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## HABITAT DISTRIBUTION AND FEEDING STRATEGIES OF FOUR SOUTH SWEDISH CORVID SPECIES DURING WINTER

**ABSTRACT:** The density of four corvids was determined for three meadow habitats during early and late winter. There was a tendency to forage more on the moister habitat in late than in early winter. The habitat niche breadth decreased from early to late winter. Rooks and jackdaws were most frequently found foraging together. Also crows often foraged together with these species. Least associated with the other species were magpies.

**KEY WORDS:** Meadow habitats, corvids (rooks, jackdaws, crows, magpies), density, habitat distribution and preference, interspecific associations, niche overlap, feeding strategies.

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## 1. INTRODUCTION

The feeding habitat of four corvids during early and late winter in south Sweden is examined. These species, hooded crow, *Corvus cornix* L., rook, *C. frugilegus* L., jackdaw, *C. monedula* L., and magpie, *Pica pica* L., constitute a guild of ground-feeding omnivorous birds. During these seasons they feed singly, in pairs or in large flocks. The *Corvus* spp. individuals frequently form mixed-species flocks.

The objective of the study was to compare the four species with respect to habitat preference and niche breadth and to calculate their mutual niche overlap. Early and late winter were compared as food can be assumed to be more scarce in late winter, and this might influence niche characteristics. It has been stated that animals become less specialized with respect to habitat when food is scarce, at least if they, in contrast to these corvids, are pursuers (MacArthur and Pianka 1966).

It has also been suggested that the best strategy is to utilize the same habitat niche, regardless of food abundance (MacArthur and Pianka 1966, Ulfstrand 1976). It could also be argued that, in times of food shortage, animals should reduce food competition by specializing (Ulfstrand 1977). This may be associated with a tendency for animals to decrease also their habitat niche with increased intraspecific competition that can be expected to occur although the within-habitat food niche is unaltered (MacArthur 1972). It is, of course, possible that there is no overriding strategy but each case must be considered separately. These and other aspects of the feeding strategy of these corvids will be discussed.

## 2. STUDY AREA AND METHODS

### 2.1. AREA

The study was carried out in part of the Revinge area in south Sweden (55°40' N, 13°30' E). This area is used for military training about ten weeks every year. At other times most of the area is grazed by cattle. For this study, three categories of open habitats were distinguished: "dry habitat" (characterized by the grass species *Corynephorus canescens* (L.) P. B.), "intermediate habitat" (*Dactylis glomerata* L.) and "moist habitat" (*Deschampsia flexuosa* (L.) Trin.). The first two habitats occur on mineral soil and the last one on peat. Still moister open habitats dominated by tall herbs and rushes, exist but as the birds there were difficult to spot, they were omitted in this study. The examined habitats covered about 80% of the study area of about 20 km<sup>2</sup>. Outside the study area there were garbage heaps, potato deposits, hay deposits, etc., that were occasionally frequented by corvids from the study area. This was especially pronounced during periods with snow cover, but no such periods coincided with the study periods.

### 2.2. FIELD OBSERVATIONS

53 plots of 1.0–19 ha each were delimited in the study area. They were chosen in order to permit a good survey from roads and to constitute a homogeneous habitat that could be assigned to one of the three categories. 21 plots with a total area of 61 ha were in dry fields, 14

plots of 108 ha in intermediate periods with up to three. The periods were October (18 counts), October 2 (1977 (18 counts)).

2.3.1. All birds of a species were treated as a flock and not as two flocks, in different measurements of individual birds in a plot, not independent of measurement.

It is difficult to determine habitat preferences of various habitats. The proportion of birds in each habitat was proportional either to the area of the habitat or to the number of birds in the areas compared with the other habitats. The distributions were tested for differences from random using chi-square tests.

2.3.2. Niche breadth

$$B = \frac{1}{\sum p_i^2}$$

(Levins 1968), the number of resource states (here habitats).

2.3.3. An index, representing the number of resource states within each habitat, was calculated for each period. The maximum number of resource states possible, I stand for the total number of groups (G).

$$\frac{1 : \sum p^2}{\sqrt{R \cdot G}}$$

2.3.4. Niche overlap

$$N.O. = 1 - \frac{1}{2}$$

plots of 108 ha in intermediate fields, and 18 plots of 61 ha in moist fields. During four census periods with up to three counts per day corvids that were feeding in the plots were recorded. The periods were October 20 to November 5, 1975 (20 counts), February 17 to March 6, 1976, (18 counts), October 25 to November 12, 1976 (16 counts), and February 22 to March 16, 1977 (18 counts).

### 2.3. UNIT OF MEASUREMENT AND CALCULATION OF NICHE PARAMETERS

2.3.1. All birds of one species in one plot were regarded as one group. In the discussion I treat this as a flock although this may not be true in every case. A group could be formed of two flocks, in different parts of a plot although this was very uncommon. The use of a number of individual birds in statistical analysis is inappropriate as the presence of one bird in a plot is not independent of that of others. Therefore, in most cases I use the group as unit of measurement.

It is difficult to decide what should be considered the expected occurrence when testing habitat preferences of the species. This difficulty arises because average plot size differed in the various habitats. The number of groups found in one habitat could be expected to be proportional either to the area covered by that habitat or (because some flocks cover fairly large areas compared with some plots) to the number of plots in that habitat. The observed distributions were tested in both ways. The results did not contradict each other, but significant differences from random distribution were sometimes only found with one of the two alternative tests.

