

Habitat selection, flocking and feeding behaviour of Hooded Crows *Corvus corone*

Anders Pape Møller

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Hooded Crows were studied during a period of 27 months in N Jutland, Denmark, in order to investigate the effect of the winter invasion of crows from Scandinavia upon resident birds. During the stay of the winter visitors, the population was several times as large as in summer, when more food was available. Aggressive interactions between Hooded Crows in winter indicated intraspecific competition for food. Residents stayed in or near their territory all the year round and knew the location of food sources. The winter visitors arrived when food resources were diminishing and had no knowledge of the distribution of food. The visitors were able to utilize scattered occurrences of abundant food, whereas the resident crows were faithful to their preferred habitats throughout the year. The visiting Hooded Crows utilized meadows and ephemeral food sources, such as newly spread dung, but sites were often visited only for a couple of days. The resident crows roosted commonly near their feeding grounds, but this rarely occurred among winter visitors (only during severe weather). The resident crows did not use energy for flying between a communal roost and the feeding grounds, and were able to start feeding at daybreak and continue until dusk. Intraspecific competition between the two Hooded Crow populations was thus reduced in extent.

Anders Pape Møller, Langelandsgade 216, DK-8200 Århus N, Denmark

Introduction

Many temperate bird species face the invasion of northern conspecifics in autumn, often in considerable numbers. At this time of the year resources are often declining and intraspecific competition results. If the resources are at all predictable, resident birds will usually benefit from their knowledge of the area (cf. Alerstam & Enckell 1979). Another common outcome of migration and residence in bird populations is leap-frog migration: some populations are sedentary and the more northern migratory ones merely rest in the area of the sedentary population on their way to southern wintering grounds. Although reduction of intraspecific competition has been suggested as a cause of leap-frog migration (Salomonsen 1955), predictable spring weather in areas near the breeding grounds and the possibility of moving to the breeding grounds during early spring have also been put forward (Alerstam & Högstedt 1980).

In the present study of Hooded Crows *Corvus corone*, the problems facing a resident population will be considered.

Study area and methods

The study was conducted near the village Kraghede (57°12'N, 10°00'E), N Jutland, Denmark. The area was covered with different kinds of crops, especially barley. Meadows (below 10 m altitude) surrounded the area on three sides. During winter most fields were left bare

after early harrowing and ploughing. A detailed description of the area is given in Møller (1982).

The Hooded Crow was investigated in the period October 1979 through December 1981 during a more intensive study of Magpies *Pica pica*. Hooded Crows had to be considered, because of their interactions with Magpies. The monthly distribution of observation hours was as follows: January 42, February 18, March 18, April 36, May 51, June 39, July 36, August 78, September 27, October 42, November 24 and December 45.

Surveys were conducted along a 6.1-km route through the area (cf. Møller 1982). Each survey usually lasted 1–3 hours. The Hooded Crows were plotted on a map and notes made of habitat use and feeding parameters (no. of pecks and steps per unit time, time being recorded with a stopwatch). Each step lasted on average 0.49 sec (N=37) and each peck 0.92 sec (N=40), no seasonal trends being recorded. Step length averaged (\pm s.d.) 23.9 \pm 7.1 cm (N=68) without seasonal trends. In more than 90 % of all cases pecks were followed by swallows, and as pecks were much more easily recorded than swallows, pecks were used as an index of food intake rates. These feeding parameters were used to calculate speed ((steps x 0.239)/time m sec⁻¹), real speed ((steps x 0.239)/(total time - pecks x 0.92) m sec⁻¹), time stationary (pecks x 0.92 x 100)/(total time) %, pecks m⁻¹ and duration of an average stop ((total time - 0.49 x steps)/(steps) sec.).

Habitat preference indices were calculated using Jacobs' formula (1974):

$$P = \frac{X_1/Y_1 - X_2/Y_2}{X_1/Y_1 + X_2/Y_2}$$

where X_1 is the number of individuals in the habitat, Y_1 is the total number, X_2 is the size of the habitat and Y_2 is the total area. The values range from +1 to -1.

