The importance of the farmland-forest edge for area use of breeding Hooded Crows as revealed by radio telemetry

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Twenty-six Hooded Crows (*Corvus corone cornix*) breeding in a fragmented farmland-forest landscape in southeastern Norway were radio-tracked between April and June in three years. The 95% home range size averaged 0.15 km². The proportional distribution of habitat categories in the home ranges was compared with that in the landscape; EDGE (forest <30 m from open habitats) and FIELD (mainly pastures and gardens) ranked first, followed by CROP (farmland ploughed annually), OLD (forest >30 m from open habitats) and YOUNG (clear-cuts and young planted forest). The same ranking was found when the habitats used were compared with those available within the home ranges. Crows devoted more time to perching, mostly in EDGE, than to foraging, mostly in FIELD and CROP. Use of EDGE increased with increasing availability of EDGE in the home range, but the crows used EDGE more than expected from availability only as long as the proportion of EDGE was <0.40. Home range decreased as the proportion of EDGE in the home range increased. The results suggest that an increase in the farmland-forest edge-to-area ratio may increase the density of breeding Hooded Crows, and thus increase the predation risk on bird nests in edge habitats.

1. Introduction

Habitat fragmentation, e.g. through agricultural development and forest harvesting, changes birds' living conditions in many ways and particularly by an increase in the edge-to-area ratio (Forman & Godron 1986, Andrén 1994). Habitat specialists may lose their living areas and become rare when fragments become too small (Hinsley *et al.* 1996), whereas generalists may be favoured by fragmentation and attain higher population densities through fragmentation. However, few studies have focused on individual-based area use of habitat generalist predators in fragmented landscapes. This limits our understanding of the effects of fragmentation (Andrén 1995, Robinson *et al.* 1995, Marzluff & Restani 1999). In particular, an understanding of the mechanisms underlying increased nest predation with increased forest fragmentation hinges on a detailed understanding of the habitat use of generalist predators.

Rates of nest predation caused by generalist predators may increase when fragmentation increases (Gates & Gysel 1978, Andrén 1992). Increased nest predation rates have been documented for both natural and artificial nests in farmland-forest edges compared to the inner forest habitats (Andrén & Angelstam 1988, Temple & Cary 1988, Huhta *et al.* 1996, Donovan *et al.* 1997, Söderström *et al.* 1998), and in small forest fragments scattered in the agricultural landscape compared to continuous forest (Wilcove 1985, Møller 1988, Donovan *et al.* 1997). There is evidence to suggest that the edge effect of increased nest predation is more important in agricultural and urban areas than in forested areas (Marzluff & Restani 1999, Jokimäki & Huhta 2000). In forest dominated landscapes with minor human influence, edge-related increase in nest predation might even be absent (Huhta *et al.* 1998).

Among the generalist predators believed to benefit from increasing landscape fragmentation are corvids in general (Preston 1957, Tenovuo 1963, Ratti & Reese 1988) and crows (*Corvus* spp.) in particular. The European Crow (*Corvus corone*) and the American Crow (*Corvus brachyrhynchos*) are regarded as potentially important predators on a wide range of bird nests in agricultural landscapes in Europe (Andrén 1992) and in fragmented forests in North America (Yahner *et al.* 1993), respectively. The widespread European Crow is regarded as both a habitat generalist (Wittenberg 1968, Andrén 1992) and a food generalist (Meidell 1943, Yom-Tov 1975, Goodwin 1986). It is found in highest densities in agricultural areas intermingled with forest (Andrén 1992, Jokimäki & Huhta 1996). To reveal the mechanisms behind the observed increased density of crows with increasing habitat fragmentation and proportion of edge habitat, we need to know more about the relationship between home range, and the use of edges between farmland and forest compared to availability at the individual level.

We studied habitat-specific area use and behaviour of breeding Hooded Crows (*Corvus corone cornix*) in a fragmented farmland-forest landscape during the breeding season in three years by use of direct observations aided by radio-telemetry in order to answer the following questions: 1) Do the crows select home ranges with more edge habitat than randomly expected from the landscape composition? 2) Do the crows use the edge between farmland and forest more than expected from availability within their home range? 3) If so, can the crows' home range size be explained by the availability of edge between farmland and forest? 4) Can the pattern of habitat use be explained by the crows' differential allocation of time to the components of behaviour across habitats?

2. Methods

2.1. Study area and trapping

The data were collected in Hamar and Ringsaker municipalities in Hedmark county in southeastern Norway (approx. 60°50′N, 11°10′E) during the Hooded Crow's breeding season in three years; from 12 April to 26 June 1993, from 19 May to 28 June 1995, and from 7 May to 21 June 1996. The study area is a mixed farmland-forest landscape with a declining farmland-forest ratio with increasing altitude (150–500 m a.s.l.) and accompanying transition from the boreonemoral to the boreal zone (Fig. 1). This gradient is similar to that through Limes Norrlandicus in Sweden (see Andrén 1992), but is much shorter due to a steeper

