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An assessment of Chough *Pyrrhocorax pyrrhocorax* diet using multivariate analysis techniques

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Abstract — This paper provides the first quantitative information on the diet of the Chough, *Pyrrhocorax pyrrhocorax*, as assessed by faecal analysis. Fifty taxa (48 invertebrate and 2 plant) were identified in subsamples of Chough faeces collected from under the roosting sites of adults and from chicks in the nest on the island of Islay. Multivariate analyses of the data indicated that the seasonal abundance and availability of prey items was the most important factor influencing Chough diet throughout the year. Soil-dwelling Tipulidae (January to July) and Bibionidae (January to April) larvae, dung-associated insects (during the spring, and late summer and autumn), and surface-active insects (during the summer) were the most abundant invertebrate components of the diet. The invertebrate taxa taken in numbers by the Chough at any particular time of year compared well with those taxa found to be numerous on pasture at that time (McCracken 1990). Cereal grains were the most frequently taken food items during the early winter months, when invertebrate availability was low. The analyses provided an objective grouping of these very heterogeneous data into useful groupings for further study and investigation of the birds behaviour. Implications for the management of Chough areas are suggested, with emphasis on livestock and pasture management and the maintenance of mixed farming including small scale cereal production.

Introduction

The Chough, *Pyrrhocorax pyrrhocorax*, is one of Europe's rarest birds with scattered populations mainly in the mountainous areas of Iberia, along the northern Mediterranean area, in Brittany, and on the west coast of Britain. It is the rarest corvid in the British Isles being confined to the western seaboards of Ireland, Scotland and Wales (Monaghan 1988a). In the past it was much more widespread, but declined throughout the eighteenth and nineteenth centuries. Choughs are now absent from England and their distribution in Scotland and Wales is very limited. In Scotland breeding birds contracted to the Inner Hebrides and the Mull of Kintyre in the 1930's, and have been confined to the Inner Hebrides since the mid 1980's. Islay and Colonsay have been the major stronghold for many years (Monaghan et al. 1989) and maintaining suitable conditions there will be crucial for the survival of the Scottish population.

The Chough is listed on Schedule 1 of the Wildlife and Countryside Act (1981), which gives it special protection in Britain, and concern for its future in Europe resulted in its inclusion in April 1985 on Annex 1 of the European Community Directive (79/409/EEC) on the conservation of wild birds. The latter confers a responsibility on member states to conserve both the bird and its habitat. Only through a full understanding of the Chough's population structure, behaviour and ecological requirements can a conservation policy for the bird be devised (Monaghan et al. 1989).

A number of researchers have employed faecal analysis during the course of their investigations into the diet of the Chough (Bullock 1980, Roberts 1982, Warnes 1982). To avoid confusion with the faeces of other birds, all used a single, fresh dropping as their basic sampling unit, and identified prey items from remains within the dropping. There is considerable bias in such an approach due to different rates of digestion of prey items. Quantitative data were not included in the analyses of these studies. Instead, faeces collected at the same time of year were regarded as belonging to a grouping, and the results presented the occurrence of each prey item in each grouping (e.g. 90% of the faeces collected in November 1980 at Coul, Islay contained earwig remains - from Warnes 1982).

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While certainly indicating the general spectrum of items taken by the Chough in the areas concerned, the lack of quantitative data means that it is not possible to determine the relative importance of a particular prey item in the Chough diet at any time of the year. Indeed, some investigations may have given a misleading impression of the relative importance of certain taxa (Warnes 1982) and generalised interpretations of bird-habitat relationships may have over-emphasised the importance of certain areas (Bullock 1980).

The main aim of the results presented here is to address this gap in knowledge by the use of alternative collection and analytical techniques. This paper attempts to achieve 3 broad objectives. Firstly, to describe and quantify the diet of the Choughs on Islay; secondly, to test the applicability of multivariate techniques to objectively analyse the data; and thirdly, to interpret the data for practical management purposes. A fuller account of an investigation into the factors affecting the availability of invertebrate food for the Chough on Islay is given in McCracken (1990).

On Islay, an individual Chough, whether roosting communally (sub- adults and non-breeders throughout the year; some breeding birds in winter) or at the breeding site (most breeding birds in summer; some in winter), tends to use one particular roost site repeatedly (Monaghan 1988b, pers. obs.). Its faeces accumulate directly below this site, and it is possible to collect these accumulations at regular intervals. Standardised subsamples from these fresh "faecal mounds" should provide more accurate indications of the types and numbers of prey items taken within that period.