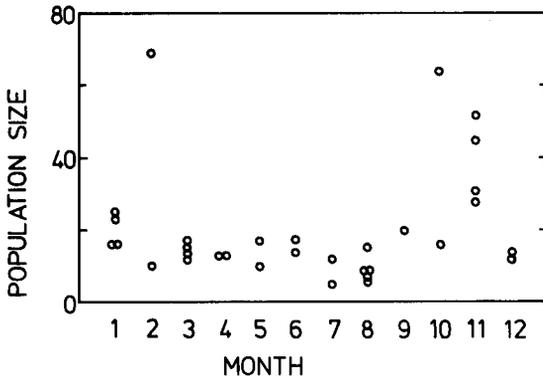


Fig. 1. Annual variation in population size of Hooded Crows within the Kraghede area. 32 complete censuses included.

During the years 1979–1981 a total of 7, 8 and 6 pairs of Hooded Crows bred within the Kraghede area (Møller 1981 and unpubl.).

Results

Annual cycle of the Hooded Crow. The Hooded Crow is generally considered a resident species in Denmark, a small fraction having been migratory in the early decades of the present century (Salomonsen 1967). In the Kraghede area pairs often remain within their territories all the year round. Nest building starts in March–April and the young fledge in May. Some replacement clutches are laid in April–May, with fledging in June. Prolonged parental care lasts until July–August. The moult takes place from June through early September, as recorded from shed primaries, secondaries and retrices. Non-breeding flocks of

immature birds are common. Migration of northern populations from Scandinavia takes place from early October through November and return migration from late February to early April. Many birds stay in the area throughout winter (Fig. 1).

Habitat use. The habitats utilized by the Hooded Crows differed during the annual cycle. Several were avoided all the year round (ploughed fields, cornfields, plantations), whereas others were preferred most of the time (grassland, stubble, potatoes) or during some seasons (harrowed fields, roadsides, fences) (Table 1).

Preferred habitats were utilized outside the breeding season (March–June) without any seasonal trends (Fig. 2). During the breeding period preferred habitats were frequented less often than at other times (March–June: 85 in preferred (indices 0.26–1.00), 230 in other habitats, July–February: 822 in preferred and 325 in other habitats, $\chi^2=209.5$, $df=1$, $P<.001$). The habitats neither preferred nor avoided (indices -0.25 to 0.25) were frequented more often outside the breeding season (March–June: 137 indifferent habitats (indices -0.25 to 0.25), 178 others, July–February: 980 indifferent habitats, 167 others, $\chi^2=241.2$, $df=1$, $P<.001$). Avoided habitats were utilized less often in winter (December–February) than at other times of the year (December–February: 16 avoided habitats (indices -0.26 to -1.00), 465 others, March–November: 98 avoided habitats, 883 others, $\chi^2=19.9$, $df=1$, $P<.001$) (Fig. 2).

Meadows are characterized by their high production of invertebrates, due to ample moisture and constant growth of grass in the same areas. Meadows were visited by Hooded Crows much more often during the stay of northern winter visi-

Table 1. Habitat selection indices (Jacobs' indices) in Hooded Crows at Kraghede. N indicates the number of birds observed in different months. – = no observations possible, as the habitat is temporarily absent.

Habitat	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ploughed	-.96	-.94	-.67	-.74	-.82	–	–	-.75	-1.00	-.81	-.80	-.83
Corn	-1.00	-1.00	-1.00	-.79	.08	-.91	-.97	-.72	-1.00	.17	-1.00	-1.00
Harrowed	.63	-.18	-.86	.14	.10	.66	-.05	-.53	-.41	-.11	.20	-.03
Stubble	.39	.83	.76	.76	–	–	–	-.12	.67	.66	-.13	.24
Grass	.50	.45	.23	-.08	-.31	.03	.60	.48	.18	.27	.40	.45
Plantation	-1.00	-1.00	-1.00	-1.00	-1.00	-.27	-1.00	-.20	-.08	-1.00	-.62	-1.00
Farmyard	-.19	-1.00	-1.00	.12	-1.00	-1.00	-1.00	-1.00	.48	-1.00	-.36	-1.00
Potatoes	–	–	–	.54	.60	.79	-.33	.39	.33	.52	.00	–
Ditch	-1.00	-1.00	-1.00	.41	.00	.41	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
Road	-1.00	-1.00	.80	-1.00	.70	.86	.73	.75	.78	.53	.50	-1.00
Beets	–	–	–	-1.00	-1.00	.68	.00	-1.00	-1.00	-1.00	–	–
Fence	-1.00	-1.00	.78	-1.00	.33	.41	.70	.83	.87	.47	.29	-1.00
Rape	–	–	–	-1.00	-1.00	.71	-1.00	-1.00	-1.00	–	–	–
Dung	–	–	.90	.98	–	–	–	–	.96	.75	.96	.99
Dunghill	-1.00	-1.00	.95	.85	-1.00	.95	.95	-1.00	.95	.98	.80	-1.00
N	151	120	50	83	98	84	106	145	56	140	219	210