Forested habitats
Agricultural habitats
Territories
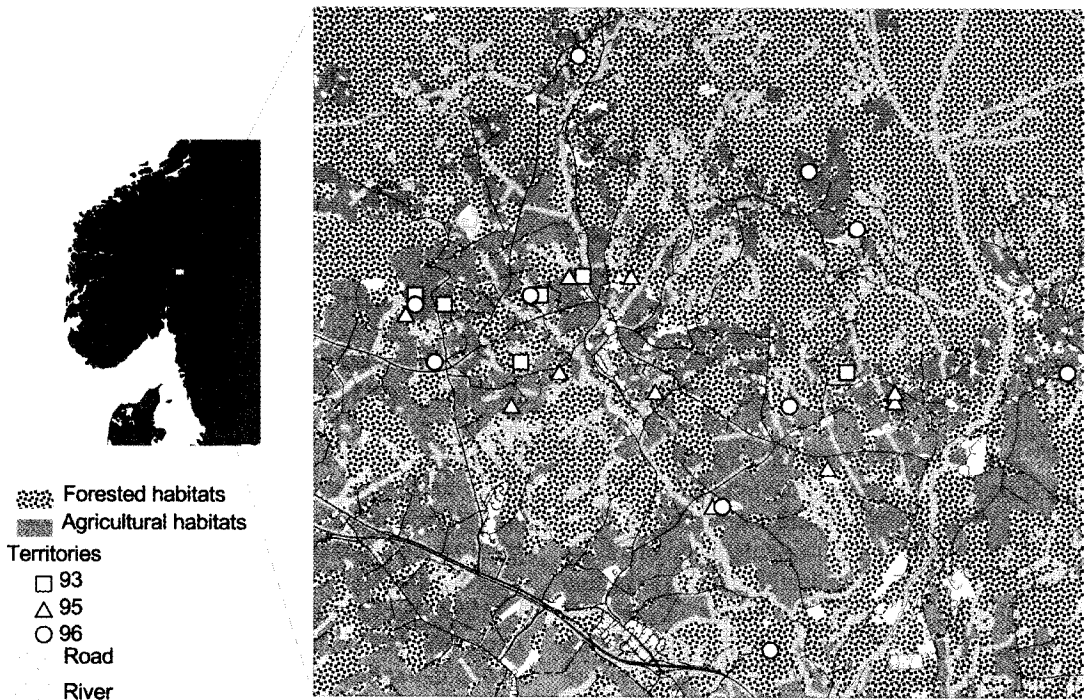□ 93
△ 95
○ 96
Road
River

Fig. 1. Map of the study area.

terrain. Three fur farms, but no rubbish tips are situated in the study area. The fur farms were used by non-breeding crows during April–May and by some breeding crows in June.

Crows were trapped in April and May by use of a modified version of the Larsen trap (Reynolds 1990, Tapper *et al.* 1991) with two large compartments (each compartment approx. 0.5m × 0.45 m × 0.5m). Traps were distributed fairly even over the study area. Trapping (for details see Hansen *et al.* (2000)) and radio-tagging were conducted with permission from the Directorate for Nature Management and from the National Animal Research Authority in Norway.

Trapped crows were weighed, measured, sexed if possible, ringed, and equipped with a radio transmitter (Biotrack, UK) mounted as a backpack and attached with a harness made of tubular teflon tape (Bally Ribbon Mills, PA, USA), locked with plier-flattened small cylinders of Sterling silver. The radio-tagged crows were located several times for the next 24 hours to ensure that the tag did not impair the bird. Of the crows included in the present study, three had a 12 g radio tag, and the remaining ones had a 18 g tag (har-

ness included). Each crow was allowed to habituate to the tag for at least 48 hours before collection of data started. Sex was determined from a combination of behaviour, body mass, body measure and brood patch (Slagsvold 1983). The median body mass of radio-tagged crows were 495 g (range 485–515, n = 9) for females and 560 g (range 515–610, n = 17) for males. The 18 g tag thus made up about 3.6% and 3.2% of the body mass of females and males, respectively. Radio-tagging may influence behaviour and mortality of birds (Paton *et al.* 1991). None of the breeding crows included in the present analysis lost their territory after tagging, and many raised offspring to independence in the same season as they were tagged. The non-breeding crows joined the flocks as usual after tagging. We therefore believe that area and habitat use of the crows included in the present study were not influenced by the tags.

2.2. Tracking

The sample analyzed consists of data from 26 breeding crows, of which six were tracked in 1993,

ten in 1995, and ten in 1996 (Fig. 1). The crows tracked included one mated pair in 1993 and another mated pair in 1995. Both individuals in each of these pairs were tracked the same year. We have regarded data collected on the mates in 1995 to be independent because their home range overlap was only ca. 33% of the male's home range. In contrast, the data collected on the mates in 1993 were judged to be dependent because their home range overlap was ca. 75% of the male's home range. Both mates in the pair tracked in 1995 were included in the present analysis, whereas the male in the pair tracked in 1993 was excluded from the analysis.

Each crow was located no more than once a day in daylight, but sometimes (<10% of the days) also on roost at night. The locations of crows at roost did not extend their calculated home range, and were not included in the habitat selection analysis. The temporal distribution of a crow's locations was systematically spaced so that within each month each crow was located at all hours of the day (Andersen & Orrin 1989, Beyer & Haufler 1994). When locating a radio-tagged crow, we aimed to get a visual confirmation of the location without disturbing or flushing the bird. This was usually possible at distances of 50–200 m by using binoculars. Because we proceeded until we could get a visual confirmation of its behaviour, we occasionally flushed a bird.

The crows' behaviour when first spotted during our approach to determine location was recorded as one of three mutually exclusive categories; perching, flying or foraging. Foraging included all movements by the crow on the ground, and consisted of the two behaviour categories "walking" and "eating" pooled. This pooling is justified by the fact that breeding crows in our study area almost always foraged when on the ground (Brekke 1994). In cases when the crows rested on a fence, stone, or a similar structure adjacent to the foraging area, their behaviour was recorded as perching. The behaviour categories perching and foraging were classified by habitat, while the behaviour category "flying" was not. The number of observations per crow equals the number of observations for the estimation of its home range.

Locations were plotted on copies of aerial photos (scale 1:22000, June 1991) in the field and later transferred to maps (1:5000 or 1:10000). Home range calculations are based on both daytime and the few (<10%) nighttime locations, whereas habitat analyses are based on daytime locations only.

