THE DIET OF THE CHOUGH (*PYRRHOCORAX PYRRHOCORAX*) AND THE ALPINE CHOUGH (*PYRRHOCORAX GRACULUS*) IN THE ALPS: SEASONALITY, RESOURCE PARTITIONING AND POPULATION DENSITY

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RÉSUMÉ

Les régimes alimentaires en hiver et au printemps du Crave à bec rouge (*Pyrrhocorax pyrrhocorax*) et du Chocard des Alpes (*Pyrrhocorax graculus*) dans l'ouest des Alpes italiennes ont été étudiés par analyse des féces. Des études antérieures, conduites dans la même zone de syntopie en été et automne ((Rolando & Laiolo, 1997 ; Rolando *et al.*, 1997a), ont montré que les régimes et les modalités de la recherche alimentaire de ces espèces peuvent souvent diverger mais c'est essentiellement durant les mois d'hiver que les différences interspécifiques sont les plus grandes. De décembre à mai, le régime du Crave est essentiellement basé sur les larves et pupes de Diptères alors que celui du Chocard s'avère plus variable, consistant principalement en fruits en hiver et, au printemps, en arthropodes et feuilles de *Sempervirum arachnoideum*. Le Crave et le Chocard diffèrent aussi dans l'organisation de leurs temps de recherche alimentaire, le premier restant plus longtemps sur ses sites de prospection. La plus grande flexibilité trophique du Chocard paraît résulter d'un comportement opportuniste qui lui permet d'exploiter chaque mois la ressource la plus profitable. Les largeurs de niches globales sont virtuellement identiques, les deux espèces exploitant sensiblement le même nombre de catégories de ressources. Toutefois, les ressources étant souvent différentes, le recouvrement des régimes est quasi nul en hiver, augmentant à partir de mars. Les régimes alimentaires sont discutés en fonction du statut de ces espèces dans les Alpes. Il est en particulier suggéré que le régime essentiellement végétarien du Chocard serait associé à ses fortes densités de population alors que le régime insectivore du Crave serait lié à ses faibles densités.

SUMMARY

We investigated the diet of the Chough (*Pyrrhocorax pyrrhocorax*) and Alpine Chough (*Pyrrhocorax graculus*) during winter and spring in the western Italian Alps by faecal analysis. Earlier studies conducted in the same area of syntopy in summer and autumn (Rolando & Laiolo, 1997; Rolando *et al.*, 1997a) have shown that diet and foraging behaviour of these species may often diverge, but it is especially in winter months that interspecific differences reach the highest levels. From December to May Chough diet mainly consisted of fly larvae and pupae, while Alpine Chough diet was found to be more variable overall, largely consisting of berries in winter and Arthropods and houseleek leaves in spring. Chough and Alpine Chough also differed in foraging times (the former staying longer in patches). The

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greater trophic flexibility of the Alpine Chough appears to result from its opportunistic behaviour which allows this species to exploit the resource that is more profitable in each month. Overall niche breadth values were virtually identical, with the two species feeding upon approximately the same number of resource items. However, since resources were often different, the overlap between the diet of the two species was close to zero in winter, increasing from March onward. Diets are discussed with respect to the different status of these species in the Alps. In particular it is suggested that the mainly vegetarian diet of the Alpine Chough might be associated with its high population densities while the insectivorous diet of the Chough might be associated with its low population densities.

INTRODUCTION

The Chough (*Pyrrhocorax pyrrhocorax*) and the Alpine Chough (*Pyrrhocorax graculus*) coexist over much of their ranges and occur in the same habitats (Goodwin, 1986). The species do, however, exploit different resources in a different fashion, at least in summer and autumn: previous studies have indicated that the short-billed Alpine Chough almost entirely forages on the surface, whilst the long and curved-billed Chough normally probes deeply in soil (Rolando *et al.*, 1997a). This behavioural divergence is associated with low trophic niche overlap, especially in the autumn months when the Chough digs out invertebrate prey and the Alpine Chough mainly relies on berries (Rolando & Laiolo, 1997). Insect prey caught by the Chough apparently provide more energy than the vegetable food collected by the Alpine Chough, but if we consider the energy required in food collection, which is, in turn, related to abundance and ease of capture, the trophic niche of the Chough is not more profitable than that of the Alpine Chough (Rolando & Laiolo, 1997). The coexistence of Chough and Alpine Chough in the Alps therefore seems to be associated with a certain degree of partitioning and different utilisation of resources. In addition the two species do not show any propensity to associate in mixed flocks, probably since flocking associations (Rolando *et al.* 1997b) achieve no benefit.

In the Alps the Chough and the Alpine Chough greatly differ in population size. The former is a rare bird, while the latter is common and widespread, reaching high population densities in some localities (Mingozzi *et al.*, 1988; Cucco *et al.*, 1996). Diet, sensu the trophic position of the species, is one characteristic that permits the prediction of population density in many mammal and bird species: for a given body size, a species relying on resources at high trophic level has less overall energy available than a species feeding on resources at low trophic level and, as a consequence, the former should maintain lower densities (Lindeman, 1942; Eisenberg, 1981; Eisenberg & Thorington, 1973; Juanes, 1986; Robinson & Redford, 1986; Damuth, 1987; Silva & Downing, 1995). In addition, more food per unit of area should be available to herbivorous species than to frugivorous ones (specialized on fruiting parts of the plant), which, in turn, rely on a more abundant food source than granivores (seeds are only part of the fruiting structure); insectivores, which are secondary consumers, and carnivores, which are often tertiary consumers, are reliant on even scarcer resources (Eisenberg, 1981; Robinson & Redford 1986). Many studies carried out on birds and mammals have demonstrated that primary consumers (herbivorous, frugivorous and granivorous species) maintain higher densities than secondary and tertiary ones (insectivorous, carnivorous) of the same size (Robinson & Redford, 1986; Silva & Downing, 1995; Silva *et al.*, 1997).

The aims of this study were: 1) to describe the foraging ecology of the Chough and the Alpine Chough in winter and spring, 2) to analyse the intraspecific temporal variation in diet and 3) to establish the degree of interspecific food niche segregation. Additionally, an attempt was made to discuss the possible consequences of foraging ecology on densities of the two species in the Alps.