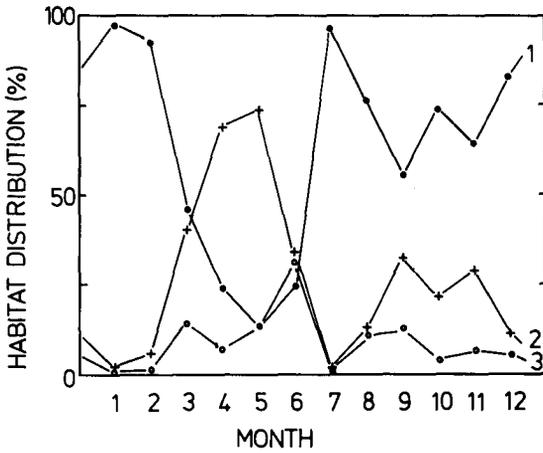


Fig. 2. Annual variation in distribution of Hooded Crows among preferred (Jacobs' indices 0.26—1.00) (1), indifferent (indices —0.25 to 0.25) (2) and avoided (indices —0.26 to —1.00) (3) habitats.

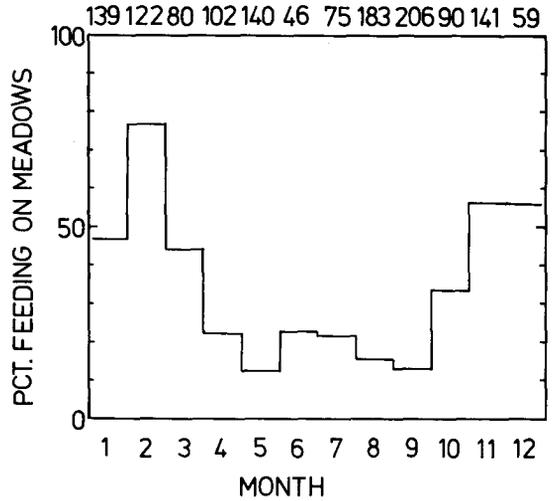


Fig. 3. Annual variation in frequency of Hooded Crows feeding on meadows. Top numbers refer to sample sizes.

tors than outside this period (October—March: 514 on meadows, 340 elsewhere, April—September: 114 on meadows, 419 elsewhere, $\chi^2=199.9$, $df=1$, $P<.001$) (Fig. 3). The fraction of crows feeding on meadows was generally connected with the numbers of birds present in the Kraghede area ($y(\text{fraction on meadows } (\%))=13.8+1.0 X$ (average monthly population size), $r=0.60$, $t=2.4$, $df=10$, $P<.05$) (Fig. 4).

During winter, mild frost-free periods alternated with cold and snowy periods. Several habitats were visited more often during snow cover and frost than during warmer periods with naked soil (e.g. grass, farmyards, dung, dunghills), whereas others were avoided (ploughed and harrowed fields) (Table 2). More birds were recorded on preferred habitats during snow cover and frost than at other times (snow cover: 316 preferred habitats, 360 others, no snow cover: 41 preferred habitats, 73 others, $\chi^2=139.1$, $df=1$, $P<.001$; frost: 229 preferred habitats, 39 others, no frost: 54 preferred habitats, 42 others, $\chi^2=34.8$, $df=1$, $P<.001$). Avoided habitats were generally visited infrequently during all kinds of weather (Fig. 2), whereas indifferent habitats were used less during unfavourable weather (snow cover: 15 indifferent habitats, 337 others, no snow cover: 73 indifferent habitats, 41 others, $\chi^2=200.9$, $df=1$, $P<.001$; frost: 13 indifferent habitats, 255 others, no frost: 32 indifferent habitats, 64 others, $\chi^2=52.9$, $df=1$, $P<.001$).

most common in April and May during the incubation and nestling periods, whereas pairs were common in March just before the breeding season and again in September after the reproductive period. Flocks with more than five birds were common in October to February, whereas flocks of 3—5 Hooded Crows were common in July—August (family flocks, flocks of immature birds) and also during the winter visitor period (October—March) (Table 3).

