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PAIR COMPOSITION AND REPRODUCTIVE SUCCESS ACROSS A HYBRID ZONE OF CARRION CROWS AND HOODED CROWS

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ABSTRACT.—The Carrion Crow (*Corvus corone corone*) and the Hooded Crow (*C. corone cornix*) have parapatric ranges in Europe with narrow areas of hybridization. Reproductive biology of populations of Carrion and Hooded crows and hybrids is described for four areas in northern Italy. Nonrandom mating was observed in a hybrid zone. Homogamic pairs were observed more frequently than expected by chance. Data on clutch size and reproductive success were analyzed for Carrion Crows and Hooded Crows in allopatry, and for parental and hybrid phenotypes in a hybrid zone. Clutch size did not vary across the hybrid zone. Pairs with Hooded Crow females in the hybrid zone produced significantly more chicks than those with hybrid females. The number of chicks recorded from Carrion Crow females was higher than for hybrid females, but not significantly. Significant variation was observed for the effect of the male's phenotype on reproductive success due to the comparatively high reproductive success of Carrion Crows in the area of allopatry. No significant difference in the reproductive success was observed in the hybrid zone between pairs containing only parental phenotypes and pairs containing at least one hybrid. Carrion Crows in allopatry produced more fledglings than Carrion Crows in the hybrid zone, whereas Hooded Crows in allopatry had a reproductive success very similar to that of Hooded Crows in the hybrid zone. Our results do not support the dynamic-equilibrium model but are compatible with the bounded-hybrid-superiority model. The hybrid zone studied coincides with an "ecotone" between the alpine valleys and the intensively cultivated plain. We conclude that the maintenance of parapatric distributions of the two morphs is due mainly to ecological factors. The hybrid zone could be considered the narrow belt in which environmental features are such that hybrids are not less fit than parental individuals, its narrowness being caused by the steepness of the environmental gradient crossing it. The nonrandom mating observed could result from heterogeneous phenotype dispersion which, in turn, reflects differential habitat selection in the hybrid zone. *Received 22 April 1991, accepted 10 January 1992.*

MANY EXAMPLES of closely related species or morphs showing parapatric distributions with relatively narrow zones of hybridization have come to light in the last few decades (for reviews about terrestrial animals see Endler 1977, Rising 1983, Barton and Hewitt 1985; for marine invertebrate examples, see Bert and Harrison 1988). Hybrid zones have been interpreted: (1) as a consequence of secondary contact between two populations of an ancestor species that have diverged to some extent during a period of geographic isolation and reexpanded their ranges; or (2) as the product of selection maintaining steep clines in contiguous populations. Whatever the origin, the fate of hybrid zones is of particular interest, since at least some of them conceivably could be considered evidence of speciation phenomena in process.

Three major hypotheses have been put forward to explain and predict the dynamics of hybrid zones. When the broad occurrence of hybrid zones among animal taxa was first appreciated, a consensus developed as to their ephemeral nature (ephemeral-zone hypothesis). Natural hybridization was predicted to evolve in either of two opposite directions—speciation or fusion of the allopatric populations through introgressive hybridization (Dobzhansky 1940, Sibley 1957, Remington 1968). Under this hypothesis, speciation inevitably would occur between populations that have diverged through differential mutations, selection and coadaptation to the extent that hybridization "would disrupt the distinctly coadapted gene pools" (Moore 1977) that had evolved during isolation (adaptive-speciation model). The adaptive-speciation model predicts that premating isolating mechanisms will evolve through selection against individuals prone to hybridize (Darwin 1859, Fisher 1930, Sibley 1957, Mayr 1963, Ayala 1978; but see Loftus-Hills 1975, Paterson 1978, Heth and Nevo 1981, Barton and Hewitt 1985, Dowling and Moore 1985). Fusion will occur if the two isolates have not diverged to the extent to which hybrids are selected against, and fully fertile hybrids will be the means of introgressive hybridization.

The other two hypotheses deal with the dynamics of the hybrid zones postulated to be persistent. Barton (1979a, b) and Barton and Hewitt (1981) refined a dynamic-equilibrium hypothesis, previously formulated by Bazykin (1969), which characterizes hybrids as having low or null fitness. Hybrids may be at a disadvantage because they have low viability or fecundity, or because they attain a low mating success. Since only populations in the hybrid zone experience selection against hybridization, gene flow from the allopatric areas into the hybrid zone could "swamp alleles which cause individuals to avoid hybridizing" (Moore 1977) and prevent the evolution of antihybridization mechanisms. No exogenous factors are supposed to play a role in the maintenance of the hybrid zone, and the hybrid zone is expected to shift geographically from the most fit towards the less fit parental population unless stabilized by a density gradient or trough (Moore and Buchanan 1985).

As a third hypothesis, which can be termed the bounded-hybrid-superiority hypothesis, Moore (1977) proposed that hybrid zones could be maintained by a "bounded hybrid superiority" in the areas of overlap of the parental populations or in areas lying between their ranges. Under this hypothesis, hybrids would be more fit within the narrow strip where they usually occur, whereas they are less fit than the parental populations in the areas of allopatry. The advantage of the hybrids is supposed to derive from a coincidence of the hybrid zone with an ecotone.