2.3. Analyses

Home ranges were calculated according to the minimum convex polygon (MCP) method (Samuel & Garton 1985) by using the Wildtrak software for Macintosh computers (Todd 1992). Home range sizes were calculated for the 95% MCP. This was drawn after the 5% most distant positions from a calculated center of activity had been removed (Todd 1992). All analyses are based on the 95% home range, because the 100% home range may have biased habitat proportions due to occasional sallies. The 95% home range is a conservative estimate with less risk of including habitats which are never used. Four of the breeding crows were located 1–4 times on a fur farm situated 3–5 km away from their home range commonly used. These locations were excluded before calculating home range size, because these crows were never observed between their home range commonly used and the fur farm.

The habitat in which a radio-tagged crow was first spotted during our approach to determine location (unless judged to have moved to this position due to our approach) was recorded as one of five mutually exclusive categories; CROP, FIELD, YOUNG, OLD and EDGE. Agricultural habitats were made up by CROP (farmland ploughed annually) and FIELD (pastures, gardens, farmyards and road sides), and forested habitats were YOUNG (clear-cuts with planted coniferous trees <3 m high), OLD (all forest with trees >3 m high, mostly mature forest, situated >30 m from CROP, FIELD or YOUNG) and EDGE (forest with trees >3 m high situated <30 m from CROP, FIELD OR YOUNG; i.e. the edge between open and closed habitat).

For each breeding crow we estimated the habitat availability from enlarged copies of aerial pho-

tos (original scale 1:22000, copy scale 1:11000) onto which its 95% MCP had been delineated. We then placed a grid over the aerial photograph and classified the habitat at each intersection within the 95% MCP (cf. Sullivan & Dinsmore 1992). This yielded a median of 131 classification points (range 48–296) per home range with ca. 35 m between classification points.

We studied the crows' habitat use at two scales (Johnson 1980). First, we determined habitat use at the landscape scale by comparing the habitat proportions within the home ranges of the breeding crows with the habitat proportions at the landscape scale. For the data from 1993, we delineated a landscape area by pooling all locations (n = 248) of five radio-tagged non-breeding crows tracked simultaneously with the breeding crows (Smedshaug 1994) and calculating the associated 95% MCP. This amounted to an area of 20.48 km², and completely included the home ranges of all the six breeding crows tracked in 1993. The same procedure was applied for the crows tracked in 1995; the 95% MCP based on the pooled locations (n = 368) of nine non-breeding crows amounted to 20.02 km² and completely included the home ranges of the ten breeding crows tracked in 1995. This procedure of defining available habitat on the landscape scale provides a conservative estimate of the area available to the radio-tagged crows, because it includes only an area that we really know is used by radio-tagged crows. Even if we were unable to sex and accurately age all the non-breeding crows, we know that they consisted of both males and females of different ages. The non-breeding crows present in 1996 were not tracked intensively enough to make a reliable landscape delineation. Therefore, for the data from 1996 we used the habitat proportions found for 1995, because the breeding crows tracked in 1996 were in the same area as those tracked in 1995.

Second, we determined the crows' habitat use within the home range by comparing the proportional distribution of habitats used with that of habitats available within the home range. However, only six of the 26 radio-tagged crows had YOUNG available in their home range. Compositional analysis (see below) is not well-designed for this problem (Alldredge *et al.* 1998).

Therefore, we included YOUNG in CROP, reducing the number of habitat categories used from five to four. Also, nine crows did not have OLD habitat within their home range. Therefore, the values for the missing cases were determined by randomization (see Aebischer *et al.* 1993).

The traditional measure of habitat selection, relating use of a habitat to its availability (e.g. Neu *et al.* 1974), has recently been challenged (Aebischer *et al.* 1993, Mysterud & Ims 1998). First, Aebischer *et al.* (1993) argued on statistical grounds that habitat preference should be substituted by habitat ranking based on individual log-ratios to overcome the unit-sum constraint. We employed such compositional analysis proposed by Aebischer *et al.* (1993) to investigate habitat selection, since it is the best method so far developed (Alldredge *et al.* 1998). Compositional analysis is a general multivariate analysis which, by reducing dimensionality through a log-ratio, overcomes the unit sum constraint arising in resource selection analysis (Aitchison 1986), and applies relative habitat use to rank the habitats. Compositional analysis also uses the individual as the sampling unit, which is desired when the aim is to draw inference on a population.

Second, Mysterud and Ims (1998) further developed the approach of Aebischer *et al.* (1993) by pinpointing the common problem in the analysis of habitat selection that both the calculation of absolute preference and that of ranking implicitly assume that use of a habitat is directly proportional to its availability. This may mask any differential allocation of time to the components of behaviour (e.g. foraging vs. resting) across habitats, and give rise to misleading conclusions concerning whether a habitat is selected or avoided (Smedshaug 1994). Therefore, Mysterud and Ims (1998) introduced the term functional response in habitat use, meaning a change in the relative use of a habitat type with changing availability of two habitat types, and defined selection of a habitat to occur only within the range of habitat availability for which the proportion of use is significantly greater than the proportion available. By applying a logistic regression model, regressing habitat use against the logit of habitat availability (i.e. log of proportion habitat available di-

vided by one minus proportion of habitat available), Mysterud and Ims (1998) argued that evidence for functional response in habitat use could be inferred by means of the regression parameter values (i.e. the intercept α and slope β). Mysterud and Ims (1998) interpreted functional response in habitat use relative to habitat availability to be present for all significant parameter estimates, except in the case where $\alpha = 0$ and $\beta = 1$ (i.e. habitat is used equal to availability), and in the case where $\beta = 0$ (i.e. the investigated habitat is used independently of its availability). In our case, the focal habitat type is EDGE, and the other habitat type consists of all the other habitat types (defined above) pooled (CROP, FIELD, YOUNG and OLD).

