

Nest distribution in a population of the Hooded Crow *Corvus cornix*

JON LOMAN

Loman, J. Nest distribution in a population of the Hooded Crow *Corvus cornix*. *Ornis Scand.* 6, 169–178, 1975.

In a Hooded Crow *Corvus cornix* population in Southern Sweden, nests were found to be weakly overdispersed. If they had a choice, the crows preferred conifers as nest trees. Nest height was determined by the branch structure, which differed between tree species. Presence of marshland (presumably containing much food) and social interactions were not found to affect nest dispersion to a significant extent.

Jon Loman, Zoological institute, Ecology Building, S-223 62 Lund, Sweden.

INTRODUCTION

The purpose of this paper is to analyse some factors that might influence the selection of nest site by the Hooded Crow *Corvus cornix* L. This problem has previously been discussed by Abshagen (1963), Tenovuo (1963), Wittenberg (1968), and Kulczycki (1973) on the basis of studies in DDR, Finland, BRD, and Poland respectively. The work of Wittenberg refers to the Carrion Crow *Corvus corone* and that of the others to the Hooded Crow. Even if, according to my opinion, the Carrion and Hooded Crow should be considered different species, it seems appropriate to include both when comparing geographical variation of ethological and ecological characters, as they seem to be ecological vicariants in all respects.

STUDY AREA

Part of the Revinge area and of the adjacent farmland in the province of Skåne in southern Sweden (55° 40' N, 13° 30' E) served as the study area. The Revinge area has been used for military training purposes since about 1967 and was earlier mixed farmland. There are numerous groves and lines of trees. The former are up to 0.15 km² in area. *Alnus glutinosa*, *Betula pubescens*, *B. verrucosa*, *Fagus sylvatica*, *Picea abies*, and *Pinus silvestris* occur in pure

stands. Also *Populus tremula*, *Quercus robur*, several species of *Salix*, and *Ulmus glabra* are found, although in mixed stands. There are several marsh areas where important food items for the crows, such as small rodents, pheasant eggs, and frogs, are particularly abundant. This presumably also applies to the invertebrates. Adjacent to the study area is a eutrophic lake covering 3 km². The part of the Revinge area on which this study was carried out is used for military training about five weeks a year. During other times it is grazed by cattle.

MATERIAL AND METHODS

The data were collected from 1971 to 1974 and refer to 188 nests (Table I). Within a fixed area of 21 km², I tried to find all crow nests during all four years. However, in 1971 and 1972 some nests were destroyed by humans before my search was completed and their number and locations are not known. In 1973 and 1974 I received information about all destroyed nests; they could therefore be included in the study. Some nests outside the fixed study area were also found, so that somewhat different areas were searched in different years. The fact that all nests were found within a restricted area rather than a lesser proportion in a wider area should reduce any bias due to

Table I. Number of crow nests included in this study. The fixed study area covered 21 km² that were searched during all four years. In 1973 and 1974 additional areas were searched; the total area comprised 22 km² in 1973 and 24 km² in 1974

	1971	1972	1973	1974	All years
The fixed study area	41	38	40	41	146
All searched areas	41	38	52	57	188

differences in conspicuousness of nests in different tree species and at different height.

As the study area comprised and was bordered by large treeless areas without any crow nests, it is difficult to give a pertinent measure of nest density. This was therefore calculated in two different ways. The results differ by approximately 10 %.

Method I provides a measure of density for an area in which it is possible to find with certainty the closest neighbour to all nests. This area is the one searched, except when this is bordered by treeless areas or includes nests, whose closest neighbour has not been found

with certainty. In the former case I included half the treeless area, and in the latter the whole area up to half way between the outermost nest with the nearest neighbour known and the nest without the nearest neighbour known (Fig. 1).

Method II provides a measure of density and variance for a number of squares. The study area is divided into 1 × 1 km large squares, and the area used in the calculation includes all such squares that were searched to at least 80 %.

To each 1 × 1 km square an 'index of wetness' is assigned. It has the value 0 if the official map lacks the symbol for 'marsh' in that particular square, 1 if it contains up to 5 %, and 2 if it contains more than that proportion. When calculating the mean number of nests per km² with respect to this index, all squares searched to at least 80 % were considered.

