29	31	41			
+M						1	1												1									
1971																										35	97	3
−M	1																											
+M		1	1	1			1																	1				
1072																										49	96	4
−M		1																										
+M				1	1	1									1			1										
1973																										61	82	18
−M	1			1		1																						
+M			1		1		1				1	1																
1974																										79	48	52
−M	1							1		1										1								
+M							2					1					1											
1975																										88	51	49
−M	1		1							1													1					
+M			1			1					1					1												
1976																										41	88	12
−M					1																							
+M				1		1			1				1															
1977																										78	41	59
−M	6	1	1					1														1						
+M		1		3	1										1						1							
1978																										81	72	28
−M	4	1						1	1																			
+M	1							1	1	1															1			
1979																										94	73	27
−M	1	2					1						1															
+M	1					1								1														
1980																										35	60	40
−M			1								1																	
																											70.8	29.2

known habitat factor had influenced the nest-site choice and consequently the breeding association of the species (this procedure eliminated 9 of the 70 squares with birch groves). For every year there is a large difference between the expected and the observed number of associated colonies (Fig. 1). This strongly suggests that the association between the two species is not mainly due to similarity in habitat requirements, but rather to a positive response by Fieldfares to the presence of a pair of Merlins.

Colony Structure

The colonies varied from elongated to circular. Though they were often elongated, the number of centrally situated nests increased with colony size ($P<0.01$, Spearman r_s, Siegel 1956).

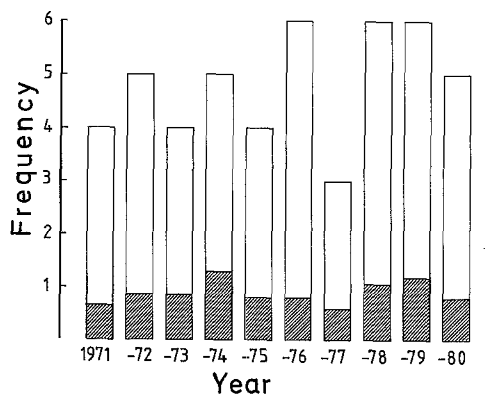

Fig. 1. The frequency of squares with both Merlins and Fieldfares. The frequency expected if Fieldfares do not respond to the presence or absence of Merlins is shown as a *shaded part* of the observed frequency. The observed association is consistently higher than expected, which indicates that Fieldfares prefer to nest near Merlins

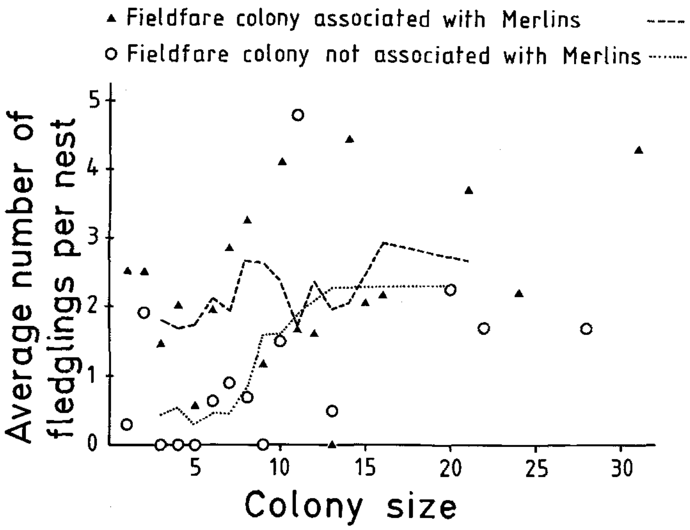

Fig. 2. Average number of fledglings produced per nest in Fieldfare colonies of different sizes. Data for Merlin-associated (▲) and non-associated (○) colonies are shown separately. The curves showing averages (constructed as the mean of 5 adjacent points) indicate that fledgling production is higher for Merlin-associated Fieldfares breeding in colonies of small-to-moderate size