The statistical tests were done by using Statwiev 4.0 (Abacus Concepts, Berkeley, USA), JMP 3.1 (SAS Institute Cary, USA) and S+ 3.3 (MathSoft, USA) software. The habitat proportions were arcsine transformed (Sokal & Rohlf 1995) before being included in a forward stepwise regression. In the stepwise regressions the F-to-enter value was 4.0. The analysis of habitat use at the home range scale was conducted with MacComp 0.90 (John Caroll, California, USA). Statistical significance was established at $P < 0.05$, and all tests were two-tailed. Means are given with $\pm 1SD$ unless otherwise stated.

3. Results

3.1. Home range

Crow average 95% home range size was $0.15 \pm 0.23 \text{ km}^2$. There was no significant difference in 95% home range size between the three years of study (ANOVA, $F_{2,23} = 1.26$, $P = 0.30$) or between sexes (unpaired t-test, $t = 0.76$, $n_1 = 17$, $n_2 = 9$, $P = 0.45$). There was no significant correlation between 95% home range size and number of locations for the breeding crows in all years combined ($r = 0.19$, $n = 26$, $P = 0.33$).

3.2. Habitat selection

The habitat composition of home ranges differed significantly from that of the landscape ($\Lambda = 0.34$, $df = 4$, $P < 0.0001$). When comparing the habitat composition in the home ranges of the breeding crows with that in the landscape, EDGE and FIELD ranked highest with no significant difference between them, followed by CROP, OLD and YOUNG, which all were ranked significantly lower than EDGE (Table 1a; Fig. 2a).

Within their home ranges habitat use by breeding crows was non-random ($\Lambda = 0.33$, $df = 3$, $P < 0.001$). EDGE was used significantly more

Table 1. Ranking matrix based on compositional analysis of a) the differences in habitat composition between the landscape and the home ranges of radio-tracked Hooded Crows, and b) the differences between habitat use and habitat availability within these home ranges. P-values are given in the upper right and the corresponding t-values are given in the lower left. See text for definition of landscape.

a)

	EDGE	FIELD	CROP	OLD	YOUNG	Rank
EDGE		0.58	0.023	<0.001	<0.001	1
FIELD	0.58		0.20	<0.001	<0.001	2
CROP	2.38	1.32		<0.001	<0.001	3
OLD	5.95	5.63	5.41		0.20	4
YOUNG	7.23	6.32	6.60	1.32		

b)

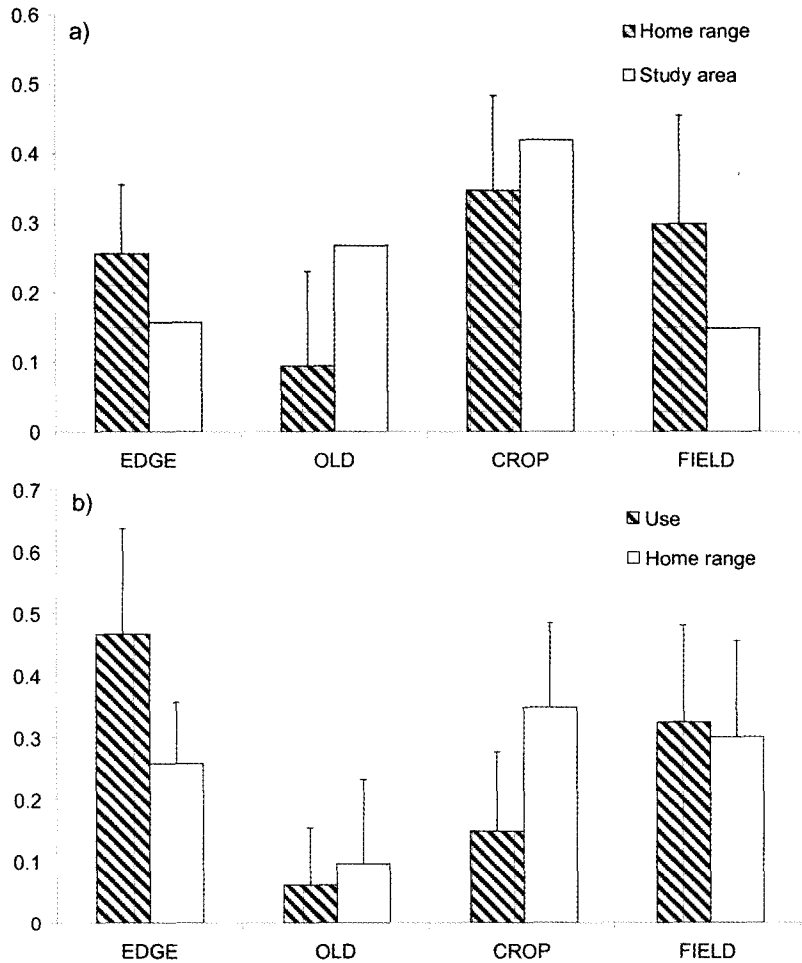|	EDGE	FIELD	CROP	OLD	Rank
EDGE		0.034	<0.001	0.002	1
FIELD	2.31		<0.001	0.01	2
CROP	5.78	4.67		0.52	3
OLD	3.71	2.85	0.69		4

Fig. 2. Habitat composition in the landscape compared with that in the home ranges of radio-tracked breeding Hooded Crows (a), and habitat use by these crows compared with habitat availability within their 95% home range (b). Data are shown as average ± 1SD.

than FIELD, which was used significantly more than both CROP and OLD, relative to that expected from the habitat composition in the 95% home ranges (Table 1b; Fig. 2b).