Use of this method on a number of "faecal mounds", accumulated at different times of the year, followed by comparison of the resulting data sets, should provide a more comprehensive analysis of the Chough's diet. The employment of multivariate techniques would allow objective analyses of the data to be made. Gauch (1982) concluded that two complementary multivariate analysis techniques, Two-Way Indicator Species Analysis (TWINSPAN: Hill 1979a), a polythetic divisive clasification technique, and Detrended Correspondence Analysis (DECORANA: Hill 1979b), a divisive ordination method based on reciprocal averaging, were by far the best techniques available for analysing complex sample- by-species data arrays. The great value of these techniques is that a large array of species and samples, with large numbers of zero values, can be dealt with in an objective way independent of any prior knowledge about the samples other than the species present (Foster et al. 1990).

It should be borne in mind that one cannot relate frequency of occurrence of prey items in the diet directly to biomass of food provided, although it may be possible to calculate this afterwards. However, such calculations are beyond the scope of this study.

Methods

Data collection

Two types of faeces were collected for analysis: adult, from "faecal mounds" at roosting sites; and chick, in the form of discrete faecal sacs produced by the chicks in the nest. Adults remove the chick faecal sacs from the nest and these only acumulate towards the end of the nestling period, when they are produced too frequently for the adults to remove them all. Fresh faecal sacs could be recognised and for the purpose of this study they were considered to contain prey provided by the adults on the day of collection.

Faeces from a total of 18 individual roosting and/or nest sites were used in this study (Table 1). For reasons of security the location of these sites on the island will not be presented here. Adult faeces were collected from 8 sites on Islay over various intervals between August 1986 and July 1989, and from 1 mainland coastal site in south-west Scotland in July 1988. The average collection period was 6 weeks, but this varied between 4 and 12 weeks and was dependant on opportunities to visit the sites (which was done in association with other work). Chick faeces were collected in May or June 1989 from 9 other sites on Islay and from 1 site on the island from which adult faeces had also been collected.

Two subsamples (each 3 ml in volume) were taken from each collection of faeces, and each was given an identification code. The final data set used in the analyses consisted of taxa abundances from 60 subsamples (40 adult and 20 chick).

Each subsample was washed through a sieve (aperture width 0.32 mm), and the associated taxa identified and counted under a binocular microscope. The presence of cereal grains and weed seeds was noted and their abundance estimated. Since earthworm chaetae may pass through a 0.32 mm sieve the washings were also examined for the presence of these.

The minimum number of each taxon present in each subsample was calculated. Beetle (Coleoptera) adults and larvae were mainly identified from head capsules, mandibles and legs. Fly (Diptera) larval and pupal stages were identified from posterior spiracles and mouthparts. Moth (Lepidoptera) larvae were distinguished by their mandibles, earwigs (Dermaptera) by their cerci, and ants (Formicidae) by their head capsules. The presence of crane fly (Tipulidae) eggs was taken to imply that an adult had been consumed.

Table 1. Roosting and/or nest sites from which Chough faeces were collected for analysis. The site and subsample codes, types of faeces collected, and the period over which the faeces accumulated are shown. Sites 1-17 were on Islay and site 18 was in south-west Scotland.

SITES AND SUBSAMPLES	TYPE OF FAECES	PERIOD OVER WHICH FAECES ACCUMULATED
1 A & B	ADULT	01/08/86 - 03/10/86
1 C & D	CHICK	31/05/89
2 A & B	ADULT	20/01/88 - 22/03/88
3 A & B	CHICK	22/05/89
4 A & B	ADULT	02/11/86 - 28/11/86
4 C & D	ADULT	13/12/86 - 12/02/87
5 A & B	CHICK	22/05/89
6 A & B	ADULT	10/03/89 - 29/04/89
7 A & B	ADULT	20/01/88 - 21/03/88
7 C & D	ADULT	10/03/89 - 30/04/89
8 A & B	CHICK	30/05/89
9 A & B	CHICK	01/05/89
10 A & B	ADULT	02/11/86 - 28/11/86
10 C & D	ADULT	14/12/86 - 12/02/87
11 A & B	CHICK	31/05/89
12 A & B	CHICK	30/05/89
13 A & B	ADULT	03/10/86 - 02/11/86
14 A & B	CHICK	05/06/89
15 A & B	CHICK	22/05/89
16 A & B	CHICK	30/05/89
17 A & B	ADULT	18/01/88 - 23/03/88
17 C & D	ADULT	23/03/88 - 29/04/88
17 E & F	ADULT	29/04/88 - 14/07/88
17 G & H	ADULT	14/07/88 - 11/10/88
17 I & J	ADULT	11/10/88 - 01/12/88
17 K & L	ADULT	19/01/89 - 10/03/89
17 M & N	ADULT	10/03/89 - 01/05/89
17 O & P	ADULT	01/05/89 - 05/06/89
17 Q & R	ADULT	05/06/89 - 19/07/89
18 A & B	ADULT	01/06/88 - 09/07/88

The phenology of potential invertebrate prey items on Islay was investigated through 1988 and 1989 by pitfall trapping, and by sampling soil and cow dung (McCracken, 1990). This knowledge was used to assist in the interpretation of the results from the analyses of the faecal subsamples.