STUDY AREA AND METHOD

DIET

Diets of sympatric and syntopic Chough and Alpine Chough were investigated in the central Aosta Valley, in the Rhêmes Valley and in the Savarenche Valley (western Italian Alps). The major habitats consist of alpine meadows and mountain cliffs at high altitude and coniferous or mixed woodland interspersed with cultivated fields and small urban areas at lower altitudes. During the breeding season the two species remain above the tree line, but after the first snowfalls (usually occurring in November) the birds come down to lower level grounds to feed in snow free patches (Rolando *et al.*, 1997a; Laiolo *et al.*, 1997).

Foraging Chough and Alpine Chough were observed from suitable vantage points and only fresh droppings were gathered. A total of 1 216 fresh faecal samples (436 of the Chough and 780 of the Alpine Chough) were collected during winter and spring (December to May) in both 1993 and 1994.

Following Rolando & Laiolo (1997), droppings were first dried and then washed in a Petri dish and examined under a binocular microscope (magnification up to 50 X). Food items were identified with the aid of reference collections or with the use of identification keys (Baroni, 1977; Chinery, 1987; Grandi, 1984, Eisenbeis & Wichard, 1987).

The quantification procedure we followed consisted of establishing the number and the relative volume of the different food categories within each sample. A unit volume was determined for every item by calculating the mean value of 30 samples of each item collected in the field, so that we did not consider the volume of remains in faeces, but the actual size of the entire item consumed. Numbers of specimens occurring in each faecal samples were usually estimated on the basis of the number of mandibles or heads (for arthropod prey) and the number of seeds or root bases (for fruits and bulbs respectively). This methodology allowed us to calculate for each faecal sample the relative percentage volume of each item. Therewith, following Kruuk (1989), as an estimate of food composition in droppings we used the Volume Percentage (V %) of a food source, calculated using the equation: $V\,\% = U\,\% \times W\,\%/100$ where U % is the percentage of occurrence (the number of times a particular food source was found in faeces divided by the total number of faeces examined) and W % is the mean of the relative volumes each item had in the faeces in which it occurred.

To compare directly the diets of the two species (and to allow comparison with other studies) we used the same level of taxonomic precision, this was set on the basis of Orders.

Interspecific niche overlaps were estimated monthly using Colwell & Futuyma (1971) index $C = 1 - 1/2 \Sigma |p_{ij} - p_{hj}|$, where p_{ij} and p_{hj} are the proportions (of volume) of the class j in the diet of species i and h; the potential measure of overlap can range from 0 (no resource used in common) to 1 (complete overlap). The above calculation was also used to estimate, for each species, the variation between the diets in consecutive months and the degree of auto-overlap; the month-to-month variation thus calculated was used to evaluate the degree of intraspecific temporal variation in diet.

The calculation of the trophic niche breadth was done using the Shannon-Weaver diversity index (B) with the equation $B = - \Sigma p_i \log p_i$, were p_i is the proportion (of volume) of class i in the diet. The index was calculated monthly on each species dietary data.

FORAGING TIMES

Birds were observed with telescopes at a magnification of X15-45 and the foraging times — or stay times, i.e. the time the focal bird foraged in a site before flying to another patch (over 50 m away) — were timed with a stopwatch. A total of 3 078 stay times (895 for the Chough and 2 183 for the Alpine Chough) were recorded. For each species a multiple regression analysis was performed on stay times using four predictor variables (month, temperature, elevation of the foraging patch, flock size). Before computing parametric tests, data were log-transformed to attain normality.

RESULTS

DIET

The detailed composition and the variation of the two species' diet during winter and spring months are shown in Table I. The diet differed significantly between the two species in every month (G-tests computed between the diets of the two species in each month: December $G = 576.8$, d.f. = 13, $P < 0.001$, January $G = 428.1$, d.f. = 14, $P < 0.001$, February $G = 162.5$, d.f. = 14, $P < 0.001$, March $G = 293.1$, d.f. = 14, $P < 0.001$, April $G = 220.9$, d.f. = 14, $P < 0.001$, May $G = 35.4$, d.f. = 14, $P < 0.01$). Chough diet consisted mainly of invertebrate prey, which constituted more than 90 % of diet volume throughout the study period (Fig. 1). The volumetrically dominant animal taxa were fly larvae and pupae. Bibionidae larvae featured prominently in every month, the highest volume percentage being in December (70.7 %). The Chough also consumed a range of beetles (the highest-ranking items being Chrysomelidae, Scarabaeoidea and Cantharidae larvae), with their amount in faeces being greater than 20 % in February, March and May. Other arthropod prey (such as caterpillars, earwigs, bugs and spiders) occurred rarely in the diet. Vegetable matter (in the form of *Gagea* bulbs) occurred occasionally in the faeces.

