Ornis Fennica 73:179–185. 1996

An analysis of the diet of Red-billed Chough *Pyrrhocorax pyrrhocorax* nestlings in NE Spain, using neck ligatures

Cristina Sánchez-Alonso, Xavier Ruiz, Guillermo Blanco & Ignacio Torre

Sánchez-Alonso, C. & Ruiz, X., Dept. de Biologia Animal, Universitat de Barcelona, Av. Diagonal 645, ESP-08028 Barcelona, Spain
Blanco, G., Dept. de Biologia Animal, Universidad de Alcalá de Henares, Alcalá de Henares, ESP-28871 Madrid, Spain
Torre, I., Museu Granollers, Ciències Naturals, C/Francesc Macià 51, ESP-08400 Granollers, Spain

Received 8 March 1996, accepted 30 May 1996

Owing to the scattered distribution and the difficulty of reaching their nesting places, Red-billed Choughs *Pyrrhocorax pyrrhocorax* still remain poorly known in many aspects of their biology and ecology, including diet. Previous diet studies for this species rely mainly on pellets and faeces, which are intrinsically biased food samples. We present data on nestlings' diet based on the analysis of undigested prey delivered to the nest by adults, gathered using neck ligatures. A total of 626 prey items belonging to 12 different taxonomic orders were collected from 63 ligatures. All food items found were animals, among them, the most important by numbers were Lepidoptera (caterpillars) and Coleoptera (also mainly formed by larval instars). In terms of biomass, consumption of Lepidoptera was much higher than that of Coleoptera, though both form, also in this case, the bulk of the nestling's diet. Secondary prey items were Araneae, Orthoptera, Diptera, Hymenoptera and Gastropoda. The remaining prey categories can be considered accidental. According to typology, preys belonging to burrowers are those most collected by parent Choughs followed by walkers, hoppers, and the miscellaneous category others, constituted by accidental prey types. Three non-mutually exclusive factors are argued to explain differences among Chough diet studies: 1) the relative availability of food resources, 2) the highest energetic demand during the breeding season, and 3) the effect of biases associated with the different food samples analysed.

1. Introduction

The Red-billed Chough (*Pyrrhocorax pyrrhocorax*) is a Palaearctic species that is valuable as an indicator of a certain type of environmental quality and stability (Wilkinson 1989). The populations of this species in central and northern Europe have declined severely during the last two centuries (Rolfe 1966, Yeatman 1976, Guillou 1981, Bullock et al. 1983a), and the largest populations are now found in the Iberian Peninsula, though much more fragmented than formerly expected (Farinha et al. 1989, Soler 1989).

Two main arguments have been invoked to explain these population declines: active human persecution and changes in soil usage in the agricultural landscapes that Choughs inhabit (Rolfe 1966, Garcia-Dory 1989, Owen 1989, McCracken et al. 1992, Meyer et al. 1994). Because of this, nesting Choughs are nowadays confined, almost exclusively, to rocky cliffs in both coastal and mountainous areas (Coombs 1978, Harrison 1982).

Owing to the scattered distribution and the difficulty of reaching their nesting places, the species remains poorly known in many aspects of its biology and ecology, including diet. The main diet studies performed to date correspond to the British Isles (but see Soler & Soler (1993)) and all of them rely mainly on the analysis of pellets and faeces, or focus mainly on feeding behaviour or habitat (Cowdy 1973, Bullock & del Nevo 1983, Bullock et al. 1983a, Roberts 1983, Piersma & Bloksma 1987, McCracken et al. 1992, Meyer et al. 1994).

More quantitative studies on diet composition and the biomass of prey items consumed are needed to assess this basic ecological trait of Chough populations (Soler & Soler 1983, Roberts 1989). Furthermore, as pointed out by Warnes and Stround (1989) pellets and faeces might represent highly biased sources of information, largely as a result of differential digestibility of prey items. To date, however, there is no study based on better sources of information. On the other hand, the diet of nestlings is even less known than that of the adult birds, since only two studies include an analysis of nestling's food (Warnes & Stround 1989, McCracken et al. 1992).

In this paper we report and analyse for the first time the diet of Chough nestlings, on the basis of the undigested prey delivered to the nest by adults. In this way we can overcome biases associated with other sources of information and obtain reliable data on the biomass supplied by each prey item. Diet composition is quantitatively described using taxonomic and typologic prey categories.