3.3. Functional response

Mean relative use of EDGE by the crows was 0.43 ± 0.15, while mean relative availability of EDGE in their home ranges was 0.25 ± 0.10. A binomial logit model was used to investigate whether the probability of use of EDGE was conditional on the proportional availability of EDGE in each individual home range. The slope (β) was nearly significantly different from zero ($\beta = 0.36 \pm 0.18$ (SE), t = 1.95, P = 0.052, whereas the intercept (α) was not significantly different from

zero $\alpha = 0.20 \pm 0.23$ (SE), t = 0.88, P = 0.38). This indicates that there was a marginally greater chance of finding an individual crow in the EDGE habitat with increasing availability of EDGE (Fig. 3). However, the model fit to the data was not optimal (N = 26, P < 0.001, G res/df = 1.73). Including year in the model did not increase the fit markedly (G res/df = 1.63), but made year become significant ($\beta_{year} = -0.24 \pm 0.12$ (SE), t = -2.02, P = 0.043).

3.4. Habitat-dependent activity

The crows devoted their time mainly to perching (mean proportion 0.61 ± 0.14) followed by foraging on the ground (0.25 ± 0.11) and flying (0.13 ± 0.07; Table 2). There was a strong asso-
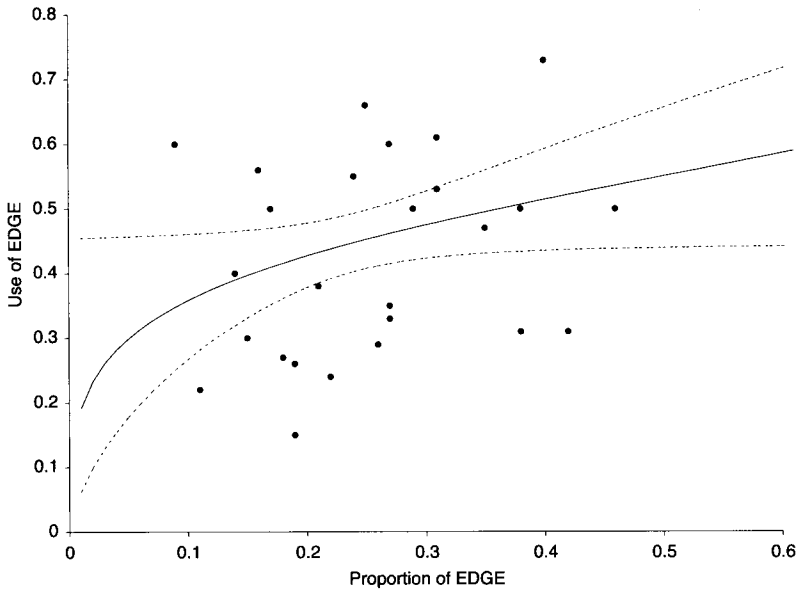
Fig. 3. Logistic regression of the proportional use of EDGE by radio-tracked breeding Hooded Crows against the proportion of EDGE available in home range. The dotted lines indicate the 95% confidence interval.

ciation between the two main behaviour categories (perching and foraging) and habitat (Table 2). The open habitat category CROP was mainly used for foraging, while the forested habitat categories OLD and EDGE were almost only used for perching (Table 2). The habitat category FIELD contained single trees and was often used by the local farmers for dumping organic offal, and the crows used this habitat almost as much for foraging as for perching (Table 2). Thus, most perching took place in EDGE (59%) followed by FIELD (27%), OLD (11%) and CROP (2%). In contrast, most foraging on the ground took place in FIELD (47%) and CROP (45%), followed by EDGE (6%) and OLD (2%).

3.5. Can habitat composition explain home range size?

In a stepwise regression model (forward selection) with the log-transformed 95% home range size as dependent variable and the arcsine transformed proportions of CROP, FIELD, OLD and EDGE in the home range as independent variables, only the proportion of EDGE was included in the model ($R^2 = 0.38$, n = 26, F = 14.48, P = 0.0009; Fig. 4), while the variables CROP (F = 0.18), FIELD (F = 1.04) and OLD (F = 0.28) were not included. The home range size declined with an increasing proportion of EDGE in the home range (Fig. 4).

Table 2. The proportion (mean ± SD) of time devoted to the main behaviour types (perching and foraging) in each habitat, and the proportion of total use of these habitats, by radio-tracked Hooded Crows. The number of individual crows on which the calculated figures are based is given if different from the total number studied (N = 26).

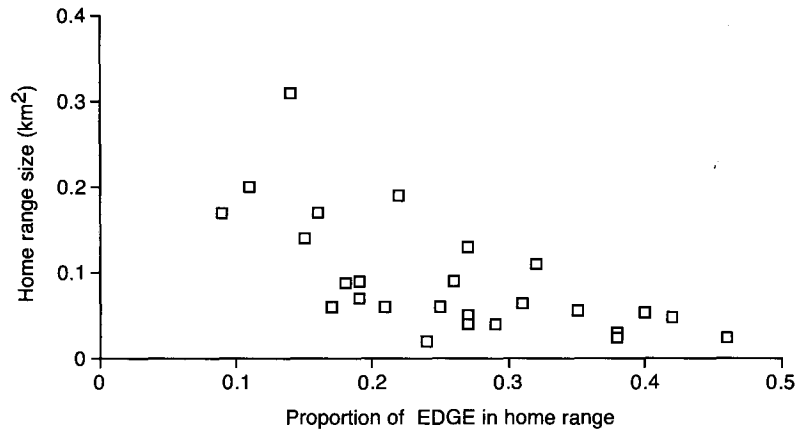| Habitat	Activity		Use
	Perching	Foraging	
OLD	0.94 ± 0.06[1]	0.06 ± 0.08	0.08 ± 0.11
EDGE	0.96 ± 0.10	0.04 ± 0.10	0.43 ± 0.25
CROP	0.10 ± 0.10[2]	0.90 ± 0.25	0.15 ± 0.12
FIELD	0.57 ± 0.28[3]	0.43 ± 0.29	0.33 ± 0.15

[1]N = 5, [2]N = 21, [3]N = 25

Fig. 4. The relationship between the 95% home range size (ha) of radio-tracked breeding Hooded Crows and the proportion of EDGE within their 95% home range.