2.3.2. Niche breadth was calculated according to the formula

$$B = \frac{1}{\sum p_i^2}$$

(Levins 1968), the  $p_i$ s denoting the proportion of all groups found in each one of the habitats. The  $B$ -value has a potential span of one to three, three reflecting the number of resource states (here habitats) and obtained if the groups are equally distributed over all habitats.

2.3.3. An index, representing the tendency of groups to concentrate their feeding on a few plots within each habitat was calculated. This index was based on the previous formula. The resource states were represented by the different plots, considered separately for the four study periods. The maximum value is equal to the least of the observed number of groups and the number of resource states. This differed between the seasons and habitats. To make comparisons possible, I standardized the values by dividing them by the geometric mean of the number of groups ( $G$ ) and the number of resource states ( $R$ ), that is:

$$\frac{1 : \sum p^2}{\sqrt{R \cdot G}}$$

2.3.4. Niche overlap was calculated according to the formula

$$N.O. = 1 - \frac{1}{2} \sum |p_i - q_i|$$

(Schoener 1970).  $p$  and  $q$  denotes species and the  $i$ 's habitats. This value has a potential range of 0 to 1.

2.3.5. The tendency to occur together in a plot, which is strongly correlated with the tendency of birds to form mixed-species flocks, was determined both for all observations and for the three habitats separately. To obtain an "index of joint occurrence" I set up a 2 · 2 contingency table for the presence or absence of species in every species pair in each plot. The number of joint occurrences ( $A$ ) was compared with the expected number of joint occurrences under random distribution,  $(A + C) · (A + B) : N$ .  $B$  and  $C$  are the number of plots where only one of the species was observed;  $N$  is the total number of plots. The plots were considered separately for each of the 72 counts.

2.3.6. The activity of potential prey invertebrates was sampled with pitfall traps at six sites in each habitat during summer and at two sites in each during early and late winter. At each site ten jars with alcohol were put in a 5 · 2 m grid with 10 m between the jars.

### 3. RESULTS

#### 3.1. DENSITY AND HABITAT PREFERENCES

The crow was the most common corvid on the open habitats within the study area followed by the jackdaw, the rook, and the magpie (Table I). However, magpies often stayed in pine plantations and were probably as common in the study area as the crow. The densities of *Corvus* sp. were the highest in the intermediate and moist habitats whereas the magpies occurred least frequently in the intermediate habitat (Fig. 1). All species exhibited habitat preferences (Table II). There was a tendency for all species to forage more in moist habitat in

Table I. Density (individuals per km<sup>2</sup>) in the study area during early and late winter  
For the mean density values, the densities in the various habitats have been given different weights according to the total area covered by each habitat in the study area: dry habitat 2.5 km<sup>2</sup>, intermediate 3.5 km<sup>2</sup>, moist habitat 4.5 km<sup>2</sup>, and other habitats (garden, forest, and reeds) 4.0 km<sup>2</sup>. For the calculations of the mean values, it was assumed that there were no birds in the latter habitats. For the magpie, this would have been quite wrong; therefore no mean value is given

Species	Early winter				Late winter			
	dry	intermediate	moist	mean	dry	intermediate	moist	mean
Crow	2.9	6.9	3.7	5.3	0.8	6.3	18.0	8.8
Rook	2.9	2.1	1.0	2.8	0.2	3.0	2.0	2.3
Jackdaw	1.8	4.3	1.6	3.1	1.0	5.2	8.4	5.5
Magpie	2.0	0.6	1.2		0.8	0.1	0.9	

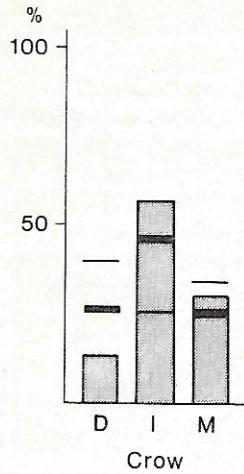


Fig. 1. The distribution of Crow with the distribution of habitats. The shaded part represents...

The distribution of groups... and the distribution of area... The degree of significance is...

Species	Period
Crow	early winter
	late winter
Rook	early winter
	late winter
Jackdaw	early winter
	late winter
Magpie	early winter
	late winter

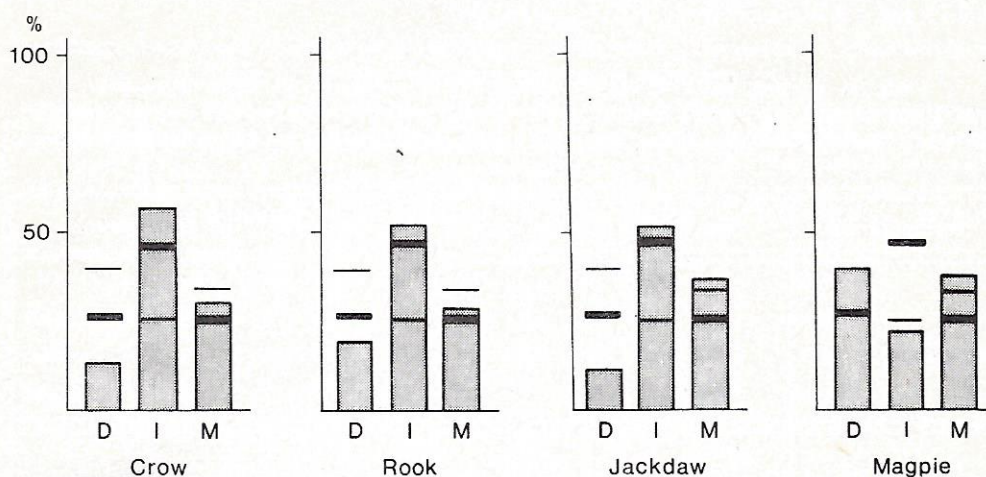


Fig. 1. The distribution of groups in different habitats (D – dry, I – intermediate, M – moist) compared with the distribution of plots and with the distribution of area of the three habitats. The shaded part represents groups, the thick bars area and the thin bars number of plots in different habitats.