The Carrion Crow (*Corvus corone corone*) and the Hooded Crow (*Corvus corone cornix*) have become a paradigmatic example of parapatrically distributed morphs whose ranges overlap in a narrow zone of hybridization. Their hybrid zone is one of the first to be described in some detail (Meise 1928). Mayr (1959) considered the hybrid belt between the Carrion Crow and the Hooded Crow to be a particularly striking example of secondary contact and interbreeding between isolates that have not yet attained the species rank. Nonetheless, there is little information about the mechanisms that determine the zone's apparent maintenance, narrowness and geographic stability in some of its parts (but see Cook 1975, Dybbro 1976). In continental Europe the Carrion Crow has a western and the Hooded Crow an eastern distribution. The two morphs meet and hybridize in a narrow region running from the Ligurian Apennines, through the southern edge of the Alps and through central Europe north to Jutland (Mayr 1942, 1963). Another hybrid zone exists in Scotland that separates Carrion Crow populations of England, Wales, and southern Scotland from the Hooded Crow populations of northern Scotland.

The distribution of the Carrion and Hooded crows in northern Italy is fairly well known from the results of recent local atlas projects (e.g. Mingozzi et al. 1989, Brichetti and Fasola 1990). However, these reports do not include information on the areas of occurrence of hybrid phenotypes and are somewhat ambiguous with respect to the distribution, on a fine scale, of the parental morphs.

The aim of our study was to analyze the reproductive biology of parental Carrion Crow and Hooded Crow populations and of hybrids. In particular, we tested the predictions that: (1) assortative mating between phenotypes occurred; (2) the mean reproductive success of hybrid phenotypes differed from that of parental phenotypes in the hybrid zone; and (3) differences in the mean reproductive success existed between the parental phenotypes living in allopatry and those in the hybrid zone.

METHODS

STUDY AREAS

The study was carried out during the springs of 1988, 1989 and 1990 in four areas chosen to correspond to the areas of allopatry of the two parental morphs and to two areas in the hybrid zone (Fig. 1).

Area of allopatry of Carrion Crow.—This was an area of 65 km^2 covering all the bottom of the Stura di Demonte River valley from 750 to 950 m above sea level and a few small lateral valleys of the Stura Valley. The extent of the different cultivations was determined over the entire study area. All the area was in meadows and pastures, except for a few small maize fields (<1%) and rye fields or vegetable gardens (<0.5%). At the bottom of the valley there were isolated or patchily distributed poplars (*Populus* spp.), alders (*Alnus* sp.), willows (*Salix* sp.), walnuts (*Juglans regia*), chestnuts (*Castanea sativa*), and a few conifers such as larch (*Larix decidua*) and spruce (*Picea abies*). "Pure" Carrion Crow phenotypes (see below and Fig. 2 for description of parental and hybrid phenotypes)

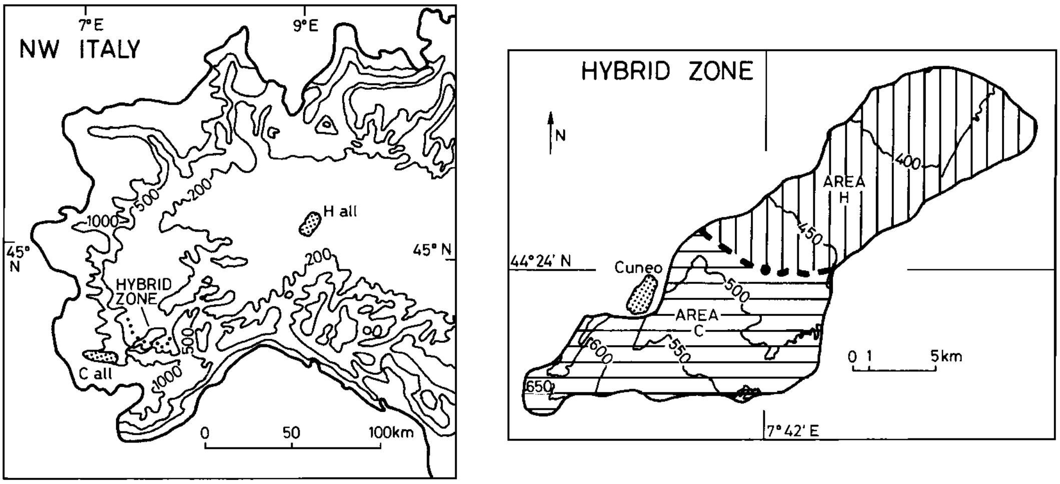

Fig. 1. Location of study areas in north-western Italy (left) and of study areas in hybrid zone (right). C all = area of allopatry of Carrion Crow; H all = area of allopatry of Hooded Crow; area C = study area on Carrion Crow side of hybrid zone; area H = study area in Hooded Crow side of hybrid zone. Dotted line (left) indicates position of axis of hybrid zone as determined by our study and deduced from Mingozzi et al. (1989). Bold dashed line (right) indicates the border between two study areas in the hybrid zone (i.e. the center of the hybrid zone). Contour levels indicated (left and right).

represented more than 99% of the crow population in this area.

Area of overlap and hybridization.—The "hybrid zone" was an area of about 250 km^2 located within the Cuneo-Turin flatland, ranging in altitude from 350 to 650 m above sea level. In this area, the parental phenotypes of the Carrion and Hooded crows live in sympatry and hybridize. All of the area was considered to lie within the hybrid zone, since the nests of the individuals of each parental phenotype (even considering only those studied) were never farther than 4.5 km from the nearest nest of an individual of the other parental phenotype (or if measured perpendicular to the estimated axis of the hybrid zone, never farther than 3 km). This area was divided into two study areas (area C located on Carrion Crow side of hybrid zone, and area H on Hooded Crow side of hybrid zone).

