

CHAPTER 5 FOOD INTAKE

5.1 INTRODUCTION

The slender decurved beak of the Chough suggests fundamental differences between it and the other British corvids (Coombs 1978, Waite 1984, and see Section 1.3.1). Choughs feed largely on epigaeal invertebrates: principally on the larvae of beetles and flies, earwigs, spiders and ants (Goodwin 1986). Cereal grain is recorded as being taken in northern areas (Warnes 1982). Until this study, earthworms have not been regarded as important prey, even though Bullock (1980) reported that 15% of 39 faecal samples from the Llyn peninsula in North Wales contained such evidence. He recorded none such from nearby Anglesey, nor did Roberts (1982) on neighbouring Bardsey Island, or Warnes (1982) from Islay. Holyoak (1967) suspected that earthworms were taken on the Calf of Man. Ussher & Warren (1900) recorded 'worms' as a food in Ireland but this was somewhat discounted by Bullock *et al.* (1983b).

The aim of this chapter is, primarily by sampling of feeding sites and faecal castings, to investigate the diet of the Chough in West Wales, and to relate these findings to the availability of the prey spectrum by season and in the Welsh and Cornish study areas. It is not here related to habitat availability. Behavioural studies (Chapter 6) demonstrate that Choughs spend virtually all their active time foraging, and areas used for this activity were the subject of the preceding chapter.

5.2 METHODS

5.2.1 PREY SAMPLING METHODS

The term 'prey' is used to describe all food items, whether animate or not. The location of all Chough feeding observations, and, if possible, the actual prey items taken were recorded. If the actual prey was not obvious, either from direct observation or from inspection of prey foci (*e.g.* ants' nests), the area was sampled to give an indication of potential prey present. In Cornwall, the background prey spectrum was sampled in areas which had historically supported Choughs, and which were all potential re-establishment sites (Chapter 7).

The physical and botanical structure of feeding sites were investigated (4.3 & 4.4) in addition to prey sampling. If pursuit of birds was in progress, their positions were marked for later investigation (2.5.3 & 2.5.4). Soil-core extraction was chosen as the primary method of sampling since it could be used both spontaneously and routinely, as determined by Chough behaviour. Although time-consuming, it was considered preferable to the pitfall-trapping used in earlier Chough studies (*e.g.* Warnes 1982) especially when hand-sorting on site. Pitfall-trapping requires pre-selection of sites, fixed equipment and frequent visitation; it is destructive and, in the short term, will alter the local distribution of certain taxa (Terrell-Nield 1986); it is also biased in favour of active ground-moving taxa which are often nocturnal and therefore not Chough food (see below); Southwood (1978) discussed other 'pitfalls' of pitfall-trapping, and Luff (1975) found considerable variation in the efficiency of various traps. However, pitfall-trapping was undertaken during a preliminary study at Rame in Cornwall (Appendix IV), and during an inquiry on Ramsey Island (Appendix V) towards the end of the main study, in which nocturnality and diurnality of the catch assemblages were examined. Suction-trapping was not employed since it samples mainly small invertebrates living on plant stems and leaves, and not larger terrestrial forms, *e.g.* Coleoptera (Galbraith 1986). To sum up, soil-sampling is imitative of Choughs' feeding behaviour, less biased in its selection, and enables instant sampling at recently vacated feeding sites. However, it also under-represents certain taxa, notably carabid ground-beetles which are opportunistically taken by Choughs from the ground surface or from under stones (Coombs 1978); earwigs are possibly also similarly taken.

When access and substrate permitted, soil cores measuring 8x6cm were extracted; otherwise (e.g. in rocky ground), an equivalent volume of earth was sampled with a knife or trowel. The depths of cores and their rapid extraction helped to ensure the capture of deep-burrowing earthworms (Galbraith 1986). Inaccessibility of some steep cliff feeding sites will have caused an indeterminate amount of bias.

