There are two distinct groups of crows *Corvus corone* in the Palearctic. The all-black *corone* group (the ‘Carrion Crows’) has two disjunct races: nominate *corone* in the west and *orientalis* in the east. The grey-and-black *cornix* group (the ‘Hooded Crows’) comprises a number of races in northern and eastern Europe, from Corsica and Italy east-

**ABSTRACT** The taxonomic status of Carrion *Corvus corone* and Hooded Crows *C. cornix* is reviewed. As well as the obvious differences in plumage between the two, there is good evidence for non-random mating and reduced fitness of hybrids between Carrion and Hooded Crows, which together provide sufficient evidence for them to be regarded as separate species under most species concepts. Differences in vocalisations and ecology support this distinction. It is therefore recommended that Carrion Crow and Hooded Crow be treated as separate species.
wards, through the Middle East to northern, western and central Asia. These include *cornix*, *capellanus*, *sharpii* and *pallescens*.

**Distribution**

‘Carrion Crow’ *C. c. corone* (Goodwin 1986; Cramp & Perrins 1994; Madge & Burn 1994) is found from England and Wales south to Iberia and the southern slopes of the Alps, and eastwards to Austria (fig. 1). It hybridises with *C. c. cornix* in several areas, including northern Scotland, southern Denmark, parts of eastern Germany and the Czech Republic, along the borders of Austria with Hungary and Slovakia, and in the southern foothills of the Alps. The eastern race, *orientalis*, occurs from Iran north to the Aral Sea, across to the western Altai. Elsewhere in Asia, it is found through south and east Kazakhstan to Kashmir, Sinkiang, Mongolia, central and northern China, Korea and Japan. Farther north, it occurs through the Yenisey valley eastwards to Kamchatka.

‘Hooded Crow’ *C. c. cornix* (Goodwin 1986; Cramp & Perrins 1994; Madge & Burn 1994) occurs in the Faeroes, Ireland and the Isle of Man, northern Scotland, Denmark and Fennoscandia, and east to the Yenisey valley (where it interbreeds with *orientalis*). It also occurs in eastern Germany, Hungary, northwest Romania, northern Croatia, northern Italy and Corsica, and northeast to about 49°N in Russia.

The race *sharpii* is found in Sardinia, Sicily and south mainland Italy; from coastal Croatia east to Romania, and Bulgaria south to Greece (including Crete); through Moldova and Turkey (except in the south), east through southern Ukraine and northern Kazakhstan to the western Altai; and through the Caucasus and northern Iran. It grades into *cornix* in Ukraine, European Russia, and Kazakhstan, overlapping and partly hybridising with *orientalis* in Turkmenistan and Kazakhstan. The race *pallescens* occurs from Cyprus and southeast Turkey to northern Iraq and Egypt. The race *capellanus* occurs in Iraq and southwest Iran.

**Geographical variation**

Within the Carrion Crow group, there is only slight variation (Cramp & Perrins 1994): *orientalis* differs from nominate *corone* by having longer wing, tail and tarsus. In Spain, *corone* is smaller than elsewhere in western Europe, especially in terms of bill depth. By contrast, those *orientalis* from the mountains and north average larger than elsewhere. The bill is slightly longer and more slender in the west, comparatively thicker and shorter in the east, but these differences are slight and clinal: no races other than *orientalis* are generally recognised in the east.

Within the Hooded Crow group, variation is also slight and clinal (Cramp & Perrins 1994),
involving the dimensions of wing, bill and tarsus, and tone of grey feathering. Birds are generally smaller in the south, and paler in the south and east. In northern Europe (including the Faeroes, Scotland and Ireland), *cornix* is typically large, close to nominate *corone* from western Europe in size, with a light ash-grey body. Those from southern and central Europe are slightly darker, and are sometimes separated as 'subcornix'. In Siberia, *cornix* averages paler, but the differences are very slight. The race *sharpii* is equal in size to *cornix*, or slightly smaller, but the grey is distinctly paler. European *sharpii* are larger than those from Asia, especially in terms of bill size: those from the Don, Ural and lower Volga rivers are sometimes separated as 'khazaricus'. Farther south and west, the situation becomes more complex. Birds from Turkey, Caucasus ('kaucasicus') and northern Iran are slightly smaller than *sharpii*, and the grey is slightly darker, intermediate between that of *cornix* and *sharpii*. Variation in the size and colour of birds from Italy through Turkey is slight and inconsistent, so all are usually included in *sharpii*. The race *pallescens* from southern Turkey through the Middle East to Egypt is the smallest race, and the grey corn be even paler than on *sharpii*. Finally, *capellanus* forms the pale end of a cline in colour, being cream or pale silver rather than grey in fresh plumage, and almost white when worn. This taxon is larger than adjacent populations, especially in terms of bill, tarsus and foot size. The throat feathers are rather long, and, as in *orientalis*, the tail is long and graduated. It is, in fact, closely similar to Pied Crow *C. albus*, but the greyish-white is more extensive and the centre of the breast is black. The race *capellanus* is sometimes considered a separate species, but the plumage pattern is similar to that of other races of the *cornix* group, its proportions are rather similar to *orientalis*, and it is said to intergrade with *sharpii* in Iran (Meinertzhagen 1926; Meise 1928; Vaurie 1959).

