Ornis Fennica 70:202–212. 1993

The population size and breeding biology of the Rook *Corvus frugilegus* in northern Finland

Seppo Rytkönen, Kari Koivula & Eero Lindgren

Rytkönen, S., Koivula, K. & Lindgren, E., Department of Zoology, University of Oulu, Linnanmaa, FIN-90570 Oulu, Finland

Received 29 June 1993, accepted 25 October 1993

We studied the number and the breeding ecology of Rooks in the surroundings of Oulu, northern Finland (65°N, 25°30′E) during 1987–1992. The number of breeding pairs was about 500 in 10 colonies. Non-breeding birds formed 15–35% of the population. Breeding started in mid April. Average clutch size (3.7) was only slightly smaller but the mean number of young produced (1.6 in successful nestings and 1.1 in all nests) was considerably smaller than in Middle Europe. The most productive clutch size varied between 4 and 6 annually. Early breeders had larger clutches and produced slightly more young than late breeders. Nest site did not affect breeding success; however, Rooks breeding in the top sites of multiple nested trees bred earlier and had larger clutches than others. Normally, repeat nesting was rare. Annual variation was very high, both in clutch and brood sizes. Mean May temperature and duration of ground frost appeared to predict rather well the forthcoming breeding success. Low success in cold springs may reflect reduced availability of earthworms (main food for the nestlings) due to the prolonged ground frost period. Nowadays, the Oulu population is at its largest, and has doubled during the last two decades. It seems that this increase can not be explained by the local reproduction, but has more obviously been based on immigration from the south and/or east. More information, especially ringing records, is needed to confirm this.

1. Introduction

Rooks *Corvus frugilegus* have been breeding in Finland only since 1885 (von Haartman et al. 1963–1972). The population size increased at least until the 1950's, when Merikallio (1958) estimated the size of the Finnish population at 3000 breeding pairs. In the 1960's, however, this number was argued to be an overestimate (Malmberg 1971). In Røskaft's (1980) paper of northern Rooks, the Finnish Rook population was estimated to be much smaller, only at 500–700 breeding pairs in the 1970's. It seems that the Finnish population has decreased in numbers at least from the first half of the 20th century (see also von Haartman et al. 1963–1972). The trend is similar to that in other parts of Europe. In Germany and the Netherlands the Rook numbers have been decreasing for the whole century (Ruge 1988), and in Great Britain the decrease began in the 1950's (O'Connor & Shrubb 1986). In Hungary the Rook numbers stayed stable until the

1980's, but thereafter, a clear decrease has followed (Kalotas 1985, 1988).

The breeding biology of Finnish Rooks is poorly known. von Haartman (1969) gave some anecdotal information about clutch sizes in southern Finland. It is unknown whether this northern population is maintained by its own reproduction, or is it a so-called sink population, which only exists as a consequence of immigration from other populations.

We studied the population size and structure, and breeding biology of the Rooks in Oulu and the surrounding communes during 1987–1992. The local population (hereafter called the Oulu population) is isolated from the two other sub-populations in Finland. The nearest Rooks breed about 250 km to the southwest (around Vaasa), and the third settlement is still 150 km further south (around Pori). On the other hand, these three sub-populations can be considered as the Finnish population, because all Finnish Rooks migrate and presumably overwinter in the same areas in Western Europe. In this paper, we review the history of the Oulu population, present the results of a study on basic breeding biology, and discuss the factors affecting the breeding success. In addition, we discuss whether the population is self-maintained or not.

2. Methods

This study was carried out in the surroundings of Oulu, northern Finland. The Oulu population consists of rookeries located in the area of four neighbouring communes: Liminka, Muhos, Tyrnävä, and Oulu (65°N, 25°30′E).

The number of breeding pairs was estimated by counting the nests found at the colonies in the middle of the breeding season during 1987–1992. The number of nests found in May, when all the pairs have started breeding, has been considered to be a good estimate of the breeding population (Malmberg 1971). However, there were always some unused nests from previous years or nests, usually incomplete ones, probably built by non-breeding birds. In the largest colony at Liminka, consistently about 10% of the nests checked were not occupied annually. Thus, the number of breeding pairs could be estimated as 90% of the total number of nests found. This applies at least to the larger colonies. In the smaller ones the percentage might be higher.

The birds living in the colonies were censused by photographing the roosting birds late in the evening. The birds were abruptly threatened, and as they flew over around the rookery, the flock was photographed. The birds were counted from the photos using a microscope. The number of Jackdaws *Corvus monedula*, also roosting in the colonies, was estimated beforehand; we could not separate Rooks and Jackdaws in the photos. The number of Jackdaws was always much smaller than that of Rooks — at Liminka, for example, less than 10% of all birds. As we could calculate the numbers of breeding Rooks and the birds present in the area, we could also estimate the number of non-breeders. These can be considered 1-year-old birds, since Rooks normally start breeding at the age of two (Coombs 1960).