Spot samples were taken to determine obvious prey (such as ants' nests, as mentioned above, also the foci of diptera larvae, especially in cow dung, and surface items such as cereal grain) at feeding points where these could be determined precisely. Cereal was the only major inanimate food, and because its collection involves surface-gleaning rather than digging or searching, it requires a different analytical approach. It is a food which requires a minimum of collection-effort in terms of time and energy by the Choughs, which offsets its lower calorific value (Richford 1978). Since the food source lies visible on the surface, it cannot be meaningfully sampled in the same way as subterranean fauna; for this reason, cereal grain is omitted from some of the results. Its true value is examined in Section 5.3.5.

Soil samples were immediately disassembled on a white tray or polythene sheet. All organisms of a size likely to be taken by Choughs (i.e. >5mm long (5.3.6)) or present in aggregations (e.g. ants) were counted; larvae could often be identified only to family or generic level; a type collection was retained for later or specialist examination. Identification was taken to as high a level as possible within available resources. Earthworms were not generally specified but assigned to one of 3 different size classes: S =small (<40mm), M =medium (40-80mm) or L =large (>80mm) (after Feare *et al.* 1974, Waite 1984) [NB. sizes are of animal in relaxed state]; based on a sample of 25 from each class, the energy content of each was S =0.76J, M =1.75J, and L =4.06J (after Waite 1984; cf. Table 5.6). The commonest species of earthworm found were *Lumbricus rubellus*, *Eisenia foetida* and *Allobophora chlorotica*; the former two occur in regions of high organic matter, whereas the latter prefers areas where the organic matter has been more broken down (P. Elliott, pers. comm.).

Where precise feeding sites could be determined, sometimes corroborated by definitive evidence of actual prey, these methods ensured that one of the main objectives of the study (the actual components of Chough diet) was adequately covered. At such sites, the method also allowed the frequencies of potential prey to be compared between the different study areas.

At less precisely determined feeding sites, nonetheless determined to exact areas of usage, a transect of 3-5 samples was taken at 1m intervals across the area (Figures 2.15 & 2.16). In order to establish whether Choughs were selecting for localised prey richness (patchiness) or for other reasons, sampling also took place in adjacent habitats which though physiographically suitable for Choughs were unused at the time. Whittaker (1947) noted that Choughs concentrated on certain patches of moorland while avoiding apparently similar patches nearby. The sampling protocol was also intended to provide general background information on prey availability. A second primary objective of the study was the investigation into the availability of potential prey in Cornwall, based on an understanding of prey selection by Choughs in Wales. For this reason, it was necessary to employ a method which could be replicated in areas where Choughs were not currently found (i.e. Cornwall), and thus provide a basis for their comparison and a means by which Cornwall and the regions sampled therein could be assessed. Some subjectivity inevitably had to be employed in the selection of equivalent Cornish areas, and this was based on empirical knowledge gained from Chough usage in Wales. The Cornish sampling always took place immediately after Welsh fieldwork to avoid seasonal effects.

Prey abundance and diversity were seen as key elements both to understanding Chough feeding

ecology in the different regions of West Wales, and to the assessment of Cornwall as potential Chough habitat. There are two main components of diversity: (i) number of species, and (ii) the spread of individuals (Putman & Wratten 1984; and see Section 5.3.2). An index to estimate availability was constructed to respond to frequency and spread of captures across the study area and region:

$$AI = \frac{(I_a + (S^a - 1)) + (I_b + (S^b - 1)) \dots}{N}$$

where AI = the Availability Index, I_a = the frequency or total number of individuals per taxon recovered from S^a = the number of +ve samples in the site A, ('b' = site B *et seq*) and N = total number of samples (-ve and +ve) per site or region. A simplified example for a given number of samples, N, is 4 individuals of Taxon F from 2 samples would produce 5/N (*i.e.* $4 + (2 - 1)/N$), as would also 3 individuals of Species G from 3 samples ($3 + (3 - 1)/N$); thus compensating for the wider occurrence of Species G.