Classification and ordination

The 60 subsamples were classified by TWINSPAN, which produces a hierarchical classification by dividing the data into two groups, followed by repeated division of each of these newly derived groups. The process was continued until either replicate subsamples were about to be separated (a process for which the term "site integrity" has been coined), or each further division produced two end-groups which were not ecologically distinct.

Since the principle aim of the analysis was to use the quantitative information in the data the "pseudo-species" function in TWINSPAN was used. This reduces the quantitative data to presence/absence data, without undue loss of information, by converting the frequency data into classes (Hill 1979a). Each class is treated thereafter as if it were a separate taxon, a "pseudo-species". In this classification, the quantitative data were converted into four classes: 1-4, 5-9, 10-24 and >24 individuals. These classes were non-exclusive, so that, for example, a subsample in which 20 *Aphodius* spp. larvae were found would be registered as containing classes 1, 2 and 3 of *Aphodius* spp. larvae.

Taxa and subsamples were ordinated in three axes using DECORANA. All taxa were considered (a) equally, and (b) after downweighting, the procedure whereby the influence of rare taxa in the data on the ordination of the subsamples is minimised (Hill 1979b). The axes of the resulting graphs can be related to known environmental parameters, which may then be used to describe characteristics of importance to the community structure, or the preferred environments of the species present (Luff et al. 1989). Downweighting of rare taxa did not substantially change the ordination of the subsamples and is therefore not considered any further here.

After analyses of the data set, groups of subsamples were interpreted as representing distinct taxa assemblages. The subsample ordination scores derived from DECORANA, measured in standard deviations of species "turnover" (Hill 1979b), were used to calculate the centroid mean score, for the first three axes, of each end-group interpreted form the analyses. The distances between end-group centroids were then calculated to give a measure of the similarity between end-groups as defined by the analyses (Luff et al. 1989).

Results

Chough faecal content

A total of 50 taxa were identified in the subsamples (Table 2). The majority of the invertebrate taxa fall into one of three "habitat" categories (surface-active, soil-dwelling or dung- dwelling) as detailed below.

Coleoptera: Carabidae, Curculionidae, Elateridae, Staphylinidae and *Serica brunnea* (Scarabaeidae) adults would mainly be found active on the soil surface, whereas Cantharidae, Carabidae, Elateridae and Staphylinidae larvae would mainly be found in the soil. The remaining beetle taxa would be found in association with livestock dung, apart from the Silphidae adults which would be found in carrion.

Diptera: Bibionidae larvae and Tipulidae larvae and puparia would be found in the soil, and Calliphoridae larvae and puparia in carrion. The remaining fly taxa would be found either in or underneath livestock dung.

Other: The Lepidoptera larvae, Araneae, Dermaptera and Formicidae would all be found on the soil surface, although some Lepidoptera larvae would also be found in the soil. The cereal seeds (barley grains) would either be found in stubble fields or at livestock feeding stations, and the weed seeds probably in pastures.

No evidence was found to suggest that earthworms are prey items on Islay.

Classification

The classification of Chough faecal content (and hence diet) on Islay, as interpreted from TWINSPAN end-groups, is given in Figure 1, together with the indicator taxa at each division. There were no indicator taxa for end-groups A, E and G. Eight end-groups were recognised as representing distinct foraging strategies. The subsamples within each end-group are shown in Table 3, and the frequency of occurrence of each taxon within these end-groups is given in Table 4. Interpretation of the end-groups was based on knowledge of (1) the ecology of the taxa that occurred frequently within them, (2) the number of individuals of these taxa within the subsamples of an end-group, and (3) the areas from which the subsamples were collected. The criterion of site integrity was used to ensure that the interpretation of the classification was meaningful.

The end-groups were described as shown below. Figures after taxa are mean percentage relative abundances (± SE) for the subsamples in the end-group.

End-group A: 6 subsamples from 3 sites, collected from adults on the Scottish mainland (July 1988), and from adults (February 1987) and chicks (May

Table 2. - Taxa identified in Chough faeces. An 8-letter abbreviation is shown for each taxon.