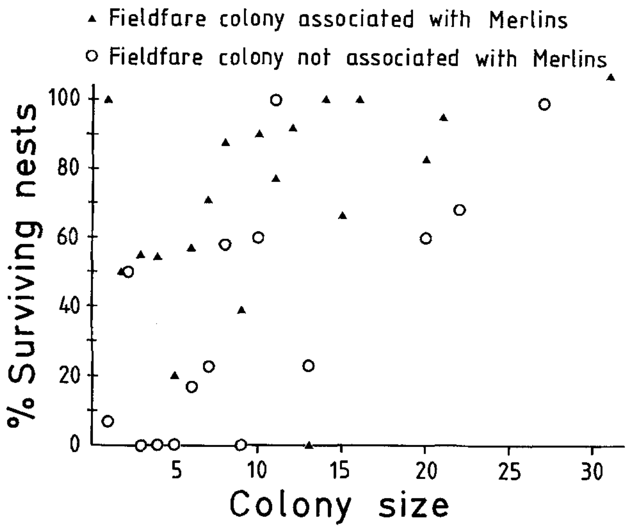

Fig. 3. Percent surviving nests in relation to colony size for Merlin-associated (▲) and non-associated (○) Fieldfare colonies

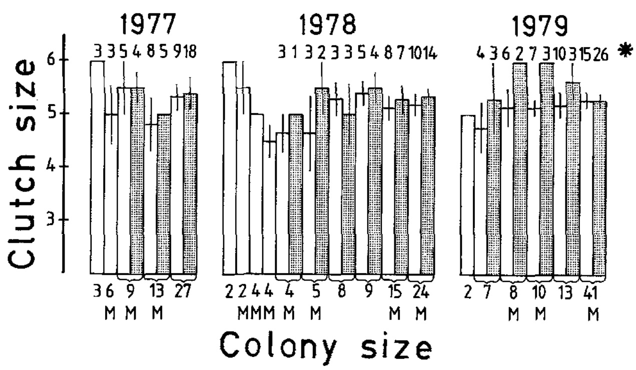

Fig. 4. Mean clutch size (±SE) for central (*shaded*) and edge pairs. *M* associated with Merlins; * number of nests used in the calculation

The number of peripheral nests was compared between colonies with and colonies without a Merlin pair. To avoid influence from colony size, colonies of equal size were compared with each other. No difference was found between colonies with and without a Merlin pair ($P = 0.27$). The presence of Merlins hence did not markedly affect the colony structure.

The Relationship Between Colony Size and Breeding Success

As indicated by earlier studies of Fieldfares (Andersson and Wiklund 1978; Wiklund and Andersson 1980), their communal defence favours nesting in colonies. An analysis of the effect of colony size on the reproductive success shows that fledgling production per nest increases with colony size ($P < 0.03$). However, beyond a colony size of about 10 nests there is only a slow increase in breeding success (Fig. 2).

To test whether nest predation varies with colony size, I examined nest survival. The test was performed, separately, on colonies associated with Merlins and on non-associated colonies. The results, summarized in Fig. 3, show that nest survival increases significantly with colony size in both categories of colonies ($P < 0.002$).

A comparison of Fig. 2 and 3 indicates that nest survival increases faster with colony size than does fledgling production per nest. Therefore, a more detailed study of the relations between colony size and breeding performance was done in 1977–1979

Clutch size did not vary with colony size ($P = 0.34$), whereas average nestling production per nest was positively correlated with colony size ($P < 0.0001$). However, chick mortality due to starvation increased with colony size ($P < 0.0001$). Similarly, proportional nestling mortality (starved young per egg hatched) increased with colony size ($P < 0.0001$). Consequently, the number of fledglings from nests escaping predation was negatively correlated with colony size ($P < 0.001$).

The Relationship Between Nest Position and Breeding Performance

When clutch sizes were compared between central and edge birds, without relating them to time of

Table 2. Number of unhatched eggs and starved nestlings in central and peripheral nests (mean ± SE)

Year		Peripheral nests clutch size			Central nests clutch size		
		4	5	6	4	5	6
1977	Unhatched		0.33 ± 0.33	1.00 ± 0.58	1[a]	0.40 ± 0.25	0.83 ± 0.48
	Starved		2.00 ± 0.00	3.00 ± 0.58	0[a]	2.00 ± 0.32	2.83 ± 0.40
1978	Unhatched	1[a] 0[a]	0.44 ± 0.18	0.75 ± 0.25	0[a]	0.36 ± 0.15	0.57 ± 0.20
	Starved	3[a] 0[a]	1.33 ± 0.37	2.75 ± 0.25	1[a]	1.55 ± 0.21	2.43 ± 0.30
1979	Unhatched	0[a]	0.15 ± 0.10	1[a] 0[a]		2[a]	0.60 ± 0.22
	Starved	3[a]	0.85 ± 0.19	4[a] 0[a]		0[a]	0.90 ± 0.38