The same formula was used both in Chough feeding areas and nearby unused areas in order that they might be compared. The samples in unused areas were arbitrarily selected, as shown in Figure 2.16. The extensive nature of the study did not permit random habitat sampling, and it was, moreover, considered not germane to the specific objectives: the central question being 'What do Choughs do?' rather than 'What do they not do?!' Given an infinite complexity of habitats and habitat mosaics, the research in Cornwall had to be based on the results from Wales.

5.2.2 FAECAL SAMPLING METHODS

Faecal samples were collected during the course of bird observation. Collection was usually restricted to fresh samples obtained immediately after the birds' departure from a feeding site. Occasionally, these were supplemented with older material, such as in the Rame study (Appendix IV), or to achieve more information on prey selection, where the actual time of defaecation and, therefore, by estimation, of ingestion, was not required. Extra faeces originated from without the main study areas, and some pellets were collected in Cornwall but no accessible roost site was found in Wales, and therefore no pellets were available from Welsh birds.

Faecal samples were usually examined within 24 hours; when this was not possible during the field trip, they were dried and stored for later examination. The collected samples were teased apart in water with the aid of dissecting needles in a glass petri dish beneath a binocular microscope. A magnification of x6.25, illuminated by incident light, was usually found to be sufficient for recording the larger fragments of chitin and other durable prey remains; but this had to be increased to x12.5 - 25.0, with transmitted light, in order to locate earthworm chaetae and, occasionally, the spiracle processes of dipteran larvae. The fragments were sorted, dried on filter paper, and stored in sealed polythene bags. An experiment was tried in which remains from individual faecal residues were 'laminated' between strips of transparent adhesive tape, but it was found that, whilst this was a convenient method of storage, it often proved difficult to examine the microsculpture, scale pattern and form of arthropod fragments, resulting in additional problems of identification.

Since the Choughs foraged over several different habitats in each of the 3 Welsh study areas (Figure 2.1) as well as in Cornwall, this made the study of a comprehensive reference collection of potential prey impossible, particularly in view of the over-riding ornithological nature of the main project. Identification has therefore relied upon direct comparison of the fragments with the extensive entomological collections housed in the University of Sheffield and Doncaster Museum, with the

expert help of Dr Paul Buckland. Thus, legs could be identified only to family level amongst most of the Coleoptera, whilst thoraces, elytra and occasionally heads might be taken to the generic or species level. For some groups, *e.g.* the Lepidoptera, insufficient data are available to facilitate identification based upon larval head capsules, and no attempt was made to speciate lumbricid or dipterous processes. Lists of species are not essential and may even be misleading when birds concentrate on a few different dominant items at different times of the year (Feare 1984), as appears to often be the case with Choughs.

In December 1988, a captive Chough was used to investigate food selection, throughput of earthworm chaetae, and calorific intake (Appendix X, and see Section 5.3.7). The results are only of limited application due to the difficulties involved in comparing captive diets with those of wild birds (where digestion of many of the prey leave no recognisable trace in the faeces or pellets), the constraints of environmental and dietary conditioning, and the increased energy costs imposed on wild birds by the need to hunt (see Chapter 6). However, such experiments might be useful if only as a basis for such comparisons and the trial of methodologies.

5.3 RESULTS

5.3.1 PREY SAMPLING AND SELECTION

A total of 1166 soil samples was taken over the course of the study in the main study areas: 658 in Wales and 508 in Cornwall (5.3.4). The discrepancy is partly explained by 138 determinations of actual prey in Wales which were not possible in the main Cornish study, although 56 such samples were collected during the preliminary Rame study (Appendix IV). The origin of samples within the main study areas is given in Table 5.1.