Breeding biology was studied in the largest colony at Liminka during 1987–1991. The nests in 10–15 m tall Scots pines *(Pinus sylvestris)* and birches *(Betula sp.)* were visited 5–6 times during the breeding season. During the first three visits, about one week apart (depending on weather) starting from the last third of April, we first recorded the laying dates of early breeders, then their complete clutches; and then we recorded the laying dates of late breeders, and finally their complete clutches. In years when the spring was late, we visited the colony once more about one week later.

Broods were divided into early and late ones according to the annual median dates for start of breeding or based on the visiting schedules (see above) — we could not always determine the exact laying dates. In 1987 and 1989 the first visits were too late, but we could calculate the earliest laying dates from the first hatching dates by assuming that incubation began after the first egg was laid and lasted 18 days (e.g., Wittenberg 1988). Generally, early broods were started during the second and third week of April, and the late broods during the last week of April and in the beginning of May. When a new clutch was started in the same nest where the earlier clutch had been lost, this was assumed to be a repeat clutch. Because part of the starting dates could only be classified between two consecutive visits (with accuracy of 1–2 days), non-parametric methods were used in statistical analyses dealing with laying dates.

The young stay in the nest for 4–5 weeks, but because older nestlings climb away from their nests when disturbed, the breeding success was based on the number of 3- to 4-week-old nestlings (hereafter called 3-week-old young) counted during two visits in late May and/or early June. This apparently was a quite good estimate of the number of fledglings produced, since the mortality of the young older than three weeks is very small (e.g. Holyoak 1967). This was also observed in the colonies: only very few over 3-week-old young were found dead under the trees, whereas numerous dead some-days-old nestlings were found.

Nest sites were classified into four categories as follows: (1) *single* nested trees; and (2) *base*, (3) *middle* and (4) *top* sites in multiple nested trees. Temperature data were obtained from Oulunsalo airport, about 15 km north from the colony in Liminka. Dates for melting of ground frost were determined from the ground temperature data (measured once a week) obtained from Ruukki, about 25 km south from Liminka. Melting was considered to start when the ground temperature (20 cm below) first time clearly increased from the 0-level. Because of the high annual variation in the clutch and brood sizes, we used standardized values for these in the statistical analyses of the combined data.

Table 1. The numbers of Rook nests in the Oulu population during 1987–1992.

Commune Colony	1987	1988	1989	1990	1991	1992
Oulu						
Krouvi	49	51	85	85	51	88
Allinpuisto	42	24	16	16	15	29
Karjasilta	17	28	42	18	9	13
Keskusta	24	30	24	19	15	11
Hevossaari	16	–	–	–	–	–
Intiö	–	–	–	20	43	41
Total	148	133	167	158	133	182
Liminka						
Kyllönen	240	241	290	275	210	214
Tyrnävä						
Kirkko	93	83	85	77	80	102
Murto	25	21	18	18	16	11
Total	118	104	103	95	96	113
Muhos						
Muhos	7	15	40	40	23	25
Total	523	493	600	568	462	534

3. Results

3.1. Rook numbers

The numbers of Rook nests found in the Oulu area are presented in Table 1. Assuming that at least 90% of the nests were occupied (see Methods), the total breeding population stayed rather stable, at about 500 pairs, over the study years. Besides the breeding birds, there were always non-breeding Rooks also present. The proportion of non-breeders in the three colonies is presented in Table 2. It seemed that in years with poor breeding success (1987 and 1991, see below) the proportion of non-breeders was higher than in good years (1988 and 1989). However, the total number of Rooks stayed rather stable (Table 2). This result can be interpreted in two ways, which do not exclude each other: either some of the 1-year-old Rooks start to breed in good years and/or some of the old (≥2 years) birds do not breed in poor years.

Table 2. The number of Rooks and the proportion of non-breeders at three colonies during 1987–1989 and 1991 (in 1990 the photos were unsuccessful). The accuracy is to the nearest 5%. The total number of Rooks in the Oulu population was estimated from the number of breeding pairs (= 90% of nests found, see Methods) and the average proportion of non-breeders in the population.

Colony	1987	1988	1989	1991
Total number of Rooks	1350	1100	1250	1300
Percentage of non-breeders				
Oulu, Krouvi	?	30	25	30
Liminka, Kyllönen	30	15	10	35
Tyrnävä, Kirkko	30	20	15	45
Average	30	20	15	35

3.2. Timing of breeding and repeat nesting

First Rooks settled at their colonies in March. Egg-laying started in the middle of April and was quite synchronous. There was very little variation in the timing of breeding: during 1987–1991 the earliest laying initiations varied between 10 or 11 April (1989–1991) and 15 April (1988). Normally, almost all the pairs (annual variation 78–98% of all the first clutches) started laying in April. Because of incomplete data (see Methods) we could not calculate exact median dates for the start of breeding, but quite reliably these varied between 15 or 16 April (1991) and 19 April (1988 and 1990). The latest nests were started in the beginning of May each year and in the second week of May in 1987 and 1989.