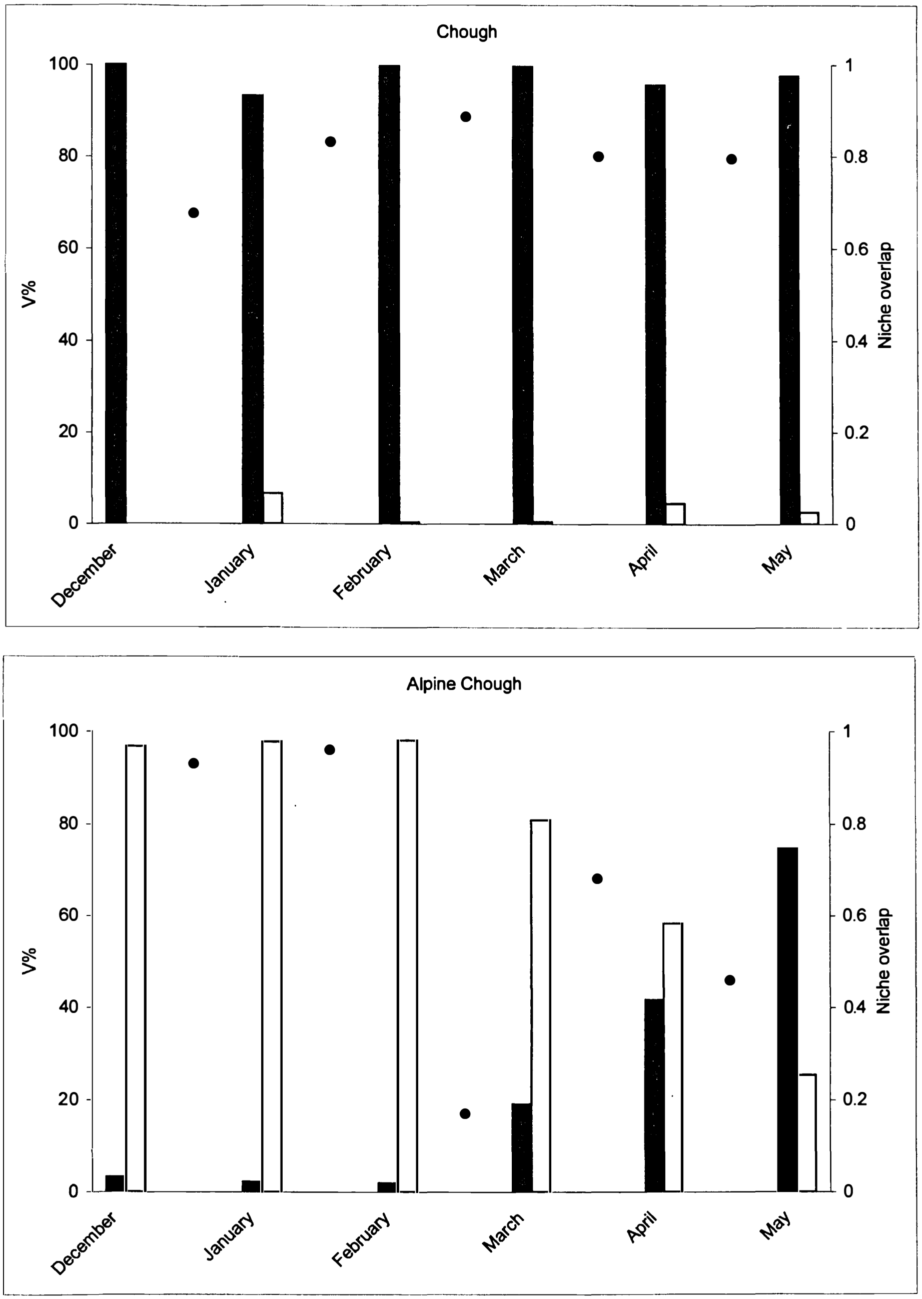

Figure 1. — Seasonal variation in the diet of the Chough and the Alpine Chough. Left axis: mean volume percentages of animal (black bars) and vegetable (empty bars) items. Right axis: niche overlap between consecutive months (filled circles).

TABLE I

Mean percentage volume of the different prey categories found in faecal samples of the Chough (C) and the Alpine Chough (AC). Taxonomic orders, in keeping with Tutin et al. *1964, Grandi 1984, and Pearse* et al., *1993, are given in bold type.*

	December		January		February		March		April		May	
	C	AC	C	AC	C	AC	C	AC	C	AC	C	AC
VEGETABLES												
— **Coniferales**	—	**2.9**	—	**6.6**	—	**4.5**	—	**0.2**	**0.6**	**1.8**	—	**4.3**
Juniperus spp.	—	2.9	—	6.6	—	4.5	—	0.2	0.6	1.8	—	4.3
— **Lilliflorales**	—	—	**4.2**	—	**0.2**	—	—	—	**0.2**	**0.1**	**1.6**	**0.6**
Gagea spp.	—	—	4.2	—	0.2	—	—	—	0.2	0.1	1.6	0.6
— **Rosales**	—	**12.2**	**0.2**	**16**	—	**15.2**	**0.1**	**80.4**	**2.2**	**53**	**0.4**	**8.6**
Rosa spp.	—	10.5	—	15.1	—	13.5	—	—	—	—	—	—
Sorbus aria	—	0.4	—	—	—	0.3	—	—	—	—	—	0.1
Sorbus aucuparia	—	1.1	—	0.1	—	—	—	—	—	0.3	0.4	0.2
Ribes spp.	—	0.1	—	0.3	—	—	—	—	—	0.2	—	—
Prunus spp.	—	—	—	—	—	0.7	—	—	—	—	—	—
Sempervivum arachnoideum	—	0.1	0.2	0.5	—	0.7	0.2	80.4	2.2	52.5	—	8.3
— **Ranales**	—	**79.9**	—	**74**	**0.1**	**78.3**	**0.3**	**0.3**	—	**0.2**	—	—
Berberis vulgaris	—	79.9	—	74	0.1	78.3	0.3	0.3	—	0.2	—	—
— **Ericales**	—	**1.8**	**2.2**	**0.8**	—	**0.1**	—	—	**1.5**	**3.2**	**0.5**	**11.9**
Vaccinium myrtillus	—	0.1	2.2	—	—	—	—	—	0.5	2.6	0.3	10.4
Vaccinium vitisidaea	—	—	—	—	—	—	—	—	—	—	—	0.1
Empetrum nigrum	—	—	—	—	—	—	—	—	1.0	0.6	0.2	1.4
Arctostaphylos uva-ursi	—	1.7	—	0.8	—	0.1	—	—	—	—	—	—
ANIMALS												
— **Stylommatophora**	—	**0.5**	**4.6**	**0.4**	**8.3**	**0.8**	**6.4**	**0.5**	**2.8**	**0**	**4.6**	**2.1**
— **Iuliformida**	**0.2**	**0.1**	**0.6**	**0**	**2.4**	**0**	**1.3**	—	**0.3**	**1.5**	**1.1**	**1.8**
— **Araneidae**	**3**	**0.1**	**5.1**	**0.1**	**4.7**	**0.1**	**5.9**	**0.6**	**3**	**2.4**	**3.1**	**1.5**
— **Orthoptera**	**2.6**	**0.5**	**0.9**	**0.5**	**2.7**	**0.2**	**1.7**	**0.4**	—	—	**0.7**	**0.4**
— **Dermaptera**	—	—	**1.4**	—	**0.2**	—	**0.5**	—	**1.3**	**0.3**	**1.9**	**1.3**
— **Hemiptera**	**2.5**	**0.3**	**2.3**	**0.1**	**3.7**	**0.2**	**4.2**	**4.8**	**2.3**	**11.4**	**1.3**	**3.9**
Heteroptera	2.5	0.3	2.3	0.1	3.7	0.2	4.2	4.8	2.3	11.4	1.3	3.9
— **Lepidoptera**	**5**	**0.1**	**4.2**	—	**8.4**	—	**4.4**	**5.5**	**3.8**	**2.3**	**3.7**	**4.5**
Pupae	0.2	—	1.3	—	1.8	—	0.3	—	0.6	0.1	1.3	0.2
Larvae	4.8	0.1	0.3	—	6.6	—	4.1	5.5	2.7	2.1	1.3	4.3
— **Diptera**	**78.5**	**0.1**	**48.9**	**0.1**	**42**	—	**51.4**	**0.6**	**65.9**	**1.9**	**50.7**	**37.3**
Pupae	7.6	0.1	10	0.1	12.4	—	16.9	0.3	9.8	0.3	4.6	0.5
Bibionidae adults	—	—	—	—	0.5	—	1.1	—	0.2	0.1	—	24.8
Bibionidae larvae	70.7	—	36.7	—	28.7	—	32.0	—	55.2	0.2	45.4	11.1
Tipulidae larvae	0.2	—	2.2	—	0.4	—	1.4	0.3	0.5	1.2	0.1	0.7
— **Hymenoptera**	**1**	**0.1**	**6.7**	**0.1**	**4.6**	**0.01**	**2.4**	**2.4**	**2.8**	**6.1**	**2**	**7.5**
Formicidae	0.6	0.02	5.3	0.06	4.4	0.01	2.3	2.1	2.3	5.6	1.6	6.4
— **Coleoptera**	**7.2**	**1.4**	**18.7**	**0.9**	**22**	**0.59**	**21.4**	**4.3**	**13.3**	**15.8**	**28.4**	**14.3**
Scarabaeoidea adults	0.8	—	1.1	—	2.6	0.07	5.2	0.4	4.0	2.2	3.6	1.1
Scarabaeoidea larvae	0.3	—	—	—	0.3	—	—	—	0.6	—	0.4	—
Silphidae	0.8	—	—	—	—	—	—	—	—	—	—	0.06
Carabidae adults	1.8	0.2	9.3	0.2	3.4	0.06	5.1	0.4	2.4	2.6	4.4	3.3
Carabidae larvae	—	—	—	—	0.1	—	0.1	—	0.2	1.1	4.7	0.07
Staphylinidae adults	—	0.03	—	—	0.2	—	0.6	0.1	1.0	1.5	0.5	0.4
Staphylinidae larvae	—	—	—	—	0.8	—	0.8	0.1	0.1	—	0.3	0.04