Table 5.1 Distribution of soil samples collected in main study areas. The Cornish areas were selected on the basis of empirical Welsh data (see text)

Study area	Number of samples collected in areas			
	Used	Adjacent unused	Feeding	Total
W1:Mwnt-Cemaes	191	44	42	277
W2:Strumble	53	15	25	93
W3:Newgale-Solva	96	6	31	133
W4:Marloes	101	14	40	155
WALES	441	79	138	658
<hr/>				
	Equivalent areas			
C1:Pentire-Cant	147	40		187
C2:West Penwith	111	12		123
C3:Lizard	126	72		198
CORNWALL	384	124		508
WALES & CORNWALL	825	203	138	1166

Availability in study areas															
Taxon	W1			W2			W3			W4			Region AI		
	I	S	AI	P	I	S	AI	P	I	S	AI	P	I	S	AI
OLIGOCHAETA															
'Small' lumbricidae	55+	31	.445	Y	3	3	.094	Y	7	6	.125	Y	20	11	.297
'Medium' lumbricidae	19	13	.162	Y	12+	5	.302	Y	12	10	.219	Y	10	9	.178
Enchytraeids	13+	7	.099	N	2	1	.038	N	12+	4	.156	N	4	4	.069
'Large' lumbricidae	3	3	.026	N	0	0	0	N	0	0	0	N	0	0	0
All OLIGOCHAETA	88+	44	.670	Y	17+	8	.415	Y	31+	14	.438	Y	34	21	.515
ARACHNIDA															
Indet. spiders	3+	1	.016	N	4+	2	.094	N	14+	7	.208	N	5	5	.089
Opiliones (harvestmen)	0	0	0	Y	0	0	0	N	15+	5	.198	N	0	0	0
Indet. mites	4	2	.026	N	0	0	0	N	0	0	0	N	0	0	0
Lycosidae	1	1	0	N	0	0	0	N	1	1	.010	N	0	0	0
All ARACHNIDA	6	4	.047	Y	4+	2	.094	N	30	13	.417	N	5	5	.089
CRUSTACEA															
indet. woodlice	4	3	.031	Y	2	2	.057	Y	1	1	.010	Y	10+	5	.139
<i>Armadillidium</i> sp.	4	1	.021	Y	2	1	.038	N	3	2	.042	N	3+	1	.030
<i>Porcellio scaber</i>	6+	2	.037	N	7	1	.113	N	0	0	0	N	2	1	.020
<i>Metoponorthus</i> sp.	11+	5	.079	N	0	0	0	N	0	0	0	N	1	1	.001
<i>Philoscia muscorum</i>	1	1	0	N	0	0	0	N	0	0	0	N	0	0	0
All CRUSTACEA	26+	12	.173	Y	11	4	.264	Y	4	3	.063	Y	16+	8	.199
DIPLOPODA															
Indet. millipedes	0	0	0	N	1	1	.019	N	8	5	.125	Y	4	4	.069
															.045

Table 5.2

Taxa, source and index of availability of potential prey recovered from Chough-used areas in Wales. 'I' = no. of individuals (+ = minimum count) recovered from 'S' (no. +ve samples); 'AI' = availability index; 'P' = recorded as possible prey from specific feeding points, 'Y' = yes, 'N' = no (see Table 5.4)

Table 5.2 (continued)