The two hybrid areas were 10 km and 13 km wide, respectively, as measured perpendicular to the estimated axis of the hybrid zone. The border between areas C and H corresponded to the center of the narrow, well-defined strip where the maximum relative frequency of breeding hybrid phenotypes was observed.

The main crops in area C, based on random sampling of 477 fields over a wide subset of the area, were: meadows and pastures (48%); maize (23%); wheat, barley and rye (22%); and seeded grassfields (*Lolium multiflorum*; 2%). Similar sampling of 724 fields in area H yielded: meadows and pastures (41%); wheat, barley and rye (26%); maize (21%); and seeded grassfields (7%). The habitat was finely patched in both areas, and the mean size of individual fields was about 3 ha. Natural woods were very rare in both hybrid study areas, and tree rows (mainly of poplars, alders, oaks [*Quercus* spp.], false acacia [*Robinia pseudoacacia*], walnuts, and planetrees [*Platanus* sp.]) existed along the edges of fields and along canals. Just a few kilometers outside of area C, towards the area of allopatry of the Carrion Crow, the crow population was composed almost entirely of pure Carrion Crow phenotypes, whereas some hybrids or even Carrion Crow phenotypes occurred outside area H towards the area of allopatry of the Hooded Crow.

Area of allopatry of Hooded Crow.—This area of 150 km^2 located near Milan and Pavia was an intensively cultivated farmland ranging in altitude from 40 to 100 m above sea level. The main crops, based on a sample of 530 fields, were: maize (39%); rice (36%); wheat and barley (7%); meadows (6%); and soybean (2%). Natural woods were absent from the area, but tree rows (mainly poplars, alders, oaks and false acacias) still existed along field edges and canals. The area is in the middle of the Po Valley at least 50 km from the nearest known Carrion Crow population in the central Alps.

DATA COLLECTED

The Eurasian Crow (*Corvus corone*) is a monogamous, territorial, large-sized passerine. It is a single-breeder species except in cases when the first clutch is lost. Egg laying usually starts at the beginning of

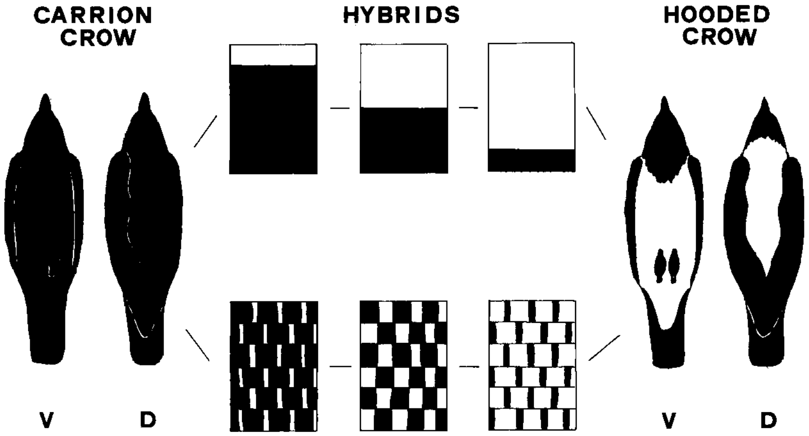

Fig. 2. Pattern of increase of black pigmentation in hybrid phenotypes, from "pure" Hooded Crow phenotype (right) to "pure" Carrion Crow phenotype (left). V = ventral view; D = dorsal view. In hybrid phenotypes, two main series of continuous variation in distribution of black pigmentation can be recognized. Boxes schematically represent body. The same amount of black pigmentation may be either uniformly scattered over grey parts of the "pure" Hooded Crow phenotype (series below) or may be concentrated, starting from posterior parts of the body (series above). See also Melde (1984) for photographs.

April. Incubation, by the female, lasts about 19 days and hatching is asynchronous. Chicks are fed by both parents and fledge at about 28 to 30 days.

Data on the reproductive biology of the crows in areas of allopatry were collected in 1988, 1989 and 1990, while data from the hybrid zone were obtained during 1989 and 1990. The nests were searched for starting on 20 March, when crows at low altitudes begin to lay eggs. The study areas were surveyed by car or on foot. The nests usually were inspected for the first time six or more days after their location to be sure that the clutch was complete. The nests were usually high in trees. When possible, they were directly inspected by climbing the tree up to the nest. The content of the nests that could not be reached directly was observed using a mirror mounted on a 6-m pole.

For each nest we recorded (when possible) clutch size, number of chicks fledged, and pair composition. Since some nests were inspected after hatching, the clutch size could not be determined. It was not possible to determine the number of chicks fledged for some of the other nests. The phenotypes of parents at each nest were scored as Carrion Crow, hybrid or Hooded Crow according to the characters of their plumage. The Carrion Crow phenotype is characterized by completely black plumage, and the Hooded Crow phenotype has a black head, throat, breast, wings and tail. Phenotypically hybrid individuals show varying degrees of intermediacy in the plumage between the Carrion and Hooded crow phenotypes in terms of the amount and dispersion pattern of black pigmentation on body feathers (Fig. 2; see Melde [1984] for detailed photograph). We classified as hybrids all those individuals showing neither completely black (Carrion Crow-like) nor "pure" Hooded Crow-like plumage.