	December		January		February		March		April		May	
	C	AC	C	AC	C	AC	C	AC	C	AC	C	AC
Cantharidae larvae	1.0	0.05	1.0	—	3.3	—	1.3	—	1.9	0.5	11.5	3.9
Chrysomelidae	2.3	1.0	4.3	0.7	8.3	0.5	0.4	3.0	1.4	6.0	0.4	1.7
Elateridae adults	—	—	1.6	—	0.3	—	0.4	0.04	0.1	—	0.9	0.4
Elateridae larvae	—	—	—	—	—	—	—	—	0.3	—	—	0.2
Curculionidae	0.2	0.02	1.3	—	—	—	0.2	0.2	1.1	2.1	1.1	2.1
Coccinellidae	—	—	—	—	—	—	—	—	—	—	—	0.02
Buprestidae	—	—	—	—	—	—	—	0.1	—	0.1	—	0.1
Cerambycidae	—	—	—	—	—	—	0.3	—	—	—	—	—
Byrrhidae	—	0.1	—	—	—	—	—	—	—	—	—	0.5
Number of faeces	**42**	**175**	**62**	**104**	**98**	**121**	**77**	**101**	**101**	**103**	**56**	**176**

By contrast, Alpine Chough diet consisted almost entirely of vegetable items in winter, with an increase in the consumption of invertebrates starting in March and reaching the highest volume (74.6 %) in May (Fig. 1). The Common Berberry (*Berberis vulgaris*) was the main food item collected in December (79.9 %), January (74.0 %) and February (78.3 %). During these months faeces also yielded Dog Rose hips (*Rosa* spp) and Juniper berries (*Juniperus* spp); other berries (*Vaccinium* spp, *Arctostaphylos uva-ursi, Sorbus* spp) were eaten occasionally. In March more than 80 % of the food collected were houseleek *Sempervivum arachnoideum* leaves; in this period many animal prey orders were eaten in approximately equal low volume (beetles, caterpillars, ants and bugs). In April *Sempervivum arachnoideum* leaves were again the dominant food class, but its amount decreased to 52.5 %; conversely, the percentage volume of prey such as beetles (mainly Chrysomelidae), bugs and ants increased. In May the Alpine Chough preyed mostly upon Bibionidae (adults 24.8 %, larvae 11.1 %), but the animal portion of the diet also included beetles, ants and caterpillars. The most abundant vegetable matter at this time was Bilberry (*Vaccinium myrtillus*).

The composition of the Chough diet remained rather constant over time, whereas that of the Alpine Chough often varied from month to month. Niche auto-overlap values calculated between consecutive months were always greater than 0.68 in the Chough whilst they were much lower between February and March (0.17) and between April and May (0.46) for the Alpine Chough (Fig. 1). Significant differences in Alpine Chough diet were found between February *versus* March and April *versus* May (G test: February v. March $G = 422.6$, d.f. = 11, $P < 0.001$; April v. May $G = 96.2$, d.f. = 14, $P < 0.001$), whereas the comparison between consecutive months was only significant between December and January for the Chough ($G = 30.4$, d.f. = 12, $P < 0.01$).

The Alpine Chough overall niche breadth was slightly larger than the Chough (0.78 *versus* 0.70). Notably, the niche breadth of the Alpine Chough proved to be lower than that of the Chough in winter months, but increased steeply from March onward (Fig. 2).

The interspecific trophic overlap was close to 0 in winter, started increasing in March and reached the highest value in May (when the overlap was more than 60 %). There was a significant departure from linearity when overlap values were analysed with a second order polynomial regression model, with (month) and $(\text{month})^2$ as independent variables ($R^2 = 0.98$, $N = 6$, overall $P < 0.005$, $P(X) = 0.04$, $P(X)^2 = 0.01$) (Fig. 3).

