Foraging success of Rooks *Corvus frugilegus* in mixed-species flocks of different sizes

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Rooks feeding in mixed-species flocks on grazed pastures foraged more successfully in large (>10 birds) than small flocks (<10 birds). Formation of large successful flocks is proposed to be a response to local changes in food distribution. Good feeding places may attract more birds and thus explain the observed correlation between flock size and success. However, the alternative hypothesis cannot be ruled out that Rooks in large flocks are more successful because they can spend more time feeding and less time scanning for predators. Furthermore, in large flocks Rooks were able to steal food from Jackdaws (kleptoparasitism).

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Introduction

Some animals commonly aggregate in foraging groups. Two major selection pressures have been proposed as the ultimate factors for the evolution of group foraging: predation, and the availability and distribution of food (Bertram 1978). In a theoretical model Pulliam (1973) predicted that the probability of detecting an approaching predator will increase with group size. This hypothesis has been generally fonfirmed by experiments and observations on birds (cf. Bertram 1978, 1980, Caraco et al. 1980, Greig–Smith 1981), mammals (Carl 1971, cf. Wilson 1975) and insects (Treherne & Foster 1980). While feeding on flocks, individuals can spend more time feeding and less time scanning for predators and hence increase their foraging success (Powell 1974, Bertram 1980). Patchily distributed food resources are not easily defended by territorial individuals, so species exploiting a food resource of this kind often live in colonies and forage in groups (Crook 1963, 1964, Brown 1964, Horn 1968, Krebs 1974). The location of food may also be enhanced by group foraging (Waite 1981, Chantrey 1982). The food density hypothesis states that when food is abundant more animals will aggregate in a given patch and the individual success will tend to be high. When the resource is depleted feeding success declines and fewer animals aggregate in the patch. These two hypotheses on the function of group foraging are not necessarily exclusive but may have different importance in different situations.

Care must be taken when interpreting grouping behavior because of many inter-correlated variables (Barnard 1983). Patterns may be confused by different individual status (age, ranking order, breeding status) and the formation of flocks of mixed species. Different individuals may have different optima and strategies (Pulliam & Caraco 1984). Thus it is difficult to discriminate between alternative hypotheses for observed patterns of aggregation.

Rooks *Corvus frugilegus* are colony-breeding birds that often forage in flocks with other corvids such as Jackdaws *C. monedula.* Rooks are particularly well suited for testing hypotheses about the costs and benefits of aggregating because their feeding rates are easily measured and they form flocks of very different sizes. In this study I examined the foraging success of individual Rooks feeding pasture land in different-sized flocks of only Rooks or Rooks and Jackdaws.

Methods

The field work was carried out at the experimental cattle farm of the Swedish University of Agricultural Sciences at Kungängen 5 km south of central Uppsala (59°50'N, 17°40'E). The corvid flocks foraged over an area that consisted of a variety of crop fields, pastures and gardens. To minimize the impact of differences in prey availability in these areas, all observations were made on a single 500 × 500 m plot of three adjacent pastures. From the third day of the study cattle were intermittently grazed on all three pastures. All observations were made between 05.00 and 09.00 in nine days between 1 and 13 July 1982.

The Jackdaws and adult and juvenile Rooks in the feeding flocks were counted every 10 min. Juvenile Rooks were distinguished by their black feathered faces, since adults have a bare white face patch. Directly after recording the flock size and its composition. I observed randomly chosen Rooks for 2 min. The foraging success was measured in terms of the number of successful pecks during 2 min (the bird was seen swallowing a food item). Every 2-min period was treated as one independent observation in the analysis, Although I could not distunguish between individual Rooks. I tried not to count the same individual more than once during each sequence of observations. The foraging birds were usually less than 500 m from me and were observed with a pair of binoculars (9 × 35) or a telescope (25 × 60). The flocks were not affected by my presence. In many cases the size and composition of the flocks changed during the course of my observations. The flock size and composition was therefore redetermined every 10 min. In the majority of the cases the flocks were so aggregated that flock membership was easy to define, but if birds were more than 200 m apart they were treated as separate groups. Perching individuals were counted as non-foraging flock members.

The availability of lumbricids, which were an important food resource, was measured twice during the investigation (3 and 14 July) using the formalin method (Raw 1959). The vegetation was removed from three randomly chosen 0.5-m^2 squares and a 0.40 % solution of formalin was poured over the squares three times at 10-min intervals. Worms from the surface down to a depth of 10 cm (Raw 1959) appeared at the surface and were collected and counted.

Results

Foraging success. The foraging success of the Rooks increased with increasing flock size (Fig.