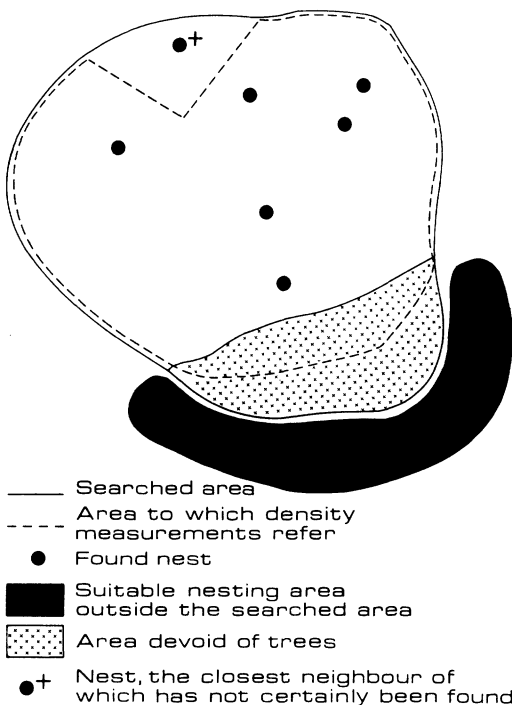


Fig. 1. Procedure used to assess nest density according to Method I, as described in the text.

Table II. Relation between nesting trees and trees in the vicinity of nests (within 40 m from the nest)

	Times served as nesting tree	Relative score of occurrence in the vicinity of nests
<i>Alnus</i>	41	38
<i>Pinus</i>	38	35
<i>Betula</i>	37	50
<i>Picea</i>	30	25
<i>Salix</i>	11	8
<i>Fagus</i>	6	7
<i>Quercus</i>	6	7
<i>Ulmus</i>	6	7
<i>Populus</i>	3	3
<i>Acer</i>	1	1
<i>Pyrus</i>	1	0
Total	180	181

To describe the tree composition in the vicinity of the nests, the following procedure was adopted. Regard was taken to trees within 40 m from the nests. The frequencies of the different trees were expressed on a scale from 0 to 1, giving a total of 1 for each unit. The

score was not directly proportional to the number of trunks, but the less common trees were overrated. Large trees were also given additional weight in the scores. The values from all nests were then added to obtain a total importance value for each tree (Table II).

Table III. Tests of the dispersion of crow nests, based on data obtained with method I and method II. All distances are expressed in km and all densities in nests per km²

Method I

	1971	1972	1973	1974	All years
N_1	33	33	41	46	153
r			0.375	0.296	
r'	0.380	0.427			0.362
m_1			2.49	2.50	
m'_1	2.29	2.07			2.37
$r_e (r'_e)$	0.331	0.348	0.317	0.316	0.325
c	1.61	2.49	2.27	0.825	1.80
P	> 0.1	< 0.01	< 0.05	> 0.1	< 0.1

- N_1 = Number of nests with the closest neighbour known.
- r = Mean value for the distance from a nest to its closest neighbour. All nests considered.
- r' = As r , but some nests destroyed by humans were omitted.
- m_1 = Density according to method I. All nests known and considered.
- m'_1 = As m_1 but some nests destroyed by humans were omitted.
- r_e = The expected mean value for the distance from a nest to its closest neighbour if random dispersion of the nests is assumed.
- r'_e = As r_e but some nests destroyed by humans were omitted.
- s_{r_e} = $0.26/\sqrt{N_1 m_1}$, standard error of the mean distance from a nest to its nearest neighbour if the nests are dispersed at random.
- c = $(r - r_e)/s_{r_e}$.
- P_1 = The probability, under the observed value of c , that the nests are dispersed at random.