CHILOPODA																	
Indet. centipedes	4	3	.031	Y	3-	1	.057	N	2	2	.031	Y	5	5	.089	Y	.046
<i>Pachymarrium</i> sp.	1	1	0	N	0	0	0	N	0	0	0	N	0	0	0	N	0
All CHILOPODA	5	4	.037	Y	3+	1	.057	N	2	2	.031	Y	5	5	.089	Y	.050
DIFLURA																	
Indet. Collembola	0	0	0	N	0	0	0	N	0	0	0	N	2	1	.020	N	0
DERMAPTERA																	
<i>Forficula</i> sp.	5-	3	.052	N	2	1	.038	N	2	1	.021	N	0	0	0	N	.032
ORTHOPTERA																	
Indet. grasshoppers	3+	1	.016	N	0	0	0	N	9+	3	.115	Y	15+	5	.188	N	.075
HEMIPTERA																	
Indet. Hemiptera	0	0	0	N	0	0	0	N	0	0	0	N	1	1	.001	N	0
LEPIDOPTERA																	
Indet. Noctuidae	1	1	0	N	0	0	0	N	1	1	.010	N	1	1	.001	N	.001
DIPTERA																	
CYCLORRHAPHA																	
Indet.	5-	2	.031	N	0	0	0	N	0	0	0	N	0	0	0	N	.014
Muscidae	3+	1	.016	Y	0	0	0	N	0	0	0	N	0	0	0	N	.001
Sphaeroceridae	3+	1	.016	Y	0	0	0	N	0	0	0	N	0	0	0	N	.001
Chloropidae	1	0	0	N	0	0	0	N	0	0	0	N	0	0	0	N	0
All CYCLORRHAPHA	12+	5	.068	Y	0	0	0	N	0	0	0	N	0	0	0	N	.029
NEMATOCERA																	
Tipulidae	35-	22	.309	Y	12+	6	.321	Y	24+	13	.375	Y	26+	12	.386	Y	.338
Bibionidae	3	2	.021	Y	0	0	0	N	3+	1	.031	N	9+	2	.099	N	.039
Chironomidae	0	0	0	N	0	0	0	N	0	0	0	N	1	1	.001	N	0
Sciariidae	0	0	0	N	1	1	.019	N	0	0	0	N	0	0	0	N	0
All NEMATOCERA	41+	24	.330	Y	13+	7	.340	Y	27+	14	.406	Y	36+	14	.475	Y	.361

Table 5.2 (continued)

Table 5.2 DIETRA (continued)

Table 5.2 (continued)

COLEOPTERA															
CARABIDAE															
Indet. carabid	9	7	.079	N	4	2	.094	N	0	0	0	1	.001	N	.048
<i>Harpalus senus</i>	6+	4	.047	N	0	0	0	N	0	0	0	0	0	N	.020
<i>Harpalus rufipes</i>	2	2	.016	N	0	0	0	N	0	0	0	0	0	N	.001
<i>Amara aena</i>	0	0	0	Y	1	1	.019	N	1	1	.010	1	.001	N	.001
<i>Nebria</i> sp.	0	0	0	N	2	2	.057	N	0	0	0	0	0	N	.001
<i>Notiophylus palustris</i>	2	2	.016	N	0	0	0	N	0	0	0	0	0	N	.001
<i>Pterostichus madidus</i>	3+	1	.016	Y	0	0	0	N	0	0	0	0	0	N	.001
<i>Harpalus latus</i>	0	0	0	N	0	0	0	N	0	0	0	1	.001	Y	0
<i>Harpalus tenebrosus</i>	1	1	0	N	0	0	0	N	0	0	0	0	0	N	0
<i>Optonus</i> sp.	0	0	0	N	0	0	0	N	2	1	.021	0	0	N	0
<i>Leistus</i> sp.	0	0	0	N	1	1	.019	N	0	0	0	0	0	N	0
<i>Carabus violaceus</i>	1	1	0	N	0	0	0	N	0	0	0	0	0	N	0
<i>Carabus problematicus</i>	1	1	0	N	0	0	0	N	0	0	0	0	0	N	0
<i>Calathus melanocephalus</i>	0	0	0	N	0	0	0	N	1	1	.010	0	0	N	0
All CARABIDAE	25+ 18	.183	Y	8	4	.189	N	4	3	.042	Y	3	.030	Y	.118
SILPHIDAE sp.	0	0	0	N	0	0	0	N	1	1	.010	1	.050	N	.014
STAPHYLINIDAE															
Indet. staphylinid	6+	4	.047	Y	3+	1	.057	Y	1	1	.010	0	0	N	.029
<i>Tachyporus hypnorum</i>	0	0	0	N	0	0	0	N	1	1	.010	0	0	N	0
<i>Philonthus varius</i>	0	0	0	N	0	0	0	N	1	1	.010	0	0	N	0
<i>Philonthus splendens</i>	0	0	0	N	0	0	0	N	1	1	.010	0	0	N	0
All STAPHYLINIDAE	6+ 4	.047	Y	3+	1	.057	Y	4	4	.042	N	0	0	N	.036
ELATERIDAE															
Indet. elaterid	6	3	.042	Y	3	1	.057	Y	0	0	0	0	0	Y	.025
<i>Agriotes</i> sp.	6	6	.058	N	0	0	0	N	0	0	0	0	0	N	.025
<i>Stenopus</i> sp.	0	0	0	N	1	1	.019	N	0	0	0	0	0	Y	0
<i>Stenicerus</i> sp.	0	0	0	N	1	1	.019	N	0	0	0	0	0	N	0
<i>Athous haemorrhoidalis</i>	0	0	0	N	0	0	0	N	1	1	.010	0	0	N	0
Indet. Athous	1	1	0	N	0	0	0	N	0	0	0	0	0	N	0
All ELATERIDAE	13 10	.105	Y	5	3	.094	Y	1	1	.010	N	0	0	N	.059
MELOIDAE sp.	0	0	0	N	0	0	0	N	3+	1	.031	0	0	N	.001