Table II. Habitat preferences of the examined corvids

The distribution of groups in different habitats is compared with the distribution of plots of the habitats and the distribution of area covered by the different habitats. The distributions are compared with  $\chi^2$ -test. The degree of significance in the deviation from random and the preferred habitat(s) is given. n.s. – not significant difference

Species	Period	Groups-plots			Groups-area		
		$\chi^2$	$p <$	preferred habitat	$\chi^2$	$p <$	preferred habitat
Crow	early winter	87.1	0.001	intermediate	9.83	0.01	intermediate
	late winter	105	0.001	intermediate and moist	30.5	0.001	intermediate and moist
Rook	early winter	6.01	0.05	intermediate	0.37	n.s.	–
	late winter	21.6	0.001	intermediate	6.17	0.05	intermediate and moist
Jackdaw	early winter	10.7	0.01	intermediate	0.64	n.s.	–
	late winter	32.0	0.001	intermediate and moist	13.5	0.01	intermediate and moist
Magpie	early winter	0.24	n.s.	–	11.7	0.01	dry and moist
	late winter	5.52	n.s.	–	11.8	0.01	dry and moist

value has a potential

correlated with the all observations and "I set up a 2 · 2 pair in each plot. The of joint occurrences of plots where only plots were considered

pitfall traps at six sites e winter. At each site

study area followed often stayed in pine ow. The densities of whereas the magpies es exhibited habitat e in moist habitat in

and late winter ven different weights 2.5 km<sup>2</sup>, intermediate km<sup>2</sup>. For the calcula- bitats. For the magpie, given

winter		
	moist	mean
	18.0	8.8
	2.0	2.3
	8.4	5.5
	0.9	

late winter than in early winter (Table III). This was significant for crows and rooks ( $\chi^2 = 13.5$  and  $6.35$ ,  $d.f. = 2$ ,  $p < 0.001$  and  $< 0.05$ , respectively) but not for jackdaws and magpies ( $\chi^2 = 4.70$  and  $= 3.14$ , respectively,  $d.f. = 2$ ,  $p > 0.05$ ).

Table III. Moisture index of habitat utilized by the corvids during different seasons. The index was obtained by giving a score of one to each group or individual observed in a plot of dry fields, two for each in intermediate, and three for each in moist, and taking the mean values of these scores

Moisture index	Species	Early winter	Late winter	Both periods
For groups	crow	2.02	2.28	2.17
	rook	1.94	2.29	2.09
	jackdaw	2.09	2.37	2.26
	magpie	1.87	2.23	1.97
For individuals	crow	2.05	2.57	2.37
	rook	1.79	2.24	2.02
	jackdaw	2.09	2.40	2.28
	magpie	1.83	2.07	1.90

3.2. GROUP SIZE

There was no consistent tendency for a change in group size from early to late winter (Table IV). The largest observed groups of crows held 80, 60, and 20, those of rooks 35, 20, and 18, those of jackdaws 45, 40, and 35, and those of magpies 6, 5, and 3 individuals.

Table IV. Mean size of groups

Species	Early winter		Late winter		Both periods	
	mean size	N	mean size	N	mean size	N
Crow	3.1	133	4.2	157	3.7	290
Rook	5.2	32	6.9	24	5.9	56
Jackdaw	8.4	34	7.9	52	8.1	86
Magpie	1.7	55	1.9	22	1.8	77

3.3. NICHE BREADTH

Considering both seasons, the niche breadth values of the *Corvus* spp. were similar and less than that of the magpie (Table V, Fig. 1). In general, there was a tendency for niche breadth to

Table V. Niche breadth of

The change is calculated s

Species	early winter
	early winter
Crow	2.23 (1)
Rook	2.84 ( )
Jackdaw	2.64 ( )
Magpie	2.83 ( )

be reduced from early winter ( $N = 8$ ) in early winter.  $U$ -test,  $U = 11$ ,  $p = 0.0$

3.

Within the habitats their feeding on some species-habitat combinations (5 cases out of 6) ( $p = 0.11$ ). The magpies around.

Table

A high index indicates that groups were concentrated (number of plots in the intermediate 28 and moist 36. The of the indices in a s

Species	Dry
	early winter
Crow	40 (25)
Rook	(50 (10))
Jackdaw	(32 (7))
Magpie	(31 (24))

Table V. Niche breadth of the corvids during the two seasons and the change in niche breadth from early to late winter  
The change is calculated separately for the two winter periods studied. The numbers of observed groups used for the calculations are given in parentheses

Species	Niche breadth			Change in niche breadth from early to late winter	
	early winter	late winter	both seasons	1975/1976	1976/1977
Crow	2.23 (133)	2.26 (167)	2.32 (300)	+0.35	-0.52
Rook	2.84 (32)	1.97 (24)	2.53 (56)	-0.57	-0.97
Jackdaw	2.64 (34)	2.22 (52)	2.43 (86)	-0.25	-0.65
Magpie	2.83 (55)	2.36 (22)	2.83 (77)	+0.12	-1.49

be reduced from early to late winter (Table V). The mean niche breadth for all species was 2.60 ( $N = 8$ ) in early winter and 2.11 ( $N = 8$ ) in late winter, a significant difference (Mann-Whitney  $U$ -test,  $U = 11$ ,  $p = 0.03$ ).