2. Material and methods

2.1. Study Area

The study was carried out in the area of South Monegros (NE Spain), in the Ebro Valley (41°20'N, 0°11'W). This is a dry steppe area situated at 300–360 m asl, encompassing a largely homogeneous area of 250 km^2 consisting of limestone and gypsum of tertiary origin and fifteen temporarily flooded saline lakes (Balsa & Montes 1991).

The climate is Mediterranean continental, semi-arid with 350 mm of rainfall concentrated in spring and autumn, extreme temperatures in summer and winter (– 5°C to 40°C), and winter thermic inversions.

The landscape is formed by an extensive cereal plain (pseudo-steppe) with wheat *Triticum* sp. and barley *Hordeum* sp. crops. Evergreen halophytic vegetation surrounds the saline lakes. The non-halophytic natural vegetation is restricted entirely to the road edges where nitrophilic conditions occur as a result of anthropogenic actions (Tella et al. 1996).

This area of the Ebro Valley holds about 75 breeding Chough pairs (pers. obs.). Their nests, mostly in abandoned buildings, are easily accessible, see Tella et al. (1996) for a complete description of bird fauna.

2.2. Sampling

In 1993 during the breeding season (nestling period, April–May) we applied neck ligatures (Mellott & Woods 1993) to 99 nestlings belonging to 23 nests. Ligatures were applied in the morning (between 9:00–12:00 h) or during the evening (between 16:00–19:00 h) to avoid the hours of maximal temperature and to homogenize the sampling procedure.

We placed the ligatures once the adults had left the building where they had their nests, and left them in position for a two-hour period in all cases. During this time a brood was fed, almost in every case, three times ($\bar{x}$ = 3.11; s.d. = 1.01; n = 28). We then collected food boluses, removed the ligatures and fed every chick with a weight of minced meat equivalent to the food removed from their guts. We applied ligatures only once (twice in six cases) in each nest, in order to minimize effects on chick-rearing and development. Nests to which ligatures were applied did not show any deleterious effect, since their average fledging success was consistently higher than that of control nests (85.5% vs. 32.1%, respectively).

Food boluses were placed in a plastic bag, labelled and frozen until analysis. In the laboratory each prey item was identified under a binocular lens (10–40×), weighed on an electronic balance to the nearest mg, measured with a digital caliper to the nearest 0.1 mm, and frozen again for further studies.

2.3. Data Analysis

To describe diet composition we used two different categorizing schemes: taxonomy and typology of prey items. Taxonomic arrangement was performed using order level, which is the most widely used in the literature. This allows comparison with other studies and provides a general system of reference. However, since taxonomic categories can include highly variable ecological typologies (e.g. larval and adult forms of Coleoptera or Lepidoptera) this categorization should be complemented by other approaches (Henspenheide 1975) more closely related to a predator's perception of the different prey items. Usually this produces mixed categorization schemes (Henspenheide 1975, Roberts 1989, Warnes & Stround 1989) and, because of the hierarchical structure of some of the descriptors employed, we prefer separate analyses for these two grouping procedures (Martínez et al. 1992). Furthermore, the analysis of typological categories, mainly based on the locomotive behaviour of prey items (walkers, burrowers, hoppers, and others), can provide a rough estimate of a predator's feeding behaviour and foraging habitats used.

To describe diet composition we used number and biomass abundances (%N, %B), occurrence (%P), and a probabilistic index (IP), developed by Ruiz and Jover (Ruiz & Jover 1981, Ruiz 1985) as $\lambda = \sum P_{ij}^2$, where P_i is the proportion of item i in the jth food sample, for j = 1 to N food samples examined. This index combines abundance and occurrence in only one value, providing a measure of the expected commonness of a particular prey in the diet. To obtain values of λ independent of sample size, we obtained $\lambda' = (\lambda/N) \times 100$ and converted it to a within-sample percentual value $IP = (\lambda'/\sum \lambda') \times 100$. In this way, larger percentage values denote more important prey items.

Dietary diversity, as an estimate of trophic niche width, was calculated applying Jackknife procedures (Zahl 1977, Jover 1989) to cumulative diversity functions obtained using the Brillouin index (Pielou 1975). In this way, variances associated to diversity values are obtained, and statistical comparisons can be performed when appropriate.

3. Results

From the 99 ligatures applied to chicks belonging to 23 different nests, we obtained food samples in 63 cases (64%). A total of 626 prey items were collected from these food samples. All food items found were animals. Prey items belonged to 12 different taxonomic orders (Table 1). Among

Table 1. Diet composition and relative importance of the different prey categories using taxonomic groups (n = 63 food boluses). N = number of prey items, %P = percentage of occurrence, %N = percentage of abundance, IP = probabilistic index (in percentage), Biomass (g of dry weight), %B = percentage of biomass.

