

# HABITAT SELECTION OF HOODED AND CARRION CROWS IN THE ALPINE HYBRID ZONE

ANTONIO ROLANDO & PAOLA LAIOLO

**ABSTRACT** Habitat selection of co-existing Hooded Crows *Corvus corone cornix* and Carrion Crows *C. c. corone* was studied in the Susa valley, an alpine valley in the Italian hybrid zone. Foraging habitat use by the two races was not significantly different during the autumn-winter whereas it was during the spring-summer when Hooded Crows preferred meadows and Carrion Crows preferred dunged fields and maize stubble. However, if similar habitat categories (e.g. meadows and dunged meadows, maize and maize stubble) were combined, differences were no longer statistically significant. Resource selection by the two crows was more differentiated when only homotypic groups were taken into account suggesting that mixed flocking serves to standardize ecological choices. Analysis of flocking behaviour showed a clear tendency to avoid heterotypic flocks. The results of habitat selection are not in keeping with those reported by Saino (1992) in another plain area of north-western Italy, where there was a clear differentiation in the use of habitat categories during the winter. These differences, together with those regarding assortative mating, suggest that the alpine hybridization zone might be a mosaic of populations differentiated in relation to the locally diverse ecological conditions.

Dipartimento di Biologia Animale, via Accademia Albertina 17, 10123 Turin, Italy

## INTRODUCTION

A hybrid zone is an area populated by hybrids between well differentiated but freely interbreeding forms which maintain, except within this area, allopatric distributions (Short 1985). The dynamics of hybrid zones are of special interest because they may be closely connected to speciation.

Hybrid zones are thought to be due to differentiation *in situ* (i.e. primary zones) as in area effect, clinal and stasipatric speciation (Endler 1977, White 1978), or due to secondary contact (i.e. secondary zones) as in allopatric speciation. Some secondary hybrid zones are thought to have been formed following the Quaternary glacial period. In the Western Palearctic it is suggested that during the spread of the Pleistocene ice caps the original populations would have been split resulting in southern refugia. The

hypothesized refuge populations would have been separated for long enough to diverge before coming together again in post-glacial times (Thorpe 1975, 1984). This formation may also apply to the Crow (*Corvus corone* L.) whose hybrid zone in Central Europe separates the Carrion Crow (*Corvus corone corone* L.) in the West from the Hooded Crow (*Corvus corone cornix* L.) in the East and South.

In northern Italy the Carrion Crow is found in alpine areas, whereas the Hooded Crow is distributed throughout the Padana plain. The bottom of the alpine valleys and plains at the foot of the Alps are areas of sympatry and syntopy where the two forms have hybridized. These areas therefore represent the alpine hybrid zone.

Some studies carried out in north-western Italy (Piedmont and the Aosta Valley) have shown that pairs with hybrid females produce fewer chicks than those with Hooded and

Carrion Crows females, even if differences were significant only for Hooded Crows (Saino 1990, Saino & Villa 1992), and that there is a more or less marked tendency for assortative mating (Saino & Villa 1992, Rolando 1993). The limited propensity to form mixed pairs should also be seen in the light of the different ecological preferences observed. In an area of plain in south-western Piedmont it was observed that during winter the two phenotypes select different foraging habitats (Saino 1992).

The principal aim of this study was to verify whether foraging habitat selection also differed in the alpine valleys, where the tendency to assortative mating, although evident, was nonetheless relatively low in overall terms (Rolando 1993). An attempt was also made to verify whether or not there is a tendency to avoid the aggregation of races in the composition of groups.

## STUDY AREA AND METHODS

The study area was the Susa valley, an Italian alpine valley some 70 km long, including only fields, meadows and scattered wooded patches at the flat bottom of the valley where the two races coexist. The area examined ranged from Caselle (45° 06' N, 7° 29' E) at the mouth of the valley, to Bussoleno (45° 08' N, 7° 09' E) some 30 km further up. The area (about 60 km<sup>2</sup>, at 340-480 m a.s.l.) is characterized by meadows (Arrhenatheretea and Cheniopodieta) and fields under cultivation (especially maize) lying next to poplar *Populus* spp. plantations and very small deciduous woods (mainly consisting of false acacias *Robinia pseudoacacia* and oaks *Quercus robur*).