Repeat nesting was normally very rare: only 1–6% of the number of first clutches; except in 1991, when out of 79 breeding attempts recorded 40 were first clutches, 26 were repeat clutches and 13 were late or repeat clutches in new nest sites. The failures or desertions of the first clutches occurred in the end of April, and the repeat clutches were laid in the beginning of May.

3.3. Clutch and brood sizes

The average clutch and brood sizes during 1987–91 are shown in Table 3. Clutch sizes varied between 2 and 6. A few one-egg clutches were found, but we were not sure whether they were complete clutches or clutches with partial egg losses. The brood sizes varied between 1 and 4 (see also Fig. 1). In 1991 (the exceptional year with a considerable number of repeat clutches, see above) the mean size for the repeat clutches was slightly, but not significantly smaller than that for the first clutches (means±SD: 3.30±0.84 and 3.69±0.85, n = 23 and 13, respectively, t = 1.04, P > 0.30). The mean number of 3-week-old young produced in repeat clutches was slightly larger than that in the first clutches (in 1991, means 0.31±0.71 and 0.23±0.70, n = 26 and 40, respectively, Mann-Whitney U-test, z = 1.29, P > 0.10). On the other hand, the late clutches (or repeat clutches in new nest sites, see above) produced significantly more young (mean 0.62±0.69,

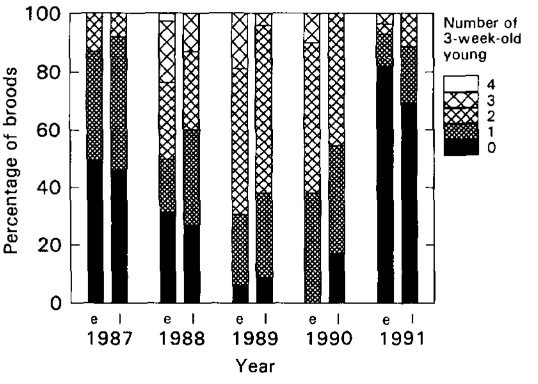

Fig. 1. Percentage distribution of different brood sizes at the end of the nestling period (when the young were 3-week-old) in early and late broods during 1987–1991. In 1991 most of the late broods were repeat nests.

Table 3. Mean clutch and brood sizes at Liminka colony during 1987–1991. Mean for the five year period[a] and mean for annual means[b] (unweighted) are presented.

	Clutches			Broods					
				Successful			All		
Year	Mean	SD	n	Mean	SD	n	Mean	SD	n
1987	3.16	0.70	82	1.23	0.46	73	0.67	0.70	134
1988	3.86	0.88	93	1.94	0.86	65	1.37	1.15	92
1989	4.20	0.82	94	1.88	0.66	88	1.74	0.80	95
1990	3.66	0.94	47	1.63	0.58	41	1.49	0.73	45
1991	3.64	0.83	36	1.47	0.62	17	0.32	0.67	79
1987–91[a]	3.74	0.84	352	1.67	0.64	284	1.06	0.83	445
1987–91[b]	3.70			1.63			1.12		

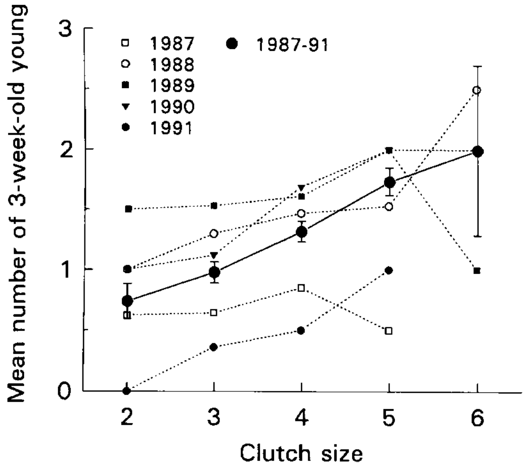

Fig. 2. Breeding success in relation to clutch size during 1987–1991. SEs are given for the means of combined data.

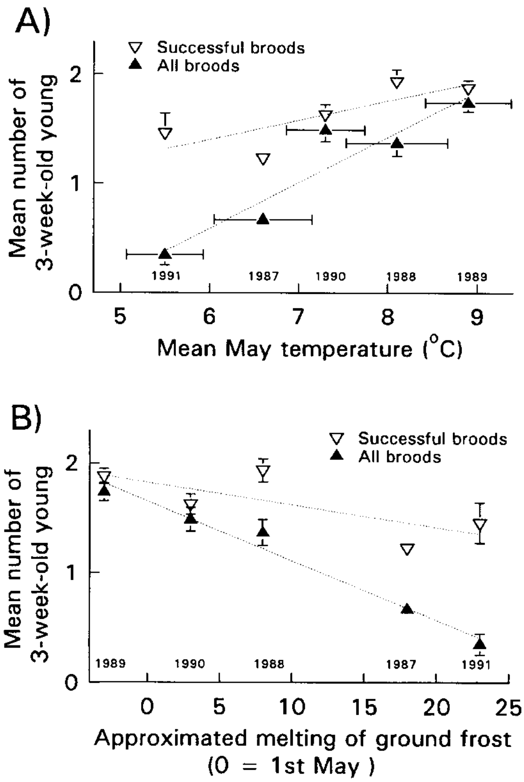

Fig. 3. Annual variation in breeding success (mean with 1 SE) in realation to A) mean May temperature and B) melting of ground frost during 1987–1991. The dotted lines show the linear regression slopes. For statistics see text. SDs for the mean temperatures are given in the above figure.

n = 13) than did early first clutches (0.23±0.70, n = 40, z = 1.99, $P < 0.05$).