Prey category	N	%P	%N	IP	Biomass	%B
Lepidoptera	218	79.4	34.7	45.7	56.3	58.4
Hymenoptera	15	12.7	2.4	3.0	0.7	0.7
Orthoptera	33	19.0	5.3	4.8	4.4	4.5
Coleoptera	214	58.7	34.0	33.0	22.5	23.3
Embyoptera	6	7.9	1.0	0.1	0.1	0.1
Neuroptera	22	7.9	3.5	0.8	2.2	2.2
Dermaptera	2	3.2	0.3	0.0	0.1	0.1
Diptera	36	7.9	5.7	3.5	1.8	1.9
Araneae	63	46.0	10.0	7.6	7.0	7.2
Gastropoda	16	6.3	2.5	1.5	0.8	0.8
Other invertebrates	3	4.8	0.5	0.0	0.5	0.6
Sauria	1	1.6	0.2	0.0	0.1	0.1

them, the most important by numbers were the Lepidoptera (exclusively caterpillars) and the Coleoptera (also mainly formed by larval instars), both prey categories present similar consumption rates in number. In terms of biomass, consumption of Lepidoptera provided significantly greater amounts of biomass than Coleoptera (Wilcoxon Matched-Pairs Single-Ranks test on biomass belonging to these prey categories in each nest $Z = 3.2881$, $P = 0.0010$, $n = 23$, two-tailed). The third category, both in numbers and biomass, was that of spiders (Araneae). These three categories formed ca. 80% of prey in numbers and ca. 90% in biomass. Consistently, the probabilistic index shows that these two categories are, by far, the most important: Lepidoptera and Coleoptera, followed by a series of secondary prey items represented by Araneae, Orthoptera, Diptera, Hymenoptera and Gastropoda. The remaining prey categories can be considered accidental. According to typology, preys belonging to burrowers are those most collected by parent Choughs followed by walkers, hoppers, and others (Table 2). Individual mean trophic diversity (0.64) was slightly larger than 0.5 indicating that diet was dominated, at the individual level, by two main prey categories (i.e., Lepidoptera and Coleoptera). Both, cumulative and Jackknifed trophic diversities, in contrast, reached much higher values that were quite similar (Table 3), indicating that the sample analysed was large enough (Pielou 1975).

4. Discussion

Choughs have been considered almost exclusively insectivore birds in some studies (Rolfe 1966, Meyer 1990), while others point out a mixed diet formed by plant and animal material, which tends to present more insects during the breeding season (Warnes & Stround 1989, McCracken et al. 1992, Soler & Soler 1993, Meyer et al. 1994). In this study, in contrast to what is known for other Iberic populations during the breeding season (Soler & Soler 1993, Blanco et al. 1994), Choughs were exclusively insectivorous.

Some authors argue that this change in diet composition is because of an increase in the availability of insect larvae in spring (Garcia-Dory 1983, Soler & Soler 1993), while Blanco et al. (1994) ascribed the drop in olive consumption in spring to depleted availability of this resource. In some studies authors found that Coleoptera were the most consumed prey items (Bullock et al. 1983b, Warnes & Stround 1989, McCracken et al. 1992, Meyer et al. 1994), while in others Coleoptera and Lepidoptera were similarly consumed (Bullock et al. 1983b, Soler & Soler 1993). In this study both prey categories presented similar consumption rates in number, but Lepidoptera (larval instars) provided significantly greater amounts of biomass than Coleoptera, which are also mainly formed by larval instars. In contrast to data obtained by Cowdy (1973) for Ramsey Is. (Wales),

Table 2. Diet composition and relative importance of the different typologic categories (n = 63). Symbols as in Table 1.

Prey category	N	%P	%N	IP	Biomass	%B
Burrower	410	92.1	65.6	78.1	65.1	81.3
Walker	164	68.2	26.2	16.3	11.8	14.8
Hopper	33	19.0	5.3	4.3	2.0	2.4
Others	18	7.9	2.9	1.3	1.1	1.4

Table 3. Trophic diversity (niche width) values for taxonomic categories (Order) in this study compared with data given by Soler and Soler (1993) for spring in his study on adult birds from south-east Spain.