The females in the hybrid zone were scored during the incubation period by observing them as they were driven from the nest when we kicked the tree trunk; we observed them in flight and when they landed. When a first scoring attempt was unsuccessful, we repeated the scoring procedure. The males were scored by observing the individuals bringing food to the nest after the eggs hatched. These observations usually were performed by two people simultaneously to minimize the errors in determining the score of the phenotype. Obviously, this procedure could not be used when the eggs failed to hatch. However, in some cases, scoring of the male was possible because, after the female was driven away from the nest, the male joined her and they were seen resting together in the fields or, in some instances, they foraged or patrolled the territory together.

In the springs of 1989 and 1990, a late snow fall occurred in the hybrid zone and in the area of allopatry of Carrion Crows. Despite the fact that there were late snow falls in two out of the three years of this study, they should be considered rare events. All nests destroyed by the snow and nests definitely depredated or destroyed by man were considered in the analysis of the clutch size, but were excluded from the analysis of reproductive success.

In the analyses of clutch size and reproductive success we adopted five area-phenotype categories (Carrion Crow in allopatry, Carrion Crow in the hybrid zone, hybrid, Hooded Crow in the hybrid zone, Hooded Crow in allopatry) and four area categories

TABLE 1. Observed and expected frequencies of pairs of nine possible compositions in two areas (C and H in Fig. 1) into which the hybrid zone was divided. C = Carrion Crow; Y = hybrids; H = Hooded Crow. Relative frequencies of the phenotypes in two areas were markedly different.

Parents		Area C			Area H		
Female	Male	Observed	Expected	X^2	Observed	Expected	X^2
C	C	28	13.7	15.0	7	1.4	2.6
H	H	23	12.8	8.2	47	41.9	
C	H	2	12.4	8.7	2	6.4	3.0
H	C	3	14.1	8.8	3	9.2	4.2
C	Y	0	4.0		0	1.3	
Y	C	0	3.2		3	2.6	
Y	Y	4	0.9	0.6	2	2.0	0.0
Y	H	3	2.9		10	10.4	
H	Y	5	4.1		9	7.7	
Total		68		41.3[a]	83		9.8[b]

[a] $P < 0.001$, df = 1.
[b] $P < 0.02$, df = 1.

(area of allopatry of the Carrion Crow, hybrid zone-area C, hybrid zone-area H, area of allopatry of the Hooded Crow). This dual approach to the analysis of the variation in the breeding parameters is similar to that adopted by Johnson and Johnson (1985) in a study of hybridization between sapsuckers (*Sphyrapicus ruber daggetti* and *S. nuchalis*), and by Moore and Koenig (1986) in a study of a flicker (*Colaptes auratus*) hybrid zone.

DATA ANALYSIS

The expected frequencies of each pair composition ($F_{x,y}$) were calculated using:

$$F_{x,y} = (X_i Y_j)/n \tag{1}$$

where X_i is the number of females of the i-th phenotype in the sample, Y_j is the number of males of the j-th phenotype in the sample, and n is the total number of pairs. Observed frequencies of pair compositions were compared to those expected using chi-square tests. Analysis of variance of the breeding parameters was carried out using a general-linear-model approach. Bonferroni's t-test (Miller 1981) was used to perform multiple comparisons among group (area-phenotype and area categories) means. All statistical analyses were performed using the SAS computer package (SAS Institute 1985).

RESULTS

Pair composition in hybrid zone.—The observation of nonrandom mating in the hybrid zone can furnish evidence for the existence of premating isolating mechanisms between the phenotypes. The observed frequencies of pairs of the nine possible types were compared to the frequencies expected under the hypothesis of random mating. The relative frequencies of the phenotypes varied markedly across the hybrid-zone study area (Table 1). To address partially the problem of geographic isolation between crows living on opposite sides of the hybrid zones, the expected frequencies were calculated and compared to the observed frequencies separately for areas C and H (also see Discussion). A significant deviation from random pair composition was observed in both areas C and H, although it is more evident in area C where the relative frequencies of the parental phenotypes were almost identical (Table 1). In each of the two areas, homogamic pairs (pairs involving two individuals of the same parental phenotype) were observed more frequently than expected. In area C the observed frequency of homogamic pairs for the Carrion Crow was 2.0 times and for the Hooded Crow was 1.8 times that expected. In area H the pooled frequencies of homogamic Carrion Crow and Hooded Crow pairs was 1.3 times the expected. Correspondingly, there was a deficiency of heterogamic pairs (Carrion Crow female × Hooded Crow male and Hooded Crow female × Carrion Crow male). In particular, in area C the observed frequency of heterogamic pairs was just 0.2 times, whereas in area H it was 0.3 times the expected frequency. Hybrids of both sexes mated in a remarkably random manner with other hybrids and with parental individuals. No sexually asymmetrical deviation from expectance was detected.

