

SOCIAL ORGANIZATION IN A POPULATION OF THE HOODED CROW

JON LOMAN

Dept. of Animal Ecology, Ecology building, S 223 62 Lund, Sweden

Received 16 February 1982, revised 8 May 1984

CONTENTS

1. Introduction	61
2. Study area	61
3. Methods	62
3.1. Trapping and tagging	62
3.2. Recording	62
3.3. Radio-tracking	62
4. Results	62
4.1. Territorial and flock crows in spring	62
4.2. Acquisition of territories and pair bond	64
4.3. Attachment to the territory	65
4.4. Seasonal variation in flock size and feeding stations	66
4.5. Distribution of crows during winter	68
4.6. Migration	70
4.7. Survival	70
5. Discussion	71
5.1. Segregation of territories and flock area	71
5.2. Pair formation	71
5.3. Territory establishment	71
5.4. Occupancy of territories during winter	72
5.5. Juveniles staying in their parents' territories	72
5.6. Distribution of feeding sites during winter	73
5.7. Function of roosting behaviour	73
6. Acknowledgements	74
7. Summary	74
8. References	74
9. Samenvatting	74

1. INTRODUCTION

Data presented in this paper will be used for two kinds of comparison that give information on the evolution of social traits in the Hooded Crow *Corvus cornix* and other species. By comparing information from studies made at different localities, it is sometimes possible to evaluate the importance of environmental variables for certain social traits. Other studies on aspects discussed in this paper are, e.g. those by Tompa (1975) in Switzerland, Kalchreuter (1971a) and Wittenberg (1968) in West Germany and Charles (1972) in Scotland. These studies refer to the Carrion Crow *C. corone*. Although I prefer to consider it a species different from the Hooded Crow, its ecological niche is sufficiently similar to justify comparisons.

It is also possible to compare the social organisation of crows with that of other, systemati-

cally related, species. Corvid social organization can roughly be classified as territorial, colonial, or communal. Territorial systems are those where the living space is split up into exclusive territories, at least during the breeding season. Colonial species have their nests concentrated and feed in a common area around the nesting colony but each nest is tended by a single pair. Communal societies are those where a family group tends one nest in a shared territory. The Hooded Crow mainly belongs to the territorial category. Abshagen (1963) has described how it can adopt a colonial nesting strategy and here I will demonstrate that Hooded Crows show some traits of communal nesting too.

Some further data are included, but not directly used for comparative purposes. This is to present a picture as complete as possible of the crow population studied. I believe this facilitates understanding of phenomena to be discussed.

I have previously reported on the breeding biology of the crow population studied (Loman 1977, 1980) and some data from these studies are given as a background. Eggs are laid in early April and mean clutch size is 4.3 eggs. About 10% of the clutches are lost or deserted. Some of these are replaced. Eggs hatch after an incubation period of about 18 days. Hatching is asynchronous, spanning over 2–3 days. Twenty-five per cent of the broods are lost to predators. A mean of 2.8 young fledge from the remaining broods. The youngest one in a brood often starves to death. The number of breeding pairs in the study area varied between 39 and 52 (1.9–2.5 pairs per km²) during 1972–1979.

2. STUDY AREA

The study was conducted in southern Sweden (55° 40' N, 13° 30' E). An "intensive study area" covered about 20 km² of the Revinge area, a military training field. It was used for military training about 5 weeks per year and for the rest of the year much of it was grazed by cattle. There were some

marsh-areas and a eutrophic lake, Krankesjön. All trapping and tagging was done in the intensive study area, where I attempted to find all nests.

As all large winter roosts and some other places of importance for tagged crows were situated outside the intensive study area, I also made observations in adjacent areas. Agricultural land dominated outside the Revinge area. Some places in the study area provided a large supply of food for crows throughout the year or during certain seasons. These places will henceforth be referred to as "concentrated feeding places", CFP. CFP in the study area were: 1. A small fenced area where pigs were kept in the open all year. The crows had opportunities to take pig's food. 2. Two centres for cattle raising in the Revinge area. Cattle were always in the vicinity of these centres during winter and were fed with hay and supplementary food in the open. The crows were often seen to feed among the hay. All calves were born in the open at these centres in spring. Dead calves and afterbirths provided important food for the crows. 3. Municipal garbage tips. 4. A dung heap that was particularly favoured by crows during winter. 5. Winter potato stores. These provided food for various months during winter.

The breeding crows were protected in the intensive study area. I was always able to detect whether or not nests belonged to tagged crows in this area. Nesting by tagged individuals outside the intensive study area could sometimes be recorded. Other common corvids in the study area were Rook *C. frugilegus*, Jackdaws *C. monedula*, Magpie *Pica pica*, and Jay *Garrulus glandularius*. The former two frequented the same winter roosts as the Hooded Crows. The density of Rooks increased considerably in the course of the study but this did not seem to influence the density or distribution of the Hooded Crow population. A pair of Hooded Crows that nested in a copse retained their nest-site despite the fact that Rooks started nesting in the same copse.

3. METHODS

3.1. TRAPPING AND TAGGING

Most results of this work are based on spot observations of tagged crows. Some supplementary information was gained from continuous observation of radio-tagged individuals.

Most crows trapped were taken in small, two-compartment traps in their territories during the period March to June. Trapping in the flock area was also done mainly during this season. Altogether 60 territorial and 25 flock crows were trapped during the springs of 1974–1979. A Norwegian crow trap (Kalchreuter 1971b) was tried during some winters. This was only successful for one short period in December 1975 when 19 crows, most of them winter migrants, were trapped. Most crows were tagged as nestlings, at the age of about 25 days. Altogether 230 nestlings were tagged during the springs of 1975, 1976, and 1977. Of these, 136 were still in the study area in July or later in the year of hatching and 45 were present in July of next year.

All crows trapped received wing tags (Picozzi 1971). The size of the tags was 33 × 70 mm. To facilitate identification and to allow calculation of the rate of tag loss, identical tags were used on both wings. For crows tagged as adults, the proportion of individuals losing both tags was calculated to be 0% after one year, 3% after two and 30% after three years. The tags could be identified at a distance of up to 300

m, using a 25× telescope. All crows received official, numbered leg rings in addition to the wing tags. This permitted identification of crows found dead or killed by people outside the study area.

3.2. RECORDING

Most observations of crows were made from a car. The data in the results section are based on all observations of tagged crows but the majority was made during two standard car routes in order to reduce bias. One, completely inside the intensive study area, comprised 40 km and was completed once every week from 1 April 1975 to 30 June 1978. The second route ran up to 5 km from the intensive study area, encircling it. This route comprised 70 km and was completed once each week from 1 September 1976 to 30 June 1978. Although the standard routes were no longer completed after this period, additional observations were made during the period 1 April to 30 June 1979 in order to determine the breeding status of tagged individuals. Each time a tagged crow was observed I recorded, among other things the size of the flock in which the tagged bird was seen. Aggregation of crows were considered as flocks, if the distance between individual birds was less than 50 m.

3.3. RADIO-TRACKING

Some observations were obtained from radio-tracking seven crows. The transmitters used operated on the 27 MHz band. They had a range of 400–800 m, a life of about 10 days and weighed, about 30 g. Each crow was tracked for up to three full days.