	This study	Soler and Soler 1993
Individual mean trophic diversity	0.64 (se = 0.07)	–
Jackknifed trophic diversity	2.49 (se = 0.16)	–
Cumulative trophic diversity	2.40	1.0

and suggestions by Meyer et al. (1994), ants did not represent an important food resource for Choughs' nestlings in Monegros, but they are not absolutely absent in their diet as reported by Warnes and Stround (1989).

We agree with Soler and Soler (1993) that these differences could be explained through variations in foraging habitat and prey availability among study areas but, in our view, may also partially come from differences in bias associated with the different food samples analysed. Therefore, at least three, not mutually exclusive factors can be considered: 1) relative availability of different prey types during the chick-rearing stage of Choughs in Monegros (April–May), 2) an insectivorous diet is favoured when the energy demand is high, since insects provide much larger amounts of energy and proteins than plant matter (Ricklefs 1974, Murphy 1994), and 3) our source of information is much less biased than pellets and faeces.

Concerning availability, during April–May in Monegros seeds in the cereal crops have not yet ripened, thus the availability of cultivated grains may be poor and, though we have no data on wild seeds, it must be taken into account that cultivated areas predominate over those that are non-cultivated (road and field margins), where the wild grains would be available. Furthermore, in this area there are no generalized insecticide treatments and insect productivity is high (pers. obs.). However, biases induced by the sources of information analysed, are also relevant as shown by data on trophic diversity given in Table 3, which are much higher in our study than in that of Soler and Soler (1993) which is based on a large amount of samples.

The only other study in which diet of nestlings is described (McCracken et al. 1992) provides data corresponding to only two categories (Diptera larvae and Coleoptera), but in a way not easily comparable, since values are not grouped per sample, therefore impeding the calculation of diversity values.

All these results are consistent with the fact that pellets and faeces are amongst the most biased diet samples, because of presenting lower prey richness, underestimation of soft-bodied prey, and overestimation of prey presenting undigestible characteristic elements which have protracted retention times (Rosenberg & Cooper 1990, Noordhuis & Spaans 1992, Harris & Wanless 1993). An example of this can be found in the Soler and Soler (1993) study, where the third category was formed by Hymenoptera (mainly ants), whereas in ours the third category in number and biomass was constituted by soft bodied Araneae, which may be underestimated in pellets or faeces analyses, despite chelicera resistence to degradation. In any case, another factor to be taken into account in the case of Soler and Soler (1993) data, is that they studied the diet of adult birds, while we analysed the nestling's diet.

As expected, according to previous descriptions of the foraging behaviour of Choughs (Cowdy 1973), the main prey category, both in numbers and biomass, at the typologic level corresponds to burrowers, i.e., larval instars of insects living in the upper part of the soil (approx. up to 5 cm in depth), followed by walkers, i.e., prey moving slowly on the soil surface that might be easily located and captured while searching for burrowers. Sherry (1984), using cluster analysis found that in the guts of several species of tropical Flycatchers, caterpillars and grasshoppers tended to co-occur, and ascribed this to the fact that predators searching for one tended to encounter the other. The rest of the prey typologies are included in the miscellaneous category others, since their occurrence is very low, meaning that they are only accidentally taken by Choughs.

The Monegros area seems to fit, to a certain extent, the requirements of ancient Chough habitats, i.e., low-intensity undisturbed pasture lands (Bullock & del Nevo 1983, Meyer et al. 1994). In the Monegros there are a noticeable proportion of patchily distributed fallow fields, a relatively low human population density, and semideserted buildings suitable for their nests scattered over the area. Therefore, the maintenance of traditional agriculture practices, such as fallow fields, which are employed as occasional pastures by sheep herds, seems crucial to the preservation of that Chough population.

Acknowledgements. The authors are very grateful to H. Pietiäinen, M. Mönkkönen, and an anonymous reviewer for comments and criticism which improved the text. To L. Jover for statistical advice. To Ignasi Oliveras for his help during the field work, to E. Mateos for help in the determination of some insects and to José Luis Tella for logistic and technic support as well. Thanks are also given to Diputación General de Aragón (DGA) for kind authorisation to work at the Chough nests. R. Rycroft (SAL, EIM Universitat de Barcelona) improved the English text.