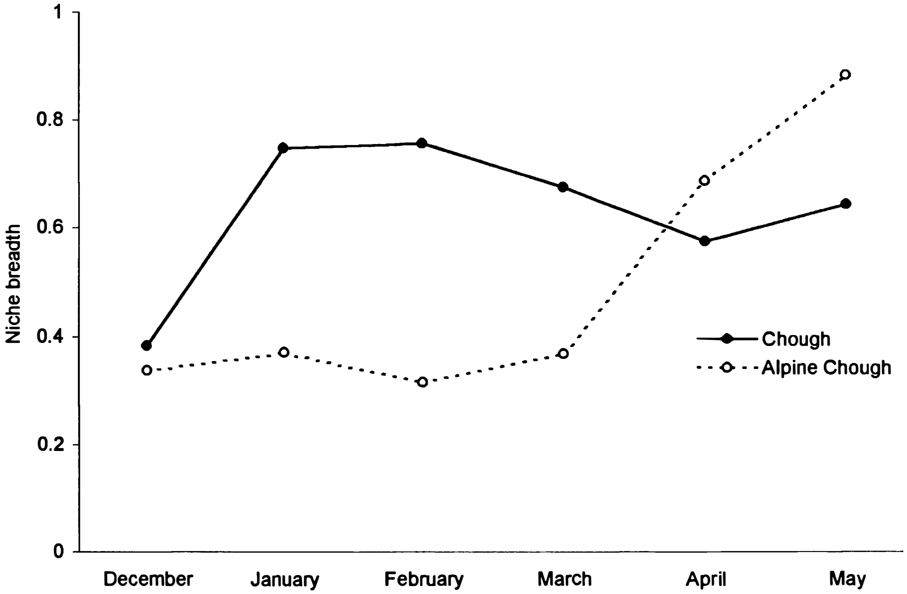

Figure 2. — Monthly niche breadth values of Chough and Alpine Chough.

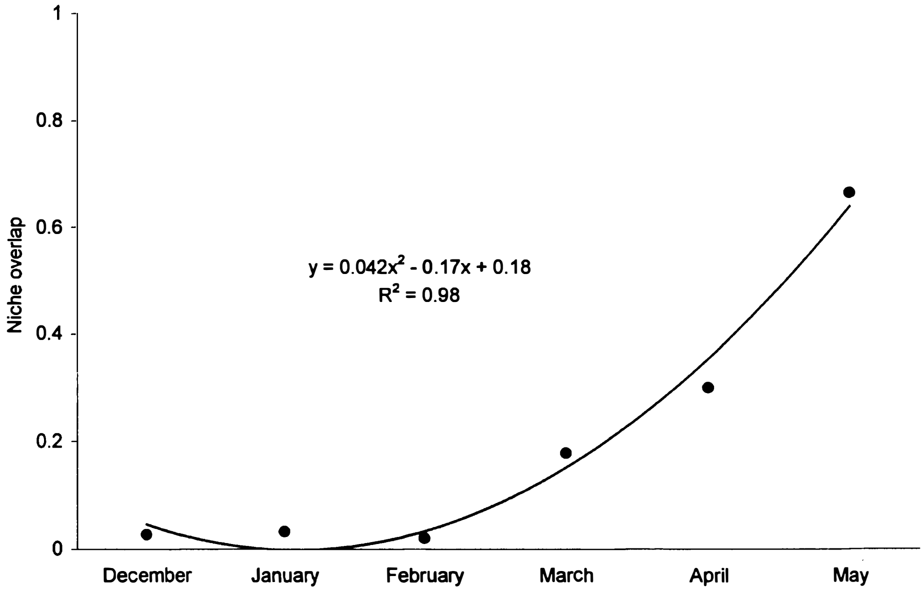

Figure 3. — Monthly interspecific trophic niche overlap between Chough and Alpine Chough diet; the trend line and its equation are shown.

Foraging times

The two species never occurred together in the same patches throughout the study period, and so only data on single species flocks appear in the analyses.

For each species a simultaneous regression of stay times on month, temperature, altitude and flock size variables produced low coefficients of multiple determination for both species ($R^2 = 0.07$ for Chough and 0.024 for Alpine Chough), but the proportion of the variance explained by the four predictors was highly significant (Chough: $F_{4,890} = 16.01$, $P < 0.001$, Alpine Chough: $F_{4,2178} = 13.40$, $P < 0.001$). The multiple regression equation obtained suggested that the Alpine Chough times were slightly but significantly negatively correlated with all the four variables (month and flock size accounting for most of the variability of the sample). Conversely, Chough stay times were positively correlated with temperature, elevation and flock sizes, but weakly decreased over time. Therefore, the two species stay times tended to vary oppositely in relation to the four variables (unequal slope: $F_{4,3067} = 33.51$, $P < 0.001$)). Differences in foraging time between the two species were tested with a one-way ANOVA: on average, the foraging times of Chough were found to be higher than those of Alpine Chough (5.58 ± 0.14 min. *versus* 2.24 ± 0.04 min., $F_{1,3076} = 970.9$, $P < 0.001$). The mean values of stay times in each species in relation to 4 categories of altitude and temperature, 7 categories of flock size and 6 months from December to May are shown in Table II; in each case Choughs stays proved to be higher than Alpine Choughs ones.

DISCUSSION

Diet

These data contribute to fill the knowledge of Choughs and Alpine Choughs diet and foraging behaviour in western Italian Alps, adding information to the antecedent study conducted by Rolando & Laiolo (1997) and Rolando *et al.* (1997a) in summer and autumn in the same study area. In June the Alpine Chough collected leatherjackets, while the Chough mainly relied on caterpillars. From July onward the bulk of Alpine Choughs diet consisted of grasshoppers, whilst Choughs consumed beetles, *Tipula* pupae, caterpillars and fly (Bibionidae) larvae. It was in autumn that diets diverged most: Alpine Choughs ate vegetable matter (berries), Choughs continued to dig up Arthropods (Rolando & Laiolo, 1997). Also in winter and spring soil-dwelling invertebrate prey dominates Chough diet: from December to May this species mostly consumed fly larvae and pupae, confirming that this species is mainly an underground feeder (digger and prober), as reported by Rolando *et al.* (1997a). In contrast, the Alpine Chough diet was more variable overall: in winter this species collected berries almost exclusively, shifting to houseleek leaves consumption in March and to arthropods predation in May, when the environmental availability of invertebrate prey increases and the breeding season starts.

Probably the diets of both species over the whole year depended on the temporal availability of locally occurring invertebrate and vegetable food in the two different habitats exploited (surface and underground niches). Seasonal

TABLE II

Alpine Chough and Chough foraging times at different altitudes, temperatures, flock sizes and months (coefficients of one-way ANOVA carried out among categories of each variable are shown).