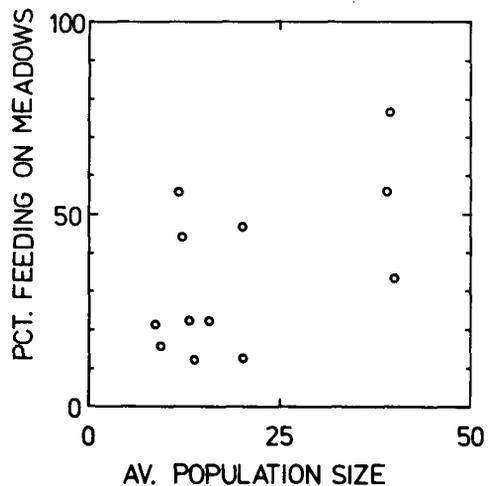


Fig. 4. Relation between frequency of meadow feeding and average population size of Hooded Crows. Values for the different months are shown.

Flocking. Hooded Crow units of one and two birds were very common and there were only a few larger flocks (Table 3). Single crows were

Table 2. Habitat preference indices (Jacobs' indices) in Hooded Crows at Kraghede in relation to soil conditions in winter (December to February).

Habitat	Soil condition			
	Snow cover	No snow cover	Frozen	Not frozen
Ploughed	-.83	-.09	-.82	-.70
Corn	-1.00	-1.00	-1.00	-1.00
Harrowed	-.24	.65	-.33	.22
Stubble	.64	.34	.08	.87
Grass	.42	-.19	.48	.06
Plantation	-1.00	-1.00	-1.00	-1.00
Farmyard	-.52	-1.00	-.46	-1.00
Ditch	-1.00	-1.00	-1.00	-1.00
Road	-1.00	-1.00	-1.00	-1.00
Fence	-1.00	-1.00	-1.00	-1.00
Dung	.98	-1.00	.98	-1.00
Dunghill	.94	-1.00	.88	.97
No. Crows	352	114	268	96

Table 3. Flock size in the Hooded Crow at Kraghede. Percentage distribution among size categories.

Month	Flock size					No. flocks
	1	2	3-5	6-10	11-60	
January	13.0	34.8	17.4	34.8	0.0	23
February	33.3	25.0	16.7	0.0	25.0	12
March	27.6	55.2	17.2	0.0	0.0	29
April	51.4	31.4	8.6	5.7	2.9	35
May	56.3	35.4	6.2	1.0	1.0	96
June	45.5	44.9	8.6	1.4	1.4	69
July	43.9	33.3	17.5	3.5	1.8	57
August	39.8	43.0	16.1	0.0	1.1	93
September	43.6	53.8	0.0	2.6	0.0	39
October	44.0	32.0	10.0	10.0	4.0	50
November	34.0	34.0	14.9	6.4	10.6	47
December	11.1	22.2	16.7	27.8	22.2	18
Total	41.8	38.8	11.7	4.4	3.4	565

Feeding behaviour. Pecking rates were high in January–February (21–23 pecks min⁻¹) compared with other months (9–16 pecks min⁻¹) (Fig. 5). The number of pecks per metre was low in late autumn (October–December), with a rise in January and a subsequent decline during the spring months. However, the stepping rate and speed rose to high levels during the same autumn months and sank again in January (Fig. 6). The average duration of stops was low in January–February and since peck rates were high, much time was spent stationary and only a little time in movement (Fig. 6).

Although the Hooded Crows were feeding their nestlings in May–June and fledglings in June–July, the pecking rates did not rise and no other changes could be detected (Figs. 5, 6). Apparently, the increase in daylength together with improved food availability allowed sufficient food to be collected without behavioural adjustments during feeding.