The annual differences were highly significant both in the clutch sizes (ANOVA: $F_{4,347}$ = 17.28, $P < 0.001$) and in the brood sizes ($F_{4,415}$ = 37.56, $P < 0.001$; see Fig. 1) — also if only the successful broods were considered ($F_{4,275}$ = 13.24, $P < 0.001$). The proportion of total losses varied drastically between the years, from 7% to 76% (χ^2-test, $P < 0.001$; see Fig. 1).

Breeding success increased with clutch size (Spearman rank-correlation: r_s = 0.316, n = 332, $P < 0.001$; Fig. 2). The number of 3-week-old young produced per egg was the same (about 1/3) in all clutch sizes ($F_{4,327}$ = 0.197, P = 0.940; r_s = 0.022, n = 332, P = 0.695).

3.4. Factors affecting breeding success

3.4.1. Weather

The annual means of the number of 3-week-old young were correlated with the mean May temperature and the approximated date of melting of ground frost (r = 0.93 and –0.98, respectively; see Fig. 3). The corresponding empirical two-tailed P-values by randomization test (see Pollard et al. 1987) after 10 000 simulations were 0.016 and 0.002, respectively. Therefore, although we had only five-year data, this result suggests with significantly low risk that the breeding success of Rooks depended on the weather during the time of nesting in May. Mean April temperature did not correlate significantly with clutch size (r = –0.03, empirical $P > 0.10$).

3.4.2. Timing of breeding

The data from 1988 and 1990–1991 (when the data were complete enough) showed a significant seasonal decline in the average clutch size (by about 1 egg), but only a seemingly significant decline in the number of 3-week-old young pro-

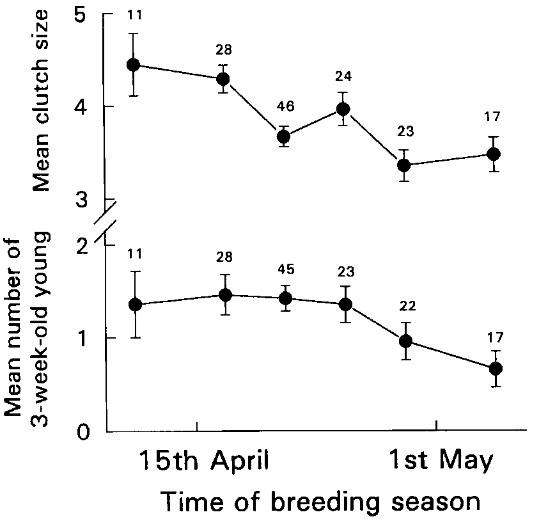

Fig. 4. Mean clutch sizes and number of 3-week-old young (with 1 SE, and sample sizes) in relation to the timing of breeding. Data are from 1988 and 1990–1991. The latter half of April is divided into four 3- or 4-day periods, and the periods before and after this are about 1 week each.

duced (Fig. 4, Table 4). For the analysis in Table 5, where the whole data were used, we classified the broods into early and late ones (see Methods). In the original data, early clutches were larger than late ones (means with 1SD, 3.85±0.95 and 3.58±0.89, respectively, $t = 2.77$, $n = 193 + 152$, $P < 0.01$). However, as Table 5 shows, when the nest site and the annual differences were taken into account by using standardized data, this difference was only seemingly significant. The same tendency, also not significant, was in the brood sizes: early breeders produced seemingly more young per nest than late breeders (1.20±1.03 vs. 1.03±0.89; original data, all nests included). However, when only the successful nests were considered this difference was significant (Table 5): early broods produced 1.77±0.73 and late ones 1.55±0.62 young per nest.

3.4.3. *Number of nests in the tree*

The number of nests in each tree varied from 1 to 9. Table 5 shows that the clutch size increased as the number of nests in the same tree increased. On the other hand, the number of nests in the same tree did not affect the number of young produced.

3.4.4. *Nest site in the tree*

The earliest breeders preferred to settle in trees with many nests (old ones from previous years) and to choose the top or middle nests. The late breeders had to settle more often in the base sites or in the single-nested trees (i.e., in many cases they had to build a new nest). This difference between early and late breeders in nest site selection was significant ($\chi^2 = 5.46$, df = 1, $P = 0.019$). The nest site itself did not significantly affect clutch or brood sizes, but when combined with the timing of breeding the effect was significant: early breeders in the top and middle sites had larger clutches (Table 5).

4. Discussion

History and population size

The first sighting of Rooks breeding at Oulu occurred in 1894, and for a long time the popula-

Table 4. Seasonal changes in clutch size and number of 3-week-old young produced as revealed by Spearman rank-correlation analyses. For the combined data standardized values were used.