3.4. PLOT-USE CONCENTRATION WITHIN HABITATS

Within the habitats, the *Corvus* sp. in late winter showed a greater tendency to concentrate their feeding on some plots than they did in early winter. This is most pronounced if only species-habitat combinations with at least 10 observed groups in both seasons are considered (5 cases out of 6) (Table VI). This tendency, however, was insignificant (binomial test,  $p = 0.11$ ). The magpies were not considered as many individuals stay in their territories the year around.

Table VI. Evenness of utilization of the habitats (see Section 2.3.3)

A high index indicates value an even utilization of all plots in the habitat while a low one indicates that the groups were concentrated in only some of the plots. The resource states ( $R$ ) in the different habitats (number of plots in the habitat times two (as each year is considered separately)) are for dry 42, intermediate 28 and moist 36. The number of groups ( $G$ ) that each index is based on is given in parentheses. If one of the indices in a seasonal pair is based on less than 10 groups, this pair is given in parentheses

Species	Dry habitat		Intermediate habitat		Moist habitat	
	early winter	late winter	early winter	late winter	early winter	late winter
Crow	40 (25)	35 (13)	37 (81)	30 (84)	31 (27)	14 (60)
Rook	(50 (10))	(17 (1))	38 (14)	32 (15)	(26 (8))	(31 (8))
Jackdaw	(32 (7))	(27 (3))	77 (17)	39 (27)	29 (10)	43 (22)
Magpie	(31 (24))	(31 (7))	(26 (14))	(33 (3))	33 (17)	43 (12)

ws and rooks ( $\chi^2 = 13.5$   
jackdaws and magpies

different seasons  
l observed in a plot of dry  
taking the mean values of

Both periods	
	2.17
	2.09
	2.26
	1.97
	2.37
	2.02
	2.28
	1.90

om early to late winter  
those of rooks 35, 20,  
d 3 individuals.

both periods	
size	N
	290
	56
	86
	77

pp. were similar and less  
ncy for niche breadth to

The flocks of crows showed a greater tendency to concentrate their feeding to a few plots in the most preferred habitat, the moist, than in the least preferred, the dry. This was pronounced in late winter when there also was a great difference in preference between the two habitats. Thus, combining all four census periods in the dry habitat, 38 groups visited 28 plots out of 84, whereas in the moist habitat 84 groups visited 36 plots out of 72 which was a significantly higher degree of concentration (comparing the number of plots visited by 0, 1, or more than one group,  $\chi^2 = 8.84$ ,  $d.f. = 2$ ,  $p < 0.05$ ). This comparison does not include the intermediate habitat as its mean plot size was twice that in the two others, which could bias the result. The number of groups of the other species was too small for a similar analysis.

3.5. NICHE OVERLAP

The niche overlap values of the three *Corvus* spp. were high whereas the magpie had a more different niche (Table VII). There was a tendency, although insignificant, for the overlap to decrease from autumn to late winter (Table VII). The mean overlap value was 0.80 ( $N = 12$ ) in early winter and 0.71 ( $N = 12$ ) in late winter (Mann-Whitney  $U$ -test,  $U = 52$ ,  $p > 0.10$ ).

Table VII. Niche overlap during the two seasons and the change in niche overlap from early to late winter

Pairs of species	Niche overlap			Change in overlap value from early to late winter	
	early winter	late winter	both seasons	1975/1976	1976/1977
Crow-rook	0.83	0.91	0.94	+0.01	-0.08
Crow-jackdaw	0.89	0.94	0.93	+0.08	+0.07
Crow-magpie	0.64	0.60	0.65	+0.11	-0.22
Rook-jackdaw	0.90	0.89	0.92	-0.07	-0.09
Rook-magpie	0.81	0.51	0.71	-0.03	-0.58
Jackdaw-magpie	0.75	0.62	0.71	-0.04	-0.18

3.6. MIXED-SPECIES GROUPS

Rooks and jackdaws had the highest tendency to occur together in plots followed by other combinations of *Corvus* spp. (Table VIII). The magpie was the species least associated with others. The tendency of the three *Corvus* spp. to form interspecific flocks was greatest in the dry, less in the moist, and least in the intermediate habitat (Table VIII). Thus, this tendency was least in the two most preferred habitats (Table IX). A similar comparison between early and late winter revealed almost no difference between the seasons in the tendency to form mixed-species flocks.

Table VII  
The index (see Section together.

Pairs of species
Crow-rook
Crow-jackdaw
Crow-magpie
Rook-jackdaw
Rook-magpie
Jackdaw-magpie

Species
Crow
Rook
Jackdaw
Magpie

3.7. DIST

Pitfall-sampling invertebrates showed late winter than in the invertebrates, it

The biomass of invertebrates at two sites sampled filled with alcohol at

Habitat
Dry
Intermediate
Moist

\*The capture sites



Table VIII. The tendency of different pairs of species to occur together in plots. The index (see Section 2.3.5) is calculated separately for each of the three habitats and for the habitats together. The number of observed mixed-species groups is given in parentheses

Pairs of species	Dry habitat	Intermediate habitat	Moist habitat	All habitats
Crow-rook	25 (7)	5.3 (25)	13 (16)	11 (48)
Crow-jackdaw	16 (4)	4.6 (33)	13 (28)	10 (65)
Crow-magpie	9.0 (7)	3.2 (9)	4.1 (8)	4.1 (24)
Rook-jackdaw	82 (6)	12 (15)	35 (14)	27 (35)
Rook-magpie	4.4 (1)	4.1 (2)	8.3 (3)	5.5 (6)
Jackdaw-magpie	9.5 (2)	2.7 (2)	8.3 (6)	5.9 (10)