Since the proportions of the two races change along the valley, we ideally divided it into six five-kilometre-long portions, in keeping with Rolando (1993). Observations on Carrion and Hooded Crows were carried out once a week from September 1987 to September 1988. Hybrid individuals were very few and, therefore, we decided only to consider the pure black and

grey phenotypes. Intermediates were discarded from the analyses. Autumn-winter data (September-February) were separated from spring-summer data (March-August). We drove along different itineraries and stopped whenever birds were encountered. Car transects were done in open habitat where all or most individuals could be seen whereas in habitats with hedgerows, poplar plantations or small wooded patches, the presence of birds was checked by walking across the habitat.

All the crows in a particular field were considered as belonging to the same flock, in keeping with Patterson *et al.* (1971) and Waite (1981). Flock composition was specified together with the kind of substratum on which the birds were foraging (meadows, ploughed fields, maize fields, etc.) or resting (poplar, oak, willow, etc.). Habitat categories were then clumped in order to meet statistical standards. Six broad categories of foraging habitats were established: (1) meadows, (2) dunged meadows, i.e. those meadows seasonally scattered with dung, (3) maize fields, (4) maize stubble, (5) ploughed fields and (6) maize and wheat sprouts. The use of the trees was described according to a further six categories: (1) poplars, (2) false acacias, (3) cherry trees, (4) apple trees, (5) oak trees and (6) willow trees.

The presence of other individuals may influence individual choices of where to feed or rest. Since it is impossible to weigh observations for the quantitatively unknown effect of flocking behaviour, data might be analysed by considering each flock or each individual as an observation, in keeping with Rolando & Giachello (1992). None the less, it is rather difficult to accept that in a social species like the crow each flock is made up of individuals that behave independently of each other and, hence, we did not consider each individual as an observation but we preferred only to consider each flock as an observation, in keeping with Loman (1980) and Patterson *et al.* (1971).

It was also considered that the foraging and habitat choices of one form may be influenced

by the presence of the other form and, accordingly, data from homotypic flocks were analysed separately.

We scored 1 for each flock. When observing heterotypic flocks we scored each race according to its relative abundance (i.e. we scored 0.75 for the Hooded Crow and 0.25 for the Carrion Crow if the flock was made up of, say, 15 and 5 individuals respectively). The percentage of habitat use by the two races was compared using the chi-square test (contingency tables), assuming that all observations were independent (all successive observations of flocks with identical composition and location were discarded from the analysis). Bonferroni's simultaneous confidence intervals test (Neu *et al.* 1974, Byers *et al.* 1984) was used to compare the frequency of one form with that of the other in the same habitat category. This technique is usually used to compare observed and expected use of habitat categories in order to check if the species selected or avoided certain resources. As a null hypothesis we assumed the habitat use of both races as identical. Since habitat use is bound to be subject to sampling error, we considered the results cautiously.

We used Principal Component Analysis (PCA) to represent and compare the use of habitat categories by the two races in the six portions of the valley. Accordingly, matrices of 12 rows (six valley portions x two races) and six column-habitat categories were subjected to these multivariate analysis using the Systat computer package (1985). Data were initially standardized so that each variable had a zero mean (Digby & Kempton 1987).

We calculated the expected frequency of heterotypic and homotypic flocks (up to 5 individuals) using both the binomial and the hypergeometric distribution. The expected frequencies obtained were then compared to those observed with the chi-square goodness-of-fit test.

## RESULTS

The relative frequencies of the two forms varied along the valley. Hooded Crows were more abundant at the mouth of the valley (at Caselette, 1st portion, about 80%) and their relative frequency decreased further up the valley (at Bussoleno, 6th portion, about 40%).

**Table 1.** Percentages of use of foraging habitat categories. C= Carrion Crow, H= Hooded Crow. Asterisks indicate that the use of the habitat category of the examined race is significantly different from that of the other. \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ . See data analysis for details.