	Clutch size			Number of 3-week-old young		
Year	r_s	n	P	r_s	n	P
1988	–0.295	75	0.011	–0.185	72	0.118
1990	–0.585	43	0.0002	–0.193	43	0.211
1991	–0.485	31	0.008	–0.109	31	0.551
1988–91	–0.310	149	0.0002	–0.154	146	0.064

tion was small, only some dozens of pairs were observed in the 1930's and 1940's (Merikallio archives, Zoological Museum of Oulu; see also Rytkönen & Koivula 1990). By the end of the 1960's the population size was about 200 pairs, and increased in the 1970's almost to 300 pairs (Siira 1977, Merilä & Merilä 1978). During the following two decades the population has almost doubled, and now there are more Rooks than ever before, about 500 breeding pairs in the surroundings of Oulu. Nowadays, these Rooks form about 40% of the Finnish Rook population, which was estimated at 1100 pairs in 1987 (Rytkönen et al. 1992). This increasing trend is opposite to what has happened during the same time in western Europe (O'Connor & Shrubb 1986, Ruge 1988). On the other hand, the total Finnish Rook population has declined since the 1950's (von Haartman et al. 1963–1972). Taking into account the history of Rooks in the Oulu area, this decrease must have occurred in the colonies located in southern Finland.

Breeding biology

Breeding at Liminka started in mid April — about one month later than in Middle Europe. In England mean dates for the first egg varied between 7 March and 23 March, and the earliest dates were at the end of February (Owen 1959, data for 1952–1957). In North Germany median dates varied between 23 March and 14 April with the earliest date being 19 March (Wittenberg 1988, data for 1962–1967). In New Zealand, where Rooks were introduced from Europe about 100 years ago, breeding starts in August and peaks in September (Purchas 1979).

Clutch sizes of Rooks at Liminka were similar to those in Norway and Germany, but a little smaller than those in England or in New Zealand (Table 6). In brood sizes the pattern was similar (Table 7). In good years, clutch sizes at Liminka were about as large as in the best areas in Europe. Brood sizes, however, were not as large as in England and Germany. Total losses were considerably numerous in some years (Fig. 1) — more numerous than for example, in North Germany (Wittenberg 1988).

In the combined data, the most productive clutch size was larger than the most common clutch size, and the breeding success increased linearly with clutch size. Owen (1959), Røskaft (1985), and Wittenberg (1988) have observed the same relationship. This difference could be explained by the costs of reproduction (e.g. Røskaft 1985). Røskaft (1985) took originally smaller broods and increased them to a brood size of four, and found that these artificially enlarged broods produced more young than did smaller control broods. The parents of enlarged nests did not suffer higher mortality, but the costs were paid during the next breeding season: the

Table 5. Results of ANCOVA for clutch and brood sizes at Liminka colony. Standardized data for dependent variables was used because of highly significant between-year differences. Factors analyzed: number of nests in the same tree (as covariable, #NESTS), timing of breeding (TIMING, early and late nests), and nest site in the tree (SITE, four levels, see Methods).

			Brood size			
	Clutch size		Successful nests		All nests	
Source of variation	F	P	F	P	F	P
Covariable						
#NESTS	7.28	0.007**	0.15	0.705	0.53	0.474
Main effect	2.85	0.024*	2.58	0.038*	2.37	0.052
TIMING	3.60	0.059	4.87	0.028*	3.61	0.058
SITE	2.30	0.077	1.20	0.311	1.79	0.149
TIMING*SITE	1.36	0.248	0.55	0.697	1.93	0.105

strained parents started breeding later and had smaller clutches than the control parents. In our data, however, the most productive clutch sizes varied between 4 and 6 annually, and in some years the largest clutches observed were not the most successful (Fig. 2). Therefore, in addition to the possible costs through future reproduction (see Røskaft 1985), at least in poor years, the present reproduction was found to be constrained by the parents' rearing ability.

One striking result of this study was the extremely high proportion of total nest losses in some years. It is obvious that these losses were not caused by predation, and neither can cannibalism explain this phenomenon. The nestling mortality is highest during the first third of the nestling period: Holyoak (1967) observed that 26 of the 28 young that were lost during the nestling period died in the first week, 2 in the second and none thereafter. A similar result has been found by Purchas (1979) in New Zealand, and the most likely reason was starvation (see also Owen 1959). This is understandable, because in Rooks the average daily weight gain in the first 10 days after hatching is as high as 35%, and nestlings may differ in weight by as much as two-fold (Purchas 1979). Thus, food shortages may rapidly lead to drastic consequences. In addition, if males must spend a lot of time defending their territories instead of foraging, the young nestlings may suffer from food shortage and perish (Purchas 1979).

Table 6. Clutch sizes of the Rook in Europe and New Zealand.