**Hybrid zones**

The boundary between the *corone* and *cornix* groups is usually sharp, with a narrow zone of hybridisation where birds of both phenotypes and various hybrid forms occur. Outside this hybrid zone, a wider border or introgression zone occurs, in which most birds are typical of one form but where some individuals show influences of the other. Detailed maps of the hybridisation zones between nominate *corone* and *cornix* can be found in Meise (1928), Richter (1958), Cook (1975), Dybbro (1976), Picozzi (1976) and Bährmann (1978). In Asia, *orientalis* and *cornix/sharpii* were perhaps originally well separated and contemporary overlap may be a result of habitat change. The zone of hybridisation here is apparently not stable (see Meise 1928; Vaurie 1954; Korelov *et al.* 1974).

The introgression zone in Scotland has been
mapped twice in the last 40 years, during fieldwork for the two Breeding Bird Atlases (Sharrock 1976; Gibbons et al. 1993). Additional observations were incorporated for the European Atlas (Hagemeijer & Blair 1997), but these are less detailed. Sharrock and Gibbons et al. both show that the hybrid zone is relatively narrow. It moved north and west during the twentieth century, with \textit{corone} displacing \textit{cornix} from the lower (agricultural) land around the North Sea coast of eastern Scotland and restricting it to more upland areas. Relatively little ecological or genetic research on crows has been carried out in this region, however (Picozzi 1975, 1976).

Hybrids show intermediate plumages, with every intergradation between typical all-black and ‘hooded’ birds, often with black dappling on the back and chest (Richter 1958; Melde 1984). Picozzi (1976) separated these into four categories, although the underlying variation is continuous:

1. Black crows. All-black, either pure Carrion Crows or hybrids indistinguishable from these.
2. Dark hybrids. Hybrids which have a dark grey back and/or belly, including those with a grey collar.
3. Pale hybrids. Hybrids with a pale back and belly. These are distinguished from Hooded Crow by uppertail- and undertail-coverts, which are concolorous with the back and belly in Hooded and darker in hybrids.
4. Grey crows. Hooded Crows or hybrids indistinguishable from these.

There is also a zone of hybridisation between \textit{cornix} and \textit{corone} in northern Italy, which was extensively studied in the 1980s and 1990s. Italian researchers (e.g. Rolando 1993) recognised a fifth category of hybrid, between Picozzi’s 2 and 3, for birds which are intermediate between pale and dark hybrids. The Italian studies investigated habitat, pair composition, vocalisations and reproductive success, and the results from these are discussed below. These and other studies have shown evidence of partial ecological segregation and slight behavioural differentiation between \textit{cornix} and \textit{corone}. There is strong evidence of non-random mating in the zones of hybridisation and, in Italy, hybrid progeny reproduce less successfully.

**Habitat preference**

There have been two studies of habitat preference in the Italian hybrid zone. The first (Saino 1992) was undertaken in two areas of Piedmont during the winter of 1989/90. The main habitats were meadows, grazed and ungrazed pastures, cereals and maize. Saino separated the birds into Carrion, Hooded and hybrids, and obtained very similar results in both study areas. Table 1 summarises the results of his highly detailed analyses in terms of the relative frequency of phenotypes in each habitat compared with that expected if the forms were distributed randomly, in an attempt to eliminate the problem of the relative abundance of the three forms. Saino found significant variation among the three types in their habitat use.

These results suggest that Hooded and Carrion Crows differ slightly, yet significantly, in their habitat use. In a separate part of the same hybrid zone, however, Rolando & Laiolo (1994) obtained rather different results. They found less difference between Hooded and Carrion Crows in winter, but marked differ-

<table>
<thead>
<tr>
<th>Table 1. Habitat preference of Carrion \textit{Corvus corone} and Hooded Crows \textit{C. cornix}, and hybrids between the two studied at two sites in northern Italy in winter. Plus (or minus) signs indicate that the form was present at a frequency above (or below) that expected if the birds had been distributed randomly across habitats. * = p&lt;0.05 ** = p&lt;0.01. Data from Saino (1992).</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Carrion</strong></td>
</tr>
<tr>
<td>Site A</td>
</tr>
<tr>
<td>Meadows</td>
</tr>
<tr>
<td>Ungrazed pasture</td>
</tr>
<tr>
<td>Maize stubble &lt;15 cm</td>
</tr>
<tr>
<td>Maize stubble &gt;15 cm</td>
</tr>
<tr>
<td>Recently seeded grass fields</td>
</tr>
<tr>
<td>Cereal</td>
</tr>
<tr>
<td>Ploughed fields</td>
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<tr>
<td>Others</td>
</tr>
</tbody>
</table>

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ences during spring and summer. Table 2 summarises the spring/summer distribution of the two forms in their study. Carrion Crows were found significantly more frequently in maize stubble and meadows treated with manure. Hooded Crows, on the other hand, were significantly more abundant in non-manured meadows and maize fields. Manure treatment comprised scattering dung across the field so that pieces lay on the surface. Birds selectively examined these for the presence of invertebrates. Rolando & Laiolo (1994) noted that the differences between habitats disappeared when meadows were pooled irrespective of fertiliser treatment, and when maize crops were pooled independent of crop state. Since the differences are significant, it is questionable whether pooling these data is valid, and evidence of differential utilisation of habitat between the two taxa still remains. In summary, the results of both of these studies suggest that Hooded Crow is a bird of poorer quality land, a finding which is supported by its displacement by Carrion Crows in northern Scotland following changes in land use during the twentieth century. These ecological differences merit further study.