Habitat Categories	Total Data				Homotypic Data			
	Autumn-Winter		Spring-Summer		Autumn-Winter		Spring-Summer	
	C	H	C	H	C	H	C	H
Meadows	60.2	59.6	66.7	71.7	66.4	60.2*	54.1**	69.3***
Dunged meadows	11.7	11.9	13.2**	4.6***	7.9	11.4	20.6***	3.8***
Maize fields	4.0	3.6	0.0***	2.9**	4.3	3.3	0.0***	4.1**
Maize stubble	15.0	16.2	5.6	3.5*	11.6	17.1*	8.7	3.1***
Ploughed fields	9.1	8.7	8.2	10.8	9.8	8.0	9.5	12.8
Maize-wheat sprouts	0.0	0.0	6.3	6.5	0.0	0.0	7.1	6.9
Total No.obs.	254	759	160	390	164	490	126	290
$\chi^2$	0.29 4 df., N.S.		18.5 5 df, $P < 0.005$		5.44 4 df, N.S.		43.0 5 df, $P < 0.001$	

**Table 2.** The effect of combining similar habitat categories. "meadows" = meadows + dunged meadows; "maize" = maize fields + maize stubble. C = Carrion Crow, H = Hooded Crow. Asterisks indicate that the use of the habitat category of the examined phenotype is significantly different from that of the other. \* =  $P < 0.05$ . Chi-squares were calculated taking into account also fields and maize-wheat sprouts categories (see table 1).

	Total Data				Homotypic Data			
	Autumn-Winter		Spring-Summer		Autumn-Winter		Spring-Summer	
	C	H	C	H	C	H	C	H
"Meadows"	72.0	71.4	80.0	76.4	74.3	71.6	74.6	73.1
"Maize"	18.9	19.8	5.6	6.4	15.9	20.4*	8.7	7.2
$\chi^2$	0.09		1.10		1.92		1.07	
	2 df, N.S		3 df, N.S.		2 df, N.S.		3 df, N.S.	

In general, Hooded Crows and Carrion Crows showed a similar pattern of resource utilization, with a marked use of meadows throughout the year. An examination of the frequency of use of cultivated areas in the various portions of the valley failed to reveal variations associated to the valley slope and the analysis of the frequency of use was therefore performed on data taken from all six valley portions.

The two races showed an almost identical frequency of use for all the various types of arable land during winter while some significant differences were observed in summer (Table 1). The number of significant differences was higher with data referring to homotypic flocks than with total data (homotypic + heterotypic flocks) (Table 1).

In general, a use of meadows irrespective of dunging and a use of maize independent of plant structure may be hypothesized. If, as a result, both categories of meadows (meadows and dunged meadows) and maize (maize fields and maize stubble) were combined, then virtually identical percentages of use were obtained for the two forms (Table 2).

Data relating to the use of trees were collected mainly during the autumn-winter when Carrion and Hooded Crows showed an almost identical use of trees irrespective of the method of analysis used (Table 3).

In overall terms, the representation of the six subpopulations of the two subspecies in the two-dimensional plane of PCA did not show any differences between the two forms during winter. In other words, irrespective of the separation of data according to group composition (keeping homotypic flocks separate or otherwise) no clusters of points which might differentiate the habitat selection of Hooded Crows from that of

**Table 3.** Percentages of use of resting habitat categories. C = Carrion Crow, H = Hooded Crow. No significant difference in the use of habitat categories between the two forms was found using Bonferroni's intervals analysis.

Categories	Total Data		Homotypic Data	
	C	H	C	H
Poplars	66.4	66.2	63.2	64.3
Robinias	5.6	7.0	7.0	8.6
Cherry trees	4.5	4.9	3.5	4.9
Apple trees	8.4	6.4	7.9	4.9
Oaks	7.8	7.9	7.9	7.8
Willow trees	7.3	7.6	10.5	9.5
Total No. obs.	129	286	114	244
$\chi^2$	1.06		1.88	
	5 df, N.S.		5 df, N.S.	