Some measurements of feeding behaviour dur-

ing varying winter weather conditions were made (Table 4). Pecking rates increased from naked soil to snow cover and again from snow cover and thaw to snow cover and frost. During snow, and snow and frost combined, both stepping rates and speeds decreased markedly.

Discussion

Habitat use. Preferred habitats were generally those available at the time of the year and/or those that were most productive. Preferred habitats were utilized most often outside the breeding season, when food was scarce. During breeding, intermediate habitats were often frequented. A trade-off between habitat preference and productivity apparently existed, as optimal habitats were utilized chiefly during the less productive winter season. Even avoided habitats were visited less often outside than in the breeding season. The marked winter influx of northern Hooded Crows led to an increase in the utilization

Table 4. Feeding parameters (average \pm SD) under different soil conditions. * - $P < 0.05$, **** - $P < 0.001$, n.s. - not significant. Only differences between average values are indicated. Pairwise comparisons between snow cover/frost and snow cover/thaw and between snow cover/thaw and no snow cover/no frost. The differences between snow cover/frost and no snow cover/no frost were all highly significant ($P < 0.001$).

Feeding	Soil condition		
	Snow cover Frost	Snow cover Thaw	No snow cover No frost
Steps min ⁻¹	20.1 \pm 9.1	**** 47.5 \pm 35.4	**** 67.8 \pm 25.7
Pecks min ⁻¹	26.3 \pm 11.8	n.s. 19.6 \pm 12.4	**** 11.0 \pm 7.9
Speed (m sec ⁻¹)	.08 \pm .04	**** .19 \pm .14	**** .27 \pm .10
Real speed (m sec ⁻¹)	.13 \pm .07	**** .26 \pm .19	* .32 \pm .10
Time stationary (log X (%))	1.56 \pm .22	n.s. 1.41 \pm .29	**** 1.09 \pm .38
Av. duration of stop (log X (sec))	.21 \pm .29	n.s. .39 \pm .39	n.s. .81 \pm .45
Pecks m ⁻¹ (log X)	1.12 \pm .28	**** .69 \pm .67	**** 12 \pm .51
No. of observations	10	59	48

of meadows as feeding sites. However, even during winter local Hooded Crow pairs remained in or near their territories and utilized the resources there.

As the weather became less favourable in winter, a marked switch occurred from indifferent to preferred habitats.

Flocking. The local adults remained in singles or pairs all the year round and the juveniles were observed to form small flocks. During the stay of the winter visitors, larger flocks were common. Flocking is generally seen as an adaptation to predator detection or to exploiting resources with a clumped and unpredictable distribution (e.g. Crook 1965). Predators were rare, with only irregular visits by Goshawks *Accipiter gentilis*. On the other hand, the resources exploited by the Hooded Crows had a scattered distribution. The crows often fed in fields where the corn had not been harvested or had been harvested with some

loss, and they then rested in one area on one day and in another the next. Similar irregular movement occurred during spreading of dung in winter. Usually large numbers of Hooded Crows turned up the same day as the dung was spread, remaining in the site for a couple of days and then leaving for another. It is not known whether these alterations of feeding sites were due to regular transfer of information at the communal roosts or to the visual impact of large numbers of black birds in the often white landscape (Ward & Zahavi 1973, Loman & Tamm 1980).