4. RESULTS

4.1. TERRITORIAL AND FLOCK CROWS IN SPRING

4.1.1. The territorial system and territory fidelity

Almost all crows could easily be classified as either territorials or flock crows during the months April to June. A crow that was always observed singly or in a pair within a restricted area during this period, was considered a territorial crow; otherwise it was considered a flock crow. These "labels" remained until the next breeding season.

During spring months, territorial pairs occupied home-ranges that did not overlap but were probably more or less adjacent. The home-ranges were therefore considered territories during the period April to June. Most of the territory was covered every day in search of food and territorials usually roosted within their territories. Territorials were occasionally observed outside their territories during the breeding season: 1. Neighbouring pairs could sometimes be seen feeding peacefully at the border between

their territories. 2. Sometimes crows were seen making short excursions outside their territories. 3. If a territorial crow was trapped, neighbours could be seen in its territory within a short period of time. A territorial crow was once slightly wounded in a trap. After release it was attacked and probably killed by a neighbouring pair. 4. Territorial crows usually roosted within their territory. However, four times tagged or radiotagged territorials were observed to participate in evening gatherings either on the ground or in trees in their own of in neighbouring territories. These gatherings probably involved mainly territorials. After these assemblies, which lasted 15 to 30 min, the crows flew off single or in pairs.

4.1.2. Distribution and home-ranges of flock crows

The home-ranges of flock crows were larger than those of territorials during the period April to June and they overlapped widely. Flock crows were mainly restricted to CFP and their surroundings. Areas much used by flock crows apart from CFP were probably situated at the intersection of several territories, far from the nests (Fig. 1). These areas were utilized by the same flock crows as those usually present at the closest CFP. Nests were in some cases found

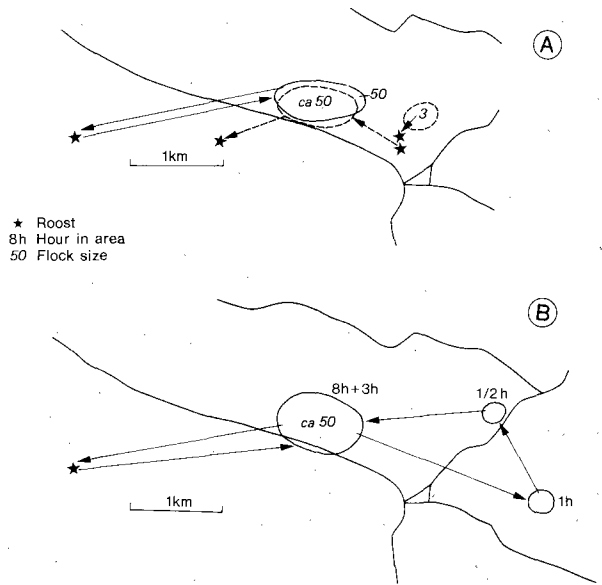
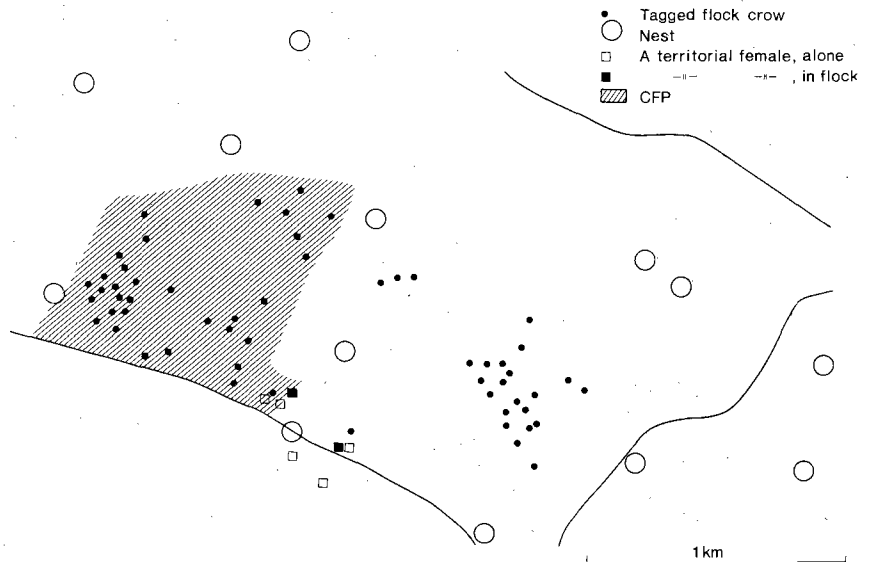


Fig. 2. Daily activity pattern of two radio-tracked flock crows. A was tracked on 18, 20 and 22 March 1977; on 18 March (broken line) during the afternoon only. B was tracked on 5 April 1978. Duration of stay is not given when entire day spent in one place.

close to CFP and, at least in one case, the home-range of a nesting pair was regularly used by flock crows too. This pair was sometimes seen feeding together with flock crows but as the pair

Fig. 1. Distribution of flock crows during spring in relation to a CFP and to nests. Sites of observation of a female that nested close to the CFP are also given.



was usually separate from others and bred, it was classified as a pair of territorial crows (Fig. 1).

During spring and summer, flock crows usually roosted within one or two kilometres from their daytime feeding areas. Observations of two radio-tracked flock crows suggest that changes of roosting place were common (Figs. 2A, 3A). Most of the day was spent feeding at one or two CFP but some flock crows did range further afield (Fig. 2B). Such excursions were made by single birds or small flocks.

4.2. ACQUISITION OF TERRITORIES AND PAIR BOND

4.2.1. Territory acquisition by flock crows

Flock crows were sometimes observed alone or in pairs. During winter these observations were more or less randomly scattered among all places where flock crows were observed. However, during spring single or paired flock crows were often observed outside the area usually frequented by flocks. Flock crows that were observed in such situations will be called "prospectors". This pattern is reflected by the relative distance of crows in flocks and prospectors to the nearest CFP during winter January—March) and spring (April—June). Considering all observations of tagged individuals, these distances were 770 m ($n = 180$) and 1100 m ($n = 10$) during winter (not significant, Median test, $\chi^2 = 0.11$) and 520 m ($n = 155$) and 1300 m ($n = 25$) during spring (significant, Median test, $\chi^2 = 5.75$, $p < 0.05$). The flock area frequented by prospectors was the one closest to the area of prospecting (13 cases). Furthermore, if a crow had been observed in a flock area the year before it became territorial, this had been in the area that was closest to its newly acquired territory (5 cases). prospecting was often followed by the occupancy of a territory at the site of prospecting, or close to it, in the following year (4 cases; territories were 100, 200, 200 and 400 m from the site of prospecting). prospecting crows were single birds in 15 out of 24 cases (62%). This was similar to the fraction of territorial crows that were observed singly during spring (Fig. 8). However the two frac-

tions may not be quite comparable as the territorial female spends much of the time on the nest or in its immediate vicinity and not with the male. I thus think that some of the 15 single prospectors really were unmated birds.