Carrion Crows were obtained (the first two factors accounted for 78.7% and 65.8% of the variance respectively). On the other hand, during the summer a slight differentiation was observed between the two forms, in particular in relation to homotypic data (74.9% of the variance). However, also summer segregation disappeared when data for meadows were combined with those for dunged fields and the data relating to maize stubbles with those for maize (87.8%).

Homotypic flocks were observed more frequently than expected and heterotypic ones less frequently than expected, both during autumn-winter and spring-summer. Differences between observed and expected frequencies were highly significant ( $P < 0.001$ ), irrespective of the methods used to calculate the expected data.

## DISCUSSION

The indications obtained by frequency analysis suggest that winter foraging habitat was almost identical for Hooded and Carrion Crows. These results are not in accordance with data obtained by Saino (1992) in a relatively plain-like zone in the province of Cuneo (south-western Piedmont). He found that the Carrion Crow showed a clear preference for meadows whereas the Hooded Crow positively selected maize fields, both in the more "mountainous" part of the zone and in the plain area, and irrespective of the method used for data analysis (each individual or each flock an observation). However, in our study area a differentiation was noted during the summer when the Carrion Crow showed a significant preference for dunged meadows and maize stubble compared to the Hooded Crow which made greater use of meadows. It is worth pointing out that this summer differentiation, seemingly the opposite of that observed during the winter at Cuneo, was observed in a constant manner in each of the six valley portions examined. Accordingly PCA highlighted two clusters of points in the two-dimensional plane of the first two principal components.

Meadows and dunged meadows were considered separate resources because it is well known that crows capture insects present in dung (Barbero *et al.* 1992) and some observations had shown that Crows turned upside down the pieces of dung scattered all over the meadows. Therefore the presence of birds in these meadows might be due to the presence of dung, irrespective of the "meadow" resource. Maize fields and maize stubble were considered separate due to the different plant structure, along the lines proposed by Saino (1992). These categories are however debatable, especially when it is observed that by combining the aforesaid resources in pairs, percentages for the use of the new resources are obtained which are relatively similar for both forms. This similarity is immediately reflected in multivariate analysis which no longer reveals any summer segregation between the two races using these data. It might be argued that the dung scattered on the meadows does not overly interest the birds and that the maize kernels are their main food both in maize crops and in the stubble (the latter hypothesis being confirmed by Saino's observations).

The picture of foraging activities must be integrated by data referring to the use of trees for resting. In this respect, the two forms are surprisingly alike in view of the different environmental characteristics of the two allopatric areas in northern Italy (poplar plantations on the plain for the Hooded Crow and coniferous woods in the mountains for the Carrion Crow).

It is well known that species with similar ecological requirements may reciprocally influence each other in their choice of foraging habitats (Eden 1987). The resource selection behaviour of the two crows was more differentiated when only homotypic groups were taken into account. It can therefore be hypothesized that in mixed flocks the two subspecies influence one another, resulting in relatively homogeneous habitat selection behaviour. In this case mixed flocking serves to standardize ecological choices, thus indirectly confirming that also individuals influence each other and that choices are shared (Loman 1980).

Even though a clear ecological segregation was not evident, the analysis of flocking behaviour showed a clear tendency to avoid heterotypic flocks. It was hypothesized that the different ecological choices between Carrion Crow and Hooded Crow evidenced at Cuneo enhanced the probability to form distinct flocks (Saino 1992). Having shown that ecological segregation is non-existent or weak, our results suggest that the tendency to avoid heterotypic flocks depends mostly on behavioural choices. We hypothesized that the selective aggressiveness of the crows (with the Carrion Crow dominant over the Hooded Crow) observed both at Cuneo (Saino 1992) and in the Susa valley (Rolando & Giachello 1992) may be responsible for the selection against heterotypic flocking.