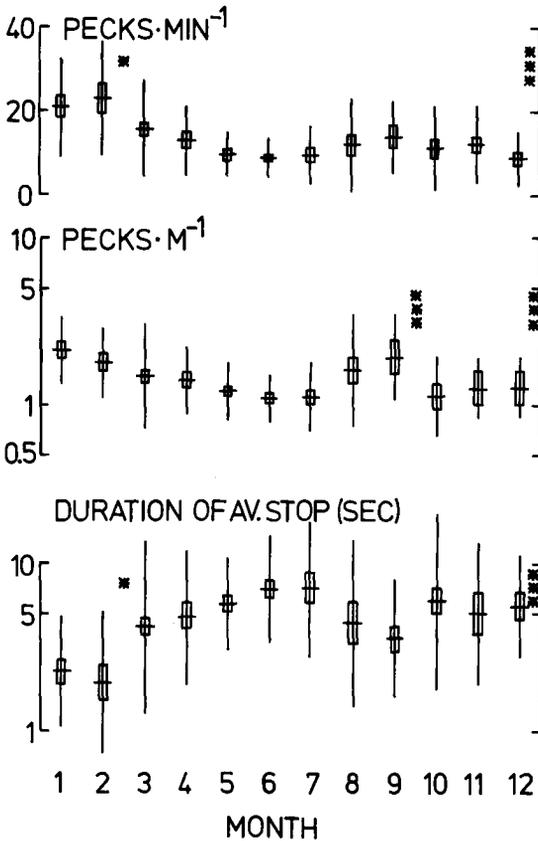


Fig. 5. Annual variation in feeding parameters of Hooded Crows. Vertical line = \pm SD, horizontal line = average, vertical bar = \pm SE * = $P < 0.05$, ** = $P < 0.02$, *** = $P < 0.01$, **** = $P < 0.001$. Only differences between average values are indicated.

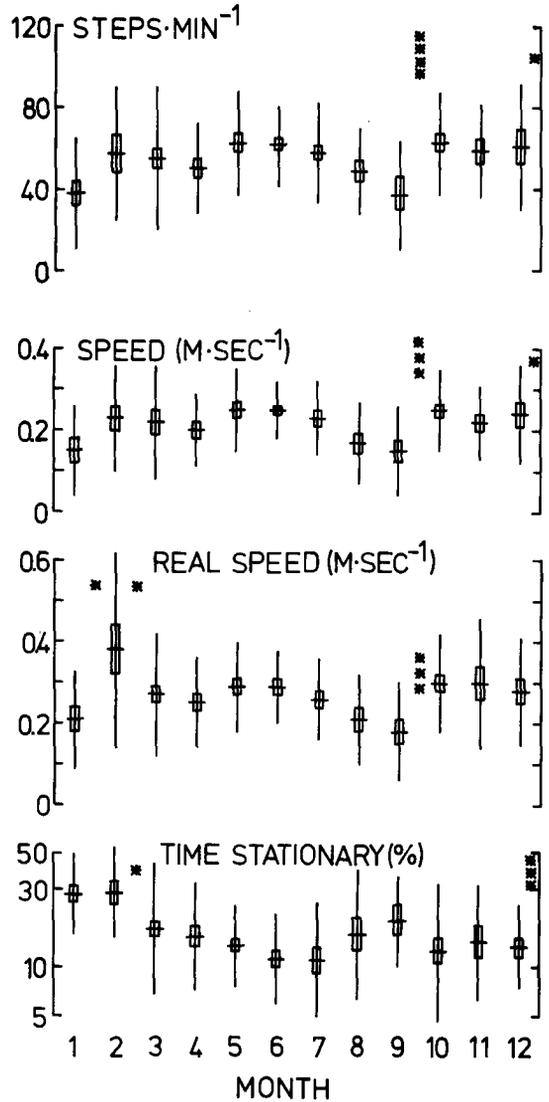


Fig. 6. Annual variation in speed and movement parameters of Hooded Crows. For further explanation, see legend to Fig. 5.

Feeding behaviour. During the winter months with short days, the rates of food intake were high and the speeds and stepping rates were generally very low. The regular movements of flocks between foraging sites on successive days were probably necessitated by the rapid depletion of resources when a large flock rested in an area.

Unlike the Magpie, whose rates of food intake increased during the breeding season (Mugaas & King 1981, Møller 1983), the Hooded Crow did not alter its feeding behaviour during reproduction. This may be due to the increased daylength and improved availability of food. Why Magpies have to increase their intake remains an open question. The larger Hooded Crow may be able to utilize a larger area in feeding, as the length of the bill allows it to explore a wider range of depths in the soil; probing was more common as a feeding technique in crows than in Magpies (Lockie 1956, Högstedt 1980, my own observations). A resource shared by the two species, but used to only a minor degree by Magpies, is invertebrates in dry cow pats. Due to their larger size the crows were able to use clod-turning as a common feeding technique, whereas Magpies only rarely did so.

Deterioration of the weather in winter led to increased pecking rates and decrease in movement rates. As described above under habitat use and flocking, a single patch may be used intensively for a short period (a couple of days) and then abandoned. As resources were probably re-established very slowly during winter, the frequent movements between sites may have been necessary to support the population of crows within an area.