COLEOPTERA:	
Cantharidae larvae	CANTLARV
Carabidae adults	CARAADUL
" larvae	CARALARV
Curculionidae	
Philopedon plagiatus (Schaller) adults	PLAGADUL
Other weevil adults	WEEVADUL
Elateridae	
Agriotes spp. adults	AGRIADUL
" " larvae	AGRILARV

Table 2. - continued

Ctenicera cuprea (F.) adults	CCUPADUL
" " " larvae	CCUPLARV
Geotrupidae	
Geotrupes spp. adults	GEOTADUL
Hydrophilidae	
Cercyon spp. adults	CERCADUL
Helophorus spp. adults	HELOADUL
Sphaeridium spp. adults	SPHAADUL
Scarabaeidae	
Aphodius ater (DeGeer) adults	APHOATER
A. contaminatus (Herbst) adults	APHOCONT
A. depressus(Kugelann) adults	APHODEPR
A. fimetarius (L.) adults	APHOFIME
A. foetidus (Herbst) adults	APHOFOET
A. fossor (L.) adults	APHOFOSS
A. rufipes (L.) adults	APHORUFI
A. rufus (Moll) adults	APHORUFU
A. sphacelatus (Panzer) adults	APHOSPAC
Aphodius spp. larvae	APHOLARV
Serica brunnea (L.) adults	SERRBRUN
Silphidae adults	SILPADUL
Staphylinidae adults	STAPADUL
" larvae	STAPLARV
DIPTERA:	
Anisopodidae larvae	ANISLARV
Bibionidae larvae	BIBILARV
Calliphoridae larvae	CALILARV
" puparia	CALIPUPA
Muscidae	
Morellia spp. puparia	MOREPUPA
Polietes spp. larvae	POLILARV
Other Muscidae larvae	MUSCLARV
" " puparia	MUSCPUPA
Scathophagidae larvae	SCATLARV
" puparia	SCATPUPA
Sphaeroceridae larvae	SPHALARV
" puparia	SPHAPUPA
Tipulidae adults	TIPUADUL
" larvae	TIPULARV
" puparia	TIPUPUPA
OTHER:	
Araneae - spiders	SPIDPRES
Cereal seed remains	CEREPRES
Dermaptera - *Forficula auricularia* L.	FORFAURI
Formicidae - ants	ANTSPRES
Lepidoptera larvae - caterpillars	LEPILARV
Weed seed remains	WEEDPRES

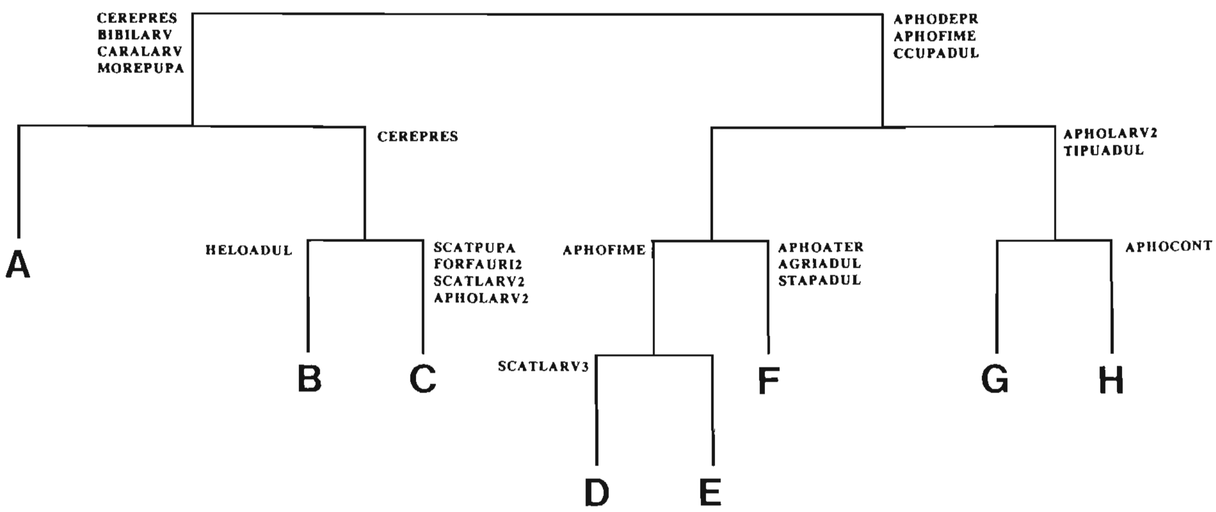

Figure 1. Dendrogram showing the eight end-groups interpreted from the TWINSPAN classification of the Chough faeces data set. The indicator taxa at each division are shown (abbreviations as in Table 2), and the numbers indicate the 'pseudo-species' class where it is other than 1.

1989) on Islay. Crane fly larvae were abundant (49.6 ± 10.1) in all these subsamples. In addition, the chicks were provided with numbers (5.4 ± 2.5) of lesser dung fly (Sphaeroceridae) puparia; and numbers of ants (33.0 ± 13.0 - mainland Scotland only), spiders (5.0 ± 2.2 - Islay only) and ground beetle (Carabidae) larvae (25.7 ± 5.0) were taken by the adults. On the basis of their taxa compositions, these subsamples were "under-represented" in the data set. They therefore proved difficult to classify within TWINSPAN, hence their position at one extreme.