Method II

	1971	1972	1973	1974	All years
N_2	19	18	19	21	77
m_2			2.42	2.24	
m'_2	1.95	1.88			2.13
s^2			1.37	1.89	
s'^2	1.61	0.93			1.44
T	14.8	8.90	10.2	16.9	51.5
P	> 0.10	< 0.10	< 0.10	> 0.10	< 0.05

- N_2 = Number of squares for which density, according to method II, and standard deviation have been calculated.
- m_2 = Density according to method II. All nests considered.
- m'_2 = As m_2 , but some nests destroyed by humans were omitted.
- s = Standard deviation of the number of nests per km². All nests considered.
- s' = As s , but some nests destroyed by humans were omitted.
- T = $\frac{s^2 (N_2 - 1)}{m_2} ; \frac{s'^2 (N_2 - 1)}{m'_2}$
- P = The probability, under the observed value of T , that the nests are dispersed at random.

RESULTS

Dispersion

Two tests were made of the hypothesis of random dispersion. The statistic $(r-r_e)/s_{r_e}$ was calculated. Here r is the mean distance from a nest to its nearest neighbour, r_e the expected mean distance from a nest to its nearest neighbour, under the actual density, if the nests were dispersed at random, and s_{r_e} the standard error of the expected mean distance from a nest to its nearest neighbour if the nests were dispersed at random. This statistic is normally distributed, and the hypothesis of random dispersion can be rejected for sufficiently large or small (negative) values (Clark & Evans 1954). The statistic $s^2(N-1)/m$, where s is the standard deviation of the number of nests per km², N the number of 1×1 km squares, and m the density of the nests according to method II, was also calculated. It is χ^2 -distributed, and the hypothesis of random dispersion can be rejected for sufficiently small or large values (Southwood 1966, p. 41).

According to the first test, the hypothesis of random dispersion could be rejected in favour of overdispersion for the years 1972 and 1973 ($p < 0.01$ and $p < 0.05$, respectively). If all four years were considered, it could be rejected at the 0.1 level. According to the second test, the hypothesis of random dispersion was only rejected if data for all four years were combined ($p < 0.05$) (Table III). Fig. 2 relates the

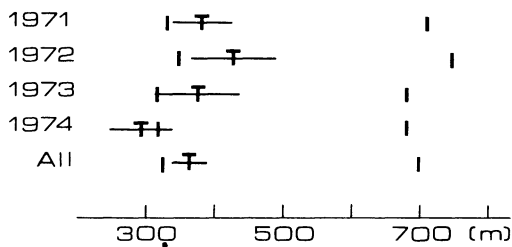


Fig. 2. The relation between the observed mean distances between the nests (T) and the expected mean distances at random dispersion (vertical bar on the left) and the mean distances at maximum spacing (vertical bar on the right). The 95% confidence interval is indicated by a thin horizontal line.

distance between the nests to the distance at maximum spacing and the expected mean distance at random dispersion. Also in this case the difference was significant if all four years were considered.

To obtain information on the dispersion type when the effect of treeless areas is eliminated, a special analysis of groves with more than one nest was carried out. The distribution of nests in these groves is presented in Fig. 3. The maximum possible distance between two points in the groves with two nests was calculated, and also the three pairwise distances between points, placed to give a maximum total of separating distances, in groves with three nests. Expressing the distance between the nests as a fraction of the maximum possible a mean value of 0.58 was obtained. When the same was done for random points (two in the groves with two nests and three in those with three nests) a value of 0.38 was obtained. These random points constituted coordinates, taken from a table of random numbers, and do not represent the expected distance between two random points in each grove. The number of cases where the distance between nests was longer than that between random points was compared to the number of cases where the opposite was the case; the former was found to be significantly larger (χ^2 -test, two-tailed, $P < 0.05$).

The distribution of distances to the nearest neighbour was bimodal during all years (Table IV). The shorter distances did not relate to nests in the same grove, but on the contrary, the majority of these distances were measured

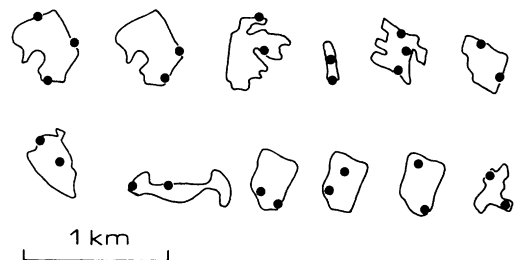


Fig. 3. Shape of groves and position of nests in the groves with more than one nest during the same year.