Records of two radio-tracked male crows further illustrate these points. One single prospecting male was tracked for three days in March 1975. He spent about half of each day alone within a restricted area, the other half in a flock at one or two places about one km away (Fig. 3A). From 1976 onwards he occupied a territory close to the area where he had been prospecting. In April 1975 the area where the single male had been prospecting was occupied by another radio-tracked crow that, with its mate, spent the whole day there and was thus territorial. This pair did not breed that year. It roosted

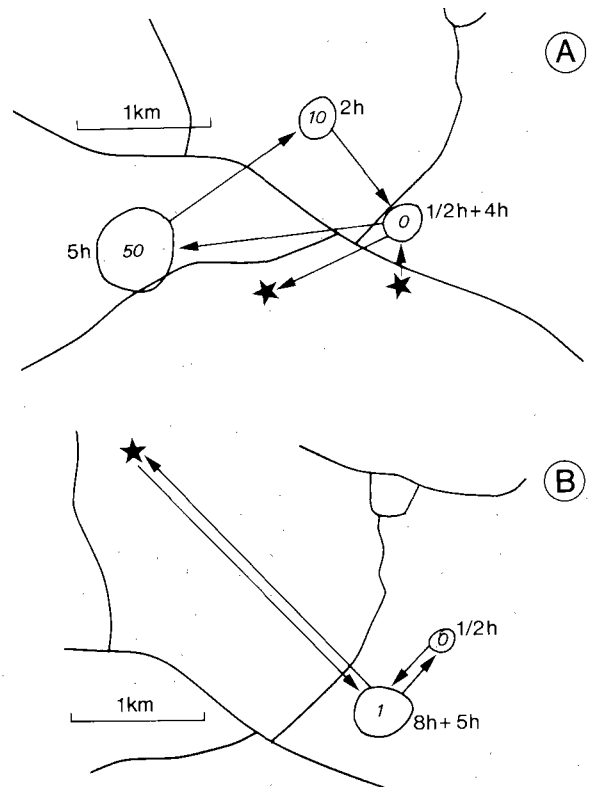


Fig. 3. A. Activity range of a prospecting male, radio-tracked on 24 March 1975. It had a similar range on 23 and 27 March.

B. Activity range of a mated male, presumably a first-year territorial, radio-tracked on 3 March 1975. It had a similar range on 27 April. Symbols as in Fig. 4

with flock crows about two km from the territory (Fig. 3B).

4.2.2. Age of newly established territorials

None of the sixty crows that had been tagged as nestlings and that were still in the study area with identifiable tags, had established a territory when about one year old. At an age of about two years, 2 out of 30 and at about three years, 5 out of 13 did possess a territory. Of the former two, one was breeding and of the latter five, three were breeding in their first year as territorials.

4.2.3. The start of breeding

Of 12 newly established territorial pairs, seven did not breed in their first year of territorial life; five of these seven did so in their second year but two did not. Those that had started breeding continued to do so in succeeding years. In eleven instances one bird was recorded breeding for the first time while its partner had already bred in the territory previously. In nine out of these eleven cases did the newly formed pair consist of two first time breeders. However, most of these pairs had been present in the territory for nearly one year while pairs of inexperienced birds sometimes had been present for less than a month only before the start of breeding.

4.2.4. Mate fidelity

Of 16 different pairs, both partners were tagged and these were observed for a total of 34 pair-years. In these years, only one pair split up. This pair had established a territory but no breeding took place. As both had been tagged in that territory, it is uncertain whether they were first-year territorials but this seems likely as they did not breed (section 4.2.3). The two crows of this pair were mated with untagged partners next year. The male was still in its original territory, the female in an adjacent one.

4.2.5. Pair formation

Some pairs probably formed between two flock crows. This was most likely the case with two crows that prospected together at several places in one spring and were also seen in the

flock area at this time. Other pairs, probably the majority, formed in the territories. All territorials that were known to have lost their mate (eight males and one female) kept their territories in the following spring. If the loss occurred during the breeding season (seven cases), the widowed crow sometimes remated in the same season. This was observed in four cases, including in the female that lost her partner. In two cases no remating was observed until the following breeding season, but such rematings may have gone unnoticed. For one case no pertinent information is available as the territory was difficult to observe.

4.3. ATTACHMENT TO THE TERRITORY

4.3.1. Territorials

Practically all territorial crows were in their territories during April to June (Fig. 4). By definition all should be, but there are a few observations that I consider exceptional (section 4.1.1). In years with a late start of breeding some territorial crows were seen in flocks away from their territories during the first week of April; July and August were transition months with an increasing number of observations of territorials from outside the territory, though mostly in its vicinity (Fig. 4). About 25% of all observed territorials were in their territory during the winter months. There was variation between pairs with respect to the tendency to stay in their territory during winter. I found no correlation between experience as territorial (first-year territorials

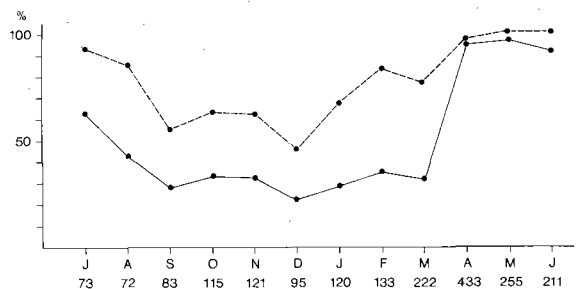


Fig. 4. Seasonal variation in the distance at which territorials were observed from their territory. The drawn line gives the fraction (%) of all observations within the territory, the broken line the fraction of observations within 1 km of the territory border. The number of observations is given below the x-axis.

vs. more experienced ones) or body weight of the crow and the proportion of all observations made within the territory from October to March. However, there was a tendency for territories that were likely to yield an adequate food supply during winter to be more adhered to than others. Such territories, *e.g.* those in the vicinity of places where cattle were fed during winter, those containing small streams, one close to a small village and even one including the ecological field station, were significantly more frequented during winter. (Mann-Whitney U-test, with territories ranked according to the proportion of all observations of territories made within their territory during winter, $U = 235, p < 0.01$).

4.3.2. Juveniles

Juveniles were virtually confined to their parents' territories in June (Fig. 5). However, comparatively few juveniles were observed together with their parents in this month (Table 1). This was because most juveniles left the nest in the beginning of June and spent their first weeks in its vicinity, waiting for their parents to feed them. Later, in July, they followed their parents but fed mainly by themselves. During July and August, increasing numbers of juveniles left their native territories and almost none were observed there from September onwards (Fig. 5). Juveniles were sometimes observed together

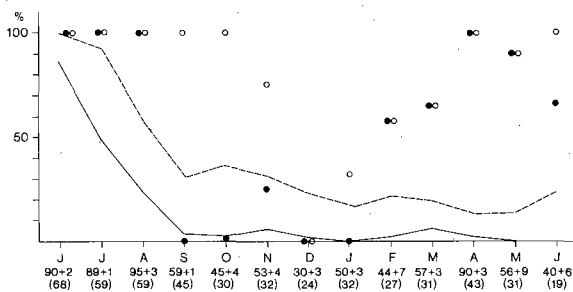


Fig. 5. Seasonal variation in the distance at which juveniles were observed from their natal territory. The drawn line refers to observations within the territory, the broken line to observations within one kilometre away from it. The circles refer to two juveniles that were regularly observed in their parents' territory during the spring when they were about one year old. Below the x-axis the number of observations is given, excluding the two atypical juveniles plus the number of observations of these latter; the number of individual juveniles involved is given in parentheses.