	Alpine Chough			Chough		
	Mean (min)	SD	N	Mean (min)	SD	N
Elevation (m a.s.l.)						
< 1 000	2.75	2.2	176	5.77	3.80	572
1 000-1 500	2.55	1.92	260	—	—	—
1 500-2 000	2.24	1.68	1 452	5.44	5.02	60
> 2 000	1.63	1.09	277	5.11	4.63	308
	$F_{3.2161} = 19.9$	$P < 0.001$		$F_{2.937} = 2.56$	n.s.	
Temperature (°C)						
< – 5°	2.28	1.59	269	4.99	3.00	71
– 5°-0°	2.86	2.01	181	5.98	3.52	82
0°-+ 5°	2.26	1.77	532	5.50	4.03	413
> + 5°	2.14	1.66	1 183	5.59	4.65	374
	$F_{3.2161} = 9.46$	$P < 0.001$		$F_{3.936} = 0.74$	n.s.	
Flock size (N)						
1-10	1.92	1.28	202	5.30	3.80	350
11-20	2.39	1.86	547	5.46	3.98	572
21-30	2.10	1.58	551	12.82	8.91	18
31-40	2.49	1.96	268	—	—	—
40-50	2.08	1.48	81	—	—	—
50-100	2.34	1.70	478	—	—	—
> 100	1.18	1.73	38	—	—	—
	$F_{6.2158} = 4.33$	$P < 0.001$		$F_{2.937} = 29.7$		$P < 0.001$
Month						
December	1.87	1.52	274	3.44	2.81	7
January	2.21	1.58	269	5.56	3.30	233
February	2.63	2.04	436	6.17	4.15	374
March	3.14	2.10	293	5.52	4.95	56
April	2.24	1.54	361	5.93	5.26	171
May	1.62	1.07	532	2.59	1.82	99
	$F_{5.2159} = 40.0$	$P < 0.001$		$F_{3.2161} = 13.0$		$P < 0.001$

turnover of availability is quite evident on the surface. Grasshoppers are available (and abundant) in alpine pastures only from July to October, when they constitute the bulk of Alpine Choughs diet. The Alpine Chough shifts to vegetable consumption in autumn, after berries start ripping and simultaneously Arthropod prey becomes scarce. Invertebrates will appear in the surface (and in Alpine Choughs diet) again only after snow melting, in spring. Likely, prey availability also changes in the apparently more constant underground niche of the Chough, but in this case seasonal turnover is less clear and harder to demonstrate.

NICHE OVERLAP

From December to May niche auto-overlap values calculated between consecutive months were constantly high (about 0.8) for the Chough diet whilst they were much lower between February and March and between April and May for the Alpine Chough diet. However, the overall trophic niche breadth values of the two species were very close; monthly values of the Alpine Chough were lower than those of the Chough during winter, but increased steeply from March onward, when they were higher than those of the Chough. The same pattern of the greater monthly variability in Alpine Chough diet (in spite of a niche breadth which is roughly equivalent to that of the Chough) was also found in the analyses of summer and autumn diets (Rolando & Laiolo, 1997).

Consequently, we can confirm that the Alpine Chough in the Alps has a greater plasticity than the Chough. In this case behavioural plasticity does not coincide with 'generalism', since the diet of both species is composed of a few dominant food classes, but rather 'opportunism'. Some prey categories appear to be taken opportunistically, according to their availability: the Alpine Chough 'specializes' in the item type that is more profitable in each month. This high plasticity is also confirmed by the Alpine Chough's ability to find alternative foraging ground (e.g. apple orchard, human dwellings), when the amount of snow cover on shrubberies is too deep (Laiolo *et al.*, 1997). In some highly tourist localities this species can almost entirely feed on man-related food such as bread and household scraps (Delestrade, 1994).

FORAGING TIMES

In addition to diet, this study has indicated that the two Corvids greatly differ in foraging times as well (the Chough resulted to stay at a feeding patch twice as long as the Alpine Chough) confirming the results obtained by Rolando *et al.* (1997a) for summer and autumn.

The results of the multivariate regressions indicate a weak but significant relationship between Choughs and Alpine Choughs stay times and the variables month, temperature, elevation and flock size. Nevertheless, the two species showed the same tendency only in the case of month (positive correlation), in all the other cases correlations were positive for the Chough and negative for the Alpine Chough.

In the case of the Alpine Chough Rolando *et al.* (1997b) obtained the same results in summer and autumn for flock size: if flock size was small, Alpine Chough stay times tended to be longer (indeed it is worth noting that the largest Alpine Chough flocks were composed of 150 birds, whilst Chough numbered 25 at the most). In the case of the Alpine Chough it may be argued that the shorter stays in larger flocks are related to the higher probability that, in a larger flock (up to 150 birds), some individuals fly away inducing the others to follow them. By contrast, in the case of the Chough foraging times could be more related to predation risk. The risk of predation might decrease at increasing flock size because large groups have a higher probability to scan and detect a predator (Pulliam, 1973) or, alternatively, in a large group a particular individual is less likely to be preyed upon when a greater number of potential prey are present (Turner & Pitcher, 1986). Therefore, Choughs might spend more time foraging (longer stay) in a large group, benefiting by the lower risk of predation.

How can diet and foraging behaviour affect status and population density?

Our study emphasizes a clear-cut differentiation in foraging ecology between the two species. During the winter months the complete niche partitioning (diet overlap close to zero) and the opposite behaviour in relation to ecological variables is astonishing, particularly when we consider that these two species are usually syntopic. Rolando & Laiolo (1997) highlighted a certain degree of dietary overlap in the summer months, but trophic differentiation greatly increased in autumn. In summer and autumn the two species sometimes occurred on the same feeding ground, even if the observed frequencies of the mixed flocks were significantly lower than those expected on the basis of a random association hypothesis (Rolando *et al.*, 1997b). In winter and spring no mixed foraging flocks occurred and the two species exploited spatially isolated patches. Winter is notably a critical period on high mountain tops, since deep snow cover and low temperatures result in permanent food shortage conditions. The Chough and the Alpine Chough are forced to retreat to feed at lower altitude, in snow free patches. Therefore, competition for food is likely to increase, unless the diet of the two species does not overlap at all. The observed niche partitioning might be the possible outcome of interspecific competition where two sympatric species had to coexist under conditions of extremely scarce food supply. However, so little is known about the processes involved in niche displacement (and indeed we do not know if a displacement ever occurred), that we can neither reject or accept this hypothesis on the basis of observational data alone.