Selostus: **Alppivariksen ravinto Koillis-Espanjassa**

Johtuen lajin hajanaisesta levinneisyydestä ja pesimäalueiden vaikeakulkuisuudesta alppivariksen biologia ja ekologia mukaanlukien ravitsemus on huonosti tunnettua. Kirjoittajat tutkivat alppivariksen pesäpoikasten ravintoa keräämällä näytteitä emojen poikasilleen kuljettamasta ravinnosta. Näytteet kerättiin laittamalla poikasille kaulaside, joka esti ruoan nielemisen. Siteitä pidettiin paikallaan kaksi tuntia, jonka jälkeen kupuun kertynyt ravinto otettiin talteen, side poistettiin ja poikasia ruokittiin vastaavalla määrällä jauhelihaa. Käsittely tehtiin yhteensä 99 poikaselle 23 pesällä. Aineisto käsitti yhteensä 626 ravintokohdetta, jotka kuuluivat 12 eläinlahkoon (Taulukko 1). Ravinto koostui yksinomaan eläinravinnosta, josta tärkeimpiä sekä numeerisesti että biomassaltaan olivat perhosen toukat ja kovakuoriaiset. Nämä ryhmät yhdessä hämähäkkien (Araneae) kanssa muodostivat 80% ravintokohteista ja 90% ravinnon biomassasta. Ekologisesti tarkasteltuna ravinto koostui suurelta osin kaivautuvista (burrower) ja maan pinnalla kävelevistä eliöistä (walker, Taulukko 2). Poiketen useista aikaisempien tutkimuksien tuloksista kirjoittajien tutkimat alppivarikset olivat kokonaan hyönteissyöjiä. Tutkimusalueen puoliaavikko-olosuhteissa alppivarikset ovat riippuvaisia perinteisistä maankäyttömuodoista, kesantopelloista ruokailu- ja autioista rakennuksista pesäpaikkoina.

References

Balsa, J. & Montes, C. 1991: Regadíos y conservación de humedales en regiones semiáridas. El caso de Los Monegros. — Quercus 64: 36–44.

Blanco, G., Fargallo, J. A. & Cuevas, J. A. 1994: Consumption rates of olives by choughs in Central Spain: variations and importance. — J. Field Ornithol 65(4): 482–489.

Bullock, I. D. & del-Nevo, A. 1983: The Choughs of the Calf. — Peregrine 5(5): 226–229.

Bullock, I. D., Drewett, D. R. & Mickleburgh, S. P. 1983a: The Chough in Britain and Ireland. — British Birds 76: 377–401.

Bullock, I. D., Drewett, D. R. & Mickleburgh, S. P. 1983b: The Chough on the Isle of Man. — Peregrine 5(5): 229–237.

Coombs, F. 1978: The Crows. A study of the corvids of Europe. — Redwood Burn Limited Trowbeidge & Ester, London.

Cowdy, S. 1973: Ants as a Major Food Source of the Chough. — Bird Study 20: 117–120.

Farinha, J. C. & Teixeira, A. M. 1989: The Chough in Portugal - Status and distribution. — In: Bignal, E. & Curtis, D. J. (eds.), Chough and land-use in Europe: 25–28. Scottish Chough Study Group, Paisley, Scotland.

García-Dory, M. A. 1983: Datos sobre la ecología del Género Pyrrhocorax (P. pyrrhocorax y P. graculus) en el Parque Nacional de la Montaña de Covadonga. — Alytes 1: 411–448.

García-Dory, M. A. 1989: Brief report on the current status of the Chough in the Cordillera Cantabrica, Spain. — In: Bignal, E. & Curtis, D. J. (eds.), Chough and land-use in Europe: 34–37. Scottish Chough Study Group, Paisley, Scotland.

Guillou, J.-J. 1981: Problèmes de la distribution du Crave (Pyrrhocorax pyrrhocorax) en Europe occidentale. — L'Oiseau et R.F.O. 51: 177–188.

Harris, M. P. & Wanless, S. 1993: The diet of shags Phalacrocorax aristotelis during the chick-rearing period assessed by three methods. — Bird Study 40: 135–130.

Harrison, C. 1982: An Atlas of the Birds of the Western Palearctic. — Collins, London.

Henspenheide, H. A. 1975: Prey characteristics and predator niche width. — In: Cody, L. & Diamond, J. M. (eds.), Ecology and evolution of communities: 158–180. The Belknap Press of Harvard University Press, Cambridge.

Jover, L. 1989: Nuevas aportaciones a la tipificación trófica poblacional: el caso de Rana perezi en el Delta del Ebro. — Ph.D.-thesis, Universitat de Barcelona.