4. Discussion

4.1. The importance of the forest edge for crows

The crows in our study used EDGE relatively more than other habitats at both the landscape scale and the home range scale. The ranking of EDGE and FIELD before CROP, OLD and YOUNG at the landscape scale indicates that the crows selected *a home range with a more diverse vegetation than* random. Similarly, Ignatiuk & Clark (1991) found a higher density of American Crows in an agricultural area with more diverse land use than in an agricultural area with more crop land and less trees.

On the home range scale the crows used EDGE relatively more than other habitats. Breeding crows use the forest edge to perch in (Preston 1957) and hunt from (Slagsvold 1980). Moreover, predators such as the Goshawk (*Accipiter gentilis*) may be easier to detect and avoid from the forest edge. In addition, breeding crows place their nests in forest edges (Wittenberg 1968, Loman 1975, own observation), which may incur a lower nest predation risk from non-breeding crows than placing the nest in single trees (Loman 1979). The need for observing intruders (Charles 1972) also implies that breeding crows increase perch time on sites with a good view, such as forest edges. The crows probably use the EDGE as a convenient look-out for prey, predators and intruders.

The home range sizes of the breeding crows in our study decreased with an increasing propor-

tion of EDGE in the home range. The EDGE habitat in this study was primarily between forested and agricultural habitats and not between forest and clearcut. According to Wittenberg (1968) the number of pairs per km forest edge would be a better density index for the European crow than number of pairs per km². Studies of non-radiotagged breeding European crows have found that home range size in cultivated landscapes increases with an increasing proportion of forest (Pinowski & Wasilewski 1962, Wittenberg 1968, Tompa 1975). The density of crows is highest in a landscape with both forest and agricultural land, where the agricultural land is the crows' main food base (Andrén 1992). Together, the results of these studies and our study suggest that the distribution of habitats within the home range, and not the forest proportion *per se,* may be important to the crows. Therefore, amount of EDGE probably is, by some mechanism, an indication of habitat quality for crows.

4.2. Habitat-related behaviour

We found a strong association between activity and habitat for the Hooded Crow. The habitat category most used within the home range was EDGE, and the main behaviour was perching, such that the Hooded Crows spent considerably more time perching in EDGE than in any other habitat. In contrast, when foraging on the ground the crows spent equal amounts of time in FIELD and CROP, and almost no time in other habitats. Because the crows devoted more than twice as much time to perching

than to foraging on the ground, and because most perching took place in EDGE which is less common in our study area and in the crows home ranges than is CROP, traditional habitat analysis would have lead to the conclusion that CROP is used less than expected from its availability and thus is selected against, while EDGE is used more than expected from the availability and thus is selected.

The 12% of the total time spent in CROP seems likely to fulfill almost half of the crows' food demand, and the crows could probably have used more time foraging there if they needed to. Hence, to conclude that CROP is selected against is probably incorrect. When the habitat definitions are such that the animal under study performs one type of behaviour in each habitat category, an analysis of habitat use also is some kind of time budget analysis (Smedshaug 1994, Mysterud & Ims 1998).

4.3. Functional response in habitat use

This interaction between behaviour and habitat poses a problem to habitat selection analysis. Therefore, Mysterud & Ims (1998) presented a test for functional response in habitat use to reveal any change in relative use of a habitat with changing relative availability of that habitat. Lack of such a functional response may be due to some time budget constraint that does not allow change in use when the availability changes. Our analysis of functional response showed that the crows used EDGE nearly significantly more with increasing proportion of EDGE in the home range. However, because the slope ($\beta = 0.36$) was < 1, the crows' use of EDGE did not increase in proportion to availability. This seemingly weak functional response was due to the crows' intensive use of EDGE even at low availability. The crows selected EDGE only as long as the proportion of EDGE available in their home range was below a certain value (ca. 0.40). Above this value, the crows no longer selected for EDGE, probably because no more time could be devoted to perching.

4.4. Implications for nest predation

Corvids have been found to be the major nest predators in several studies of nest predation in edges and forest fragments in agricultural and urban landscapes in both Europe (Angelstam 1986, Andrén & Angelstam 1988, Møller 1989, Andrén 1992, Jokimäki and Huhta 2000) and North America (Temple & Cary 1988, Robinson et al. 1995, Hannon & Cotterill 1998), as well as in managed forest in North America (Yahner & Wright 1985, Yahner 1991, but see also Marzluff & Restani 1999). However, most of these studies have used artificial nests and they may not be representative of real nests (Willebrand & Marcström 1988, Valkama et al. 1999). Furthermore, there is reason to believe that corvids rob ground nests to a lesser extent than tree nests. There are fewer predator species foraging in trees than on the ground, so the proportional predation risk posed by corvids is possibly higher in trees than on the ground. In edges corvids may also be more efficient predators on tree-nests than on ground-nests.

Andrén (1992) showed that the Hooded Crow was the most important predator on artificial nests among corvids in landscapes with agricultural land. Hannon & Cotteril (1998) found that predation by corvids was highest in edges and small woodlots, and suggested this to be due to corvids foraging in forest edges. Our radio-tagged crows did not use much time foraging on the ground in the forest edge, but rather spent their time there perching. The crows' differential allocation of behaviour across habitats, with perching located to forest edge, would facilitate their discovery of and predation on bird nests in the forest edge.