The apparent lack (or scarcity) of segregation between the two races in habitat selection in the Susa valley is in line with results obtained in this and a further three adjacent alpine valleys where there was a slight tendency to assortative mating (Rolando 1993). A marked tendency to mate assortatively was, on the contrary, reported in the zone near Cuneo (Saino & Villa 1992). Perhaps at Cuneo ecological segregation and the different behavioural choices are synergic, resulting in a clear separation of the two forms, which, therefore, mated at a low degree. The few data available for the Scottish hybrid zone have not shown a lower level of fitness in hybrids nor a tendency towards assortative mating (Picozzi 1976). It may therefore be hypothesized that in the three areas examined (two in Italy and one in Scotland) the two forms co-exist and hybridize differently because of the different local ecological conditions. It should be noted that the environmental characteristics of the three areas studied to date are different. The two Italian areas of the alpine hybrid zone (only 90 km apart by straight line) are situated in different environments: the area near Cuneo, well outside the alpine valleys, resembles a plain area (in spite of the fact that it is a plateau lying at an altitude of 500-600 m) whereas our study area, which lies entirely within one of these alpine valleys, is a mountain

area. In the first case it can be seen that the presence of the Carrion Crow is due to a slight expansion onto the plain starting from the mountain, whereas, on the contrary, in the Susa valley the Hooded Crow's presence may be seen as the result of infiltration into a mountain area achieved by exploiting the "plain-like" environment of the valley floor. Major differences between the areas suggest that the alpine hybrid zone is a mosaic of populations differentiated in relation to locally different ecological conditions. The mosaic hybridization model was first described by Harrison (1986) for crickets but other examples of mosaic hybrid zones were also later described for grasshoppers (Tosto & Bidau 1991) and newts (Arntzen & Wallis 1991). At Cuneo the hybrid zone is about 15 km in width whereas in the Susa valley it extends for about 60 Km long. In general, with low topographic diversity hybrid zones narrow considerably (Howard & Waring 1991). Accordingly, in alpine valleys with a flat bottom, the two races may coexist for many kilometres, since the environmental features are suitable for both.

## ACKNOWLEDGEMENTS

We wish to thank E. Balletto, A.P. Møller, I.J. Patterson, N. Saino and S. Ulfstrand who made useful criticisms of a first draft of the manuscript. G. Allasia kindly discussed the mathematical properties of binomial and hypergeometric distribution. P. Giachello and R. Ferro were of great help in collecting data in the field.

## REFERENCES

- Arntzen, J.W. & G.P. Wallis 1991. Restricted gene flow in a moving hybrid zone of the newts *Triturus cristatus* and *T. marmoratus* in western France. *Evolution* 45:805-826.
- Barbero, E., C. Palestini & A. Rolando 1992. Variability of the entomatic diet of the Hooded Crow *Corvus corone cornix* in the Western Po Valley. *Avocetta* 17:29-33.
- Byers, R.C., R.K. Steinhorst & P.R. Krausman 1984. Clarification of a technique for analysis of