Area	Year(s)	Clutch size mean	(range)	Min–max	Study
Finland	1987–91	3.7	(3.2–4.2)	2–6	This study
Norway	1979–82	3.5			Røskaft et al. 1983
North Germany	1963–67	3.7	(3.4–4.2)	1–6	Wittenberg 1988
Middle Germany	?	4.8		4–6	Mildenberger 1984
Czechoslovakia	?	4.0		2–6	Hudec 1983
North Scotland	–1965	3.6			Holyoak 1969
North England	–1965	4.4			Holyoak 1969
South England	–1965	4.3		1–7	Holyoak 1969
England	1952–57	4.4	(4.2–4.7)	2–7	Owen 1959
England	1952–54	4.4	(4.4–4.4)		Lockie 1955
New Zealand	1966–68	4.3	(4.1–4.6)	1–7	Purchas 1979
New Zealand[1]	1966–68	3.7	(3.6–4.0)	1–6	Purchas 1979
New Zealand[2]	?	3.4	(2.9–3.7)		Coleman 1972

[1]replacement clutches
[2]exceptionally poor habitat

Table 7. Brood sizes of the Rook in Europe and New Zealand.

Area	Year	Fledged young: Mean (range) Successful nests		Fledged young: Mean (range) All nests		Study
Finland	1987–91	1.6	(1.2–1.9)	1.1	(0.3–1.7)	This study
Norway	1979–82	1.6				Røskaft et al. 1983
Netherlands	?	1.8	(1.8–1.9)			Van Koersveld 1958
Germany	1959–67	2.3				Wittenberg 1988
England	1952–57	2.9[1]				Owen 1959
New Zealand	1966–68	2.4	(1.6–2.7)	1.5	(1.0–2.5)	Purchas 1979

[1]approximated from the given information

Factors affecting breeding success

The relationship between breeding success and mean May temperature indicates that Rooks are not well adapted to northern conditions. The colder climate and the extra losses in cold springs seem to explain the lower breeding success of the northern Rooks compared with the southern ones. In cold springs northern Rooks seemed to begin to breed too early. Contrary to this, clutch sizes were always larger in early breeders and also their breeding success normally was slightly better (except in the poor year 1991). There is, however, an obvious explanation for this: first breeders are older than late ones, and old breeders have larger clutches and better breeding success (Røskaft et al. 1983).

The relationship between breeding success and spring temperature may only reflect the more important relationship between breeding success and duration of ground frost (Fig. 3b). Only after the frost melts can Rooks feed on earthworms *(Lumbricidae)*, which are the chief food for the nestlings (Lockie 1955). Even cold and dry weather can cause nestling losses, because earthworms burrow deeper into the ground and are not any more available (Owen 1959). In 1991 when the spring was very cold, Rooks began breeding in mid April, as normally. The cold weather continued and the ground frost stayed until the end of May. Most of the early breeders deserted their nests (with eggs, and perhaps some with hatchlings) at the end of April, and began a new breeding attempt in the beginning of May. Clutch sizes of those late re-breeders were considerably smaller than normal (this, however, can also be explained by the seasonal decline in clutch size), and the breeding success was very low. In another cold spring in 1987, similar, but not so adverse losses were observed.

The nest site in the colony seemed to be connected with the timing of breeding and clutch size. According to the information in Røskaft et al. (1983) this result can be interpreted as follows: old and fit birds that are dominant choose the best nest sites (top ones in multiple nested trees), and lay earlier and larger clutches than young and less fit birds (subordinates). However, the number of 3-week-old young produced was not affected by the nest site, indicating that factors other than the nest site (e.g., weather dependent availability of food for nestlings) were of more importance in determining the breeding success. This result may suggest that in harsh environmental conditions the experience, or better body condition of early breeding old birds (Røskaft et al. 1983) can not assure their better breeding success, when compared with the younger and inexperienced, or weaker birds — especially when the total losses are frequent (see Table 5).

Growing sink-population?

Our results have led us to doubt whether northern Rooks can maintain their population size by their own reproduction. As Rooks normally start breeding at the age of two years (Coombs 1960), the number of young surviving until that age must be equal to the number of adults that do not survive during the same time. Unfortunately, we do not know the mortality rates of Rooks in the Oulu population. According to Richardson et al. (1979) annual adult mortality is rather low, only 21%. Saether (1989) gave a very high estimate for post-fledging mortality (based on English data): about 75% of the young die during the first winter. Patterson and Grace (1984) gave a maximum estimate of 69–71% for mortality and disappearance during the first year. According to these mortality estimates, none of the study years could have maintained the population size stable in the Oulu population (all nesting attempts included). On the other hand, the above mortality estimates may be too high for this northern population, where density is much lower than in England, and thus, density-dependent mortality is of less importance. But, even if we consider post-fledging mortality as being similar to the adult mortality, still in three years out of five the population size should have decreased, which also should have been the overall trend during the study years.