However, niche segregation by different trophic levels did occur and may have resulted in important consequences for the status of each species. The population density of a species in a given area is limited to the number of animals the area can support (Robinson & Redford, 1986). Many factors have been shown to account for the variation in population densities: body size, habitat, biogeography, and phylogeny of the species (Eisenberg, 1980; Silva *et al.*, 1997; Peters & Raelson, 1984). Diet is also an important factor: previous studies have shown that primary consumers (herbivorous, frugivorous and granivorous species), which have access to greater abundance of resources than secondary or tertiary ones (insectivorous, carnivorous), have higher average population densities (Juanes, 1986; Robinson & Redford, 1986; Silva & Downing, 1995). Hence, for a given body mass, population of herbivorous species would be expected to be greatest, followed in descending order by frugivorous, granivorous, omnivorous, insectivorous and carnivorous species (Robinson & Redford, 1986).

This paper together with previous research carried out in the Alps (Rolando & Laiolo, 1997) has shown that the Alpine Chough is mainly frugivorous (more than 50 % of berries) from September to February, is herbivorous-omnivorous in March and April (> 50 % *Sempervivum* leaves) and insectivorous from May to August (i.e. during the breeding season); in other words it is mostly vegetarian in 8 out of 12 months of the year. Conversely, the Chough can be regarded as insectivorous given that it is specialized to catch soil-dwelling insects, and, noticeably, keeps digging throughout the winter, despite the greater availability of vegetable items on the surface. The different trophic levels occupied by the Chough and the Alpine Chough in autumn, winter and early spring might therefore account for their different densities in the Alps. The Alpine Chough, in fact, is a common bird in every mountain valley, and large flocks are often observed (winter flocks over 1800 birds have been recorded on apple orchards at valleys bottom) (Mingozzi *et al.*, 1988; Cucco *et al.*, 1996; Laiolo *et al.*, 1997). Conversely, the Chough is rather rare, with up to 20-40 individuals in each valley; winter flocks rarely contain more than 50 individuals (Rolando & Laiolo, 1997; Cucco *et al.*, 1996).

Despite the fact that no other specific studies on the relationship between diet and population densities has been conducted for these species to date, the literature on dietary and population density data from other areas appear to confirm our hypothesis (at least for the Chough). In Spain, where high local densities of Chough are reported in many areas, the Chough has a more variable diet, including wild grains and cultivated cereals throughout the year, in amounts accounting for up to 60 % of the total diet volume (Soler & Soler, 1993; Soler *et al.*, 1993); olive consumption also appears to be important in some areas (Blanco *et al.*, 1996). La Palma (Canary Islands) holds a large Chough population (300-400 pairs) (Bignal, 1994); here Choughs normally gather figs *Ficus carica* and oranges *Citrus sinensis* in autumn and winter (Cullen *et al.*, 1952). The stronghold of the Chough in Italy occurs in the Apennines, where there are rather high population densities (De Sanctis *et al.*, 1997): vegetable items (olives) appear to be an important resource (De Sanctis, unpublished data). British Choughs appear to rely more on animal prey (Holyoak, 1967, 1968; Roberts, 1982; Bullock *et al.*, 1983; Meyer, 1990) and population densities are low; on the Scottish island of Islay, the main Scottish stronghold (Monaghan, 1986), seed consumption is high in autumn and winter (Warnes & Stroud, 1989; McCracken *et al.*, 1992).

However, trophic position apart, Chough numbers in the Alps could be maintained at low levels by other factors. The habitat required by the Chough (e.g. semi-natural pastures) is not widespread at the low altitudes used to forage in winter. Pastures tend to be abandoned and are replaced by shrubs and cultivation, which are favourable to the Alpine Chough but unfavourable to the Chough in the Alps. In most of its Palearctic distribution the Chough is associated with a low intensity, pastoral and agricultural system (Monaghan, 1986); the continuing loss of the traditional pastoral farming is consequently considered one of the major threat to Chough populations in many areas (Bignal, 1994). Moreover, severe winter conditions may also affect the ecology of the Chough more than that of the Alpine Chough: when the ground is frozen for extended periods the Chough is likely to find feeding extremely difficult. Likewise, the fact that digging apparently requires greater expertise — yearlings only gradually improve their foraging skills by learning from the adults, and they can only peck prey on the surface after fledging (Rolando *et al.*, 1994) — may determine a lower winter survival of yearlings. An ultimate contributory factor might be the increasing development of human-related activities (mainly tourist expansion) on mountain tops, which could create disturbance. Alpine tourism improves the year-round food supply, but only Alpine Choughs seems to profit by this; the higher behavioural plasticity and the greater ability of this species to find trophic alternatives (often directly provided by man) might allow large populations to survive or even create long term population increase (Sackl, 1997).

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REFERENCES

BARONI, E. (1977). — *Guida Botanica d'Italia.* Licinio Cappelli Editore. Bologna.

BIGNAL, E. (1994). — Chough. Pp. 420-421, *in:* Tucker, G.M. & Heaths, M.F. (eds.). *Birds in their their conservation status.* BirdLife Conservation series No 3, Cambridge.

BLANCO, G., FARGALLO, J.A. & CUEVAS, A. (1996). — Consumption rates of olives by Choughs *Pyrrhocorax pyrrhocorax* in central Spain. Variations and importance. *J. Field Orn,* 65: 482-489.

BULLOCK, I.D., DREWETT, D.R. & MICKLEBURGH, S.P. (1983). — The Chough in Britain and Ireland. *British Birds,* 76: 377-401.

CHINERY, M. (1987). — *Guida degli Insetti d'Europa.* Muzzio Editore. Padova.

COLWELL, R.K. & FUTUYMA, D. J. (1971). — On the measurements of niche breadth and overlap. *Ecology,* 52: 567-576.

CUCCO, M., LEVI, L., MAFFEI, G. & PULCHER, C. (1996). — *Atlante degli uccelli di Piemonte e Valle d'Aosta in inverno (1886-1992).* Monografia XIX, Museo Regionale di Scienze Naturali, Turin.

CULLEN, J.M., GUITON, P.E., HORRIDGE, G.A. & PEIRSON, J. (1952). — Birds on Palma and Gomera (Canary Islands). *Ibis,* 94: 68-89.

DAMUTH, J. (1987). — Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy use. *Biol. J. Linn. Soc.,* 31: 193-246.

DE SANCTIS, A., DE MARINIS, F., LIMONGELLI, L., PELLEGRINI, M. & SPINETTI, M. (1997). — The status and breeding biology of the Chough (*Pyrrhocorax pyrrhocorax* Linnaeus) in the Central Apennines - Abruzzo, Italy. *Avocetta,* 21: 157-164.