Breeding parameters of five area-phenotype categories.—Variations in clutch size and reproductive success (measured as the number of

TABLE 2. Clutch size ($\bar{x}$, SE of clutch size, and n) of female area-phenotype categories and significance of variation in clutch size among area-phenotype categories.[a]

Area-phenotype category	$\bar{x}$	SE	n
Carrion Crow allopatry	4.4	0.09	118
Carrion Crow hybrid zone	4.7	0.13	41
Hybrid	4.2	0.20	29
Hooded Crow hybrid zone	4.5	0.09	88
Hooded Crow allopatry	4.5	0.09	114

[a] $F = 1.1$, df = 4 and 385, $P = 0.36$.

chicks fledged/nest) were evaluated among the area-phenotype categories. Since no clear variations in the breeding parameters of the five area-phenotype categories were observed among years (see below), data were pooled. The variances of the breeding variables for the area-phenotype categories were found to be homoscedastic.

Clutch size.—Significant variation in clutch size among years was found only for the Carrion Crow in allopatry ($F = 5.2$, df = 2 and 115, $P < 0.01$). In particular, the mean clutch size in 1990 was significantly larger than in 1989 ($P < 0.01$, Bonferroni t-test), and no differences were found with 1988. There was no variation in the mean clutch size among the five female area-phenotype categories (Table 2). Carrion Crows in allopatry laid fewer eggs than Carrion Crows in the hybrid zone and hybrids laid fewer eggs than parental females, but these differences were not statistically significant.

Apparently abnormal eggs were found in five nests of hybrid females. The abnormalities consisted of unusual egg-shell pigmentation and frailty. All but two of the eggs found in these nests were completely depigmented and very light blue, whereas the eggs observed in the other nests were usually much darker and spotted, streaked or mottled by olive-green or olive-brown (see Harrison 1985). More importantly, the eggs in these nests apparently had a brittle shell. In two nests containing three eggs each, the eggs were found broken at the time of the first or second inspection, while the female was still incubating. In a third nest, two of the five eggs were found broken, and just one egg hatched. In a fourth nest with three eggs, two had an extremely thin shell and failed to hatch, and the third egg produced a fledgling. In the fifth nest, three out of four eggs were depigmented and all failed to hatch. Apparently, no similar abnormalities in shell frailty were observed in more than 1,400 eggs observed in parental female nests in the hybrid zone or in allopatry.

Reproductive success.—We defined the reproductive success of a breeding pair as the number of chicks reared to about the age of fledging. Therefore, our tests of reproductive success are not independent of those on clutch size. The success of the breeding pairs was analyzed first by considering separately the effect of the phenotype of the female and of the male on the number of chicks fledged per nest. No significant variation in the number of chicks fledged among years was detected for any of the female or male area-phenotype categories.

The number of chicks fledged varied significantly among the five female area-phenotype categories (Table 3). The Bonferroni t-test revealed that there was no significant difference in reproductive success between the parental females in allopatric areas and those in the hybrid zone. However, a marked difference in reproductive success was found between Carrion Crow females in allopatry and those in the hybrid zone. The females of the two parental phenotypes in the hybrid zone showed a similar reproductive success, but the Hooded Crow females had significantly higher reproductive

TABLE 3. Reproductive success ($\bar{x}$, SE of number of chicks fledged/nest, and n) of female area-phenotype categories, and significance of comparisons between categories (Bonferroni t-test).[a]

				Probability			
Area-phenotype category	$\bar{x}$	SE	n	CY	Y	HY	H all
Carrion Crow allopatry	3.1	0.11	91	ns	<0.001	<0.05	<0.05
Carrion Crow hybrid zone (CY)	2.5	0.19	37		ns	ns	ns
Hybrid (Y)	1.6	0.28	24			<0.01	<0.005
Hooded Crow hybrid zone (HY)	2.6	0.13	89				ns
Hooded Crow allopatry (H all)	2.6	0.12	118				

[a] $F = 7.9$, df = 4 and 354, $P < 0.001$.

TABLE 4. Reproductive success ($\bar{x}$, SE of number of chicks fledged/nest, and n) of male area-phenotype categories, and significance of comparisons between categories (Bonferroni t-test).[a]

				Probability			
Area-phenotype category	$\bar{x}$	SE	n	CY	Y	HY	H all
Carrion Crow allopatry	3.1	0.11	91	<0.01	ns	<0.01	<0.05
Carrion Crow hybrid zone (CY)	2.3	0.20	41		ns	ns	ns
Hybrid (Y)	2.7	0.33	20			ns	ns
Hooded Crow hybrid zone (HY)	2.5	0.13	84				ns
Hooded Crow allopatry (H all)	2.6	0.12	118				

[a] $F = 4.5$, df = 4 and 349, $P < 0.005$.

success than hybrid females. The difference between Carrion Crow and hybrid females was similar to that between Hooded Crows and hybrids but was not statistically significant.

Significant variation in the reproductive success was found also among the male area-phenotype categories overall (Table 4). However, the comparisons by the Bonferroni t-test revealed a significant difference only between Carrion Crow males in the area of allopatry and the males of the other parental area-phenotype categories. Figure 3 shows the reproductive success of pairs of different compositions in the hybrid zone and in the areas of allopatry.

Significant variation in the mean number of chicks fledged was observed among the 10 types of pairs considered ($F = 3.4$, df = 9 and 344, $P < 0.001$). However, the only comparison to give a significant difference was that between Carrion Crows in allopatry and pairs with hybrid females and Hooded Crow males ($P < 0.005$, Bonferroni t-test). Homogamic pairs had a similar intermediate reproductive success within the hybrid zone. Pairs with a Hooded Crow female and a Carrion Crow male had relatively low reproductive success, and those with Carrion Crow female and Hooded Crow male had relatively high success, but the difference was not statistically significant. Figure 3 also shows a sharp difference between pairs with a hybrid female, irrespective of the phenotype of the male, and those with a hybrid male and a Hooded Crow female.