### Table 2. The proportion of Carrion Corvus corone and Hooded Crows C. cornix observed feeding in a variety of habitats in northern Italy in spring/summer. * indicates that the frequencies are significantly different. Data from Rolando & Laiolo (1994).

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Carrion (m)</th>
<th>significance</th>
<th>Hooded (f)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meadows</td>
<td>54.1%</td>
<td>*</td>
<td>69.3%</td>
</tr>
<tr>
<td>‘Dunged’ meadows</td>
<td>20.6%</td>
<td>*</td>
<td>3.8%</td>
</tr>
<tr>
<td>Maize fields</td>
<td>0.0%</td>
<td>*</td>
<td>4.1%</td>
</tr>
<tr>
<td>Maize stubble</td>
<td>8.7%</td>
<td>*</td>
<td>3.1%</td>
</tr>
<tr>
<td>Plough</td>
<td>9.5%</td>
<td>-</td>
<td>12.8%</td>
</tr>
<tr>
<td>Cereal shoots</td>
<td>7.1%</td>
<td>-</td>
<td>6.9%</td>
</tr>
</tbody>
</table>

### Pair composition

Mated pairs were identified during the breeding season and the phenotype of both partners recorded by Rolando (1993), although he could not distinguish the sexes. In the zone of hybridisation in Italy, there was clear evidence that pair composition was not random (table 3). Omitting the hybrid birds, of which there are small numbers and whose mating preferences are not *a priori* predictable, there is clear evidence of non-random pair composition between Hooded and Carrion Crows (or at least ‘Grey’ and ‘Black’ crows) (table 4). Random pair formation would result in far more mixed pairs than were observed.

Interestingly, fewer of the intermediate forms backcrossed to the black (9) than to the grey (24) crows. This would be expected to be equal, and the difference is significant (p<0.01). This suggests that the visual appearance of the birds is important in mate selection. Hybrid individuals preferentially choose ‘grey’ rather than ‘black’ crows as mates. Since black is, genetically, at least partially dominant (see below), grey hybrids are likely to be closer to ‘pure’ Hoodeds, than black hybrids are to ‘pure’ Car-
rions. Since the progeny of mixed genetic composition are selectively disadvantaged (see below), hybrids which choose a Hooded Crow as a mate will maximise the proportion of ‘Hooded’ genes (~75%), and consequently the fitness, of their progeny. Those that choose a black crow may have a partner with a heterogeneous genetic constitution, and consequently may produce progeny of lower fitness.

Similar evidence for non-random pairing was reported in the zone of hybridisation between Corvus corone and C. cornix in central Siberia (Kryukov & Blinov 1989; Blinov & Kryukov 1992), and between corne and corone in Schleswig-Holstein, Germany (Risch & Andersen 1998). In Siberia, Kryukov and Blinov found an excess of homotypic (like-with-like) pairs, and a deficiency of mixed pairs. Risch & Andersen (1998) recorded the phenotypes of pairs of birds on the island of Amrum, Germany. The island is in a region on the corone side of the hybrid zone, so that grey phenotypes were rare. They found that hybrids and black crows were paired assortatively, again with fewer mixed pairs than would be expected if mating was simply random. Saino (1992) also recorded the composition of groups of crows in the Italian hybrid zone, away from the nest. He examined the composition of groups of two and of more than two birds separately, and in both he found highly significant evidence for a lack of mixing compared with what would be expected at random. He extended this analysis to allow for differences in the distribution of phenotypes across habitats. Even when looking only at meadowland, there was still evidence that the association of phenotypes was not random, with a significant deficiency of mixed flocks of grey and black crows (table 5).

### Composition of populations within the hybrid zone

When the individual colour patterns of the breeding birds reported by Rolando (1993) within the Italian hybrid zone are summed, there is evidence of a deficiency of hybrid...
phenotypes (table 6).

Little is known of the genetics of pigmentation in crows, but Picozzi (1976) recorded the phenotypes of some parents and their broods in the hybrid zone in northern Scotland (table 7). These nests came from the southern (i.e. Carrion Crow) end of the hybrid zone, so grey birds were sufficiently rare that pure Hooded Crows were not present in his study area. He recorded 36 nests over three years, and categorized the birds by phenotype as black (‘Carrion’), dark hybrid, pale hybrid and grey (‘Hooded’; see above). The majority of pale hybrid nestlings occurred in broods where at least one adult was also pale.

Although based on relatively little data, these results support the idea that there is genetic control of plumage colour, with black being dominant over grey. This conforms with other studies of plumage polymorphism where the darker phenotype usually seems to be dominant, for example in Snow Geese Anser caerulescens (Cooke et al. 1995), Arctic Skuas Stercorarius parasiticus (O’Donald 1983) and Rock Dove Columba livia (Murton et al. 1973). Recently, Theron et al. (2001) have shown that melanic plumage in Bananaquits Coereba flaveola (which is also dominant over non-melanic plumage; Wunderle 1981) is perfectly associated with a mutation in the melanocortin-1-receptor gene. It is not possible to be more precise about the finer details of genetic control in crows without information from controlled crosses, but the broad spread of intermediate patterns among hybrids suggests a degree of multi-gene control, rather than the simple pattern of inheritance in skuas, Bananaquits, etc.