Martínez, C., Ruiz, X. & Jover, L. 1992: Alimentación de los pollos de Martinete (Nycticorax nycticorax) en el Delta del Ebro. — Ardeola 39(1): 25–34.

McCracken, 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.

Mellott, R. S. & Woods, P. E. 1993: An improved ligature technique for dietary sampling in nestling birds. — J. Field Ornithol 64(2): 205–211.

Meyer, R. M. 1990: Observations on two Red-Billed Choughs Pyrrhocorax pyrrhocorax in Cornwall: Habitat use and food intake. — Bird Study 37: 199–209.

Meyer, R. M., Buckland, P. & Monaghan, P. 1994: The diet of the Chough Pyrrhocorax pyrrhocorax as indicated by analysis of digested prey remains. — Avocetta 18: 95–106.

Murphy, M. E. 1994. Amino acid compositions of avian eggs and tissues: Nutritional implications. — J. Avian Biol. 25: 27–38.

Noordhuis, R. & Spaans, A. L. 1992: Interspecific competition for food between Herring Larus argentatus and Lesser Black-backed Gulls L. fuscus in the Dutch Wadden sea area. — Ardea 80: 115–132.

Owen, D. A. L. 1989: Vigilance by foraging choughs in relation to tourist disturbance. — In: Bignal, E. & Curtis, D. J. (eds.), Chough and land-use in Europe: 57–62. Scottish Chough Study Group, Paisley, Scotland.

Pielou, E. C. 1975: Ecological diversity. — John Wiley & Sons, New York.

Piersma, T. & Bloksma, N. 1987: Large flock of Choughs Pyrrhocorax pyrrhocorax harvesting caterpillars in pinewood on La Palma, Canary Islands. — Bird Study 34: 127–128.

Ricklefs, R. E. 1974: Energetics of reproduction in birds. — In: Paynter, R. A. (ed.), Avian Energetics: 152–297. Publ. Nuttall Ornithological Club, Cambridge, Massachusetts.

Roberts, P. J. 1983: Feeding habitats of the Chough on Bardsley Island (Gwynedd). — Bird Study 30: 67–72.

Roberts, P. J. 1989: Foods and feeding behaviour of choughs on Bardsey Island, North Wales. — In: Bignal, E. & Curtis, D. J. (eds.), Chough and land-use in Europe: 42–45. Scottish Chough Study Group, Paisley, Scotland.

Rolfe, R. 1966: Status of the Chough in Scotland. — Scottish Birds 12: 238–246.

Rosenberg, K. V. & Cooper, R. J. 1990: Approaches to avian diet analysis. — Studies in Avian Biology 13: 80–90.

Ruiz, X. 1985: An analysis of the diet of Cattle Egrets in the Ebro Delta, Spain. — Ardea 73: 49–60.

Ruiz, X. & Jover, L. 1981: Sobre la alimentación otoñal de la garcilla bueyera – Bubulcus ibis (L.) – en el Delta del Ebro, Tarragona (España). — Publicaciones del Departamento de Zoología de la Universidad de Barcelona 6: 65–72.

Sherry, T. W. 1984: Comparative dietary ecology of sympatric insectivorous neotropical flycatchers (Tyrannidae). — Ecol. Monogr. 54: 313–338.

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

Soler, M. 1989: The Chough in Oriental Andalusia with special mention of the Guadix Area. — In: Bignal, E. & Curtis, D. J. (eds.), Chough and land-use in Europe: 29–33. Scottish Chough Study Group, Paisley, Scotland.

Tella, J. L., Torre, I. & Sánchez-Alonso, C. 1996: Habitat fragmentation and Roost-site selection by the Storm Curlew (Burhinus oedicnemus) in an arid cultivated landscape (Los Monegros, NE Spain). — Rev. Ecol. Terre Vie 51: 153–159. (In press.)

Warnes, J. M. & Stroud, D. A. 1989: Habitat use and food of choughs on the islands of Islay, Scotland. — In: Bignal, E. & Curtis, D. J. (eds.), Chough and land-use in Europe: 46–51. Scottish Chough Study Group, Paisley, Scotland.

Wilkinson, W. 1989: Foreword. — In: Bignal, E. & Curtis, D. J. (eds.), Chough and land-use in Europe: IV. Scottish Chough Study Group, Paisley, Scotland.

Yeatman, L. 1976: Atlas des Oiseaux nicheurs de France. — Societé Ornithologique de France, Paris.

Zahl, S. 1977: Jackknifing and index of diversity. — Ecology 58: 907–913.