The statistical power of the above analysis clearly is reduced by the extremely different sample sizes obtained for pairs of the different types (Fig. 3). One of the main aims of our study was to compare the reproductive success of the hybrids to that of the parental populations. Therefore, the analysis was repeated by pooling all the pairs containing only parental individuals in the hybrid zone and all the pairs containing at least one hybrid. Parental populations in allopatry were considered separately for these analyses. Significant variation was observed in the reproductive success among the four groups thus obtained (Table 5). However, the only statistically significant differences were those between Carrion Crows in allopatry and the other groups. Therefore, there was no significant difference in the reproductive success between "pure" parental pairs and pairs containing hybrid individuals within the hybrid zone. Overall, the data showed that an asymmetry existed outside the hybrid zone due to

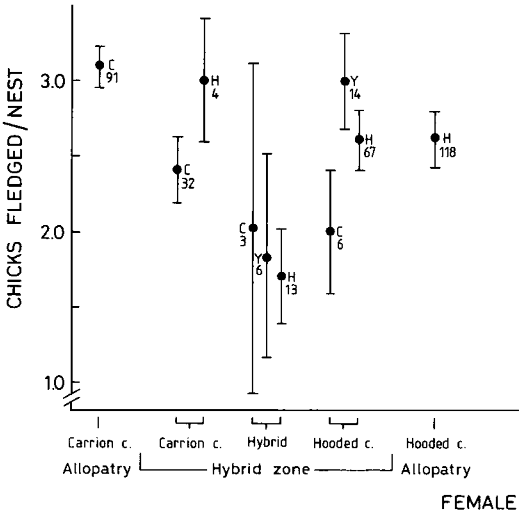

Fig. 3. Mean and standard-error bar of reproductive success of parental populations in allopatry and of pairs of different composition in hybrid zone. Abscissa indicates phenotype of female. C = Carrion Crow male; Y = hybrid male; H = Hooded Crow male. Numbers indicate size of sample. No pairs with Carrion Crow female and hybrid male were recorded.

TABLE 5. Reproductive success ($\bar{x}$, SE of number of chicks fledged/nest, and n) of homogamic pairs of Carrion Crows in allopatry, of pairs containing only parental individuals in the hybrid zone, of pairs containing at least one hybrid individual, and of homogamic pairs of Hooded Crows in allopatry. Significance of comparisons between categories (Bonferroni t-test).[a]

Parents	$\bar{x}$	SE	n	P	Y	H all
Carrion Crow in allopatry	3.1	0.11	91	<0.005	<0.005	<0.05
Both parental in hybrid zone (P)	2.5	0.11	109		ns	ns
At least one hybrid (Y)	2.3	0.23	36			ns
Hooded Crow in allopatry (H all)	2.6	0.12	118			

[a] $F = 6.2$, df = 3 and 350, $P < 0.001$.

the comparatively higher reproductive success of Carrion Crows in allopatry than in the hybrid zone, and the similar reproductive success of the Hooded Crows in allopatry and in the hybrid zone.

Breeding parameters in four areas.—No statistical variation in the clutch size among the four areas was found ($F = 0.6$, df = 3 and 386, $P > 0.6$). There was significant variation in reproductive success among the study areas (Table 6). Again, this result was due to the comparatively high reproductive success of the Carrion Crows in allopatry, whereas no significant differences were found between the two hybrid areas and the area of allopatry of the Hooded Crow. The two hybrid areas appeared to be similar with respect to the variables studied.

DISCUSSION

In both hybrid areas, homogamic pairs were more frequently observed than expected under the hypothesis of random mating. However, a methodological problem in assessing assortative mating needs consideration. The composition of the crow population, in terms of relative frequency of the phenotypes, varied with position in the hybrid zone (Table 1; Saino in press). The pooling of pair-composition data obtained from opposite sides of the hybrid zone or the inclusion in the analysis of parental morphs living at the outer edge of the hybrid zone could overemphasize the occurrence of positive assortative mating. Assortative mating can reliably be determined only where geographic effects are negligible. The crow is considered a sedentary, philopatric species, but movements over distances greater than 13 km (i.e. width of widest hybrid study area) are very common for yearlings and adults (Holyoak 1971, Picozzi 1975). Nonetheless, movements could be anisotropic in the hybrid zone and their prevalent direction could be morph-related. Thus, it is difficult to evaluate the extent to which geographic effects influenced the observed pair composition frequencies.

On the other hand, Saino (in press, unpubl. data) has shown that habitat composition varies gradually across the studied hybrid zone. Importantly, the phenotypes differed in their ecology, and their relative frequency across the hybrid study areas was statistically dependent on the abundance of the prevalent habitats (Saino in press). Therefore, the gradual variation of the relative frequencies of crow phenotypes across each of the hybrid areas seemed to be proximately controlled by ecological factors. Partial ecological segregation may promote positive assortative mating, thus acting as an imperfect premating isolating mechanism (Mayr 1970, Bert and Harrison 1988).