With this rather limited knowledge of the genetics of plumage pattern in crows, it is difficult to predict the likely array of phenotypes in a hybrid zone where random mating occurs, but there can be little doubt that, under any genetic model, intermediates should be more abundant. The ‘deficiency’ of hybrids in Rolando’s (1993) data clearly suggests non-random mating and/or some selective disadvantage to the hybrid forms.

Aspects of reproductive biology

Saino & Villa (1992) recorded the breeding performance of pairs of crows across the hybrid zone in northern Italy over a number of years. They recorded the phenotype of each bird as ‘Carrion Crow’ (all black), ‘Hooded Crow’ (black head, throat, breast, wings and tail) or ‘hybrid’ (intermediate between the two in amount or extent of black feathers in the body plumage). They separated the area into three parts: the hybrid zone, and the areas on either side where only Hooded or Carrion Crows were found (i.e. ‘in allopatry’). They recorded the composition of each pair, and (where possible) the clutch size and the number of chicks which fledged successfully (table 8).

a. Clutch size of Carrion and Hooded Crows in northern Italy

Saino & Villa (1992) found no evidence of variation in clutch size across years, so they pooled their data relating to clutch size of individual pairs (table 8, a). It is possible that, in some instances, the same pairs were recorded in successive years, so the data may not be entirely independent, but the effects of this are likely to be slight. Although there is evidence that hybrid females laid fewer eggs than either Carrion or Hooded Crows in the hybrid zone, the differ-
ences are not statistically significant. The ‘hybrid’ category will be heterogeneous, including birds recorded by Rolando (1993) as pale or dark hybrids. It is interesting to note that the variance of clutch size for hybrids is higher than that for Carrion or Hooded Crows, either in allopatry or in the hybrid zone. ‘Variance’ is an estimate of variability which, in a trait such as this, can be genetic, environmental or (usually) a combination of the two.

b. Egg volume of Carrion and Hooded Crows in northern Italy
Using essentially the same criteria, Saino & Bolzern (1992) showed that, unlike clutch size, egg volume varies significantly among phenotypes (table 8, b). They found evidence of bimodality in hybrids and (again) the variance is higher in this category.

Comparing egg volume by phenotype shows that Carrion Crows outside the hybrid zone (in allopatry) laid significantly larger eggs than those in the hybrid zone. Furthermore, inside the hybrid zone, Carrion Crows laid significantly larger eggs than Hooded Crows, and both Hooded and Carrion Crows laid significantly larger eggs than the hybrids. As with clutch size, the variance of the egg volume of hybrids is greater than for either parental form, whether inside or outside the hybrid zone.

c. Reproductive success of Carrion and Hooded Crows in northern Italy
Saino & Villa (1992) reported the number of chicks which were reared to ‘about the age of fledging’ in the three areas. They found that female Carrion Crows outside the hybrid zone reared significantly more young than either hybrids or Hooded Crows, whether inside or outside the hybrid zone. Hybrids reared significantly fewer young than Hooded Crows inside or outside the hybrid zone (table 8, c).

Male Carrion Crows outside the hybrid zone reared significantly more young than those inside the zone, and significantly more than Hooded Crows in either area, although other comparisons were not significant (table 8, d). In both sexes, hybrids showed a higher variance in brood size than did either parental form.

In a similar study, Saino & Bolzern (1992) reported chick survival in another part of the hybrid zone in Italy (table 8, e). They estimated the proportion of the clutch that survived to fledge, which is effectively the probability of each egg in the nest becoming a fledged bird. They related this back to the phenotype of the female parent, and again examined the areas separately across the hybrid zone. They found that the fledging success was significantly higher for Carrion Crows in allopatry; no other significant differences were found, although the value for hybrids was lower than for the other categories. Yet again, the variance was higher for hybrids. Interestingly, Saino & Villa (1992) described, albeit anecdotally, the presence of abnormal eggs in five nests of hybrid females. These included unusual, or even a complete lack of pigment in the shells. They also reported that shells were brittle, such that most of them broke during incubation and thus failed to hatch. Nothing akin to this was found among Hooded or Carrion Crow pairs nesting in the same hybrid zone. The sample sizes concerned were too small for these differences to be statistically significant.