End-group B: 18 subsamples from 5 sites, all from adults and covering the period December to April. Cereals, probably either gleaned from stubble fields or taken at cattle feeding stations, were the most frequently taken (48.4 ± 6.6) prey items at this time of year, with Bibionidae and crane fly larvae being taken in numbers (20.5 ± 6.6 and 6.0 ± 0.8, respectively) from pastures, probably as they become bigger and, presumably, easier to find. Other pasture insects taken included ground beetle larvae (4.9 ± 1.4) and adults (1.9 ± 0.5).

Table 3. - End-groups with associated sites and subsamples interpreted from TWINSPAN analysis. See Table 1 and text for further information.

END-GROUP	SITES AND SUBSAMPLES									
A	4C	4D	9A	9B	18A	18B				
B	2A	2B	6A	6B	7A	7B	7C	7D	10C	10D
	17A	17B	17C	17D	17K	17L	17M	17N		
C	4A	4B	10A	10B	17G	17H	17I	17J		
D	3A	3B	15A	15B						
E	1C	1D	5A	5B	11A	11B	16A	16B		
F	8A	8B	12A	12B	17E	17F	17O	17P	17Q	17R
G	13A	13B	14A	14B						
H	1A	1B								

Table 4. The frequency of occurrence of taxa within the TWINSPAN end- groups, where a taxon occurs in >20% of the subsamples in one of the end- groups (D = 21-40%; C = 41-60%; B = 61-80%; A = 81-100%). The taxa order is derived from the TWINSPAN analysis and the abbreviations are as shown in Table 2.

TAXA	TWINSPAN END-GROUP							
	A	B	C	D	E	F	G	H
BIBILARV	-	A	C	-	-	-	-	-
HELOADUL	D	C	-	-	-	-	-	-
CEREPRES	-	A	A	-	-	-	-	-
MOREPUPA	D	C	C	-	-	-	-	-
POLILARV	-	-	D	-	-	-	-	-
SCATPUPA	D	-	B	-	-	-	-	-
APHOSPHA	-	D	D	-	D	D	-	C
CARALARV	A	A	C	-	D	D	-	A
FORFAURI	A	B	A	C	-	C	B	C
ANISLARV	-	-	D	-	-	-	-	-
ANTSPRES	D	D	C	-	-	-	-	-
SPHAPUPA	D	-	-	-	-	-	-	-
SPIDPRES	C	-	-	-	-	-	-	-
APHOCONT	-	D	B	-	-	-	-	A
CARAADUL	C	A	A	B	D	C	B	A
WEEVADUL	D	C	D	-	-	D	D	-
LEPILARV	B	C	D	C	D	A	A	A
STAPADUL	C	D	D	-	-	B	D	-
TIPULARV	A	A	A	A	A	A	B	A
APHORUFI	-	-	D	-	-	D	D	A
SCATLARV	-	D	B	A	D	-	C	-
TIPUPUPA	D	-	D	-	B	-	-	A
APHOLARV	-	C	A	-	-	D	A	A
TIPUADUL	-	D	C	-	C	-	A	A
APHOFOET	-	-	-	-	-	-	C	-
APHOFOSS	-	-	-	-	-	-	C	-
GEOTADUL	-	D	D	-	C	C	B	A
AGRIADUL	B	-	-	-	D	B	-	-
CCUPLARV	-	-	-	-	-	D	C	-
PLAGADUL	C	-	C	A	D	B	B	-
SILPADUL	D	-	-	-	-	D	D	-
STAPLARV	B	D	C	B	B	C	D	-
APHOATER	-	-	-	-	-	B	D	-
CERCADUL	-	-	-	-	-	D	-	-
APHODEPR	-	-	-	A	A	B	B	A
CCUPADUL	-	-	-	A	B	C	-	-
SPHAADUL	-	-	-	A	-	-	-	C
APHOFIME	-	-	-	B	A	-	A	-
CALILARV	-	-	-	-	B	-	B	-
CALIPUPA	-	-	-	-	-	-	D	-
APHORUFU	-	-	-	-	-	-	C	-
ATHOADUL	-	-	-	-	-	-	D	-
SERRBRUN	-	-	-	-	-	-	C	-
WEEDPRES	-	-	-	-	-	-	C	A

End-group C: 8 subsamples from 3 sites, all from adults and mainly collected between October and December. Cereals were abundant (43.5 ± 9.0) in the diet at this time of year, along with insects obtained from feeding in dung. Taxa taken in numbers included dung fly (Scathophagidae) larvae (8.7 ± 2.7) and puparia (3.6 ± 1.0), and dung beetle (*Aphodius* spp.) larvae (6.6 ± 1.8) and adults (4.4 ± 1.1). Dermaptera also featured prominently (10.8 ± 3.6) during this period.