The Oulu population, however, has almost doubled its size during the past two decades. The years studied represented normal variation in spring weather: the mean spring temperatures in the study years did not differ from normal spring temperatures during 1970–1992, and the range was the same. Therefore, as the mean May temperature seemed to predict the breeding success rather well, we can assume that the average breeding success has been the same during the time when the population growth occurred; i.e., breeding success can not explain the population growth. Our results suggest that the Oulu population has grown because of immigration from other colonies. These newcomers may have come or may still come from southern Fennoscandia, or from Middle Europe where Rook numbers have declined due to unfavorable changes in environmental conditions; but where breeding success still has been good enough to produce potential emigrants. Alternatively, or in addition, these immigrants may also be of Baltic or Russian origin: Røskaft (1980) suggested that northern "satellite" colonies may have been established by immigrating Baltic Rooks. This kind of immigration occurred in 1976/77 (see Røskaft 1980). Eastern Rooks migrating along the Baltic Sea coast to their wintering grounds (Germany and France) were blown off course over the Baltic Sea by an autumn storm in 1976. Most of these birds probably overwintered in the same areas where Fennoscandian Rooks and Hooded Crows *Corvus corone cornix* stay for the winter (Denmark and the Netherlands). In the spring of 1977 they undertook their usual northeastward migration route which now was parallel to their original route and led them to Fennoscandia. This was evidenced by the unusual numbers of Rooks reported from Sweden and Finland (Røskaft 1980). Can this particular occurrence explain the growth of the Oulu population observed during the last two decades, or is the southern immigration the most important factor, or are there some other explanations? Unfortunately, because we lack ringing records, answers for these questions remain uncertain.

Acknowledgements. We thank Seppo Sulkava, Eino Merilä and Jouko Siira for valuable information about the history of the Rooks in Oulu area, and Eino Erkinaro for the possibility to examine the Merikallio archives at the Zoological Museum of Oulu. A lot of people have helped us in the field. We are grateful to Juha Korpinen, Mika Koskinen, Kimmo Kumpulainen, Kirsi Laakso, Kimmo Lahti, Mikko Mönkkönen, Anna Norja, Jouni and Vesa Rytkönen, Mikael Soppela, Pertti Tikkanen, Hannele Tuominen and Petteri Welling. We wish to thank Juha Tiainen and Hannu Pietiäinen for useful comments on the manuscript. This study was financially supported by the Department of Environment.

Selostus: **Mustavariksen kannankehitys ja pesimisbiologia Oulun seudulla**

Tutkimme mustavariksen pesimisbiologiaa Oulun seudulla 1987–92. Tarkoituksemme oli määrittää paikallisen populaation koko sekä selvittää lajin pesimisbiologiaa ja pesimismenestykseen vaikuttavia tekijöitä. Pohdimme lisäksi miten viimeaikainen kannan kasvu on tapahtunut.

Mustavariksia pesi neljä kunnan (Oulu, Liminka, Muhos ja Tyrnävä) alueella 10 yhdyskunnassa noin 500 paria vuosittain (Taulukko 1). Keväisestä kokonaisyksilömäärästä (1100–1350) oli vuosittain 15–35% pesimättömiä, ilmeisesti pääasiassa yksivuotiaita lintuja.

Keskimääräinen pesyekoko (3.7) oli vain hieman pienempi kuin Keski-Euroopassa, mutta keskimääräinen poikastuotto sekä onnistuneissa (1.6) että kaikissa aloitetuissa pesinnöissä (1.1) selvästi huonompi (Taulukot 3, 6 ja 7). Vuosittainen vaihtelu oli hyvin suurta sekä pesye- että poikuekoossa, ja kahtena vuotena viidestä pesimistulos oli erittäin huono (kuva 1). Aikaisin pesintänsä aloittaneilla pareilla pesyekoko oli suurempi kuin myöhäisillä (Taulukko 4, Kuva 4). Kokonaisaineistossa pesimismenestys kasvoi pesyekoon kasvaessa, mutta eri vuosina menestyksekkäin pesyekoko vaihteli välillä 4–6 (Kuva 2). Pesäpaikka yhdyskunnan sisällä ei vaikuttanut poikastuottoon, mutta parit, jotka pesivät useampipesäisten puiden yläpesissä, aloittivat pesinnän aikaisemmin ja munivat suurempia pesyeitä kuin muut (Taulukko 4). Uusintapesiminen oli harvinaista (1–6%), paitsi vuonna 1991, jolloin yli puolet ensimmäisistä pesinnöistä tuhoutui tai hylättiin huhtikuun lopussa, ja näistä lähes kaikki aloittivat uusintapesinnän toukokuun alussa. Toukokuun keskilämpö ja roudan sulaminen näyttivät ennustavan varsin hyvin tulevan pesimismenestyksen (Kuva 3). Huono menestys kylminä keväinä saattaa selittyä sillä, että normaalia pidempään pysynyt routa esti lierojen (*Lumbricidae*) — tärkeimmän poikasravinnon — saatavuuden kriittisessä vaiheessa poikasajan alussa.

Nykyään Oulun seudun mustavarispopulaatio on suurempi kuin koskaan aikaisemmin. Viimeisen kahden vuosikymmenen aikana populaatio on kaksinkertaistunut. Tämä kasvu ei voine selittyä paikallisella poikastuotolla, vaan perustunee

muualta tulleeseen muuttovirtaan. Ilmiön todentamiseksi tarvitaan kuitenkin rengastushavaintoja, jolloin myös mahdollisten tulokkaiden alkuperä saataisiin selville.