Table 5.2 (continued)

Table 5.2 COLEOPTERA (continued)

TENEBRIONICIDAE											
<i>Cylindronotus</i>											
<i>jaevioctostriatus</i>	5	5	.047	N	3	3	.094	N	0	0	N
<i>Cylindronotus striatus</i>	3-	1	.016	N	0	0	0	N	0	0	N
All TENEBRIONIDAE	8-	6	.063	N	3	3	.094	N	0	0	N
SCARABAEIDAE											
Indet. scarabid	11+	9	.099	Y	4+	2	.094	Y	2	1	.021
<i>Aphodius</i> sp.	6+	2	.037	Y	0	0	0	N	0	0	0
All SCARABAEIDAE	17+	11	.141	Y	4+	2	.094	Y	2	1	.021
Indet. beetles	0	0	0	N	1	1	.019	Y	1	1	.010
All COLEOPTERA	69+	49	.516	Y	24+	13	.547	Y	12	10	.125
GASTROPODA											
Indet. slug	5+	3	.037	N	0	0	0	N	2	2	.031
<i>Remoralis</i> sp.	2	2	.016	N	0	0	0	N	0	0	0
Indet. snail	0	0	0	N	0	0	0	N	0	0	0
All GASTROPODA	7+	5	.052	N	0	0	0	N	2	2	.031
Diversity index	D	19.6	14.5	14.6					12.6		26.6
Total no. samples		191	53	96					101		441

Diversity index after Margalef (1951), see text p.128

Table 5.2 (continued)