Vocalisations
The acoustics of birds may give an indication of their phylogenetic relationships. In particular, playback experiments can assist in the clarifica-

<table>
<thead>
<tr>
<th>Trait</th>
<th>CC allopatry</th>
<th>CC sympatry</th>
<th>Hybrids</th>
<th>HC sympatry</th>
<th>HC allopatry</th>
<th>Ref</th>
</tr>
</thead>
<tbody>
<tr>
<td>a Clutch size</td>
<td>4.4 (0.09) 118</td>
<td>4.7 (0.13) 41</td>
<td>4.2 (0.20) 29</td>
<td>4.5 (0.09) 88</td>
<td>4.5 (0.09) 114</td>
<td>1</td>
</tr>
<tr>
<td>b Egg volume</td>
<td>18.7 (0.08) 447</td>
<td>18.2 (0.12) 163</td>
<td>17.3 (0.21) 104</td>
<td>17.9 (0.10) 334</td>
<td>17.7 (0.09) 459</td>
<td>2</td>
</tr>
<tr>
<td>c Chicks/female</td>
<td>3.1 (0.11) 91</td>
<td>2.5 (0.19) 37</td>
<td>1.6 (0.28) 24</td>
<td>2.6 (0.13) 89</td>
<td>2.6 (0.12) 118</td>
<td>1</td>
</tr>
<tr>
<td>d Chicks/male</td>
<td>3.1 (0.11) 91</td>
<td>2.3 (0.20) 41</td>
<td>2.7 (0.33) 20</td>
<td>2.5 (0.13) 84</td>
<td>2.6 (0.12) 118</td>
<td>1</td>
</tr>
<tr>
<td>e Survival/female</td>
<td>0.71 (0.027) 75</td>
<td>0.53 (0.045) 35</td>
<td>0.38 (0.067) 24</td>
<td>0.57 (0.030) 81</td>
<td>0.56 (0.027) 101</td>
<td>2</td>
</tr>
</tbody>
</table>

References:
1 Saino & Villa (1992); 2 Saino & Bolzern (1992)
tion of taxonomic status (e.g. Irwin et al. 2001). Playback studies have not been undertaken with Hooded and Carrion Crows, but sonogram analyses have been reported by Palestrini & Rolando (1996) examined the characteristics of a call comprising a short series of ‘caws’ separated by short intervals. These were analysed by dissection of the sonograms, recording caw duration, lowest and highest frequency, harmonic duration and total frequency range. These were then examined both individually and by discriminant function analysis (DFA). Data were collected from an area where Hooded and Carrion Crows occurred in sympatry, but insufficient recordings were available from hybrids for these to be included in the analysis. Palestrini & Rolando found significant differences in five of the six parameters, and DFA permitted Hooded and Carrion Crows to be differentiated on their acoustic characters. They suggested that these differences might be ecological or geographic rather than taxonomic, but presented no evidence in support of this. In some species, acoustics have been shown to covary with body size (e.g. larger birds having deeper voices); there was no evidence of this for the crows, either within or between taxa. There is also no evidence as to whether the two taxa themselves can differentiate between their calls.

Molecular studies
The molecular research undertaken into this group has been limited and piecemeal. Most work has involved birds from Siberia in the hybrid zone between Hooded Crows of the race cornix and Carrion Crows of the race orientalis. Chelomina et al. (1991) examined restriction fragment variation in nuclear DNA from Hooded and Carrion Crows and their hybrids. A subsequent investigation (Kryukov et al. 1992) extended this to include an electrophoretic investigation of serum proteins. Neither they nor Saino et al. (1992) discovered any major differentiation between the parental forms, although Kryukov et al. (1992) reported that ‘new variants’ were identified among the hybrids in albumin, post-transferrin and esterase. It is, however, possible that these also occur among the parental forms but that the samples were simply too small to detect them. A further study, based upon DNA fingerprinting (Ufyrkina et al. 1995), found considerable variation among 15 Hooded and Carrion Crows and hybrids from the area of sympatry in Siberia. There were, however, no diagnostic DNA fragments, and the genetic structure of the hybrid population was consonant with panmixia, despite field evidence of assortative mating. Once again, however, the sample sizes were too small for detailed analysis to be possible. Chelomina et al. (1995) claimed to find further evidence of difference in patterns generated using a slightly different technology. They suggested that Hooded Crows (cornix) from Novosibirsk and Large-billed Crows C. macrorhynchos from Sakhalin were more similar

![Image of a Carrion Crow](image_url)
to each other than either was to Carrion Crows (orientalis) from Sakhalin. Although this suggests that Hooded and Carrion Crows might have diverged genetically, the sample sizes again are small and the data hard to interpret.

A more extensive study by Kryukov & Suzuki (2000) examined the DNA sequence of a short fragment (336 bp) of the cytochrome b gene in a series of individuals from Paris, France, to Hokkaido, Japan. They found uniformity in sequence from France (corone) across eastern Europe and western Siberia (cornix) and through to northern Sakhalin (orientalis). Inter-population differentiation was between 0 and 2.5%, although this is difficult to assess since they do not give detailed results. Birds from southern Sakhalin, from the far southeast of Siberia (Primorye) and from northern Japan showed similarly limited differentiation, although (again) the extent of this is not entirely clear from their data. Nonetheless, Kryukov & Suzuki reported that birds from the two regions (southern Sakhalin/Japan and the rest of Eurasia) are strikingly different in their DNA sequences. They found 4-8 substitutions (in c. 330 bases) between the birds on either side of a divide in central Sakhalin, although this is based upon fewer than ten individuals. It would be preferable to see more individuals in the analysis (especially since they also suggested that at least one sequence was found on both sides of the divide). A more detailed analysis, involving a longer sequence of the cytochrome b gene or a more variable region such as the ‘D-loop’, is required.