Therefore, our data show that pair composition within the hybrid zone was nonrandom and suggest that assortative mating was partly

TABLE 6. Reproductive success ($\bar{x}$, SE of number of chicks fledged/nest, and n) in four study areas (see Fig. 1), and significance of comparisons between areas (Bonferroni t-test).[a]

Area	$\bar{x}$	SE	n	Area C	Area H	H all
Carrion Crow allopatry	3.1	0.11	91	<0.01	<0.005	<0.05
Hybrid zone area C	2.5	0.15	67		ns	ns
Hybrid zone area H	2.4	0.15	83			ns
Hooded Crow allopatry (H all)	2.6	0.12	118			

[a] $F = 6.4$, df = 3 and 355, $P < 0.001$.

the outcome of differential habitat selection by the phenotypes. Admittedly, these data are not conclusive because the effects of geographic and ecological isolation are hardly distinguishable. However, nonrandom pair composition also could be achieved through social behavior. Selective aggressiveness occurred in heterotypic flocks; Carrion Crows were dominant and often drove away Hooded Crows and hybrids from flocks (Saino and Scatizzi 1991). This was probably one of the causes that determined nonrandom assortment of winter flocks (Saino in press) in which pair formation takes place (Wittenberg 1968, Kalchreuter 1971, Charles 1972).

Some differences in breeding parameters among the area-phenotype categories have been demonstrated in our study. Clutch size did not show a clear pattern of variation across the hybrid zone. Although clutch size is an important component of fitness, the mean clutch size of a population (e.g. Carrion Crows in allopatry) can be markedly lower than that of another population (Carrion Crows in hybrid zone) and, yet, the former can show a higher reproductive success than the latter.

The result of a lower reproductive success of the hybrid females with respect to Hooded Crow females in the hybrid zone and also to the parental females in the areas of allopatry was partly determined by hatching failures due to egg shell frailty in some hybrid female nests. Frailty, that was probably due to thinness, could cause the shell to fracture under the weight of the incubating female. The influence of thickness on the physical properties of the shells (such as permeability to gases) is not obvious, but homeostatic development of the embryo also may not be possible in eggs with abnormally thin shells, thus hindering embryo survival. It was not likely that any of the eggs found broken had been damaged by a predator, because when predation occurs the whole egg is usually stolen from the nest. However, brightness and depigmentation of the shell probably are not neutral characteristics as regards natural selection. Bright azure shells, which we found in some hybrid-female nests, are much more visible to an aerial predator flying over the nest than darker and maculated shells, which we found in all the parental-female nests.

The comparisons of the mean reproductive success of the different kinds of pairs failed to show major significant differences. Nonetheless, the reproductive success of pairs with a hybrid male and a Hooded Crow female seemed higher than that of the three types of pairs with a hybrid female. The lack of statistical significance could be attributed to a type II statistical error due to relatively small sample sizes and to the high number of comparisons implied in the analysis. Overall, however, hybrid males exhibited a higher reproductive success than hybrid females. Sexual asymmetry in selection against hybrids is known to occur in birds and other animal taxa. Moore and Koenig (1986) showed that hybrid males Yellow-shafted × Red-shafted flickers (*Colaptes auratus auratus* × *C. a. cafer*) sired significantly smaller broods than nonhybrid phenotypes. Alatalo et al. (1990) have shown that pairs involving one hybrid between the Pied and the Collared flycatchers (*Ficedula hypoleuca* and *F. albicollis*) were reproductively disadvantaged when compared to pure parental homospecific and heterospecific pairs. As observed for crows in our study, the disadvantage was more severe for pairs involving a hybrid female and one of the causes of low fledging success was hatching failure. Hybrid males between pairs of *Drosophila* and *Glossina* (Diptera) subspecies are known to be fully or partially sterile (e.g. Dobzhansky 1974, Gooding 1987, 1990, Challier et al. 1990), whereas females are not.

The results of a previous study (Picozzi 1976) carried out inside the Scottish crow hybrid zone are only partly in accord with our findings. In particular, no evidence of assortative mating existed in Scotland, while nonrandom mating was observed in the hybrid zone of the present study. In both studies, no significant evidence of reduced hybrid reproductive success was apparent, but no clear signs of differences in the reproductive performance between hybrid males and females were detected in Scotland (Picozzi 1976). There are at least two major differences between the Scottish and the Alpine hybrid zone. First, in the western Alps the hybrid zone is narrower than that in Scotland. Second, there is no evidence of a geographic shift of the hybrid zone for southern Europe, whereas in Scotland and Jutland the hybrid zone has been moving in this century (Cook 1975, Dybbro 1976, Sharrock 1976). The reasons for the differences in the crow reproduction and in the general features between the two hybrid zones are not clear, but further comparative

TABLE 7. Crow breeding-pair densities (pairs/km²) in sampling areas of allopatric ranges and in hybrid zone in northern Italy.

Density (pairs/km²)	Area	Year	Reference
	Carrion Crow allopatry		
5.5	Stura di Demonte Valley	1990	This study
	Hybrid zone		
5.3, 5.6	Two transects across zone	1988	Durio (pers. comm.)
5.3, 6.0	Two transects across zone	1989	Durio (pers. comm.)
4.7, 6.5	Two transects across zone	1990	Durio (pers. comm.)
	Hooded Crow allopatry		
3.2	Central Po Valley	1979–81	Fasola and Brichetti (1983)
<2.0	Central Po Valley	1979–81	Fasola and Brichetti (1983)
2.2	Central Po Valley	1984	Prigioni et al. (1985)
1.1	Central Po Valley	1985	Prigioni et al. (1985)
1.9	Central Po Valley	1982	Fasola et al. (1988)
7.1	Central Po Valley	1983	Fasola et al. (1988)
3.5	Northern Apennines	1984	Saino and Meriggi (1990)

studies on the reproductive biology as well as on the ecology of crows within and outside the hybrid zones could clarify this point.