Tab. IV. Distribution of the distances between a nest and its closest neighbour of the same year

Distance (metres)	1971	1972	1973	1974	total
50	0	0	0	4	4
100	0	0	2	2	4
150	0	2	2	7	11
200	1	2	4	6	13
250	4	4	9	4	21
300	7	3	9	4	22
350	9	0	3	6	18
400	3	2	1	0	6
450	2	8	2	1	13
500	1	4	4	6	15
550	4	2	1	6	13
600	1	2	1	0	4
650	0	1	0	0	1
700	1	2	0	0	3
750	0	1	1	0	2
800	0	0	1	0	1
850	0	0	1	0	1
Mean (m)	380	427	375	296	362
Standard deviation of mean	20.5	28.4	30.6	23.0	13.7

between nests in different groves. The two closest pairs of nests were situated 70 m from each other.

Distance to deserted nests

Renestings are defined as nestings in the im-

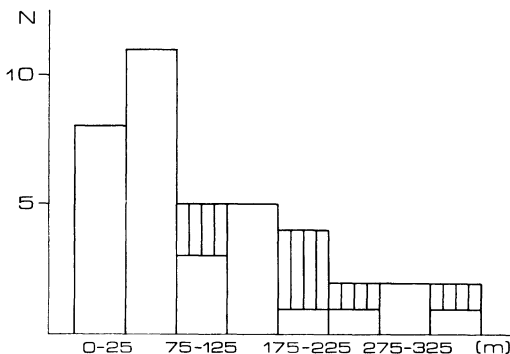


Fig. 4. Distribution of distances from nests of 1974 to the closest nesting site of the previous year. If that nesting site is closer to another nest from the same year, the bar has been striped.

mediate neighbourhood of a previous nesting failure. The distances between such a nest and the presumed first nest of the same pair were 20, 30, 30, 50, and 200 m (mean 66 m). Tenovuo (1963) gives for six renestings a mean of 48 m.

Distance to last year's nest site

The modal value for the distance from a nest to the closest nest site of the previous year was 75 m (Fig. 4). In two cases out of 120 the same nest was used during two successive years and in one case the same fork was used when the nest had been destroyed the year before.

Relation to wet areas

The mean number of nests in squares with wetness indices 0, 1, and 2 were 1.9 ($N = 40$), 1.8 ($N = 12$), and 1.9 ($N = 25$), respectively. The number of nests per km² of non-marshy areas was 1.7 while in the marshes proper it was 12 (mean for all years in the fixed area).

The nests were not closer to the marshes than a set of points distributed at random over the fixed area. However, the mean distance to the closest nest from one point in a set of points distributed at random over the marshes was shorter than that from a point in a set distributed at random over the non-marshy areas. The same difference applied also if one compared the mean distance to trees instead of nests (Table V). Trees were chosen as they are assumed to be the only acceptable nest sites in the study area.

Nest tree

As shown in Table II, the dominating nest trees in the study area were in order of importance: *Alnus*, *Pinus*, *Betula*, and *Picea*.

The distribution of nests on different tree species was not significantly different from the distribution of importance values ($P > 0.05$) (Table II). When all tree species were successively compared singly against the rest of the trees, the number of nests in *Betula* was found to be less than expected ($P < 0.05$). However, when making several comparisons, random fluctuation may produce one divergence at the 0.05 level. If all 180 nest sites are considered,

Table V. Type of distances compared to analyse the degree and kind of correlation between nests and marshes

Distance compared	No of comparisons	Mean distance (m)
From nest to closest marsh	146	750
From a random point to closest marsh	30	640
From a random point in non-marshy areas to closest nest	30	260
From a random point in marshes to closest nest	15	120
From a random point in non-marshy areas to closest tree	30	150
From a random point in marshes to closest tree	15	60

the preference for conifers was not significant ($P > 0.05$), but if only the 18 sites that offered a choice between conifers and deciduous trees are considered, it is highly significant ($P < 0.001$).