End-groups D and E contained subsamples collected from chicks at the end of May 1989.

End-group D: 4 subsamples from 2 sites in an area of dunes and sand-grassland coastal pasture heavily grazed by cattle and sheep. On the day of collection the chicks received large numbers of dung fly larvae, *Philopedon plagiatus* adults (a weevil occuring mainly in sandy places), and crane fly larvae (43.6 ± 8.2, 22.7 ± 8.9 and 10.8 ± 2.0, respectively). Small numbers of dung-associated (*Aphodius* spp.: 6.9 ± 1.2) and surface-active (Elateridae: 3.2 ± 0.6, and Carabidae: 3.4 ± 1.2) adult beetles were also provided.

End-group E: 8 subsamples from 4 inland areas. These chicks were provided with blow fly (Calliphoridae) larvae, probably obtained from carrion, *Aphodius* spp. adults and large numbers of crane fly larvae on the collection days (12.4 ± 4.2, 14.5 ± 3.8 and 33.9 ± 4.1, respectively). Small numbers of rove beetle (Staphylinidae: 7.0 ± 2.0), and click beetle (Elateridae: 6.6 ± 1.6) adults were also provided.

End-group F: 10 coastal subsamples from 3 sites, collected from both adults and chicks between May and July. As in end-group D, crane fly larvae and *P. plagiatus* adults were abundant (24.6 ± 3.1 and 16.1 ± 7.5, respectively) in these subsamples, and dung- asociated insects (*Aphodius* spp. adults: 14.6 ± 4.3, and larvae: 4.1 ± 2.4) were also numerous. Being later in the year, a greater variety of surface-active insects were taken, including moth larvae, and click and rove beetle adults (4.1 ± 0.9, 6.2 ± 1.5 and 2.9 ± 0.8, respectively).

End-group G: 4 subsamples collected from 2 different sites in the same area as end-group D - from adults at the beginning of November 1986, and from chicks at the beginning of June 1989. Although a variety of taxa were present in these subsamples, very high numbers of *Aphodius* spp. larvae and adults were found (57.9 ± 6.1 and 15.4 ± 4.0, respectively), indicating that dung-associated taxa were extremely common prey items in this area at these times.

End-group H: 2 subsamples collected at the beginning of October 1986 from adults at an inland site. Weed seeds were present in numbers (59.2 ± 1.0) from this area at this time, along with numbers of *Aphodius* spp. adults and larvae (12.5 ± 2.0 and 8.2 ± 1.0, respectively).

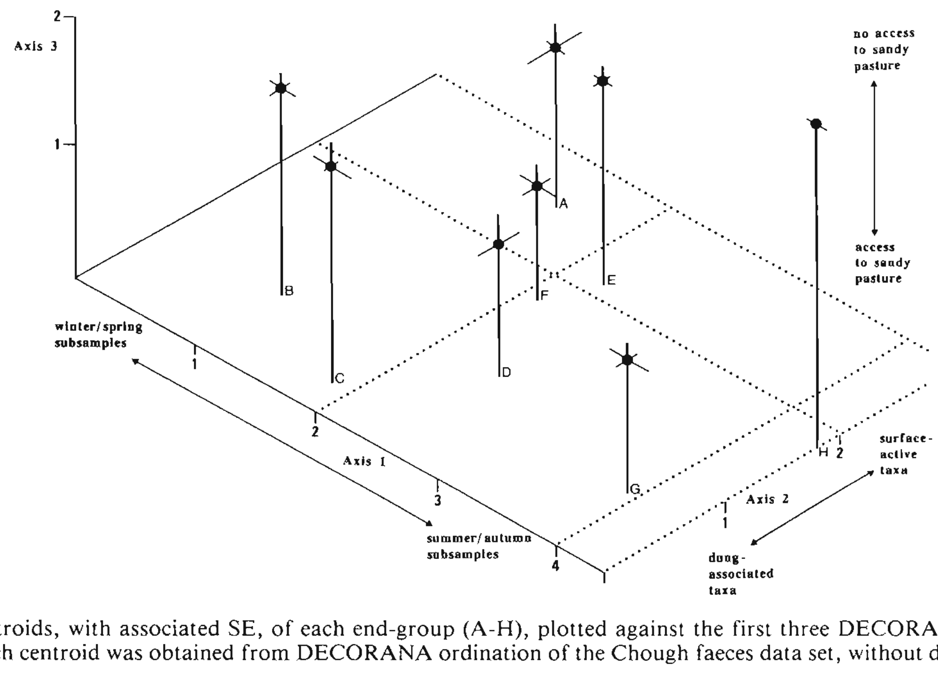

Figure 2. Centroids, with associated SE, of each end-group (A-H), plotted against the first three DECORANA axes. The position of each centroid was obtained from DECORANA ordination of the Chough faeces data set, without downweighting of rare taxa.