The breeding Hooded Crows used EDGE relatively more than other habitats on the scales of both landscape and home range, devoted their time in EDGE to perching, and showed a nearly significant functional response in use of EDGE habitat. The selection of EDGE declined with increasing proportion of EDGE available and disappeared above c. 40% EDGE in the home range. The size of home ranges declined with increasing proportion of EDGE in the home range. Our results suggest that an increased edge-to-area ratio as an effect of fragmentation will increase Hooded Crow density until saturation due to social intolerance, and that this might cause an increased predation risk from perching crows on bird nests in the farmland-forest edge. Whether increased crow density is the main mechanism explaining elevated nest predation in the farmland-forest edge needs further study.

Sammanfattning: **Betydelsen av kantzonen mellan odlad mark och skog för häckande kråkors arealbruk, avslöjat med användning av radiotelemetri**

Hemmaområdet och habitatselektionen för 26 häckande kråkor (*Corvus corone cornix*) uppmättes med använding av radiotelemetri i ett fragmenterat jord- och skogsbrukslandskap i sydöstra Norge i april-juni i 1993, 1995 och 1996. Hemmaområdet (95% minimum konvex polygon) baserat på en lokalisering per dag var i genomsnitt 0.15 km². Habitatsammansätningen i kråkornas hemmaområde avvek från habitatsammansätningen i studieområdet, och kråkornas habitatanvänding avvek från habitatsammansätningen i deras hemmaområde. I bägga dessa fall av habitatselektion rangerade kantzonen (skog < 30 m från öppna habitat) och betesmark högst, efterföljd av åker, skog (> 30 m från öppna habitat) och avverkningsytor och planterade ytor. Kråkorna använde mer tid på att sitta stilla än på att furagera, och använde för det mesta kantzonen för att sitta stilla och nästan bara betesmark och åker till att furagera. Kråkornas använding av kantzonen ökade med ökad tillgång av kantzon i hemmaområdet, men kråkorna använde kantzonen mera än tillfälligt förväntat blott så länge kantzonen utgjorde < 40% av habitattilgången i hemmaområdet. Kråkornas hemmaområde minskade, när andelen av kantzon i hemmaområdet ökade. Detta antyder, att en ökning av andelen av kantzon mellan odlad mark och skog ökar tätheten av häckande kråkor, och således ökar predationsrisken från sittande kråkor på fågelbon placerade i denna kantzon.

References

Aebischer, N. J., Robertson, P. A. & Kenward, R. E. 1993: Compositional analysis of habitat use from animal radio-tracking data. — Ecology 74: 1313–1325.

Aitchison, J. 1986: The statistical analysis of compositional data. — Chapman and Hall, London.

Alldredge, J. R., Thomas, D. L. & McDonald, L. L. 1998: Survey and comparison of methods for study of resource selection. — Journal of Agricultural, Biological and Environmental Statistics 3: 237–253.

Andersen, D. E. & Orrin, J. R. 1989: Home-range estimates of red-tailed hawks based on random and systematic relocations. — J. Wildl. Manage. 53: 802–807.

Andrén, H. 1992: Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. — Ecology 73: 794–804.

Andrén, H. 1994: Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. — Oikos 71: 355–366.

Andrén, H. 1995: Effects of landscape composition on predation rates at habitat edges. — In: Hansson, L., Fahrig, L. & Merriam, G. (eds.) Mosaic landscapes and ecological processes, pp. 225–255. Chapman and Hall, London.

Andrén, H. & Angelstam, P. 1988: Elevated predation rates as an edge effect in habitat islands: experimental evidence. — Ecology 69: 544–547.

Angelstam, P. 1986: Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. — Oikos 47: 365–373.

Beyer, D. E. & Haufler, J. B. 1994: Diurnal versus 24-hour sampling of habitat use. — J. Wildl. Manage. 58: 178–180.

Brekke, A. 1994: Time budget for territorial and non-territorial Hooded crows (Corvus corone cornix) during the breeding season in an agricultural landscape in southern Norway. — Cand scient thesis, University of Oslo.

Charles, J. 1972: Territorial behaviour and the limitation of population size in the crow, Corvus corone and Corvus cornix. — Ph.D. thesis, University of Aberdeen.

Donovan, T. M., Jones, P. W., Annand, E. M. & Thompson, F. R. 1997: Variation in local-scale edge effects: mechanisms and landscape context. — Ecology 78: 2064–2075.

Forman, R. T. T. & Godron, M. 1986: Landscape ecology. — John Wiley & Sons, New York.

Gates, J. E. & Gysel, L. W. 1978: Avian nest dispersion and fledgling outcome in field-forest ecotones. — Ecology 59: 871–883.

Goodwin, D. 1986: Crows of the world. — British Museum, London.

Hannon, S. J. & Cotterill, S. E. 1998: Nest predation in aspen woodlots in an agricultural area in Alberta: the enemy from within. — Auk 115: 16–25.

Hansen, H., Smedshaug, C. A. & Sonerud, G. A. 2000: Pre-roosting behaviour of hooded crows (Corvus corone cornix). — Can. J. Zool. 78: 1813–1821.

Hinsley, S. A., Bellamy, P. E., Newton, I. & Sparks, T. H. 1996: Influence of population size and woodland area on bird species distributions in small woods. — Oecologia 105: 100–106.

Huhta, E., Mappes, T. & Jokimäki, J. 1996: Predation on artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure. — Ecography 19: 85–91.

Huhta, E., Jokimäki, J. & Helle, P. 1998: Predation on artificial nests in a forest dominated landscape — the effects of nest type, patch size and edge structure. — Ecography 21: 464–471.

Ignatiuk, J. B. & Clark, R. G. 1991: Breeding biology of American crows in Saskatchewan parkland habitat. — Can. J. Zool. 69: 168–175.

Johnson, D. H. 1980: The comparison of usage and availability measurements for evaluating resource preference. — Ecology 61: 65–71.

Jokimäki, J. & Huhta, E. 1996: Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. — Orn. Fenn. 73: 97–113.