Nest height

The modal value for the nest height was 10 m (Fig. 5). The nest height did not differ significantly between the different years (t-tests between all pairs of years; $P > 0.05$) (Table VI). The height relative to the top of the canopy was less in 1974 than in 1971 and 1972 (t-tests; $P < 0.01$ and $P < 0.05$, respectively) (Table VI).

The nests at Revinge were placed at a lower height than those in Poland (Kulczycki 1973) and Rostock, DDR (Abshagen 1963) (t-tests; $P < 0.001$ in both cases). The mean height values of the nests in these two latter studies are not significantly different. There was a slight but significant difference between the nest height at Revinge and on the Finnish

mainland (Tenovuo 1963) ($P < 0.05$). The nests at Revinge were also in this comparison those placed at the lowest height (Table VI).

If the crows prefer to build their nest at a certain height, they should tend to build relatively lower in high trees than in low. This was not the case if the mean height of each tree species is compared to the mean nest height in the same tree species (Fig. 6). To test the hypothesis with respect to one species at a time the correlation coefficient between the height of individual nest trees and the nest height was calculated for *Alnus* ($r = -0.40$, $N = 25$), *Betula* ($r = -0.32$, $N = 25$), *Pinus* ($r = 0.41$, $N = 21$), and *Picea* ($r = 0.31$, $N = 17$). There is a significant negative correlation, as the hypothesis predicts, only for nest sites in *Alnus*. However, the hypothesis is supported by the fact that the relative nest height is lower in *Alnus* and *Betula* in the Revinge area than in the Finnish archipelago where the trees are lower (Tenovuo 1963, Tables VII and VIII).

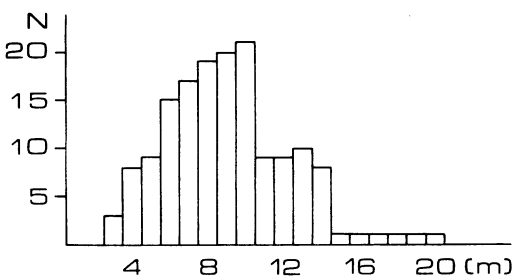


Fig. 5. Distribution of nesting heights.

Measurements of the nests

The inner diameter of nests at the Revinge area is smaller than in Finland and Poland (Tenovuo 1963, Kulczycki 1973) (t-tests; $P < 0.01$ and $P < 0.001$, respectively (Table IX)). The differences, however, are not larger than may be caused by differences in method of measurement. The depth of the nests at the Revinge area and in Poland are smaller than in Finland (t-tests; $P < 0.001$ in both cases) (Table IX). These differences are probably real.

Table VI. The height of crow nests – absolute and in relation to the top of the canopy. For comparison, data from some other countries are also given: Poland (Kalczychin 1973), Germany (Abshagen 1963), and Finland (Tenovuo 1963)

Year	Absolute height (m)	Mean error	Relative height	Mean error	Sample size
1971	9.0	0.51	0.68	0.024	40
1972	9.4	0.57	0.69	0.019	35
1973	8.7	0.58	0.65	0.020	42
1974	9.2	0.53	0.60	0.026	39
All	9.0	0.38	0.66	0.012	156
Poland	14.5	0.85			36
Germany	12.6	0.81			25
Finland, mainland	9.9				199
Finland, archipelago	4.9				192

DISCUSSION

Selection of nesting area

References indicate a great variability of the crows with respect to territoriality and dispersion type. Abshagen (1963) describes a wood of 0.075 km², where at least 37 pairs of Hooded Crows nested. This means that the mean distance to the closest neighbour must have been less than 45 m. There seemed to be little aggression between these crows. However, Abshagen considered this 'colony' to be exceptional. The Carrion Crows that Wittenberg (1968) studied at Braunschweig (BRD) lived in an area with underdispersed possible nest sites (groves of areas around 1 km² situated in open

fields). Though the territories had a mean size of 0.25 km² compared to a mean size of 0.45 km² (assuming non-overlapping, abutting territories) for the crows at Revinge, the mean distance to the nearest neighbour was only the half, 190 m compared to 360 m. The value of $m_1 \times r^2$ is 0.14 at Braunschweig and 0.31 at the Revinge area. This indicates a higher degree of aggregation at the former area (Southwood 1966, p. 41). In spite of this, the territories were clearly defended against other nesting crows