Availability in study areas														
Taxon	W1			W2			W3			W4			Region	
	I	S	AI	I	S	AI	I	S	AI	I	S	AI	I	AI
OLIGOCHAETA														
'Small' lumbricidae	26	14	.884	0	0	0	0	0	0	0	0	0	0	.494
'Medium' lumbricidae	17	10	.591	0	0	0	0	0	0	0	0	0	0	.329
'Large' lumbricidae	5	4	.182	1	1	.067	0	0	0	0	0	0	0	.114
All LUMBRICIDAE	48	28	1.659	1	1	.067	0	0	0	0	0	0	0	.937
ARACHNIDA														
Lycosidae	0	0	0	0	0	0	0	0	0	2	2	.214	0	.038
CRUSTACEA														
Metoponorthus sp.	2	2	.068	0	0	0	0	0	0	1	1	.053	0	.051
Amphipod	0	0	0	0	0	0	0	0	0	2	2	.214	0	.038
All CRUSTACEA	2	2	.068	0	0	0	0	0	0	3	3	.357	0	.101
DIPLOPODA														
Indet. millipedes	2	1	.045	0	0	0	0	0	0	0	0	0	0	.025
CHILOPODA														
Indet. centipedes	0	0	0	0	0	0	0	0	0	2	2	.214	0	.038
DERMAPTERA														
Forficula sp.	0	0	0	0	0	0	3+	1	.500	0	0	0	0	.038
DIPTERA														
NEMATOCERA														
Tipulidae	12	8	.432	5	4	.533	0	0	0	0	0	0	0	.342
Bibionidae	2	1	.045	0	0	0	0	0	0	0	0	0	0	.025
All NEMATOCERA	14	9	.500	5	4	.533	0	0	0	0	0	0	0	.367
Indet. Diptera	1	1	.025	0	0	0	0	0	0	0	0	0	0	.013
All DIPTERA	15	10	.500	5	4	.533	0	0	0	0	0	0	0	.443

Table 5.3

Taxa, source and index of estimated availability of potential prey recovered from unused sites adjacent to feeding areas in Wales. 'I' = no. of individuals (+ = minimum count) recovered from 'S' (no. +ve samples); 'AI' = availability index

Table 5.3(continued).

HYMENOPTERA										
<i>Lasius flavus</i>	8+	3	.223	0	0	0	0	0	0	.127
Indet. <i>Lasius</i>	7+	1	.159	0	0	0	0	0	0	.089
<i>Lasius mixus</i>	0	0	0	0	0	0	0	0	0	.076
Indet. Symphyta (sawflies)	0	0	0	0	0	0	0	0	0	.013
All HYMENOPTERA	15+	4	.386	0	0	0	0	1	1	.304
COLEOPTERA										
CARABIDAE										
Indet. carabid	1	1	.023	2	1	.133	0	0	0	.038
<i>Amara curta</i>	2	2	.068	0	0	0	0	0	0	.038
<i>Pterostichus madidus</i>	2	2	.068	0	0	0	0	0	0	.038
<i>Harpalus anxius</i>	0	0	0	0	0	0	1	1	.167	.013
Indet. <i>Harpalus</i>	1	1	.023	0	0	0	0	0	0	.013
All CARABIDAE	6	6	.182	2	1	.133	1	1	.167	.139
STAPHYLINIDAE										
<i>Philonthus</i> sp.	1	1	.023	0	0	0	0	0	0	.013
ELATERIDAE										
<i>Agriotes</i> sp.	3	1	.068	0	0	0	0	0	0	.038
Indet. elaterid	1	1	.023	1	1	.067	0	0	0	.025
<i>Gtenicerus aeneus</i>	1	1	.023	0	0	0	0	0	0	.013
All ELATERIDAE	4	3	.114	1	1	.067	0	0	0	.063
TENEBRIONIDAE										
<i>Cylindronotus</i> sp.	2	2	.068	0	0	0	0	0	0	.036
SCARABAEIDAE										
Indet. scarabid	0	0	0	0	0	0	0	0	0	.038
Indet. beetles	1	1	.023	0	0	0	0	0	0	.013
All COLEOPTERA	15	13	.409	3	2	.267	1	1	.167	.316
GASTROPODA										
Indet. slug	2	2	.068	0	0	0	0	0	0	.038
Diversity index	D	10.0	3.1	2.9	4.4	13.3				
Total no. samples		44	15	6	14	79				

Diversity index after Margalef (1951), see text p.128

Table 5.3 (continued)