DELESTRADE, A. (1994). — Factors affecting flock size in the Alpine Chough *Pyrrhocorax graculus. Ibis,* 136: 91-96.

EISENBEIS, G. & WICHARD, W. (1987). — *Atlas on the Biology of Soil Arthropods.* Springer-Verlag, Berlin.

EISENBERG, J.F. (1980). — The density and biomass of tropical mammals. *In:* Soulé, M.E. and Wilcox, B.A. (eds.). *Conservation biology, an evolutionary - ecological perspective.* Sinauer, Sunderland, Mass.

EISENBERG, J.F. & THORINGTON, R.W. (1973). — A preliminary analysis of Neotropical mammal fauna. *Biotropica,* 5: 150-161.

EISENBERG, J.F. (1981). — *The mammalian radiation.* University of Chicago Press, Chicago.

GOODWIN, D. (1986). — *Crows of the world.* British Museum (Natural History).

GRANDI, G. (1984). — *Introduzione allo studio dell'Entomologia.* Edagricole, Bologna.

HOLYOAK, D. (1967). — Food and feeding action of choughs. *Bird study,* 14: 61-62.

HOLYOAK, D. (1968). — A comparative study of the food of some British Corvidae. *Bird study,* 15: 147-153.

JUANES, F. (1986). — Population density and body size in birds. *Am. Nat.,* 128: 921-929.

KRUUK, H. (1989). — *The Social Badger. Ecology and behaviour of a group-living carnivore* (Meles meles). Oxford University Press.

LAIOLO, P., CAVAGNETTO, V., SOSSO, M., ROLANDO, A. & PERACINO, V. (1997). — Ranging behaviour of the Alpine Chough *Pyrrhocorax graculus* during winter in the Alps. *First meeting of the European Ornithological Union, Bologna, Italy, 28-30 August 1997.* Meeting Abstract. 87.

LINDEMAN, R.L. (1942). — The trophic-dynamic aspect of ecology. *Ecology,* 23: 399-418.

MCCRAKEN, D.I., FOSTER, G.N., BIGNAL, E.M. & BIGNAL, S. (1992). — An assessment of Chough *Pyrrhocorax pyrrhocorax* diet using multivariate analysis techniques. *Avocetta,* 16: 19-29.

MEYER, R.M. (1990). — Observation on two Red-billed Choughs *Pyrrhocorax pyrrhocorax* in Cornwall. habitat use and food intake. *Bird Study,* 37: 199-209.

MINGOZZI, T., BOANO, G. & PULCHER, C. (1988). — *Atlante degli uccelli nidificanti in Piemonte e Val d'Aosta.* Monografia VIII-Museo Regionale di Scienze Naturali, Turin.

MONAGHAN, P. (1989). — The background of Chough studies in Britain. Pp. 4-8, *in:* Bignal, E. and Curtis, D.J. (eds.) *Choughs and Land-use in Europe.* Scottish Chough Study Group.

PULLIAM, H.R. (1973). — On the advantage of flocking. *J. Theor. Biol.,* 38: 419-422.

PEARSE, V., PEARSE, J., BUCHSBAUM, M. & BUCHSBAUM R., (1993). — *Invertebrati viventi.* Zanichelli, Bologna.

PETERS, R.H. & RAELSON, J.V. (1984). — Relationship between individual size and mammalian population density. *Am. Nat.,* 128: 665-680.

ROBERTS, P. (1982). — Foods of the Chough on Bardsey Island, Wales. *Bird Study,* 29: 155-161.

ROBINSON, J.C. & REDFORD, K.H. (1986). — Body size, diet, and population density of neotropical forest mammals. *Am. Nat.,* 128: 665-680.

ROLANDO, A. & LAIOLO, P. (1997). — A comparative analysis of the diets of the Chough Pyrrhocorax pyrrhocorax and the Alpine Chough *Pyrrhocorax graculus* coexisting in the Alps. *Ibis,* 139: 388-395.

ROLANDO, A., LAIOLO, P. & FORMICA, M. (1997a). — A comparative analysis of the foraging behaviour of the Chough *Pyrrhocorax pyrrhocorax* and the Alpine Chough *Pyrrhocorax graculus* coexisting in the Alps. *Ibis,* 139: 461-467.

ROLANDO, A., LAIOLO, P. & FORMICA, M. (1997b). — The influence of flocking on the foraging behaviour of the Chough (*Pyrrhocorax pyrrhocorax*) and the Alpine Chough (*Pyrrhocorax graculus*) coexisting in the Alps. *J. Zool.,* Lond., 242: 299-308.

ROLANDO, A., PATTERSON, I.J. & LAIOLO, P. (1994). — The foraging behaviour of the Chough *Pyrrhocorax pyrrhocorax* in two contrasting habitats. *Avocetta,* 18: 45-51.

SACKL, P. (1997). — Alpine Chough. Pp. 675, *in:* Hagemeijer, W.J.M. and Blair, M.J. (eds.), *The EBCC Atlas of European Breeding Birds.* T & AD Poyser, London.

SILVA, M. & DOWNING, J.A. (1995). — The allometric scaling of density and body mass, a nonlinear relationship for terrestrial mammals. *Am. Nat.,* 141: 704-727.

SILVA, M., BROWN, J.H. & DOWNING, J.A. (1997). — Differences in population density and energy use between birds and mammals: a macroecological perspective. *Journal of Animal Ecology,* 66: 327-340.

SOLER, J.J. & SOLER, M. (1993). — Diet of the Red-billed Chough *Pyrrhocorax pyrrhocorax* in south -east Spain. *Bird Study,* 40: 216-222.

SOLER, J.J., SOLER, M. & MARTINEZ, J.G. (1993). — Grit ingestion and cereal consumption in five corvid species. *Ardea,* 81: 143-149.

TURNER, G.F. & PITCHER, T.J. (1986). — Attack abatement: a model for group protection by combined avoidance and dilution. *Am. Nat.,* 128: 228-240.

TUTIN, T.G., HEYWOOD, V.H., BURGES, N.A., VALENTINE, D.H., WALTERS, S.M. & WEBB, D.A. (1964). — *Flora Europaea.* Cambridge University Press, UK.

WARNES, J.M. & STROUD, E. (1989). — Habitat use and food of choughs on the island of Islay, Scotland. *In:* Bignal, E. and Curtis, D.J. (eds.) *Choughs and Land-use in Europe.* Scottish Chough Study Group.