Jokimäki, J. & Huhta, E. 2000: Artificial nest predation and abundance of birds along an urban gradient. — Condor 102: 838–847.

Loman, J. 1975: Nest distribution in a population of the hooded crow Corvus cornix. — Orn. Scand. 6: 169–178.

Loman, J. 1979: Nest tree selection and vulnerability to predation among hooded crows Corvus corone cornix. — Ibis 121: 204–207.

Marzluff, J. M. & Restani, M. 1999: The effects of forest fragmentation on avian nest predation. — In: Ruchelle, J. A., Lehman, L. A. & Winsniewski, J. (eds.), Forest fragmentation: wildlife and management implications. pp. 155–169. Brill Academic Publishing, Leiden.

Meidell, O. 1943: Undersøkelser over kråkas ernæring. — Nytt Magasin for Naturvitenskapene 84: 1–91 (In Norwegian with English summary.)

Mysterud, A. & Ims, R. A. 1998: Functional responses in habitat use: availability influences relative use in trade-off situations. — Ecology 79: 1435–1441.

Møller, A. P. 1988: Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of magpies and blackbirds. — Oikos 53: 215–221.

Møller, A. P. 1989: Nest site selection across field-woodland ecotones: the effect of nest predation. — Oikos 56: 240–246.

Neu, C. W., Byers, C. R. & Peek, J. M. 1974: A technique for analysis of utilization-availability data. — J. Wildl. Manage. 38: 541–545.

Paton, P. W., Zabel, C. J., Neal, D. L., Steger, G. N., Tilghman, N. G. & Noon, B. R. 1991: Effects of radio tags on spotted owls. — J. Wildl. Manage. 55: 617–622.

Pinowski, J. & Wasilewski, A. 1962: Einfluss einiger Faktoren auf die Zahl der Nebelkrähen (Corvus corone cornix L.) in verschiedenen Biotopen. — Acta Ornithol. 6: 231–251.

Preston, F. W. 1957: The lookout perch as a factor in predation by crows. — Wilson Bull. 69: 368–370.

Ratti, J. T. & Reese, K. P. 1988: Preliminary tests of the ecological trap hypothesis. — J. Wildl. Manage. 52: 484–491.

Reynolds, J. 1990: Crows and magpie control: the use of call birds in cage traps. — The Game Conservancy Review of 1989: 48–49.

Robinson, S. K., Thompson, F. R., Donovan, T. M., Whithead, D. R. & Faaborg, J. 1995: Regional forest fragmentation and the nesting success of migratory birds. — Science 267: 1987–1990.

Samuel, M. D. & Garton, E. O. 1985: Home range: a weighted normal estimate and tests of underlying assumptions. — J. Wildl. Manage. 49: 513–519.

Slagsvold, T. 1980: Egg predation in woodland in relation to the presence and density of breeding fieldfares Turdus pilaris. — Orn. Scand. 11: 92–98.

Slagsvold, T. 1983: Morphology of the hooded crow Corvus corone cornix in relation to age, sex and latitude. — J. Zool. Lond. 199: 324–344.

Smedshaug, C. A. 1994: Home range use and habitat selection of territorial and non-territorial hooded crows, Corvus corone cornix, during the breeding season. — Cand. scient thesis, University of Oslo.

Sokal, R. R. & Rohlf, F. J. 1995: Biometry. — Freeman, New York.

Sullivan, B. D. & Dinsmore, J. J. 1992: Home range and foraging habitat of American crows, Corvus brachyrhynchos, in a waterfowl breeding area in Manitoba. — Can. Field-Nat. 106: 181–184.

Söderström, B., Pärt, T. & Rydén, J. 1998: Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. — Oecologia 117: 108–118.

Tapper, S., Swan, M. & Reynolds, J. 1991: Larsen traps: a survey of members' result. — Game Conservancy yearbook 1990: 82–86.

Temple, S. A. & Cary, J. R. 1988: Modeling dynamics of habitat interior bird populations in fragmented landscapes. — Conserv. Biol. 2: 340–347.

Tenovuo, R. 1963: Zur brutzeitlichen Biologie der Nebelkrähe (Corvus corone cornix L.) im äussern Schärenhof Südwestfinnlands. — Ann. Zool. Soc. Vanamo 25: 1–147.

Todd, I. A. 1992: Wildtrak. — Dept. of Zoology, University of Oxford, U.K.

Tompa, F. S. 1975: A preliminary investigation of the Carrion Crow Corvus corone problem in Switzerland. — Orn. Beob. 72: 181–198.

Valkama, J. & Currie, D. 1999: Low productivity of Curlews Numenius arquata on farmland in southern Finland: causes and consequences. — Ornis Fenn. 76:

65–70.

Wilcove, D. S. 1985: Nest predation in forest tracts and the decline of migratory songbirds. — Ecology 66: 1211–1214.

Willebrand, T. & Marcström, V. 1988: On the danger of using dummy nests to study predation. — Auk 105: 378–379.

Wittenberg, J. 1968: Freilandsuntersuchungen zu Brutbiologie und Verhalten der Rabenkrähe (Corvus c. corone). — Zoologischer Jahrbuch Systematich 95: 16–146.

Yahner, R. H. 1991: Avian nesting ecology in small even-aged aspen stands. — J. Wildl. Manage. 55: 155–159.

Yahner, R. H. & Wright, A. L. 1985: Depredation of artificial ground nests: effects of edge and age. — J. Wildl. Manage. 49: 508–513.

Yahner, R. H., Mahan, C. G. & Delong, C. A. 1993: Dynamics of depredation on artificial ground nests in habitat managed for ruffed grouse. — Wilson Bull. 105: 172–179.

Yom-Tov, Y. 1975: Food of nestling crows in north-east Scotland. — Bird Study 22: 47–51.