References

Coleman, J. D. 1972: The breeding biology of the Rook Corvus frugilegus L. in Canterbury, New Zealand. — Notornis 19:118–139.

Coombs, C. J. F. 1960: Observations on the Rook Corvus frugilegus in southwest Cornwall. — Ibis 102:394–419.

von Haarman, L. 1969: The nesting habits of Finnish birds. I. Passeriformes. — Comm. Biol. Soc. Sci. Fenn. 32:1–187.

von Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–72: Pohjolan linnut värikuvin. Otava. Helsinki. (in Finnish).

Holyoak, D. 1967: Breeding biology of the Corvidae. — Bird Study 14:153–168.

Hudec, K. (ed.) 1983: Fauna CSSR. Ptáci Aves. Díl III/2. — Nakladatelství Ceskoslovenské Akademie Véd.

Kalotas, Z. 1985: Feeding habitat and economic importance of the Rook (Corvus frugilegus L.) in Hungary. — Aquila 92:175–239.

— 1988: Saatkrähe in Ungarn, ein Vergleich der Jahre 1980 und 1984. — Beih. Veröff. Naturschutz Landschaftspflege Bad. — Württ. 53:67–74.

Koersveld, E. van 1958: A few data on the reproduction of the Rook, Corvus frugilegus L. — Ardea 46:58–62.

Lockie, J. D. 1955: The breeding and feeding of Jackdaws and Rooks with notes on Carrion Crows and other Corvidae. — Ibis 97:341–369.

Malmberg, T. 1971: Censuses of the Rook Corvus frugilegus L. in Scania, Sweden, 1955–70. — Ornis Scand. 2:89–117.

Merikallio, E. 1958: Finnish Birds. Their distribution and numbers. — Fauna Fenn. 5:1–181.

Merilä, E. & Merilä, M. 1978: Mustavaristen esiintymisestä sekä niiden aiheuttamasta harmista ja haitasta Oulun seudulla. — Oulun Luonnonystäväin Yhdistys ry. Tiedotuksia 3:18–22. (in Finnish).

Mildenberger, H. 1984: Die Vögel des Rheinlandes. Band II. — Beiträge zur Avifauna des Rheinlandes 19–21.

O'Connor, R. J. & Shrubb, M. 1986: Farming and birds. — Cambridge University Press. Cambridge.

Owen, D. F. 1959: The breeding season and clutch-size of the Rook Corvus frugilegus. — Ibis 101:235–239.

Patterson, I. J. & Grace, E. S. 1984: Recruitment of young rooks, Corvus frugilegus, into breeding populations. — J. Animal Ecol. 53:559–572.

Pollard, E., Lakhani, K. H. & Rothery, P. 1987: The detection of density-dependence from a series of annual censuses. — Ecology 68:2046–2055.

Purchas, T. P. G. 1979: Breeding biology of rooks (Corvus frugilegus L.) in Hawke's Bay, New Zealand. — N. Z. J. Zool. 6:321–327.

Richardson, S. C., Patterson, I. J. & Dunnet, G. M. 1979: Fluctuations in colony size in the Rook (Corvus frugilegus). — J. Animal Ecol. 48:103–110.

Røskaft, E. 1980: Size of peripheral populations of Rooks (Corvus frugilegus) in Fennoscandia with special reference to Norway. — Fauna norv. Ser. C, Cinclus 3:9–15.

— 1985: The effect of enlarged brood size on the future reproductive potential of the Rook. — J. Animal Ecol. 54:255–260.

Røskaft, E., Espmark, Y. & Järvi, T. 1983: Reproductive effort and breeding success in relation to age by the Rook (Corvus frugilegus). — Ornis Scand. 14:169–174.

Ruge, K. 1988: Saatkrähe — Problemvogel auf der Roten Liste. — Beih. Veröff. Naturschutz Landschaftspflege Bad.-Württ. 53:21–30.

Rytkönen, S. & Koivula, K. 1990: Oulun seudun mustavariksista. — Oulun Luonnonystäväin Yhdistys ry. Tiedotuksia 15:7–14. (in Finnish).

Rytkönen, S., Koivula, K., & Lindgren, E. 1992: Mustavaris-yhdyskuntien ekologia Oulun seudulla. — Ympäristöministeriön ympäristönsuojeluosasto, Selvitys 78/1990 (D). (in Finnish).

Saether, B.-E. 1989: Survival rates in relation to body weight in European birds. — Ornis Scand. 14:169–174.

Siira, J. 1977: Limingan luonto. — In: Korte, S. (ed.), Liminka 1477–1977. Oulu. (in Finnish).

Wittenberg, J. 1988: Brutbiologishe Daten von der Restpopulation der Saatkrähe (Corvus frugilegus) bei Braunschweig. — Beih. Veröff. Naturschutz Landschaftspflege Bad.-Württ. 53:109–118.