[a] Indicates single observations

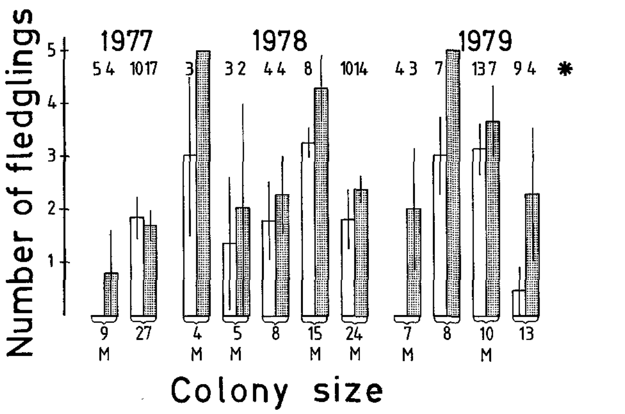

Fig. 5. Mean number of fledglings produced (± SE) for central (*shaded*) and edge birds. Data were omitted from those colonies, which were totally extinguished by predation. *M* associated with Merlins; * number of nests used in the calculation

laying, central birds produced more eggs than edge birds ($P < 0.05$, Fig. 4). However, the clutch size was negatively correlated with time of laying ($P = 0.0006$). Central and edge birds equal in time of laying and from colonies of comparable sizes did not differ in egg production ($P = 0.26$). This suggests that the smaller average clutch size in peripheral pairs was due to late laying. Further, the two categories of Fieldfares did not differ in nestling production ($P = 0.50$).

Since clutch size differences might indicate differences in quality between birds (Coulson 1968), nestling mortality and the number of nests with unhatched eggs were investigated (Table 2). There were no differences in frequency of nests with unhatched eggs between central and edge birds with a clutch of either five eggs ($P = 0.79$, Mann-Whitney *U*-test, Siegel 1956) or six eggs ($P = 0.54$, Mann-Whitney *U*-test). Similarly, with respect to clutch size, the two categories of Fieldfares did not differ in nestling mortality ($P = 0.27$ and $P = 0.36$, Mann-Whitney *U*-test).

Central pairs produced more fledglings than edge pairs ($P < 0.004$, Fig. 5). The production of fledglings per egg laid was also significantly larger in central birds ($P < 0.03$, Fisher's Permutation Test, Bradley 1968). The difference in fledgling production between central and edge birds thus resulted partly from the lower number of young produced per egg and partly from lower clutch size, in peripheral pairs.

To find out whether predation enhanced the difference in fledgling production, nest survival was compared between the two categories. Central birds had higher nest survival ($P < 0.001$) than peripheral birds, showing that edge birds suffered from higher nest predation than central pairs.

The Advantage of Breeding Association Between Fieldfares and Merlins

Merlins associated with a Fieldfare colony produce more fledglings than do non-associated pairs (Wiklund 1979). To test whether Fieldfares also improved their breeding success when associated, I compared clutch size and reproductive success between Fieldfares breeding near Merlins, and Fieldfares breeding away from Merlins. Comparable colony sizes were tested against each other, and then the data were weighted together. No difference in clutch size was found between the two categories of Fieldfares, neither in tests of colonies of comparable size, or of weighted data ($P > 0.40$). On the other hand, fledgling production was significantly larger for Fieldfares breeding close to a Merlin pair ($P < 0.01$, Fig. 2). Since the data in Fig. 2 show a great variation, curves were fitted to each category. A sliding average was calculated from the mean of 5 adjacent points. In colonies of small or moderate size, Fieldfares associated with Merlins on average produced about one more fledgling per pair than did their non-associated conspecifics. For larger colonies, the difference was less clear-cut.

What was the reason for the higher success of Merlin-associated Fieldfares? Figure 3 shows that they were favoured by increased nest survival ($P < 0.01$), probably due to reduced predation.

Density-Dependent Reproductive Success

Since the study covered two population cycles of rodents, it was possible to investigate the influence of associated changes in the population density of Fieldfares on their production of fledglings. Population density did not influence clutch size ($P > 0.38$). A similar test on reproductive success versus population size yielded an inverse correlation ($P < 0.001$). Such correlations are often taken to demonstrate density-dependent regulation of offspring production (Lack 1966). During Fieldfare population peaks the year after the rodent crash, Fieldfare nests were subject to heavy predation (Wiklund, in preparation). The correlation between Fieldfare population size and nest-predation rate is significant ($P < 0.05$).