Table IX. The number of groups per km<sup>2</sup> in different habitats

Species	Dry habitat	Intermediate habitat	Moist habitat
Crow	0.88	2.1	2.0
Rook	0.26	0.37	0.37
Jackdaw	0.23	0.57	0.74
Magpie	0.72	0.22	0.67

3.7. DISTRIBUTION OF INVERTEBRATES AND OTHER FOOD SOURCES

Pitfall-sampling in six sites in each of the three habitat types indicated that the availability of invertebrates showed more intra- than inter-habitat variation (Table X). The catch was less in late winter than in early winter. As the catch depends both on the density and the movement of the invertebrates, it should have some positive correlation to the availability of this prey to

Table X. Invertebrate food availability

The biomass of invertebrates captured at six sample sites in each habitat in July and the mean capture at two sites sampled in July, October, and February are given. At each site 10 jars (diameter 6 cm) filled with alcohol at a distance of 10 m from each other served as pitfalls. The pitfalls were operated for 72 hours

Habitat	Biomass (g) captured at each of six capture sites						Mean biomass (g) captured at two sites		
	July	October	February	July	October	February	July	October	February
Dry	2.0	4.0	11	12	15	15	11.5	1.4	0.09
Intermediate	4.2	8.1	8.7	12	12	13	6.6	7.9	0.41
Moist	7.1	9.7	9.9	10	12	23	9.8	3.2	*

\*The capture sites were flooded during this month.

feeding to a few plots in y. This was pronounced between the two habitats. 28 plots out of 84, which was a significantly by 0, 1, or more than include the intermediate could bias the result. The

the magpie had a more ant, for the overlap to ue was 0.80 (N = 12) in 52, p > 0.10).

from early to late winter

Overlap value from to late winter	
1976	1976/1977
	-0.08
	+0.07
	-0.22
	-0.09
	-0.58
	-0.18

plots followed by other s least associated with cks was greatest in the ). Thus, this tendency mparison between early the tendency to form

predators that hunt by sight, such as the corvids. During autumn the catch was highest in the intermediate, followed by the moist and the dry habitat, roughly parallel with the density of the *Corvus* spp. (Tables I, II).

Though this was not measured, it can be taken for granted that the amount of seeds and edible vegetable matter in the study area was less in late winter than in early winter, as production between the early and the late study period is negligible.

#### 4. DISCUSSION

##### 4.1. FORAGING STRATEGY MODELS

For the following discussion, I distinguish three foraging strategies. Two strategies are subdivided in parts. The following assumptions and simplifications are made: (1) The total feeding area can be divided into a limited number of definable habitats. (2) Each habitat is structurally homogeneous. (3) The birds are able to distinguish between habitats. (4) Each habitat is divisible in a number of patches. (5) Patches differ in terms of food density, but are internally homogeneous in that respect.

1a. The most straight-forward feeding strategy consists of feeding in each patch until a certain amount of food has been harvested. This is the strategy of hunting by expectation, as suggested by Gibb (1962). As it means that the searching animal will have to spend more time in patches, the less rewarding they are, this strategy seems, in most situations, to be implausible. Krebs (1973) modified it by assuming that the animal feeds in each patch for a fixed time. I will henceforth refer to this strategy as "hunting by expectation". It is illustrated in Figure 2: 1a.

1b. If the searching animal knows which habitat has the highest mean food density, it might restrict its foraging to patches within the superior habitat (Fig. 2: 1b).

2a. If the animal, from previous experience or by an inherited mechanism (as could be possible in stable habitat complexes), knows the food density distribution of patches, it could sample the food density of each patch and continue feeding only in the most profitable patches. If sampling is done by a trial feeding bout, there is no time lost if the patch is accepted for continued feeding. If it has no previous knowledge but a good memory, it could start by sampling all patches and then return to the most profitable ones. It could also take advantage of more experienced individuals and join a flock that feeds according to this pattern (Fig. 2: 2a).

2b. If sampling is costly compared with feeding, or if the differences between the mean food density of habitats are great and the animal knows the food density distribution of patches or at least the mean food density of different habitats, it could choose to sample and feed only in the best habitat (Fig. 2: 2b). This could be the best strategy even if the most profitable patches of the poorest habitat are better than the poorest ones in a better habitat if sampling is sufficiently costly, e.g., in terms of time.

3. If the animal knows the food density distribution of all patches and is able to determine the density of each patch by sight, with no cost in time or energy for sampling, or knows this density from previous experience, it should feed in the best patches only and leave each when the food density is similar to that in the best non-acceptable patch (Fig. 2: 3). Patches from all habitats should be utilized unless even the best one if a habitat is too poor (Fig. 2: 3).

Fig. 2. (The shaded part of the addition to what is assumed is available in a p

atch was highest in the  
 el with the density of  
 e amount of seeds and  
 an in early winter, as

Two strategies are sub-  
 : (1) The total feeding  
 a habitat is structurally  
 s. (4) Each habitat is  
 sity, but are internally

in each patch until a  
 ing by expectation, as  
 ll have to spend more  
 most situations, to be  
 ds in each patch for a  
 ation". It is illustrated

food density, it might

mechanism (as could be  
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 n the most profitable  
 f the patch is accepted  
 ory, it could start by  
 also take advantage of  
 is pattern (Fig. 2: 2a).  
 ces between the mean  
 istribution of patches  
 sample and feed only  
 if the most profitable  
 r habitat if sampling is

nd is able to determine  
 mpling, or knows this  
 y and leave each when  
 2: 3). Patches from all  
 (Fig. 2: 3).