- utilization-availability data. *J. Wildl. Manage* 48: 1050-1053.
- Digby, P.G.N. & R.A. Kempton 1987. Multivariate analysis of ecological communities. Chapman and Hall, London.
- Eden, S.F. 1987. The influence of carrion crows on the foraging behaviour of magpies. *Anim. Behav.* 305:608-610.
- Endler, J.A. 1977. Geographic variation, speciation, and clines. Princeton University Press, Princeton.
- Harrison, R.G. 1986. Pattern and process in a narrow hybrid zone. *Heredity* 56:337-349.
- Howard, D.J. & G.L. Waring 1991. Topographic diversity, zone width, and the strength of reproductive isolation in a zone of overlap and hybridization. *Evolution* 45:1120-1135.
- Loman, J. 1980. Habitat distribution and feeding strategies of four south Swedish Corvid species during winter. *Ekol. Polska* 28:95-109.
- Neu, C.W., C.R. Byers & J.M. Peek 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38:541-545.
- Patterson, I.J., G.M. Dunnet & R.A. Fordham 1971. Ecological studies on the Rook (*Corvus frugilegus* L.) in north-east Scotland: Dispersion. *J. appl. Ecol.* 8:815-833.
- Picozzi, N. 1976. Hybridization of Carrion and Hooded crows *Corvus c. corone* and *Corvus c. cornix* in northeastern Scotland. *Ibis* 118:254-257.
- Rolando, A. 1993. A study on the hybridization between Carrion and Hooded Crow in Northwestern Italy. *Ornis Scand.* 24:80-83.
- Rolando, A. & P. Giachello 1992. Interspecific coexistence in corvids in an alpine valley of northwestern Italy. *Boll. Zool.* 59:281-288.
- Saino, N. 1990. Low reproductive success of the Carrion Crow *Corvus corone corone* - Hooded Crow *Corvus c. cornix* hybrids. *Avocetta* 14:103-109.
- Saino, N. 1992. Selection of foraging habitat and flocking by Crow *Corvus corone* phenotypes in a hybrid zone. *Ornis Scand.* 23:111-120.
- Saino, N. & S. Villa 1992. Pair composition and reproductive success across a hybrid zone of Carrion Crows and Hooded Crows. *Auk* 109:543-555.
- Short, L.L. 1985. Article "Hybridization, zone of secondary". In: Campbell, B. & Lack, E. (eds). *A Dictionary of Birds*. Calton & Vermillon.
- Thorpe, R.S. 1975. Biometric analysis of incipient speciation in the ringed snake, *Natrix natrix* (L.). *Experientia* 31:180-182.
- Thorpe, R.S. 1984. Primary and secondary transition zones in speciation and population differentiation: a phylogenetic analysis of range expansion. *Evolution* 38:233-243.
- Tosto, D.S. & C.J. Bidau 1991. Distribution of chromosome frequencies within a hybrid zone of *Dichroplus pratensis* (Melanoplinae, Acrididae). *Heredity* 67:299-306.
- Waite, R.K. 1981. Local enhancement for food finding by rooks (*Corvus frugilegus*) foraging on grassland. *Z. Tierpsychol.* 37:15-36.
- White, M.J.D. 1978. Modes of speciation. W.H. Freeman & Co., San Francisco.

## SAMENVATTING

In het dal van Susa, in de Italiaanse Alpen ten westen van Turijn, broeden Zwarte- en Bonte Kraaien samen. Er treedt daar ook hybridisatie op tussen beide ondersoorten. De meeste paren blijken echter te bestaan uit individuen van dezelfde ondersoort. Dat zou verband kunnen houden met een verminderde voortplantingscapaciteit van hybriden zoals aangevoerd voor sommige populaties. Het kan ook samenhangen met een verschil in habitatkeuze.

In het najaar en de winter blijken er in dit gebied geen significante verschillen te bestaan in de keuze van het fourageergebied, maar in het voorjaar en de zomer geven Bonte Kraaien de voorkeur aan onbemest grasland, terwijl Zwarte Kraaien dan meer voorkomen op bemeste velden en op de stoppel van mais (Tabel 1). Dat verschil wordt duidelijker wanneer de gegevens van gemengde groepen buiten beschouwing worden gelaten. Het verschil verdwijnt echter wanneer naar wat bredere habitat-categorieën wordt gekeken (Tabel 2). Verder blijken er geen verschillen te bestaan in voorkeur voor rustplaatsen (Tabel 3). Groepen waarin beide ondersoorten voorkomen, komen overigens wel veel minder dikwijls voor dan men verwacht. De verwachting dat de beslissing van een kraai om zich aan te sluiten bij een groep onafhankelijk is van de samenstelling van die groep, gaat dus niet op.

De uitkomst van dit onderzoek - dat er in de winter geen habitatdifferentiatie optreedt en in de zomer slechts in beperkte mate - strookt niet met onderzoek op een andere lokatie in de hybridisatiezone, ongeveer 100 km zuidelijker. Wellicht bestaat er in deze zone een mozaïek van populaties, elk aangepast aan de lokale ecologische omstandigheden. De mate waarin hybridisatie voorkomt verschilt tussen populaties en lijkt te verminderen naarmate er meer verschillen zijn in habitatkeuze.