Table 1. Seasonal variation in the association of juveniles with their parents. N refers to the number of observations of tagged juveniles of which the mother or father was also tagged. "% with mother/father" gives the proportion of these observations when a parent was recorded in the vicinity of the juvenile

Month	N	% with mother	N	% with father
June	13	31	22	9
July	13	38	19	37
August	16	0	28	21
September	13	15	15	20
October	13	46	15	7
November	11	9	18	0
December	78	0	86	3

with their parents in flocks during autumn but there was almost no association after November (Table 1).

Two juveniles, of different parents, were atypical. During their second and third calendar years they were both still associated with their parents' territories during the breeding season (Figs. 5, 6). At least one of these two crows seemed less restricted to the parents' territory when two years than when one year old (Fig. 6B), still it was more associated with it than were „typical” juvenile crows (Fig. 5). Both these crows were heavier at fledging than average (480 and 510 g, average 460 g) suggesting they were males.

4.4. SEASONAL VARIATION IN FLOCK SIZE AND FEEDING STATIONS

Flocks were largest in winter and smallest during the breeding season (Fig. 7). Though territorial and flock crows were often seen in the same flocks there was a tendency for territorials to be in smaller flocks. Juveniles were mainly together with their parents in July and August and the size of the flocks in which the two categories were observed was similar. Later, juveniles behaved more like older flock crows with respect to flock size. In late winter, juveniles were even found in larger flocks than older flock crows. The fraction of crows seen in pairs or alone during different seasons showed a similar pattern (Fig. 8). Older flock crows very rarely were alone or in pairs during the period October to December and thus showed no tendency to prospect at this time. Juveniles observed alone

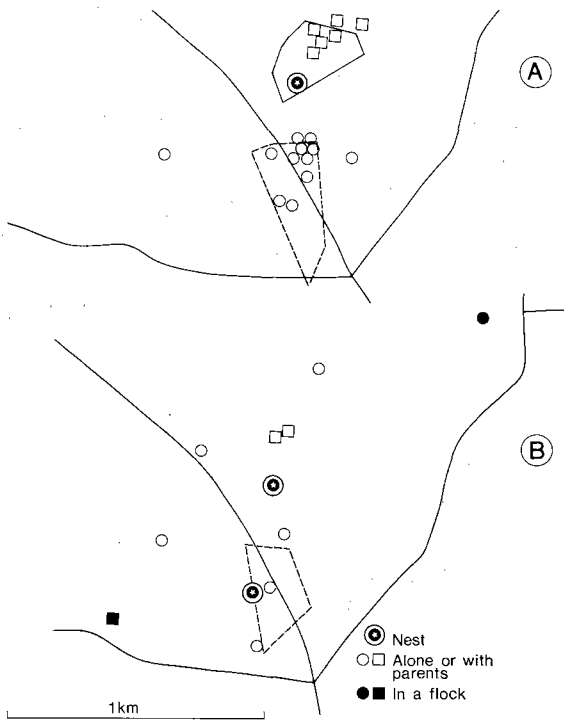


Fig. 6. Spring (April to June) distribution of two crows (square and circular symbols) that remained associated with their natal territories. The situation in their second (A) and third (B) calendar-year is shown. The father's (drawn polygon) and mother's (broken polygon) home-ranges are given. Only one parent was tagged in each pair and the tagged father had lost its tag in the third calendar-year.

or in pairs (the partner may well have been a sibling or a parent) were usually still in their native territory during late summer or autumn. Territorial crows were usually alone or in pairs when observed in their territories (73%, $N = 1193$). This was especially pronounced during the breeding season (88%, $N = 846$). When far from their territories (> 1000 m) they were nearly always in flocks (only 5% single or in pairs, $N = 322$). This fraction was similar to that for flock crows (Fig. 8).

Most crows fed in places where no obvious concentration of food was found (Fig. 9E). A considerable proportion was seen at CFP during winter (Fig. 9A). In some months, many crows utilized fields where, for a short period of time, food was plentiful as well as well dispersed over an extensive area, e.g. newly sown fields in April and field where manure had been spread

in November (Fig. 9D). Rabbits that had been killed by cars were used as a food source in December and January, usually when snow covered the ground (Fig. 9C). There were differences in these respects between the three categories of crows. Comparing the two most important feeding site categories, CFP and fields without concentrations, flock crows frequented CFP more than did territorial crows (36%, $N = 615$ and 4%, $N = 1761$ respectively). There was no obvious seasonal variation in this respect; the proportion of territorial crows at CFP varied between 0 and 18% and that of flock crows between 19 and 44%. In both categories, a maximum occurred in the period November—December. Juveniles behaved similar to territorial crows during their first months (13%, $N = 139$, at CFP in July—August) but more like older flock crows later on (40%, $N = 484$, during the rest of their first year). During midwinter and early spring they were even more associated to CFP than were older flock crows (56%, $N = 191$ during January to April). These tendencies should be compared to another juvenile tendency, viz., to stay with the parents in July and August (Table 1) and to the difference in size between flocks joined by juveniles and older flock crows during the period January to March (Fig. 7).

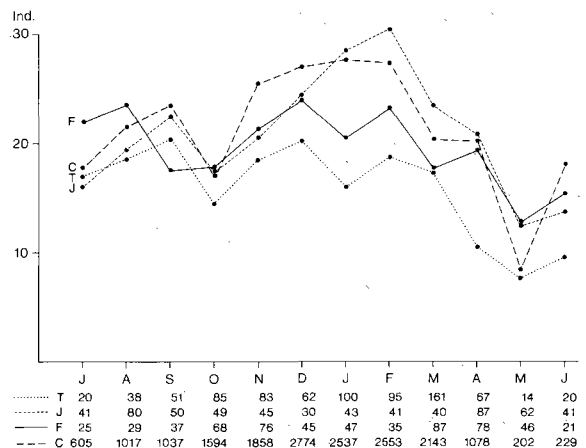


Fig. 7. Mean size of flocks. T: Territorials, J: Juveniles, F: Flock crows, C: All crows observed during weekly censuses, regardless of whether tagged or not. Crows observed singly or in pairs excluded. Number of crows given below x-axis.

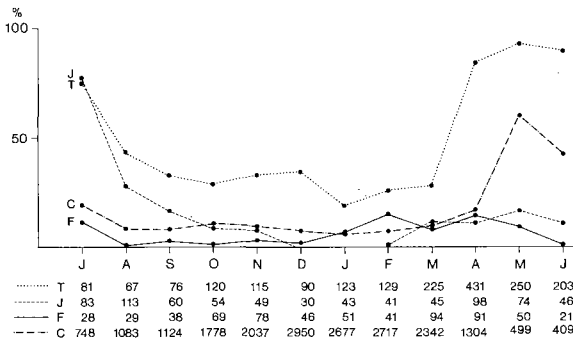


Fig. 8. Fractions (%) of crows observed alone or with family (mate, parents, young of the year). Letters as in Fig. 7. Number of observations given below x-axis.

4.5. DISTRIBUTION OF CROWS DURING WINTER

4.5.1. Size, distribution, and characteristics of roosting places

Most crows were in large roosts during winter and these roosts remained in the same place from year to year. Crows sometimes also roosted in smaller groups during winter as exemplified by one radio-tracked crow (Fig. 13B). All three large winter roosts in the study area were in small plots of spruce forest as were two out of three other known roosts in the vicinity of the study area.