To some extent, this has been provided by Kryukov & Odati (2000) in a phylogenetic analysis of various species of corvid, using about 1000 bp of cytochrome b, although again the number of individuals was limited. In a study which included 12 other species, they analysed one each of corone (Paris), orientalis (southern Primorskiy, Russia), orientalis (Sakhalin) and cornix (Moscow). Their analysis indicates that corone and cornix are sister-taxa, but that the two orientalis samples are not: the Sakhalin sequence clusters with corone/cornix, but that from Primorye is more different. ‘Carrion Crows’ from Japan and adjacent parts of eastern Asia may be genetically divergent from the rest of the taxon ‘orientalis’, but much more research is needed to resolve this.

**Diagnosability**

The black and grey forms of adult C. corone/cornix are documented thoroughly in Cramp & Perrins (1994). In summary, corone is completely black, and the grey forms of the cornix group have the head, tail and wings black, while the nape, sides of neck, back and shorter uppertail-coverts are ash-grey. In juvenile corone, the entire body is dull, sooty black, apart from the head, which has a slight oily gloss. The mantle, scapulars, tail-coverts and median coverts have glossy purplish-black tips, and light grey feather-bases may be visible, especially on the mantle and rump. The underparts are matt black, although again grey
feather-bases may be visible. The remiges, rectrices, greater wing-coverts and alula are black, less intensively glossed than in adults. The head, tail and wing of juvenile cornix are similar to those of corone, but the lesser and median upper- and underwing-coverts are grey, with dull black towards the tips. The body is grey, tinged brown on the upperparts, and appears less uniform than in adults. The remainder of the underparts are light brownish-grey.

Discussion

Helbig et al. (2002) discussed operational criteria for the assignment of specific rank to avian taxa. They recognised that populations will remain distinct only if they are reproductively isolated to the extent that their gene pools do not merge. Such populations can be regarded as following separate evolutionary trajectories, in line with the Evolutionary Species Concept (Mayden 1997) or General Lineage Concept (de Queiroz 1998). Thus, Carrion and Hooded Crows should be regarded as separate species if barriers to gene flow can be demonstrated. These barriers might be prezygotic, such as differences in courtship behaviour or species recognition through vocalisations. Alternatively, they might be postzygotic, for example if hybrids show reduced fitness. Sympatric or parapatric taxa are easier to deal with since the frequency and consequences of hybridisation can sometimes be recorded directly. Care is needed, however, to distinguish between hybrid zones and clinal variation. In the latter, when two morphologically differentiated taxa come into contact, there may be a smooth and clear transition from one through to the other. Such a situation is typified by a gradual change in the phenotypic composition of the populations from one extreme to the other, as exemplified by many species conforming to Bergmann’s or Allen’s biogeographic rules. A hybrid zone is clearly distinct when populations across the zone of transition include both parental forms as well as hybrids.

Diagnosability

‘Pure’ Hooded and Carrion Crows are diagnosable in both adult and juvenile plumages, but hybrids show varying degrees of intermediacy. It could be argued that hybridising taxa can never be 100% diagnosable since there will always be intermediates which do not meet the diagnostic criteria of either parental taxon. The hybrid zones of crows are somewhat mosaic, but it seems that many local populations within these zones contain not only hybrids, but also more or less of the ‘pure’ phenotypes, or at least birds which are indistinguishable from these, found outside the hybrid zone. Consequently, they differ from clines where the populations change progressively from one phenotype to the other, and are more akin to the ‘bimodal hybrid zone’ of Jiggins & Mallet (2000). In the light of this pattern of variation within a hybrid zone, the Biological Species Concept would regard
Hooded and Carrion Crows as semispecies, whereas the Evolutionary and Phylogenetic Species Concepts would treat them as specifically distinct.

The molecular studies are insufficient to support this, however. Nonetheless, the markers which have been used (enzymes, DNA fingerprinting and the mitochondrial cytochrome *b* gene) are less sensitive to slight genetic differentiation, and a lack of difference across the hybrid zone is unsurprising. More rapidly differentiating markers, such as microsatellites or the mitochondrial control region, might be more appropriate to such relatively recent divergences.

**Ecological/behavioural differentiation**

Taxa can be regarded as specifically distinct if there are intrinsic barriers to gene flow which ensure that the gene pools do not merge. There is strong evidence for prezygotic barriers between Hooded and Carrion Crows, at least in

198 & 199. A range of hybrid crows *Corvus corone* × Hooded Crow *C. cornix*, Northeast Scotland, 1967. Although rather grisley, these two photos illustrate the variability of hybrid types in the Northeast Scotland hybrid zone, grading from black to grey. The dark hybrids in particular are subtle, and only close views reveal the evidence of mixed parentage.
northern Italy. Although sympatric, they show partial ecological separation at some times of the year. In two separate valley systems in the region, there were consistent and statistically significant differences in distribution between meadows and maize fields. There were differences in flock composition, with a deficiency of mixed flocks even within the same habitat (meadow). Finally, pair formation was distinctly non-random; in three different studies, fewer mixed pairs were recorded than would be expected given random mating patterns. In one study (Rolando 1993), birds of intermediate plumage mated preferentially with the grey phenotype rather than with the black.