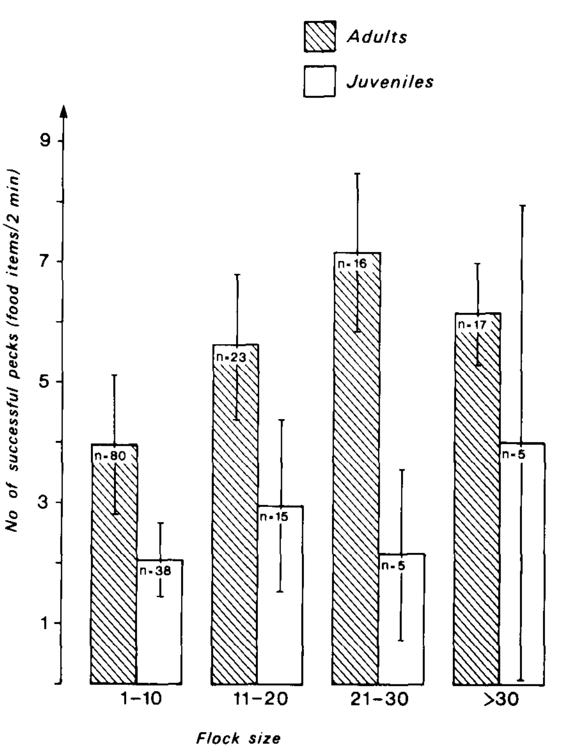

Fig. 1. Mean foraging success (food items (2 min^{-1})) of rooks. given as means (± SE) of all the birds studied, in relation to flock size of rooks and jackdaws (see text).

Table 1. Mean foraging success (food items (2 $min)^{-1}$) of adult and juvenile Rooks in different flock-size categories (see text)

Flock size	No. of Adults	No. of Juveniles	Mean foraging success Adults	Mean foraging success Juveniles	P<*
1–10	80	38	3.93	2.03	0.001
11–20	23	15	5.62	2.93	0.001
21–30	16	5	7.31	2.61	0.01
>30	17	5	6.29	4.00	0.01

* Mann-Whitney U-test, two-tailed

1). Adult Rooks in flocks consisting of more than 10 individuals were more efficient in their foraging than were adults in flocks of 1–10 birds (Mann-Whitney U-test, z=3.39, P<0.001,two-tailed, Fig. 1). A comparison of flocks of 11–20 birds with larger flocks showed that individuals in larger flocks tended to be more successful, but the difference was not significant (Mann-Whitney U-test, z=1.68, P>0.05, two-tailed, Fig. 1). There was no difference in individual feeding success between the two larger flock sizes (21–30 and >30) (Mann-Whitney U-test, z=0.90, P>0.1, two-tailed, Fig. 1) and hence there was no well-defined optimal flock size. The feeding success of adult Rooks in small flocks (<10 birds) did not vary significantly during the study (Spearman rank correlation, r_s =—0.4, P>0.05, two-tailed). A comparison of flocks of 1–10 birds with larger flocks were more successful (Mann-Whitney U-test, U^s=31, P<0.002, two-tailed). Adult birds were significantly more successful than juveniles when foraging in flocks of less than 21 birds (Mann-Whitney U-tests, z=2.98, P<0.001, two-tailed. Table 1) and also in larger flocks (Mann-Whitney U-test, z=2.40, P<0.01, two-tailed, Table 1). There were no differences in the foraging success of juvenile Rooks in different flock sizes.

Flock composition. Flock composition varied with

Table 2. The total number of individuals observed in different flock-size categories and the ratio of Rooks to Jackdaws in these. Flock composition changed as flocks became larger (X^2=237.9, df=3, P<0.001, two-tailed).

Flock size	No. of flocks	No. of Rooks	No. of Jackdaws	Ratio Rooks/ Jackdaws
1–10	88	263	167	1.57
11–20	34	161	294	0.55
21–30	19	90	386	0.23
>30	18	48	>260	<0.18
Total:	159	562	>1107	<0.51

flock size. As flock size increased the ratio of Rooks to Jackdaws decreased ($\chi^2=237.9$, df=3, $P<0.001$, two-tailed, Table 2). Foraging groups almost invariably consisted of both species except when very small, in which case they sometimes consisted of only Rooks. Small flocks (<10 birds) were frequently observed during the whole study period, whereas large flocks were observed only during the last seven days. There was a positive correlation between mean flock size and date (Spearman rank correlation, $r_s=0.82$, $P<0.02$, two-tailed). There were no significant differences in the age composition of Rooks in different flock sizes ($\chi^2=4.89$, df=3, $P>0.1$, two-tailed, Table 3). However, there was a clear trend towards a higher proportion of juveniles in larger flocks (Table 3).