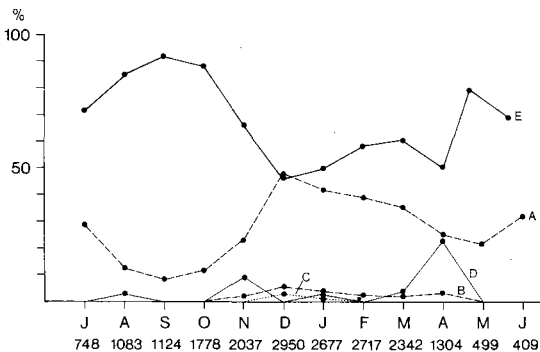


Fig. 9. Fractions (%) of all crows using distinct types of feeding site in the course of a year. A: Places with concentrated food of permanent or long-term availability (CFP). B: Places with concentrated food available for more than a few days. C: Places with concentrated food available for one or a few days. D: Extensive but temporary feeding sites with plenty of food. E: Other sites, mainly fields with no apparent concentrations of food. F: Food. Number of crows observed given below x-axis.

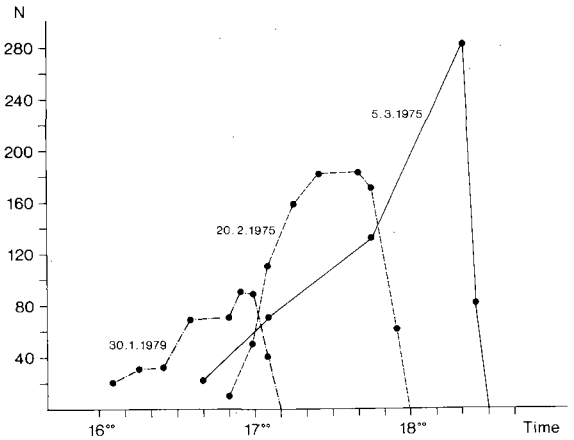


Fig. 10. Number of crows (N) at different days on evening gathering places, from arrival of the first crows to departure for the roosts.

4.5.2. Flights to and from roosts

The crows usually arrived at the roosts about 30 min after sunset. The final flight to the roost usually started from one or a few gathering places in the neighbourhood (Fig. 11). In winter several hundred crows, and also Jackdaws and Rooks, left the gathering places together. Roosting places were traditional ones, changing position a few hundred of metres at most within or between winters. The number of crows at a gathering place usually increased gradually during the hour before roosting. Departure for the

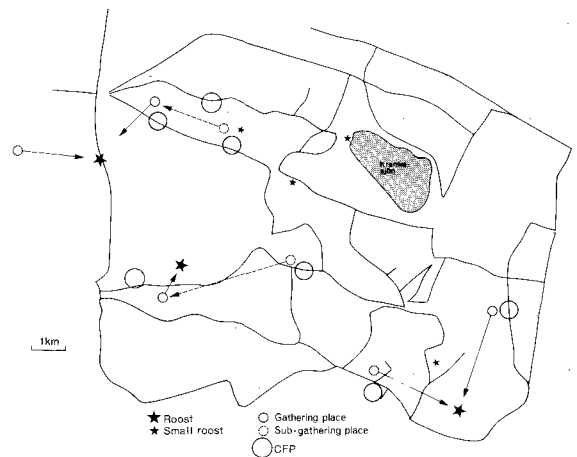


Fig. 11. Location of large, permanent winter roosts and of some smaller roosts, used irregularly during winter.



Fig. 12. Roost-recruitment areas. Daytime feeding sites are indicated for all tagged crows identified at each of four gathering places (large symbols) during October—March. Included are all sites where these birds were observed within one month from the date when first seen at a gathering place. Use of a longer time interval would have increased the possibility of confusion due to occasional changes of gathering place within one season. Roost-recruitment areas are separated by thick lines, based on the distribution of the observation sites. Crows flew to the same roost from two of the gathering places.

roost, on the other hand, took only about ten min for the whole flock (Fig. 10). Crows arriving at the gathering places sometimes from traditional sub-gathering places, usually came in flocks that were larger than those observed during daytime feeding. Gathering places, and also traditional sub-gathering places, were situated 100—300 m from the CFP (Fig. 11). The flight pattern in the morning was approximately the reverse of that in the evening. The same gathering places and sub-gathering places were used. However, less time was spent before reaching

the feeding places in the morning than on the evening flights away from these.

4.5.3. Roost-recruitment and winter activity range

Crows utilizing gathering places in winter were observed feeding in different areas during daytime. These areas are here termed roost-recruitment areas. These were roughly adjoining (Fig. 12). The home-range of an individual crow usually covered only a part of one roost-recruitment area. Some crows changed recruitment

Table 2. Frequency of roost-recruitment area change (see Fig. 12) for different crow categories during different seasons. A: Percentage of observations in the area where each individual crow was observed most frequently. B and C: Percentage in the second and third most frequented area for each crow. N: Total number of observations

	October—March				April—June				July—September			
	N	A	B	C	N	A	B	C	N	A	B	C
Juveniles	297	95	4	1	198	89	8	3	233	96	4	0
Flock crows	423	95	4	0	213	95	5	0	106	97	3	0
Territorial crows	829	99	1	0	903	100	0	0	230	100	0	0

Table 3. Frequency of observations for various categories of crows during winter. The expected model distribution is also given in parentheses together with χ^2 -value for a test of fit between observed (zero-truncated) distribution and the model distribution. For juveniles and flock crows, the Poisson distribution served as a model; for territorial crows the distribution obtained by taking the mean value of the Poisson distribution and the Geometric distribution. These models gave the best fit to the data

Number of observations during winter (October—March)	Number of individuals observed the given number of times		
	Juveniles	Flock crows	Territorials
0	26 (1.3)	12 (0.5)	11 (14.8)
1—2	11 (8.6)	8 (5.9)	27 (28.7)
3—4	10 (11.3)	8 (10.7)	32 (28.3)
5—6	3 (5.5)	8 (7.2)	13 (17.8)
≥ 7	3 (1.7)	2 (3.3)	16 (11.7)
χ^2	2.95	2.03	3.46
d.f.	3	3	3
P	0.5—0.3	0.7—0.5	0.5—0.3

area in the course of one winter. This was most common for juveniles, less common for older flock crows and least for territorials (Table 2). Juveniles and older flock crows sometimes changed roost-recruitment area during spring and summer but territorials never did during these seasons. During winter, the crows usually spent the whole day at one or two CFP, usually in large flocks (Fig. 13). They sometimes moved more extensively in smaller flocks within the roost-recruitment area (Fig. 13B). These data from radio-trackings are corroborated by information on the size of flocks at different types of

feeding sites. Mean flock size at a CFP in December to February was 27, at other sites 6.3 birds. Furthermore, most winter home-ranges comprised at least one CFP.