Table VII. The height over ground for crow nests in different trees in the Revinge area and in the Finnish archipelago. Relative height refer to the ratio height of tree/height of nest

	Sample size	Height (m)	Mean error	Relative height
<i>Alnus</i>	34	8.0	0.32	0.68
<i>Betula</i>	26	8.3	0.46	0.57
<i>Pinus</i>	22	11.3	0.89	0.78
<i>Picea</i>	17	10.1	0.75	0.68
<i>Salix</i>	8	6.8	1.15	0.66
<i>Quercus</i>	6	8.3	0.86	0.45
<i>Ulmus</i>	4	9.4	1.07	0.53
<i>Fagus</i>	4	14.0	1.18	0.53
<i>Populus</i>	3	10.2	0.95	0.63
Nests from the Finnish archipelago (Tenovuo 1963)				
<i>Alnus</i>	126	5.5		0.77
<i>Sorbus</i>	22	2.7		0.69
<i>Betula</i>	31	4.5		0.64

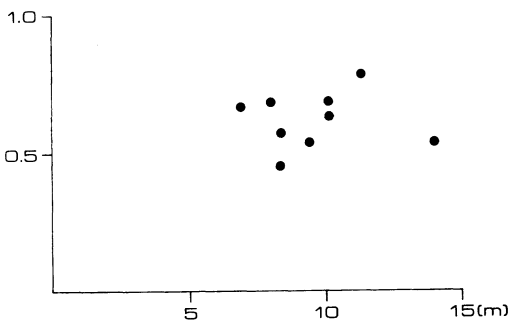


Fig. 6. Relation between the absolute nesting height (m) and the nesting height in relation to the top of the nest tree for nine different kinds of tree.

Table VIII. Degree of significance in the differences in relative height for nests in separate tree species. The values given are not exceeded by P. n.s. = not significant

	<i>Alnus</i>	<i>Pinus</i>	<i>Betula</i>	<i>Picea</i>	<i>Salix</i>	<i>Fagus</i>	<i>Quercus</i>	<i>Ulmus</i>
<i>Pinus</i>	0.01							
<i>Betula</i>	0.001	0.001						
<i>Picea</i>	n.s.	0.05	0.001					
<i>Salix</i>	n.s.	n.s.	n.s.	n.s.				
<i>Fagus</i>	0.001	0.001	n.s.	0.001	n.s.			
<i>Quercus</i>	0.001	0.001	0.05	0.001	0.01	n.s.		
<i>Ulmus</i>	0.05	0.001	n.s.	0.05	n.s.	n.s.	n.s.	
<i>Populus</i>	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

(Wittenberg 1968, p. 63). By contrast, during my work, I have only witnessed one clear case of a territorial fight. In spite of this low rate of aggression, the dispersion of the crows in my study area was less aggregated. One could hypothesize that the higher degree of aggregation caused the higher frequency of aggressions. In any case, this supports my contention that social relations are less important in determining the dispersion type than the distribution of suitable nesting trees.

Tenovuo (1963, p. 17) mentions groups of nests that he regards as instances of loose social aggregations because of their relative proximity.

Similar groups were found in my study area, but as the dispersion was still not aggregated,

Table IX. Measurements of crow nests from Revinge (this study), Poland (Kulczycki 1973), and Finland (Tenovuo 1963). The measurements from Revinge, and presumably also from Poland and Finland, refer to the cup

	Revinge	Poland	Finland
<i>Inner diameter</i>			
Number of nests	29	31	57
Mean value (cm)	18.5	19.41	19.8
Span (cm)	17–20	15.5–25.0	18–22
Standard deviation	0.79	1.95	0.83
S.d. of mean	0.15	0.35	0.11
<i>Depth</i>			
Number of nests	29	31	52
Mean value (cm)	10.4	10.35	12.6
Span (cm)	7–13	8.0–15.0	10–15
Standard deviation	1.18	1.88	1.15
S.d. of mean	0.22	0.34	0.16

they can be explained as random fluctuations of dispersion and do not presuppose social forces of attraction.