Food abundance. More lumbricids were available at the beginning of the study than at the end ($\bar{x}=47.4 \pm 2$ SE=16.22 and $\bar{x}=6.6 \pm 2$ SE=5.33 worms per m^2 respectively). As a result, the main food resource for all the corvids after 6 July was insects associated with cowpats. This meant that foraging birds were restricted to pasture lands and a more localized food supply; there were no other pastures with grazing cattle within a radius of 2.5 km. The abundance of insects associated with cowpats was difficult to quantify because cattle grazing in the study plot was intermittent and hence the distribution and prey contents of cowpats varied considerably.

Kleptoparasitism. On 17 occasions Rooks were observed chasing Jackdaws or stealing their food. Jackdaws were never seen attacking Rooks and only once were two Rooks seen in an intraspecific fight.

Discussion

Foraging success of Rooks. Adult Rooks foraged more successfully than juveniles. This finding is expected, age-related differences in competence being well known in birds (Orians 1969, Ulfstrand 1979, Burger 1980). Moreover, the juvenile Rooks were still dependent on adult Rooks for food; throughout the study young birds were often fed by adults.

Rooks foraging in large flocks were more successful than Rooks in small flocks, yet large flocks occurred only at the end of the study. This change in flock size was correlated with a dramatic decline in earthworms. After this decline foraging corvids probably had to shift to a more profitable food source, in this case cowpats. This shift probably accounts for the formation of larger flocks at the end of the study; the studied pastures were isolated and hence highly localized and attractive foraging sites. In the other words, food resources were more patchily distributed after the decline in earthworms. Whether food became more abundant was not possible estimate.

Table 3. The total number of adult and juvenile Rooks observed in different flock-size categories and the ratio of juveniles to adults in these. No significant trends were detectable (see text). Two flocks were omitted from this analysis because the age of composition was not determined.

Flock size	No. of flocks	No. of adults	No. of juveniles	Ratio juv./ad.
1–10	87	162	99	0.61
11–20	34	95	66	0.69
21–30	19	48	42	0.88
>30	17	18	21	1.17
Total	157	323	228	0.71

Thus, the foraging success of individual Rooks was clearly affected by the local distribution of food. However, if foraging success depended solely on the distribution and abundance of food, one might predict that small flocks during a given day would be just as successful as large flocks. This was not the case, because members of small flocks were always less successful than members of large flocks. The improved foraging success of birds in large flocks therefore also seems to be due to the possibility of spending more time on feeding and less on predator vigilance.

Interactions between Rooks and Jackdaws. Large flocks always consisted of both Rooks and Jackdaws, and large flocks were more frequent when food resources were localized. Since Jackdaws were often parasitized by Rooks, they probably did not benefit from feeding in large flocks. Why then were they commonly seen in large flocks? The Jackdaws were perhaps forced into large flocks by patchily distributed food in the same way as the Rooks. The patterns of both the size and composition of the flocks are indicative of this. It would be interesting to study the feeding success of Jackdaws in large and small monospecific and mixed flocks. I would predict the success to be lower in large mixed flocks.

Kleptoparasitism (i.e. one species stealing food from another) often occurs in mixed-species flocks (Brockman & Barnard 1979). Rooks stealing food from Jackdaws have not previously been reported, but there are reports of Rooks being robbed by crows (Brockman & Barnard 1979).

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Selostus: **Mustavariksen ruokailutehokkuus erikokoisissa sekaparvissa**

Parvikoon vaikutusta ruokailutehokkuuteen tutkittiin Uppsalassa sekä lajipuhtaina että naakkojen kanssa sekaparvina ruokailevilla mustavariksilla. Vanhojen mustavaristen ruokailutehokkuus kasvoi sekaparven koon kasvaessa mutta ei enää yli 30 yksilön parvissa (kuva 1). Nuorilla linnuilla parvikoko ei vaikuttanut ruokailutehokkuuteen (taul. 1).

Naakkojen osuus ruokailuparvissa kasvoi parvikoon suurentuessa, vain joissain pienimmissä parvissa ei ollut naakkoja mukana (taul. 2). Mustavaristen havaittiin 17 kertaa ryövänneen naakoilta ruokaa.

Lintujen kerääntyminen suuriksi parviksi tietyille alueille voi johtua ravinnon epätasaisesta jakaantumisesta. Mahdollisesti suuret parvet ruokailivatkin paremmilla paikoilla, mikä selittäisi niissä olevien yksilöiden korkeamman ruokailutehokkuuden. Myös predaation tehokkaampi välttäminen isommissa parvissa voisi selittää tulokset. Monella lintulajillahan parvessa ruokailevien yksilöiden on todettu käyttävän enemmän aikaa itse ruokailuun ja vähemmän ympäristönsä (oletettavasti petojen) tarkkailuun kuin yksinään ruokailevien.

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