4.6. MIGRATION

A large fraction of the juveniles and older flock crows that were tagged before winter and observed later one were never observed during the winter months (October to March) (Table 3). This suggests they had left the study area. Practically all territorials were observed in the study area during winter and I conclude that most, probably all, stayed. Twelve ringed crows were recovered dead or shot during winter outside the study area. Five of these were found in Denmark (islands of Sjaelland, Lolland and Fyn), the other seven in the Swedish province Skåne, where the study area is situated. All seven summer recoveries outside the study area came from Skåne. The latter probably represent permanent emigration while the winter recoveries may have resulted from both emigration and temporary migration. Out of 19 crows trapped and ringed during winter, three were later shot in Finland.

4.7. SURVIVAL

Survival was calculated as the proportion of birds observed in the study area during one breeding season (April to June) and observed again during the next season. Only crows whose tags were not older than two years were included as tag loss was negligible during this period of time. These values thus represent minimum survival as missing crows may have emigrated.

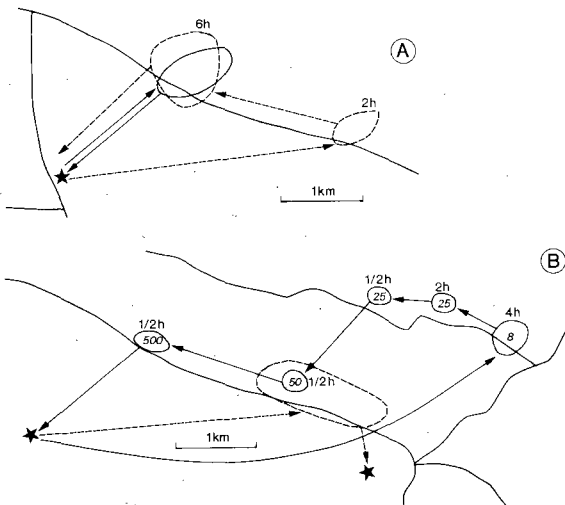


Fig. 13. Daily activity ranges of two crows radio-tracked during winter: A was tracked on 26 and 27 December 1975 and B on 2 and 7 January 1977. Symbols as in Fig. 4. Duration of stay is not given when entire day was spent in one place.

Survival was 92% for territorial crows (based on 57 birds and 132 bird-years); some birds were re-tagged in the course of the study. For flock crows (excluding the first year of life) survival was 73% (bases on 54 birds and 62 bird-years). Two of the territorials that disappeared and one flock crow are known to have been shot during winter, while the fate of the others remains unknown.

5. DISCUSSION

5.1. SEGREGATION OF TERRITORIES AND FLOCK AREA

In spring most flocks were found at or around a CFP. This phenomenon was also observed by Charles (1972) and Böhmer (1976). Territorial pairs probably have no influence on the distribution of flocks (Böhmer 1976). Flocks were also found elsewhere, at places away from crows' nests. This agrees with Charles' (1972) observation that "group intrusions" mainly take place at the borderline between territories. The fact that territorial crows restrict the movements of flock crows outside the flock area was also evident from an experiment; after territorial females were removed in May, flock crows invaded in the territories (Göransson & Loman 1982).

Charles (1972) regularly observed "group intrusions at nests" too. This was not recorded in my study area, which may explain the low rate of predation on eggs and chicks (Loman 1980) as compared to that recorded by Charles (1972) and Wittenberg (1968). They suggested that flock crows were responsible for this predation. The fact that pairs nesting in the flock area raised young to fledging suggests that predation from flock crows was of minor importance in my study area. The reasons for these differences are not clear.

The function of evening gatherings of territorial crows remains obscure; the phenomenon may constitute some kind of defence against predation, similar to the function suggested for pre-roost gatherings (section 5.7).

5.2. PAIR FORMATION

Most previous investigators have stated that pairs are formed in flocks (Wittenberg 1968, Kalchreuter 1971a, Charles 1972). This was also true in my study area, at least in some cases.

However, it seems likely that single birds prospect too as was also suggested by Kalchreuter (1971a). If these single birds are successful in establishing a territory, they probably find a mate in this territory. However, successful territory-establishment by single birds was never observed and it is difficult to see how this would be possible in competition with prospecting pairs. It may be significant that the single male that was radio-tracked while prospecting lost his potential territory to a pair. It is possible that prospecting by single birds is beneficial to them by becoming acquainted to the area, something that may be useful when prospecting with a mate later on.

All widowed males (and one such female) in my study area were able to maintain their territories and form new pairs. Pair-formation most likely took place within the territory. This is in contrast to Charles' (1972) observation that a single crow cannot defend its territory. If the female died during the breeding season, flock crows appeared in the territory (Göransson & Loman 1982). This could actually benefit the single male, enabling him to find a new mate quickly without having to leave its territory open to competing pairs.

5.3. TERRITORY ESTABLISHMENT

Evidently, the occupancy of a territory is a prerequisite for breeding. Besides, territory ownership might increase survival. However, the figures showing higher survival rate for territorial crows than for flock crows are biased by differences between both groups in the tendency to emigrate. Also, the difference could simply be due to higher survival rate of individual crows that are particularly fit and therefore are the one's most likely to establish territories.

A young non-territorial crow has two options: to remain in the natal territory most of the time, using it as a base for acquisition of its own territory, or to join a flock and spend most of the time in the flock area. The advantages and disadvantages of the two options are discussed in section 5.5.

Do flock crows select a preferred territory or do they settle more or less at random? The situation in my study area suggests that there probably is little opportunity for birds to choose at

all. Competition for a territory was intense as few territorials died, leaving vacancies to the number of flock crows present. The availability of territories may have been even more limited, since flock crows usually restricted prospecting to one roost-recruitment area. Within the study area crow territories are situated in different habitat types. In dry areas clutch size has been shown to be relatively small (Loman 1977). Since no differences have been found in breeding experience of crows inhabiting different habitats (dry vs other), clutch size differences can be regarded to reflect differences in habitat quality. It is striking that territorial crows were not found to attempt exchanging their territory for a better one. This could be because the establishment of a new territory implies less attention for the one already occupied, with the risk of losing both territories. These observations stress the difficulties crows have to obtain territories. Despite the comparatively high survival rate (for passerines) of flock crows, it is likely that many never succeed in acquiring a territory.

5.4. OCCUPANCY OF TERRITORIES DURING WINTER

The tendency for territorial crows to stay in the territory during winter differs between the various populations studied. In Scotland (Charles 1972, Spray 1978), Switzerland (Tompa 1975), and northern West Germany (Wittenberg 1968) territorials stay and defend their territories throughout the winter. In southern West Germany the crows remain in their territories most of the winter but depart under snow conditions (Kalchreuter 1971a). In my study area most crows were confined to their territories only in the period April to June. There was little snow but it is possible that during winter there were less opportunities for feeding than in the three study areas mentioned above as these were situated in farming areas. Lack of food cannot explain the crows' absence from their territories during summer in my study, but it is possible that new territories are seldom established during this season and thus there is no need to defend a territory. This is supported by Wittenberg's (1968) finding that territorial crows (in his study population) are absent from

their territories during summer but return later in autumn.