Intraspecific competition between residents and winter visitors? On many occasions outside the breeding season the population became several times as great as during the breeding season, when food was more easily available. The growth of the population could lead to intraspecific competition for food. An indication of this was regular aggressive interactions between Hooded Crows feeding in flocks. Aggressive encounters were especially common under adverse weather conditions in winter.

Resident crows have an advantage over winter visitors, since they know the surroundings and the sites with plenty of food when the weather deteriorates in autumn. At this time of the year, the winter visitors suddenly appear. Although some migrant species may use the same wintering areas in successive years, this can hardly be the case in Hooded Crows, as the tendency to migrate decreases from yearlings to juveniles and to adults (Rendahl 1960).

One disadvantage of staying in or near the territory all the year round is the inability to use

ephemeral occurrences of food, which may be more plentiful than the sources visited daily. The great mobility of the winter visitors allows them to exploit irregular food supplies.

Intraspecific competition may be diminished if different habitats are frequented by two populations to varying degrees. In the present case meadows are visited frequently by the winter visitors, whereas resident Hooded Crows remain in or near their territory throughout the year.

Hooded Crows are known to roost communally outside the breeding season and immature birds even do so in the season (e.g. Eggers 1968). One advantage of residence and territorial behavioural is knowledge of available food resources. This may allow a longer territorial existence for Hooded Crows. Local crows frequently use their territories all the year round and roost singly or in pairs nearby (c.f. Clergeau 1981 for 'non-roosting' in the Starling *Sturnus vulgaris*). Among winter visitors 'non-roosting' is only rarely seen. In severe frost and falling snow large flocks of Hooded Crows may keep on foraging up to one hour after sunset in midwinter. At this late hour flight to the communal roost is probably impossible and small groups of roosting birds can be seen scattered in windbreaks and plantations. When local Hooded Crows roost near their feeding grounds, they are able to start feeding at daybreak and do not need to cover a large distance (frequently up to 40–50 km) between the roost and feeding grounds twice a day (Stork & Jänicke 1977).

Selostus: Muuttovaristen vaikutus paikallisten variskantojen elinympäristöön, parveutumiseen ja ravinnonhakukäyttäytymiseen Tanskassa

Pohjois-Juutinmaalla Tanskassa tutkittiin 27 kuukauden ajan varisten elinympäristön valintaa, parveutumista ja ruokailukäyttäytymistä. Työn tarkoituksena oli osoittaa Skandinaviasta saapuvien muuttovaristen vaikutusta paikallisten variskantojen elintapoihin. Huolimatta talvien ravintovarojen niukkuudesta talviset varispopulaatiot kohosivat moninkertaisiksi kesäisin kantoihin verrattuna. Talviset varisyksilöiden väliset aggressiot voitiin tulkita lajinsisäiseksi ravintokilpailuksi. Paikalliset varikset pysyttelivät vuoden ympäri reviirillään tai sen välittömässä läheisyydessä, jolloin niillä oli hyvä tuntemus ravintolähteiden sijainnista. Talviset vieraat tulivat sen sijaan ajankohtana, milloin ravintovarot olivat nopeasti vähenevässä, eikä niillä voinut olla minkäänlaista ennakkotietoa ravinnon sijainnista. Paikalliset varikset pysyttelivät läpi vuoden pesimähabitaattillaan, kun taas talvivieraat käyttivät laajempaa habitaattivalikoimaa ja satunnaisia, runsaitakin ravintolähteitä kuten vasta levitettyä lantaa. Satunnaisten ravintolähteiden käyttöikä oli kuitenkin vain joitakin vuorokausia. Muuttovarikset yöpyivät parvittain etenkin ankarina talvina, kun taas paikalliset varikset harvoin yöpyivät parvissa. Niiden ei myöskään tarvinnut käyttää energiaa ruokailupaikan ja

yöpymispaikan väliseen lentämiseen, ja ne saattoivat siten käyttää ruokailuun mahdollisimman runsaasti aikaa, hämärästä hämärään. Lajinsisäistä kilpailua pystyttiin siis välttämään muuttovarien ja paikallisten varisten välillä.

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