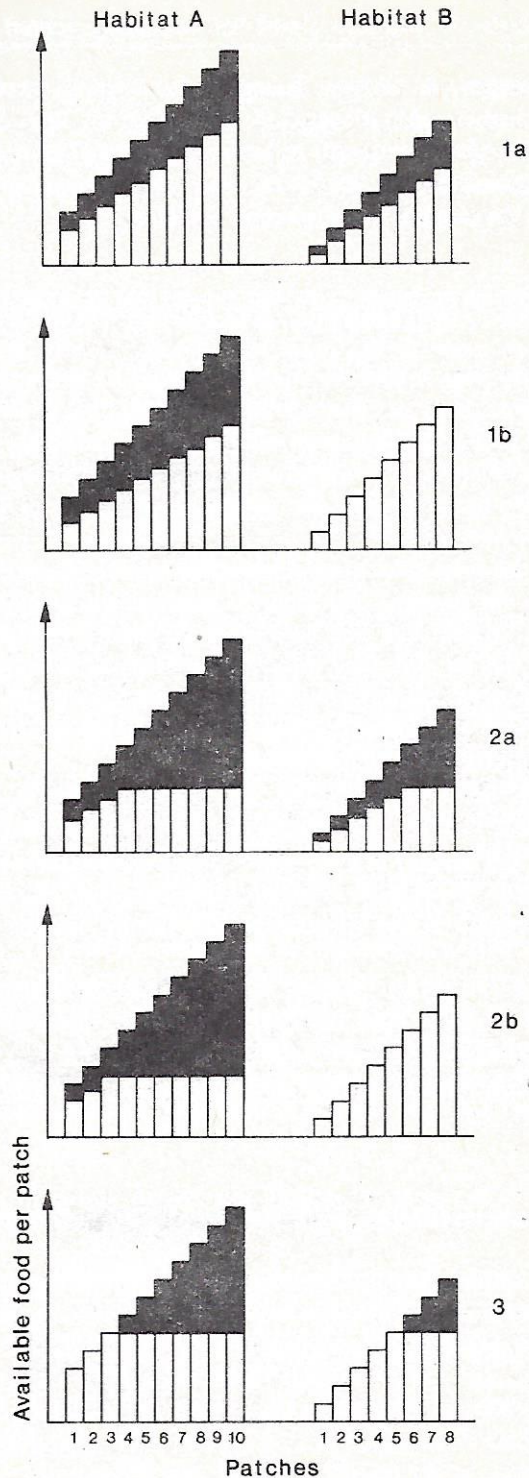


Fig. 2. Graphic models of five feeding strategies (1a-3) described in the text. The shaded part of the feeding area represents the part of the food in the patches that is consumed. In addition to what is assumed in the text, I assume the less food is consumed per unit time the less food there is available in a patch. In the depicted example, there are 10 patches in habitat A and 8 in B

The last three strategies (2a, 2b and 3) require increasingly more information. They are variations of "the optimal foraging strategy" (Krebs, Ryan and Charnov 1974). I will, however, reserve this term for strategy (3) and refer to (2a) and (2b) as "foraging by sampling". The term optimal in this context should be used with care; actually all strategies may be optimal, depending on the amount of information available.

4.2. NICHE BREADTHS AND SEARCH STRATEGIES

A clear pattern in my data is that the corvids switched to the moist habitat and decreased their niche breadth from early to late winter (Tables III, V). A likely explanation is that, although food became scarcer in the course of the winter, this change was less marked in the moist habitat, perhaps because of the gradual thinning of its initially dense vegetation cover. This change might even have reversed the relative profitability of the moist and the intermediate habitats for the corvids.

The crow, which is the only species for which sufficient data are available, showed a stronger tendency to distribute the foraging evenly in the least preferred habitat, the dry, than in the other ones (Table VI). Unless food was very unevenly distributed in the other habitats, this suggests that sampling was an important part of the activity in the dry habitat. The increased concentration on some plots in late winter compared with early winter contradicts the hunting by expectation strategy; if this applied, the tendency to concentration on some plots should be low and equal in all habitats and in both seasons.

The birds', especially the winter migrants', knowledge of their feeding area might increase from early to late winter. If so, the feeding pattern should conform more to the optimal foraging model in late winter than in early winter when it should conform more to the feeding by sampling model. Such a switch is consistent with the decrease in habitat niche breadth (Table V) and the observed increased tendency to concentrate on some patches within a habitat (Table VI).

MacArthur and Pianka (1966) suggested that animals spending relatively more time on pursuing and handling than on searching, should widen their patch utilization at reduced food levels. However, corvids mainly consume food that requires no pursuit or handling and the fact that they do not conform to this model in the present study (Table VI) does not contradict it.

4.3. FLOCKING TENDENCIES AND COMPETITION

A discussion of the different species tendency to associate is dependent on the index used. Table XI contains my data on the relations between groups of rooks and crows, and rooks and jackdaws. The index of association according to my method is 10.9 and 26.9, respectively. Employing the index of Cole (1949),  $(AD - BC) : (A + B)(B + D)$ , the relation is reversed, the index values being 0.81 and 0.40. Cole's (1949) index stresses that the distribution of rooks is nearly completely "contained" in that of crows but disregards that most crows were not associated with rooks. If the large number of crows compared with rooks was due to a sampling error I consider Cole's (1949) approach justified, but in the present case, the difference was certainly real one. My index stresses the fact that rooks and jackdaws were often found together despite the large number of empty plots. In the context of this study, I consider

this to be important. The distributions were not uniform. It may be a common feature, although, (Pyrrhonorhinus 1973).