If the territorial area that I studied really offered relatively little food, especially as compared to the flock area, this could explain three other differences between my study and others': 1. Kalchreuter (1971a) and I found that juveniles left their natal territories in late summer while Charles (1972) and Tompa (1975) found that they stayed in the territory for a longer period of time, to leave it only gradually during their first winter. A difference between my findings and those of Kalchreuter (1971a) is that he found that juveniles formed exclusive flocks in summer. I found no indication of this; juveniles were found in flocks with older flock crows and territorials. 2. In Charles' study, flock crows established small and temporary territories during winter and early spring. Later on, during the breeding season, they were usually back in the flocks. I did not observe this. 3. Charles (1972) also found that persistent intruders were tolerated during winter as third birds in the territories but they were evicted before the following breeding season. This was not observed in my study area.

5.5. JUVENILES STAYING IN THEIR PARENTS' TERRITORIES

Only Tompa (1975) has previously observed crows, apart from the pair, that stayed permanently in a territory during the breeding season. Two out of 36 territories observed by him held three crows. He had no further observations concerning origin or nature of these birds. The third birds that Charles (1972) observed were obviously of different status. They were recruited from the flock and evicted by the start of the breeding season. I observed juveniles that has some connection to their natal territory throughout the winter and, like their parents, became a permanent resident there during the breeding season. The function of this behaviour for juveniles and parents is not clear but I will discuss some possibilities. 1. The juvenile that remains in the parents' territory could serve as a helper (Skutch 1935), defending its parents' territory and assisting with feeding the new brood. No observations were made specifically to determine this, but at least in one of the territories

under observation, the juvenile was never observed in the vicinity of the nest, making it unlikely that it was feeding its younger siblings. 2. The juvenile may be better off with respect to food in the parents' territory than having to compete with other crows in the flock area. By staying within the territory, the juvenile crow may even be able to occupy part of it as a new territory, especially if the parents' territory is large. This was observed for Scrub Jays *Aphelocoma coerulescens* by Woolfenden & Fitzpatrick (1978). By having a stable base in the territorial area, establishment of a separate territory could be facilitated. Charles (1972) reports that during winter, juveniles remaining in the natal territory were better tolerated by neighbouring territorials than were unfamiliar crows. If this applies to my study area in spring, prospecting by these juveniles would be facilitated. This hypothesis is supported by the fact that one of the juveniles observed to remain in the natal territory established a territory of its own about 500 m from its parents' territory when three years old.

5.6. DISTRIBUTION OF FEEDING SITES DURING WINTER

In general, juveniles feed mainly at CFP and in large flocks during winter while territorials visit CFP less frequently and feed in smaller flocks. Older flock crows appear to be intermediate in these respects. Flock size is probably strongly influenced by the nature of the feeding site. Territorials and older flock crows, which are dominant and therefore are able to compete successfully for food, could be expected to be more often present at a CFP. However, the reverse is true. I suggest this is because territorials need to guard their territory, whereas older flock crows which are capable to defend a vacant territory should be informed about the situation in the territorial area.

5.7. FUNCTION OF ROOSTING BEHAVIOUR

Several positive effects on survival of roosting behaviour can be envisaged: 1. A roost utilized during winter may be a place with a particularly favourable microclimate, thereby reducing energy loss during night (Swingland 1977). This cannot be the only function as more energy is lost while flying to the roost than can be saved

during night (Gyllin *et al.* 1977). 2. Communal roosting could serve as a defence against predators. This could be accomplished in two ways: a) Detection of predators is probably facilitated where a large number of crows has gathered. b) If the predators are more or less territorial, communal roosting may result in a reduction of the number of predators present relative to the number of crows (Bertram 1978). Gathering places are always situated in open landscapes suggesting defence against predators to be an important factor. Roosts, on the other hand, are situated in copses where potential predators like the Goshawk *Accipiter gentilis* and the Great Horned Owl *Bubo bubo* will have good opportunities to strike unnoticed. Gathering places could be important because they allow crows to gather at a comparatively safe place and reach the roosting place simultaneously. If they arrived singly at the roost, those arriving first would face the risk of being taken by predators. Interrupting their flight to the roost at a safe place, and only continuing when sufficiently many other crows are likely to follow, may have started the evolution of a gathering place system. I think, the pattern of arrival to and departure from the gathering places supports this (Fig. 10). 3. Individual crows which have failed in finding food at a particular day, may follow other crows when departing from the roost next morning. In this way roosts may function as an information centre for food-finding (Ward & Zahavi 1973). It has been previously suggested that this is not likely to play an important role in my study area, except perhaps under very severe weather conditions (Loman & Tamm 1980).

There was no congruence between roost-recruitment areas and winter home-ranges, thus they cannot be considered group territories. This is hardly surprising as both areas are likely to be determined by different factors. Home-ranges can be expected to be primarily determined by food-availability, whereas roost-recruitment areas seem to depend on the distribution of suitable roosting places, which in turn depends on the distribution of predators. Most territorial crows in my study area had their winter home-range restricted to part of a roost-recruitment area, whereas part of the flock crows,

especially the juveniles, visited several roost recruitment areas in one winter. The latter probably were low-ranking birds, which were forced to move from one place to another under the pressure of food competition.

6. ACKNOWLEDGEMENTS

Sam Erlinge, Hans Kristiansson and Olof Liberg suggested improvements to the manuscript. Assistance in the field was given by many people, especially Thomas Madsen and Niklas Törnlund. The illustrations were prepared by Steffi Douwes. Jonathan Thornton and R. van Halewijn helped me with the English language. I thank them for their assistance. Grants were received from the Swedish Natural Science Research Council (to Sam Erlinge).

7. SUMMARY

A population of wing-tagged Hooded Crows *Corvus cornix* was studied in southern Sweden during the years 1974–79. Interest was focused on aspects of their social organization and behavioural ecology. Only part of the population studied were breeding birds. Breeding pairs were territorial during spring when non-breeding crows lived in flocks, mainly in rather restricted areas. If a territorial crow died, its mate kept the territory and obtained a new partner, usually within a month. Pairs which had recently established a territory had usually spent the previous breeding season in the flock-area that was closest to their territory. It was also common for a pair to visit occasionally an area in the year before they established a territory there. Some crows became territorial at the age of two years but the majority had not acquired a territory at the age of three.

Some pairs were usually found in their territories throughout winter whereas others were less restricted to it. This difference was probably related to differences between territories in possibilities to find food in winter. Most juveniles had ceased altogether to visit their natal territories by September in the year of hatching.

I observed two juveniles which to some extent remained associated with their natal territories throughout their first winter. Juveniles fed in large flocks in places with concentrations of food during winter. Territorial crows were usually observed in smaller flocks and fed in areas without obvious concentrations of food. Older flock crows behaved intermediately in these respects. Most crows frequented large winter roosts situated up to several km from the crows' daytime feeding ranges. The crows assembled at gathering places before roosting. They left these more or less simultaneously for the roost. Smaller roosts, within two km from feeding places, were used in summer. Some flock crows but no territorials migrated during winter. Most migrants apparently wintered in Denmark.

Annual survival was at least 92% for territorial crows and 73% for flock crows more than two years old.

8. REFERENCES

Abshagen, K. 1963. Über die Nester der Nebelkrähen, *Corvus corone cornix*. Beitr. Vogelk. 8: 325–338.
 Bertram, B. 1978. Living in groups: Predators and prey. In: J. Krebs & N. Davies (eds.). Behavioural Ecology. Blackwell, Oxford.