As there are no more nests in km²-squares with marshes than in those without marshes, and as the distance from a nest to the closest marsh proper is not markedly less than that from a random point to the closest marsh, the presence of marshes did not influence the distribution of nests when larger areas are considered. As, however, the density of nests is higher in marshes proper than elsewhere and the distance from a random point in a marsh to the closest nest is less than that from a random point elsewhere, some association between nests and marshes does exist. Without contradicting the first proposal this may be explained on the assumption that the crows, once their general nesting area is chosen, prefer to build their nests in marshes. This association can, however, be fully explained by the distribution of trees that show the same degree of association to marshes (Table V). Assuming that food is more abundant in marshes than elsewhere, the lack of importance of the marsh areas indicates either that food is less vulnerable to crow predation here than elsewhere, or that in the Revinge area food availability does not significantly influence the breeding density of crows. Yom-Tov (1974) in Scotland did not find any relationship between food abundance and nest site selection in the crow.

The nests cannot definitely be considered overdispersed, but as the dispersion pattern is superimposed on that of possible nesting sites, that is trees which are usually aggregated in

groves, it seems probable that, in a theoretical homogenous environment, nests would be overdispersed. This is to be expected if the crows defend territories against other nesting crows. The degree of overdispersion, however, is not high, and the presence of nesting trees appears to be an overriding factor for the selection of nesting area.

If one wishes to compare the effects of territoriality with that of heterogeneity of the wooded habitat, the effect of the treeless areas has to be eliminated. One way to do this is to consider each grove with more than one nest separately. To do so would eliminate some nests that might express the effects of territoriality, namely nests in single trees and nests that are the only ones in their grove. If the territoriality effect operates unrestrictedly, the distance between the nests should be as great as possible. If this prediction is not fulfilled, this may be due to the following circumstances: 1) territorial influences from nesting crows in neighbouring groves; 2) the fact that the territoriality has no influence on other crows, nesting at a distance from the nest greater than D , where D is a distance less than the maximum possible in that particular grove; 3) the influence from a heterogenous habitat with respect to some factor of importance for the selection of nesting sites, for instance, particularly good nesting trees. If 3) is important and territoriality lacks importance, the mean distance could be less than the mean distance between random pairs of points in the groves. This is not the case. On the contrary, the distance is more than that between random pairs of points. However, the mean distance is considerably less than the maximum possible, suggesting that some combination of the factors 1-3 operates. In only one case was a nest outside the groves under examination closer to a nest than the other nest(s) in the grove, so 1) cannot be very important. If 2) is important, this means that, under the observed density, territoriality is not important and the observed deviation from maximum distance is the result of random dispersion. The preliminary result is that, according to this analysis, territoriality operates but is not a very strong force, and that other