Table XI. The distribution of rooks and crows. The values represent the number of rooks present and absent.

Rook	pres abs
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This tendency to separate this effect from the distribution in the other habitats compared. For this magpie only. The effect of their presence (Table VI) distribution with a difference at the absence of crows. The magpie, being small (Charnov 1974) is forced on a realized niche in the inter-specific flocking groups of magpies. territorial individuals. personal communication reflect the competition.

Table XII. Distribution of rooks with jackdaws.

Habitat
Dry Intermediate Moist
$\chi^2$ P

this to be important. All species occur together in plots more often than expected if the distributions were random (Table VIII). This tendency to form mixed-species flocks appears to be a common feature of corvids, e.g., chough, *Pyrrhocorax pyrrhocorax* (L.), and alpine chough, *Pyrrhocorax graculus* (L.) (Lovari 1978), and Australian corvids (Rowley 1973).

Table XI. The distribution of single-species and mixed-species groups with respect to the species pairs crow-rook and rook-jackdaw  
The values represent observed patches with individuals of either species present or absent

Rook	Crow		Rook	Jackdaw	
	present	absent		present	absent
present	48	10	present	35	51
absent	242	3516	absent	21	3709

This tendency may by itself explain the high degree of habitat niche overlap observed. To separate this effect from the habitat preferences of the different species, their habitat distribution in the presence and in the absence of individuals of the other species may be compared. For this purpose the number of observations was sufficient for the crow and the magpie only. The crow had the same habitat distribution at the absence of other species as at their presence (Table XII). The result for the magpie is surprising; the tendency to a bimodal distribution with a preference for dry and moist habitats became significantly more pronounced at the absence of other species. This contradicts the otherwise reasonable expectation that the magpie, being smaller than the crow and the rook and probably socially subdominant (Morse 1974) is forced out in the marginal habitats (Morse 1970). Thus, it seems that the magpies realized niche in the study area was modified by attraction to other species. This suggests that inter-specific flocking is advantageous. However, another explanation is possible. Single species groups of magpies were often pairs or single birds. These may to a large extent have been territorial individuals. These usually stay in their territories all the year round (G. Högstedt – personal communication), possibly for social reasons. Their pattern of distribution might thus reflect the competitive situation at other times of the year, e.g., the breeding period.

Table XII. Distribution of groups on different habitats for groups of crow and magpie unassociated with other corvid species and for groups associated with other species

Habitat	Crows		Magpies	
	in single-species groups	in multi-species groups	in single-species groups	in multi-species groups
Dry	26	12	28	3
Intermediate	113	50	8	9
Moist	57	34	18	11
$\chi^2$	0.90		11.2	
$p$	> 0.10		< 0.01	

The two species that had the strongest tendency to form inter-specific flocks were rook and jackdaw. Competition between them, however, is reduced as they differ in their modes of food capture (Lockie 1956).

The crow differs from both the rook and the jackdaw in being more prone to utilize carrion (G. Göransson, G. Jansson, O. Liberg, J. Loman, T. v. Schantz and M. Sylvén – unpublished data). The advantages of flocking might apply only to a limited degree when feeding on carrion, because competition is high and it is improbable that low rank individuals would have much success (Charles 1972). This difference in feeding behaviour may contribute to the lower mean group size of the crow compared with rook and jackdaw (Table IV).

Lockie (1955) observed that crows utilize habitats with a higher vegetation than was acceptable to rooks and jackdaws. In my data on the distribution of groups, no such difference is evident (Table IX). However, the distribution of individuals agrees with his data (Tables I, III).

The degree of inter-specific association was highest in the least preferred habitat, the dry one (Table VIII). This may indicate that many plots in this habitat have a food level below some minimum requirement for all three *Corvus* spp. This will lead to concentration in the remaining plots, more mixed-species groups formed by pure chance and a high value at inter-specific association. Another explanation is that, for some reason, it might be more rewarding to form inter-specific flocks in the dry habitat. It may be that proportionally more time is spent for sampling than for feeding in this, on an average more inferior habitat and that the value of information gained from observing other individuals, even of other species, is comparatively high in this habitat.

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## 5. SUMMARY

The distribution of crows, rooks, jackdaws and magpies on plots representing dry, intermediate and moist meadows was determined for an early and a late winter period. There was a tendency for the corvids to forage more on moister meadows in late winter than in early winter (Tables II, III).

The flocks were of similar size in both seasons (Table IV). The habitat niche breadth was less in late winter than in early winter (Table V).

There was a tendency for the *Corvus* spp. to concentrate their feeding to fewer plots in each of the habitats in late winter than in early winter (Table VI). This suggests that food was more patchily distributed in late winter or that the birds, during the course of the winter, learned the relative profitability of patches in the study area.

Rooks and jackdaws had the highest tendency to feed together followed by other combinations of *Corvus* spp. The magpie was least associated with the other species (Table VIII).

The results suggest that the corvids do not forage according to the "hunting by expectation strategy" (Gibb 1962) (Fig. 2: 1a, b) but rather to the "foraging by sampling strategy" (Section 4.1. and Fig. 2: 2a, b) or, in late winter, to the "optimal foraging strategy" (Section 4.1, Fig. 2: 3, and Krebs, Ryan and Charnov 1974).