Böhmer, A. 1976. Zur struktur der schweizerischen Rabenkrähenpopulation *Corvus corone corone*. Orn. Beob. 73: 109–136.
 Brown, J. L. 1974. Alternate routes to sociality in Jays — with a theory for the evolution of altruism and communal breeding. Am. Zool. 14: 63–80.
 Charles, J. 1972. Territorial behaviour and the limitation of population size in the Crow, *Corvus corone* and *Corvus cornix*. Ph. D. thesis Aberdeen University.
 Göransson, G. & J. Loman. 1982. Does shooting of breeding Crows influence Pheasant production? — An experiment —. Trans. Intern. Congr. Crame Biol. 14: 331–334.
 Gyllin, R., H. Källander & M. Sylvén. 1977. The microclimate explanation of town centre roosts of Jackdaws *Corvus monedula*. Ibis 119: 358–361.
 Kalchreuter, H. 1971a. Untersuchungen an Populationen der Rabenkrähe (*Corvus c. corone*). Jb. Ges. Naturkde. Württemberg 126: 284–339.
 Kalchreuter, H. 1971b. Untersuchungen an der Krähenmassenfalle. Z. Jagdwiss. 17: 13–19.
 Loman, J. 1977. Factors affecting clutch and brood size in the Crow, *Corvus cornix*. Oikos 29: 294–301.
 Loman, J. 1980. Reproduction in a population of the Hooded Crow *Corvus cornix*. Holarc. Ecol. 3: 26–35.
 Loman, J. & S. Tamm. 1980. Do roosts serve as "information centers" for Crows and Ravens? Am. Nat. 115: 285–289.
 Picozzi, N. 1971. Wing tags for raptors. Ring 68/69: 169–170.
 Skutch, A. F. 1935. Helpers at the nest. Auk 52: 257–273.
 Spray, C. J. 1978. Territorial behaviour of the Carrion Crow, *Corvus corone* L., in relation to food supply: An experimental study. Ph. D. thesis. Aberdeen University.
 Swingland, I. R. 1977. The social and spatial organization of winter communal roosting in Rooks (*Corvus frugilegus*). J. Zool. Lond. 182: 509–528.
 Tompa, F. S. 1975. A preliminary investigation of the Carrion Crow *Corvus corone* problem in Switzerland. Orn. Beob. 72: 181–198.
 Ward, P. & A. Zahavi. 1973. The importance of certain assemblages of birds as "information-centres" for food-finding. Ibis 115: 517–534.
 Wittenberg, J. 1968. Freilanduntersuchungen zur Brutbiologie und Verhalten der Rabenkrähe (*Corvus c. corone*). Zool. Jb. Syst. 95: 16–146.
 Woolfenden, G. E. & J. W. Fitzpatrick. 1978. The inheritance of territory in groupbreeding birds. Bio Science 28: 104–108.

9. SAMENVATTING

In the province Skåne, zuidelijk Zweden, werd van 1974 tot 1979 onderzoek gedaan in een gebied van ruim 20 km² aan de lokale Bonte Kraai populatie. Voor zover vogels konden worden gevangen werden ze voorzien van ringen en vleugelmerken. In enkele gevallen kon gedurende enige dagen het bewegingspatroon van individuele vogels geregistreerd worden m.b.v. zendertjes. Het veldwerk bestond vooral uit het documenteren van het verspreidingspatroon en het gedrag van gemerkte vogels gedurende een aantal opeenvolgende jaren, waarbij gebruik werd gemaakt van twee vaste auto-routes in en rondom het studiegebied.

Onderscheid wordt gemaakt tussen territoriale- en groepsvogels: territorialen worden, tenminste in de periode april—juni, praktisch uitsluitend gezien binnen een gebied van beperkte omvang, en solitair of met hooguit één andere vogel. Alle vogels welke (in april—juni) niet aan dit criterium voldeden werden beschouwd als groepskraaien; deze kunnen worden aangetroffen in een groter areaal dan territoriale vogels, maar toch was hun areaal tamelijk beperkt, althans in voorjaar en zomer, en wel tot plaatsen met geconcentreerde voedselbronnen ("CFP" in de tekst; afvalhopen, mestvaalten, aardappel wintervorraden, open varkens- en koeiestallen). Arealen van territoriale- en groepskraaien overlappen 's zomers soms enigszins, terwijl arealen van individuele groepskraaien onderling dan in hoge mate overlappen. Groepskraaien roesten in voorjaar en zomer op korte afstand van hun foerageergebied en deze vogels gebruiken in de loop van een seizoen meestal meerdere roestplaatsen. In voorjaar en zomer werden groepskraaien soms enigszins buiten het groepsareaal aangetroffen, en waren dan solitair of met een partner. Deze vogels, die meestal ouder dan drie jaar zijn, worden beschouwd als verkenner: een jaar later broeden zulke vogels veelal in het eerder verkende gebied, maar niet alle broedvogels hebben een lange verkennerperiode achter de rug.

Paarvorming kan plaatsvinden tussen twee groepskraaien, maar treedt veelvuldiger op binnen een territorium. Bonte Kraaien blijken in hoge mate trouw te zijn aan hun territorium zowel als aan hun partner. Een kwart van alle gemerkte territoriale kraaien verbleef het gehele jaar binnen het territorium; er zijn aanwijzingen dat dit vooral zo is bij vogels met territoria met een relatief ruim, betrouwbaar voedselaanbod.

Jonge vogels verliezen in de periode september-novem-

ber de binding met de ouders en het ouderlijk territorium. In twee gevallen werd echter geregistreerd dat jonge vogels geassocieerd bleven met het territorium van hun ouder, in hun tweede en derde kalenderjaar.

In de winter worden territoriale kraaien — voor zover ze de binding met hun territorium tijdelijk hebben opgegeven — vooral in kleinere groepen aangetroffen, jonge vogels en groepskraaien in grotere groepen. Beide laatstgenoemde categorieën vogels werden in de winter naar verhouding ook veel meer op CFP waargenomen dan territoriale kraaien.

's Winters frequenteren de meeste kraaien in het studiegebied enkele grote, traditionele roestplaatsen gelegen in stukjes sparrenbos. Vogels arriveren hier massaal een half uur na zonsondergang, komend vanaf één of meer voorverzamelplaatsen. Deze laatste zijn veelal eveneens traditioneel, en liggen op korte afstand van CFP, en tot op enige kilometers afstand van de grote roestplaatsen. Bij voorverzamelplaatsen behoren bepaalde foerageerarealen welke onderling nauwelijks overlappen. Vooral jonge vogels wisselen in de loop van de tijd nogal eens van voorverzamelplaats en het daarbij behorende foerageergebied.

De meeste jonge vogels en groepskraaien waren niet in het studiegebied aanwezig tussen oktober en maart. Ringvondsten suggereren dat deze vogels elders in zuid-Zweden en in Denemarken overwinteren, en dat Finse vogels 's winters in het studiegebied voorkomen.

De cijfers berekend voor overleving liggen op minimaal 92% voor territoriale kraaien, en op minimaal 75% voor groepskraaien.

In de discussie worden de Zweedse gegevens vergeleken met resultaten van soortgelijk onderzoek in West-Duitsland, Schotland en Zwitserland en worden deze geïnterpreteerd in een algemener, theoretisch kader. — R. v. H.