Ordination

Figure 2 shows the centroids of the end-groups interpreted from the TWINSPAN analysis plotted against the first three DECORANA axes, without downweighting. Their positions (with associated standard errors) and relative distances from one another are given in Table 5. The eigenvalues for the ordination, which give some indication of the amount of variation associated with each axis, were 0.707, 0.467 and 0.332 for axes 1, 2 and 3 respectively. In other words 47% of the between-subsample variation in taxa assemblages accounted for by these axes was explained by axis 1, 31% by axis 2 and 22% by axis 3.

Axis 1 appears to be related to seasonality, since the winter/spring subsamples (end-groups B and C) lie at one extreme, the summer/autumn subsamples (end-groups G and H) lie at the other, and the spring/summer subsamples (end-groups D, E and F) lie in between.

Axis 2 appears to be related to foraging strategy. The subsamples within which large numbers of dung-associated taxa were found had the lowest scores along this axis, whilst those containing more surface-active taxa, or taxa not associated with dung, had the highest.

Axis 3 is possibly related to the location of the subsamples on the island. Coastal subsamples, with access to sandy pastures, had the lowest scores on this axis, whilst those occurring inland, or without access to sandy pasture, had the highest.

From the calculated distances between end-groups (Table 5) it can be seen that end-groups B and C were close, as were end-groups D and F; E and F; and A and E. In all cases however, the standard errors of the mean subsample scores on each axis were small relative to the distances between centroids, indicating that the definitions of these end-groups were valid.

Discussion

The majority of the taxa found in the Chough faecal subsamples in this study are in some way associated with pastures - they either occur in the soil and/or are surface-active in pastures, or live in the dung of livestock grazing these areas. This compares well with the findings of Bignal et al. (1988b) who, as part of their study of land use and birds on Islay, considered the relationships between the Chough and its environment. They reported that the majority of summer and winter sightings of Chough were in some form of grassland vegetation (58 and 63%, respectively), with the highest proportion in species-poor grassland during the breeding season and in species-rich grassland in winter. Species-poor grassland included permanent pastures on raised beach terraces as well as rough hill grazing. Over 50% of these grasslands were grazed by cattle, with both sheep and red deer also present. The species-rich grasslands were also heavily grazed, with over 26% holding cattle and 73% holding sheep. These species-rich swards were developed over limestone or blown sand.

In addition, the taxa taken in numbers by the Chough at any particular time of year compared well with those taxa found to be abundant on pasture at that time (McCracken 1990). Only fewer ground beetle adults appeared to be taken than would be predicted from the numbers present, as, for example, indicated by the use of pitfall traps (McCracken and Foster in prep.). These beetles

Table 5. Positions, with associated SE, on each DECORANA axis and distances between centroids of each TWINSPAN end-group. All positions and distances are in DECORANA axisunits.

END-GROUP	POSITION			DISTANCE FROM END-GROUP						
AXIS:	1	2	3	B	C	D	E	F	G	H
A	148 ± 8	255 ± 24	121 ± 14	193	234	183	95	110	308	329
B	98 ± 21	72 ± 8	154 ± 12		96	161	191	166	297	371
C	183 ± 17	27 ± 6	160 ± 19			116	191	166	218	313
D	246 ± 2	102 ± 17	97 ± 23				125	80	148	260
E	227 ± 6	213 ± 6	153 ± 10					81	225	237
F	211 ± 14	173 ± 10	85 ± 16						209	284
G	390 ± 17	66 ± 9	102 ± 9							196
H	439 ± 9	180 ± 1	254 ± 3							

possess chemical defence mechanisms (Dettner 1987), which may make them distasteful to predators, and in addition, many are nocturnally active (Thiele 1977) and therefore not readily available to the birds.

The smallest prey items detected in Chough faeces from Islay were ants, at about 4-5 mm in length. Other potential prey items, such as moth fly (Psychodidae) larvae which are of this size or even smaller, may have been taken by the birds, but would have been too easily crushed to leave any recognisable remains in the faeces.

The results presented in this paper provide the first analyses of quantitative data on Chough diet. The data collection methods used were very time-consuming and consequently fewer and smaller subsamples were investigated than would normally be desirable. However, it was felt that the benefits gained from the increased amount of information obtained on taxa abundances vastly outweighed any negative effects attributable to the small sample size. It should also be borne in mind, that when one is dealing with rare species it is inevitable that the number of individuals available for study will be small.