We have argued that plumage colour is under genetic control. Consequently, the positive assortative mating which Rolando demonstrated would in itself produce a deficiency of intermediate phenotypes in the population, even without differences in fitness. Theoretical population genetics (e.g. Crow & Kimura 1970) tells us that positive assortative mating leads to a steady decrease in heterozygosity until an equilibrium is reached which depends upon the strength of the assortment. If the hybrids have reduced fitness, then any genetically determined behavioural attribute which reduces the likelihood of mixed pairings will be selectively advantageous. Such ‘isolating mechanisms’ will be favoured since progeny resulting from homotypic pairs will survive better and carry any genes which caused the positive assortative mating in the first place (e.g. Butlin 1989).

**Fitness of the hybrids**

The Italian studies examined several aspects of reproductive success, including clutch size, egg volume, number of chicks raised to fledging, and the probability of survival to fledging of individual eggs. Although there were no statistical differences in clutch size, hybrid females laid fewer eggs than did either ‘parental’ form in the hybrid zone, and the variance of the hybrids was much higher. Egg volume differed significantly among phenotypes. Hybrid crows laid smaller eggs than did either parental form in the hybrid zone. There was no difference between Hooded Crows inside and outside the zone, but Carrion Crow eggs were significantly smaller inside the hybrid zone, compared with those outside it. If egg volume reflects the provision of nutrients for the developing embryo, these differences might have considerable biological significance. These results are summarised in table 9, where each character is ranked from 1 to 5 across the five categories of crow. For example, clutch size is highest for Carrion Crows inside the hybrid zone (rank = 1) and lowest for hybrids (rank = 5).

There is a degree of consistency in these rankings across fitness parameters which can be analysed statistically using Kendall’s coefficient of concordance (W). Carrion Crows outside the hybrid zone tend to have the highest fitness and hybrids the lowest, although overall the result is not significant (W = 0.40, p>0.05). The data are, however, slightly heterogeneous: four of the parameters are essentially ‘female’ – clutch size and egg volume are both maternal characters, and two of the measures of chick survivals (from different studies) are related to the phenotype of the mother. In addition, of course, there is non-random mating between the sexes so the phenotypes of the parents are correlated. If we omit the data relating to paternal phenotype, we have four aspects of female fitness, and these are significantly concordant (W = 0.59, p<0.05). Female Carrion Crows outside the hybrid zone have the highest fitness; hybrids (which live inside the hybrid zone) have the lowest.

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Table 9. This table shows the data from each row of table 8 converted to ranks: 1 = largest value, 5 = smallest. The mean rank for all five variables is given, and also the mean rank based upon the female parent only (i.e. rows a, b, c and e). See text for details.

<table>
<thead>
<tr>
<th>Trait</th>
<th>CC allopatry</th>
<th>CC sympatry</th>
<th>Hybrids</th>
<th>HC sympatry</th>
<th>HC allopatry</th>
</tr>
</thead>
<tbody>
<tr>
<td>a  Clutch size</td>
<td>4</td>
<td>1</td>
<td>5</td>
<td>2.5</td>
<td>2.5</td>
</tr>
<tr>
<td>b  Egg volume</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>c  Chicks/female</td>
<td>1</td>
<td>4</td>
<td>5</td>
<td>2.5</td>
<td>2.5</td>
</tr>
<tr>
<td>d  Chicks/male</td>
<td>1</td>
<td>5</td>
<td>2</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>e  Survival/female</td>
<td>1</td>
<td>4</td>
<td>5</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Mean Rank</td>
<td>1.6</td>
<td>3.2</td>
<td>4.4</td>
<td>2.8</td>
<td>3.0</td>
</tr>
<tr>
<td>Females only</td>
<td>1.75</td>
<td>2.75</td>
<td>5.0</td>
<td>2.5</td>
<td>3.0</td>
</tr>
</tbody>
</table>
Ranking of variances

We can also examine the variation in reproductive characters within the five groups of birds (table 10). The best estimate of this is the variance, which reflects the variability of individuals within a sample, and can be determined from the data in the original papers. These also show a striking consistency (W = 0.77, p<0.01), a result which is not affected by omitting the ‘male’ character. In general, hybrids have the highest variance (i.e. are most variable), followed by Hooded Crows outside the hybrid zone, Hooded Crows inside the hybrid zone are next, and the least variable (most uniform) are Carrion Crows, both inside and outside the hybrid zone.

It has long been known (e.g. Dobzhansky 1951) that crosses of individuals from different populations often show differences in ‘fitness’ (fecundity, fertility, longevity, etc.) compared with crosses within the same population. This has been demonstrated experimentally (e.g. Vetukhiv 1956), and has been explained as follows. Populations become adapted to the area which they inhabit, owing to natural selection. One form (allele) of a gene (A) is favoured in locality L_A and spreads through that population, and another allele (B) in locality L_B spreads there. This may happen for several (or many) genes so that the two populations diverge in genetic structure. But genes do not act in isolation, and the effect of replacing A with B may have secondary effects upon other genes functioning elsewhere in the animal’s body. These genes will also be selected, so that the entire genetic structure of the population evolves to produce a harmonious array of genes and alleles (a ‘coadapted gene complex’) which interact to produce a functioning organism, well adapted to exist in that place. Crossing individuals from different populations will result in ‘hybrid’ progeny and cause the coadapted complexes to begin to break up. In successive generations, progeny are produced.