Discussion

Location of Fieldfare Colonies

Fieldfares usually nest in colonies of varying size (e.g. Hohlt 1957b), but there are no indications that limited habitat availability forces them to nest in colonies (Lübcke 1975). During times of population increase in the present area, the Fieldfares established new colonies instead of enlarging existing ones. Furthermore, the total breeding area occupied each year was small compared to the total area available. These features are hard to explain by shortage of nest sites. Yet, each year most of the breeding Fieldfares were associated with Merlins. Therefore factors other than shortage of nest sites must cause the association between Merlins and Fieldfares. Association with birds of prey also occur regularly in other areas of the Fieldfare's breeding range (Diesselhorst 1955; Peitzmeier 1955; Hohlt 1957a).

Since Merlins used nests of the Hooded Crow, the most important predator on Fieldfare nests (Wiklund, in preparation), the crows might also have indirectly influenced the nest-site selection of the Fieldfares. Merlins preferred new or 1-year-old crow nests. As Hooded Crows usually nested in approximately the same area each year, Fieldfares associated with a Merlin pair often were only a few hundred metres away from an active crow nest. Both Merlins and Fieldfares attacked crows near their nest area.

The Importance of Large Colony Size and Central Nest Site

The number of mobbing birds has been shown to increase with colony size (Hoogland and Sherman 1976), and an inverse relationship probably exists between mobbing frequency and predator success (Kruuk 1964; Robertson 1973; Andersson 1976).

This study shows that fledgling production is positively correlated with colony size. Solitarily and colonial Fieldfares defend their nests in the same manner (Andersson et al. 1980). Therefore, increased nest survival in Fieldfare colonies seems to result from an increased rate of communal attacks on predators in colonies as compared to solitary pairs (Wiklund and Andersson, in preparation).

Alternatively, increased foraging efficiency via food information from successful foragers might favour colonial breeding (Horn 1968; Ward and Zahavi 1973; Krebs 1978). However, nestling mortality due to starvation increased with colony size, and there was an inverse relationship between colony size and fledgling production in nests escaping predation. These relationships make it unlikely that colonial breeding is an adaptation for increased foraging efficiency in the Fieldfare. Other evidence against this probability was given by Wiklund and Andersson (1980). Besides, the information-centre hypothesis is controversial (e.g. Bayer 1981; Evans 1982; Mock, in preparation), and experimental evidence suggests that it may not apply to gulls, for which it has also been proposed (Andersson et al. 1981).

There are indications that the mobbing of predators increases towards the centre of a colony (Balda and Bateman 1972; Hoogland and Sherman 1976). In the present study, the production of fledglings in all cases but one was larger in central than in peripheral nests, regardless of colony size. Centrally breeding Fieldfares were also favoured by reduced nest predation, probably caused by both improved nest defence and selfish herd effects (Hamilton 1971).

Another possible explanation for the difference between central and peripheral pairs is that central birds are of higher quality than peripheral ones (Coulson 1968). The results indicate that such a difference was not the only reason for the difference in success between the two categories of Fieldfares. Among pairs with similar laying dates, peripheral pairs had clutches as large as central pairs. On the other hand, the later start of laying in edge birds might be a consequence of lower breeding experience and, in this respect, there may be a qualitative difference. However, the higher risk of predation for edge pairs also contributed to their lower success.

Increased probability of nest survival hence favoured breeding in large colonies and in central position. Pairs breeding in small colonies were partly compensated by reduced nestling mortality due to starvation, probably as a consequence of reduced competition for food. The results strongly indicate that colonial breeding in the Fieldfare is an antipredator adaptation.

Social Mutualism

Together with an earlier report (Wiklund 1979), this study demonstrates a mutual benefit in the breeding association between Fieldfares and Merlins. Fieldfares breeding near Merlins fledged on average about one more chick per pair than those breeding away from Merlins. As nest survival was considerably increased for Fieldfares breeding together with a Merlin pair, defence of the nesting area by both Fieldfares and Merlins seems to be the reason for the mutual advantage.

Although the Merlins are able to catch both adult Fieldfares and their nestlings (Hagen 1947; Sperber and Sperber 1963; Hård and Enemar 1980), they rarely did so in my study area. During this 10-year study, I observed only one successful hunting attempt of a Merlin pair in their associated Fieldfare colony. This occurred in a colony where the young had fledged from all but one nest; the remaining nest was plundered by the Merlins. Fieldfares often attack the associated Merlins as they fly to and from their nest.

Since Fieldfare fledgling production initially increased with colony size (Fig. 2), nest predation probably exerted a stronger selection pressure than nestling mortality due to starvation at small-to-moderate colony sizes. However, Fieldfares did not always join the largest associated colony, but also bred in smaller ones. This, and the levelling off of fledgling production in larger colonies (Fig. 2), suggest that reduced nest predation and increased nestling starvation balance when colony size becomes large.

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