The diet of the Chough on Islay as interpreted from the analyses may be summarised as follows:

(1) the seasonal availability of prey items is the most important factor influencing Chough diet through the year. A similar situation has been described for Choughs in the Cordillera Cantabrica mountains of Spain (Garcia-Dory 1983), on Anglesey (Bullock 1980), on Islay (Warnes 1982), and on the island of Bardsey (Roberts 1982);

(2) cereals are extremely abundant in the diet from October to April;

(3) crane fly and Bibionidae larvae, together with cereals, were most frequently taken between January and April, with crane fly larvae taken in large numbers until July;

(4) dung-associated insects are abundant components of the diet during the spring (when young are in the nest), and late summer and autumn (in association with cereals);

(5) during the summer a greater variety of surface active insects is exploited.

Warnes (1982) also investigated the diet of the Chough on Islay, and concluded that dung beetle (*Aphodius* spp.) adults and their larvae formed the staple diet throughout the year. It is clear, however, from the present study, that although Aphodius spp. are eaten throughout the year, they only assume real dietary importance in spring when adults are taken, and during late summer and autumn when larvae are available in large numbers. Crane fly larvae (in the spring only) and dung fly larvae are also of great importance in the diet at these times.

Warnes also suggested that cereals (oats) were an important winter food source for flock-feeding birds, but not for breeding pairs which she considered to remain on their breeding grounds. All the winter faeces examined in the present study were collected from such pairs, and the abundance of cereals (barley) in their diet has already been stated. However, as in Warnes, no evidence of earthworm remains were found in the Chough faeces, and ants did not appear to be important prey items on Islay at any time of the year.

Paired Chough are highly territorial during the breeding season but the degree to which pairs tolerate other Choughs within their home ranges is not fully understood (Bignal et al. 1988a). However breeders certainly exclude some other Choughs and therefore, although potential prey items may be abundant at a site during the spring and summer, if that site lies within a pair's breeding territory, then other Chough within flying distance may not necessarily have access to that site at this time. Moreover, in many bird species there are age-related differences in habitat selection and foraging ability (Gauthreaux 1988). Field observations of the Chough on Islay suggest that newly fledged birds and sub-adults may depend more heavily on easily obtained prey items associated with animal dung than breeding pairs (E. Bignal pers. obs., A. Rolando pers. comm.).

With reference to the 3 broad objectives set out at the beginning of this paper:

(1) the diet of the Chough on Islay has been quantified and described and the data indicates that, contrary to previously published studies, it is highly variable both in relation to area and time of year;

(2) although the data used were "noisy" (in that the faecal samples were collected over a number of years), interpretable classifications and ordinations of subsamples on taxa composition were obtained, and the analyses provided an objective grouping of this very heterogeneous data into useful groupings for further study and investigation of the birds behaviour;

(3) the presence of an agricultural sector based on relatively low-intensive livestock rearing, especially cattle, on Islay would appear to be of great importance to the continuing survival of the Chough population there, (a) because of the invertebrates that colonise livestock dung, (b) because the practice of feeding out-wintered cattle provides an important source of cereal foodstuffs at a time when few potential invertebrate prey items are available, (c) the combination of cattle and sheep grazing pressure produces short swards in which Choughs can exploit soil and surface invertebrates, and (d) such low-intensity systems enable a wide range of natural and semi-natural vegetation to survive, which in turn contribute to the range of feeding habitats available to Choughs.

Conclusions

One cannot generalise about the diet of the Chough - diet is not a matter of specialised feeding strategy (at the prey species level) but of prey availability. The birds do, however, specialise on invertebrates and, from a management point of view, it will be important to target livestock and pasture management on Islay in order to enhance prey availability. In addition, cereals provide a crucial food source during the early winter months, when invertebrate availability is low, and on Islay cereal growing would probably only continue if livestock, especially cattle, rearing was maintained.

The interpretation of these results show that the survival of the Chough on Islay is related to its need for an availability of a wide range of invertebrate prey throughout the year. Agricultural monocultures produce habitat and land-use simplification, and it would appear that the Chough, unlike other corvids, is unable to adapt to such conditions.

Finally, the collection and analytical techniques described would appear to provide an attractive method of objectively assessing the Chough's (and other birds) dietary requirements throughout the year. In this study the time available for both fieldwork and laboratory assessment of the faeces was limited, and therefore for future studies (with greater resources) it is recommended that accumulation/collection periods are standardised at shorter intervals (e.g. 4 weekly) to provide a greater number of subsamples.

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Riassunto — Questo lavoro fornisce dettagliate informazioni quantitative sulla dieta del Gracchio corallino in Scozia. Analisi multivariate dei dati indicano che l'abbondanza stagionale e la disponibilità delle prede sono i fattori che maggiormente influenzano la dieta nel corso dell'anno. Larve di Tipulidi (da gennaio a luglio) e Bibionidi (da gennaio ad aprile), insetti associati allo sterco (primavera, estate ed autunno) ed insetti epigei (estate) costituiscono i gruppi di invertebrati più abbondanti nella dieta. Le implicazioni gestionali delle aree frequentate dal Gracchio corallino vengono analizzate e discusse.

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