Crow hybrid zone and hypotheses on hybrid-zone dynamics.—There are three main findings of the present study: (1) in the areas where parental phenotypes coexisted, they showed positive assortative mating; (2) hybrid phenotypes did not experience a significantly lower reproductive success than parental phenotypes, but some hybrid females suffered peculiar maladies in their reproductive performance; and (3) an asymmetry in reproductive success existed outside the hybrid zone. The two parts of the hybrid zone seemed similar with respect to the reproductive parameters studied.

The main prediction of the dynamic-equilibrium model (Barton 1979a, b, Barton and Hewitt 1981) is the reduced fitness of hybrids. Owing to the small sample size, no clear conclusions can be drawn about the reproductive success of crosses between individuals of the two parental morphs. Indeed, no clear signs of low reproductive success were observed for such pairs. The observation that hybrid females experienced low reproductive success might be considered as proof of depressed fitness of hybrids. However, hybrid-female failures were counterbalanced by slight hybrid-male advantages over the parental phenotypes. The observed difference in the reproductive success between pure parental pairs and pairs containing hybrid individuals (0.2 chicks per nest) was too small to conclude that hybrid fitness was inferior to that of parental pairs. Another prediction of the dynamic-equilibrium model is that the hybrid zone, unless trapped by a density trough or gradient, should shift geographically. The asymmetry existing outside the hybrid zone (assuming isotropic dispersal and equal dispersal rate from the parental populations) should cause the hybrid zone to shift towards the Hooded Crow range. No detailed historical data are available on the position of the hybrid zone in northern Italy. However, data on the origin of specimens in museum collections show that at least during the last century the ranges of the two morphs have remained substantially unchanged (Saino unpubl. data). Therefore, even this prediction of the dynamic-equilibrium model was not supported by the results of our study. The densities of reproductive pairs in the Po Valley and in the Alps are fairly well known (Table 7). The breeding-pair density in the hybrid zone was strictly similar or even higher than those in the areas of allopatry (Table 7), and no density gradient or trough seemed to be involved in determining the geographic stability of the hybrid zone.

The bounded-hybrid-superiority model predicts that ecological factors enhance hybrid fitness in the hybrid zone. Hybrid phenotypes in our study were at a slight reproductive disadvantage with respect to the parental phenotypes, but the differences were not significant. This evidence does not contrast Moore's (1977) bounded-hybrid-superiority model. Furthermore, it should be emphasized that hybrids could have an advantage over parental-type individuals in other phases of their life cycle if, for example, they are better adapted to forage in the hybrid zone (Saino in press).

The theory that hybrid zones are ephemeral phenomena is not assessable for the crow hybrid zone owing to the lack of information about its temporal dynamics. Indeed, the ephemeral-zone hypothesis has been falsified by many examples of hybrid zones that apparently have remained stable and have maintained constant width for relatively long periods (Rising 1970, Littlejohn et al. 1971, Watson 1972, Hunt and Selander 1973; but also see Barrowclough 1980). As Moore (1977) pointed out, stability of the hybrid zones is the rule rather than the exception.

Inferences about the mechanisms that promote the apparent geographic stability, localization and narrowness of the Alpine crow hybrid zone can be drawn by comparing the reproductive success of the allopatric and sympatric populations of the two morphs. The observation that Carrion Crows were more successful in the area of allopatry than within the hybrid zone suggests that a negative selection gradient runs across the hybrid zone that is paralleled by a steep environmental and altitudinal gradient from the alpine valleys to the intensively cultivated plain. No such environmental gradient existed on the other side of the hybrid zone, and Hooded Crows showed very similar reproductive success in the hybrid zone and in allopatry. Therefore, ecological factors seem to have affected reproductive success.

Differences in the foraging ecology of the two morphs in the hybrid zone have been evidenced by Saino (in press), who showed that each of the parental phenotypes in the hybrid zone selected habitats similar to those prevailing in its area of allopatry in northern Italy. Hybrids exploited the available foraging habitats less selectively than parental phenotypes. The role played by ecological features in determining the persistence, position, and narrowness of several hybrid zones has been widely acknowledged both for animals and plants (e.g. see Grant 1971, Moore 1977, Bert and Harrison 1988). The coincidence of the crow hybrid zone in northwestern Italy with an ecotone, and patterns of variation in reproductive success and of foraging-habitat selection, support the idea that the parental populations are adapted to different environments, or that each of them is competitively superior to the other in its own range. The existence of such ecological selection gradients could prevent the area of sympatry and hybridization of the parental morphs from broadening, thus promoting the maintenance of essentially parapatric distributions.

As shown here, selection is not significantly more severe against hybrids than against parental phenotypes within the hybrid zone, but hybrids are presumably less fit outside the hybrid zone. In this sense, the hybrid zone could be considered as the narrow belt, where ecological features are such that hybrids are not at a selective disadvantage with respect to the crows in parental populations. Its narrowness was probably due to the fact that it coincided with an ecotone that was also narrow.

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