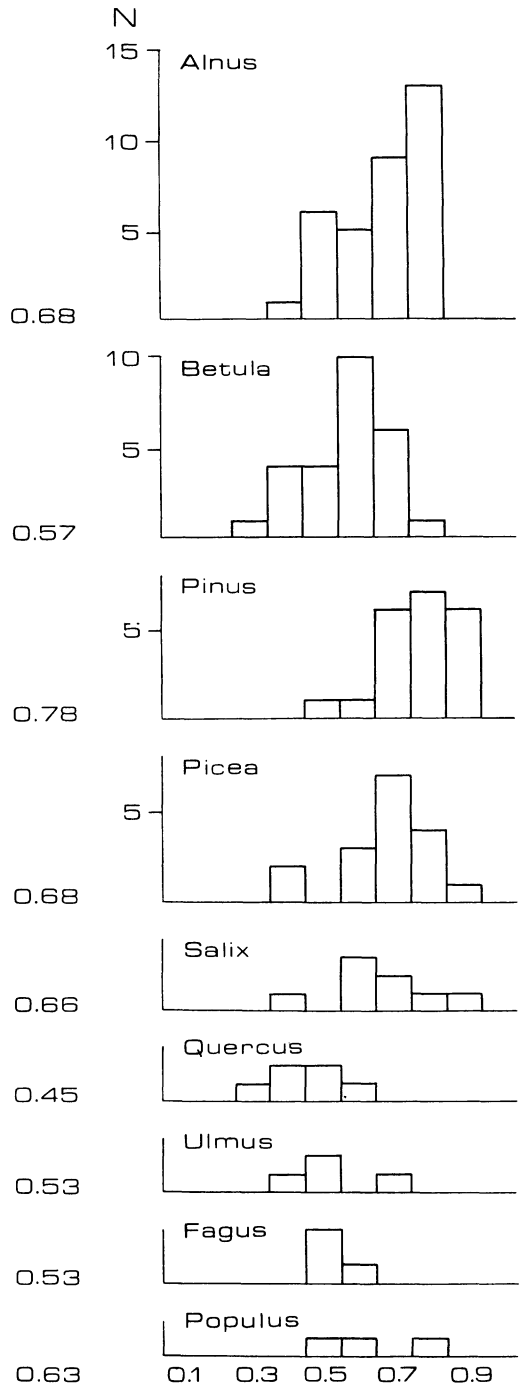


Fig. 7. Distribution of nesting heights in relation to the top of the nest tree (vertical axis: number of nests; horizontal axis: height ratio). The mean is given to the left of each diagram.

factors must be considered, such as the distribution of the trees. Assuming that also 'the second best' can be accepted as a nesting tree, which seems reasonable as most nesting trees are not used during two consecutive years, another conclusion could be that there is a surplus of possible nesting sites.

Selection of nest tree and site in the tree

In the study area, the crows exhibited a tendency to nest at the edge of groves. However, because of the small size of the groves, the study area is not suitable for a study of edge effects. Most authors, however, agree that edges are preferred as nest sites (e. g. Wittenberg 1963).

The specific kind of tree seems to have little importance for the crow's selection of nest site. The preference for conifers is, however, clear and consistent with the findings of, among others, Tenovuo (1963) and Wittenberg (1968). The preference for conifers was only manifest when mixed coniferous-deciduous groves were considered, suggesting that the crows did not prefer coniferous to deciduous groves but, within a given grove, preferred a coniferous tree if such was available.

The most important factor determining the location of the nest in the tree seems to be the position of a suitable fork. A fork that is to support a crow nest must have special properties that are certainly not found in all trees. Two branches must join the trunk at a vertical distance that should not exceed 5–6 cm. This applies to the nests at the main trunk. In the present study 172 nests were of this type while 8 were situated away from the main trunk. These demands cause every tree species to have a characteristic relative nest height (Table VII,

VIII, Fig. 7). If several suitable forks exist, the crows might prefer the highest, as Tenovuo (1963) suggested. Another factor that might influence the nesting height would be a preference for a particular height. However, my data did not demonstrate any such preference.

ACKNOWLEDGEMENTS

Claes-Thore Andersson shared the work during the first field season. Sam Erlinge, Staffan Ulfstrand, and several others offered valuable criticism of the manuscript. The study has been supported in part by grants from the Swedish National Science Research Council to S. Ulfstrand.

REFERENCES

- Abshagen, K. 1963. Über die Nester der Nebelkrähen, *Corvus corone cornix*. *Beitr. Vogelk.* 8, 325–338.
- Clark, P. J. & Evans, F. C. 1954. Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology* 35, 445–453.
- Kulczycki, A. 1973. Nesting of the members of Corvidae in Poland. *Acta Zool. Crac.* 18, 583–666.
- Southwood, T. R. E. 1966. *Ecological Methods*. Methuen & Co., London.
- Tenovuo, R. 1963. Zur brützeitlichen Biologie der Nebelkrähe (*Corvus corone cornix* L.) im äusseren Schärenhof Finnlands. *Ann. Zool. Soc. 'Vanamo'* 25, 1–147.
- Wittenberg, J. 1968. Freilanduntersuchungen zu Brutbiologie und Verhalten der Rabenkrähe (*Corvus c. corone*). *Zool. Jb. Syst.* 95, 16–146.
- Yom-Tov, Y. 1974. The effect of food and predation on breeding density and success, clutch size and laying date of the Crow (*Corvus corone* L.). *J. Anim. Ecol.* 43, 479–498.

Received January 1975

Published November 1975