Badano rozmieszczenie średnie i wilgotne łąki nego żerowania na bar zimowym (tab. II, III).

Wielkość stad była zimą niż w okresie wczesnej zimy.

*Corvus* spp. odznaczają siedlisku późną zimą i późną zimą, lub to, że w pewnych płatach badano.

Gawrony i kawki w kombinacje gatunków (Table IX).

Wyniki badań sugerują (Gibb 1962) (rys. 2: okresie późnej zimy – Ryan i Charnov 1974).

1. Charles J. 1972. *Corvus corone* and *Corvus*
2. Cole L. C. 1949.
3. Gibb J. 1962 –
4. Krebs J. 1973. Klopfer) – Plenum
5. Krebs J. R., Ryan study of patch use
6. Levins R. 1968
7. Lockie J. 1955 other Corvidae – I
8. Lockie J. 1956 Ecol. 25: 421–428
9. Lovari S. 1978
10. MacArthur R.
11. MacArthur R. 100: 603–609.
12. Morse D. 1970 40: 119–168.
13. Morse D. 1974-
14. Rowley I. 1970 behaviour – C. S.
15. Schoener T. 1951: 408–418.
16. Ulfstrand S. tion in winter and
17. Ulfstrand S. Swedish coniferous

## 6. POLISH SUMMARY

Badano rozmieszczenie wron, gawronów, kawek i srok na powierzchniach reprezentujących suche, pośrednie i wilgotne łąki w okresach wczesnej i późnej zimy. Wykazano tendencję krukowatych do wzmożonego żerowania na bardziej wilgotnych łąkach w ciągu późnej zimy w porównaniu z wczesnym okresem zimowym (tab. II, III).

Wielkość stad była podobna w obu okresach (tab. IV). Pojemność niszy siedliskowej była mniejsza późną zimą niż w okresie wcześniejszym (tab. V).

*Corvus* spp. odznaczają się tendencją do skupiania żerowania na mniejszej liczbie powierzchni w każdym siedlisku późną zimą niż wczesną zimą (tab. VI). Sugeruje to, że rozkład pokarmu był bardziej płatowy późną zimą, lub to, że ptaki uczyły się w przebiegu zimy rozpoznawać względne korzyści z żerowania na pewnych płatach badanego obszaru.

Gawrony i kawki wykazują największą tendencję do wspólnego żerowania, a mniejsze tendencje inne kombinacje gatunków *Corvus*. Sroka była najmniej stowarzyszona z innymi gatunkami (tab. VII).

Wyniki badań sugerują, że krukowate nie żerują zgodnie ze „strategią polowania przez oczekiwanie” (Gibb 1962) (rys. 2: 1a, b), lecz raczej żerują według „strategii prób” (rozdz. 4.1 i rys. 2: 2a, b), lub – w okresie późnej zimy – zgodnie ze „strategią optymalnego żerowania” (rozdz. 4.1., rys. 2: 3 oraz Krebs, Ryan i Charnov 1974).

## 7. REFERENCES

1. Charles J. 1972 – Territorial behaviour and the limitation of population size in the crow, *Corvus corone* and *Corvus cornix* – Unpublished Ph.D. Thesis, University of Aberdeen.
2. Cole L. C. 1949 – The measurement of interspecific association – *Ecology*, 30: 411–424.
3. Gibb J. 1962 – L. Tinbergen's hypothesis of the role of specific search images – *Ibis*, 104: 106–111.
4. Krebs J. 1973 – Behavioural aspects of predation (In: Perspectives in ecology, Eds. P. Bateson, P. Klopfer) – Plenum Press, New York–London, 73–112.
5. Krebs J. R., Ryan J., Charnov E. L. 1974 – Hunting by expectation on optimal foraging? A study of patch use by chickadees – *Anim. Behav.* 22: 953–964.
6. Levins R. 1968 – Evolution in changing environment – Princeton Univ. Press, Princeton.
7. Lockie J. 1955 – The breeding and feeding of jackdaws and rooks with notes on carrion crows and other Corvidae – *Ibis*, 97: 341–369.
8. Lockie J. 1956 – The food and feeding behaviour of the jackdaw, rook and carrion crow – *J. Anim. Ecol.* 25: 421–428.
9. Lovari S. 1978 – Flocking behaviour of the chough and the alpine chough – *Gerfaut*, 68: 163–176.
10. MacArthur R. H. 1972 – Geographical ecology – Harper and Row, New York, 269 pp.
11. MacArthur R. H., Pianka E. R. 1966 – On optimal use of a patchy environment – *Am. Nat.* 100: 603–609.
12. Morse D. 1970 – Ecological aspects of some mixed-species foraging flocks of birds – *Ecol. Monogr.* 40: 119–168.
13. Morse D. 1974 – Niche breadth as a function of social dominance – *Am. Nat.* 108: 818–830.
14. Rowley I. 1973 – The comparative ecology of Australian corvids. II. Social organisation and behaviour – *C. S. I. R. O. Wildl. Res.* 18: 25–65.
15. Schoener T. 1970 – Non-synchronous spatial overlap of lizards in a patchy environment – *Ecology*, 51: 408–418.
16. Ulfstrand S. 1976 – Feeding niches of some passerine birds in a south Swedish coniferous plantation in winter and summer – *Ornis scand.* 7: 21–27.
17. Ulfstrand S. 1977 – Foraging niche dynamics and overlap in a guild of passerine birds in a south Swedish coniferous woodland – *Oecologia (Berl.)*, 27: 23–45.