<table>
<thead>
<tr>
<th>Trait</th>
<th>CC allopatry</th>
<th>CC sympatry</th>
<th>Hybrids</th>
<th>HC sympatry</th>
<th>HC allopatry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clutch size</td>
<td>0.956 2</td>
<td>0.693 5</td>
<td>1.160 1</td>
<td>0.713 4</td>
<td>0.923 3</td>
</tr>
<tr>
<td>Egg volume</td>
<td>2.861 4</td>
<td>2.347 5</td>
<td>4.586 1</td>
<td>3.340 3</td>
<td>3.718 2</td>
</tr>
<tr>
<td>Chicks/female</td>
<td>1.101 5</td>
<td>1.336 4</td>
<td>1.882 1</td>
<td>1.504 3</td>
<td>1.699 2</td>
</tr>
<tr>
<td>Chicks/male</td>
<td>1.101 5</td>
<td>1.640 3</td>
<td>2.178 1</td>
<td>1.420 4</td>
<td>1.699 2</td>
</tr>
<tr>
<td>Survival/female</td>
<td>0.0547 5</td>
<td>0.0709 4</td>
<td>0.1077 1</td>
<td>0.0729 3</td>
<td>0.0736 2</td>
</tr>
<tr>
<td>Mean Rank</td>
<td>4.2 4.2</td>
<td>1.0 3.6</td>
<td>2.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female only</td>
<td>4.0 4.2</td>
<td>1.0 3.25</td>
<td>2.25</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
which contain varying proportions of alleles from each parental population, to give increased variability. This disruption of the genetic structure in subsequent generations has been shown experimentally to have profoundly debilitating effects upon fitness. The situation which we observe in the crows is akin to this. Hybrids are much more variable, and often inferior – for example in clutch size, shell thickness and chick survival. It is strong evidence that the genetic structure of Hooded and Carrion Crows differs by more than just the colour of their feathers, and the increased variance within the area of overlap indicates a hybrid zone rather than a cline.

In the case of the crows, there are few data relating to the post-fledging survival of nestlings, but there is certainly evidence of differences prior to fledging. In separate studies, hybrid females have been shown to lay fewer and smaller eggs, and to rear fewer progeny to fledging than the parental forms. Although there was little difference in chick survival between Hooded (i.e. ‘grey’) Crows inside and outside the hybrid zone, it is striking that, in these studies, Carrion (i.e. ‘black’) Crows inside the hybrid zone performed less well than outside. If the genetic model suggested above is broadly correct, and black is at least partly dominant over grey in the hybrid zone, the black Carrion Crow phenotype might mask a variable fraction of recessive ‘Hooded’ genes. On the other hand, the recessive nature of the Hooded phenotype will be less likely to conceal a genetic contribution from a Carrion Crow ancestor. It is, therefore, perhaps not surprising that black crows inside the hybrid zone will reveal a pattern of fitness intermediate between that of ‘pure’ Carrion Crows and undoubted hybrids. These patterns also lend support to the fitness differences observed between hybrids and parental forms. These again presumably reflect genetic differentiation between Hooded and Carrion Crows on either side of the hybrid zone. Where these birds come into contact, there is some hybridisation. The crows which are produced are likely to be intermediate in phenotype. The genetic dominance of the black alleles will mean that hybrid birds will tend towards the Carrion (‘black’) Crow phenotype, yet they contain alleles from both populations.

Whether the reduced viability of hybrid and ‘backcross’ crows extends beyond the nestling stage is not known. There was, however, a deficiency of intermediate phenotypes among the adults recorded in the hybrid zone by Rolando (1993). Perhaps it is not surprising that non-random mating has evolved in these regions. Hybrid progeny are selectively disadvantaged, so any behavioural characters which result in assortative mating will spread in the hybrid zone (Butlin 1989).

Conclusions and recommendations

The differences in plumage, the non-random mating and the reduced fitness of hybrids are sufficient to regard Hooded and Carrion Crows as specifically distinct under most species con-
cepts (Helbig et al. 2002). The differences in vocalisations and ecology support the differentiation but are, of themselves, not sufficient. Under the Biological Species Concept, they would be treated as ‘semispecies’, because gene flow occurs constantly between them, albeit counteracted by assortative mating and natural selection (the reduced fitness of hybrids). The deficiency of mixed pairs indicates a strong prezygotic barrier to gene flow which is reinforced by the fitness differences between the parental and hybrid phenotypes. These differences would also support taxonomic separation of the two types under most species concepts.

It is recommended that Hooded and Carrion Crow be treated as separate species. As they overlap locally with only limited hybridisation, Russian authors (e.g. Korelov et al. 1974, Stepanyan 1990) consider the two groups to be full species; orientalis is then usually combined with the corone group into a single species C. corone, which comprises two races. Nominate corone and orientalis may, however, be less closely related to each other than nominate corone is to cornix (Eck 1984); and the limited molecular results from eastern Asia (Kryukov & Odati 2000; Kryukov & Suzuki 2000) lend some support to this. The form capellanus, which in some structural characters is closer to orientalis than to cornix, may form a fourth group in the corone complex (Cramp & Perrins 1994), while Collared Crow C. torquatus (synonym C. pectoralis) from China, which is similar to orientalis, may form a fifth. There are, however, few data at present to support these observations. Until further data emerge, it is perhaps wise to err on the side of conservatism and to retain orientalis as a subspecies of C. corone.

References


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