Taxon	Frequency in				
	Study areas				Region
	W1	W2	W3	W4	
OLIGOCHAETA					
'Medium' lumbricidae	.071	.042	.065	.100	.072
'Small' lumbricidae	.143	.042	.032	0	.058
Enchytraeidae	0	0	0	.075	.022
All Oligochaeta	.190	.040	.097	.175	.130
ARACHNIDA					
Indet. spiders	0	0	0	.075	.022
<i>Oedothorax fuscus</i>	.024	0	0	0	.001
Thomisidae	.024	0	0	0	.001
Opiliones	.024	0	0	0	.001
All ARACHNIDA	.071	0	0	.075	.043
CRUSTACEA					
Indet. woodlice	.048	.167	.032	.050	.065
<i>Armadillidium</i> sp.	.024	0	0	.025	.014
Amphipoda	0	0	0	.05	.014
All CRUSTACEA	.071	.167	.032	.125	.094
DIPLOPODA					
Indet. millipedes	0	0	.032	.150	.051
CHILOPODA					
Indet. centipedes	.024	0	.032	.025	.022
ORTHOPTERA					
Indet. grasshoppers	0	0	.032	0	.001

Continued

Table 5.4

Taxa, source and frequency (number of positive samples / total number of samples) of prey recovered from precise feeding sites in Welsh study areas.

Table 5.4 continued

Taxon	W1	W2	W3	W4	Region
DIPTERA					
CYCLORRHAPHA					
Sphaeroceridae	.119	0	0	0	.036
Muscidae	.024	0	0	0	.001
Agromyzidae	.024	0	0	0	.001
All CYCLORRHAPHA	.167	0	0	0	.051
NEMATOCERA					
Tipulidae	.167	.240	.032	.175	.152
Ribionidae	.095	0	0	0	.029
Mycetophilidae	0	.040	0	.025	.014
Ceratopogonidae	0	0	0	.025	.001
All NEMATOCERA	.262	.280	.032	.225	.203
BRACHYCERA					
Empididae	.071	0	0	0	.022
Piophilidae	0	.040	0	0	.001
Bombyliidae	0	0	0	.025	.001
All BRACHYCERA	.071	.040	0	.025	.036
Indet. diptera	.048	.240	0	.025	.065
All DIPTERA	.405	.440	.032	.275	.290
HYMENOPTERA					
<i>Lasius alienus</i>	.167	.040	.419	.200	.210
<i>Lasius flavus</i>	.095	.040	.065	.150	.094
Indet. ants	0	.080	.172	.161	.065
Indet. <i>Lasius</i>	0	.080	0	0	.014
<i>Myrmica rubra</i>	0	0	.065	0	.014
Indet. <i>Myrmica</i>	0	.080	.032	0	.014
<i>Lasius niger</i>	0	0	.032	0	.014
<i>Myrmica sulcinodes</i>	0	0	0	.025	.001
<i>Lasius brunneus</i>	.022	0	0	0	.001
<i>Tapinoma erraticum</i>	.022	0	0	0	.001
Symphyta/sawflies	.022	0	0	0	.001
All HYMENOPTERA	.310	.320	.774	.425	.442

Continued

Table 5.4 (continued)

Table 5.4 continued

Taxon	W1	W2	W3	W4	Region
COLEOPTERA					
CARABIDAE					
<i>Amara consularis</i>	0	.040	0	0	.001
<i>Harpalus rufipes</i>	0	0	.032	0	.001
<i>Harpalus latus</i>	0	0	0	.025	.001
<i>Amara aenea</i>	.024	0	0	0	.001
<i>Pterostichus</i> sp. (?madidus)	.024	0	0	0	.001
Indet. <i>Amara</i>	.024	0	0	0	.001
All CARABIDAE	.071	.040	.032	.025	.043
HYDROPHILIDAE					
<i>Sphaeridium lunatum</i>	.024	0	0	0	.001
STAPHYLINIDAE					
Indet. Staphylinidae	.024	.080	0	0	.021
ELATERIDAE					
Indet. Elateridae	.024	.040	0	.050	.029
<i>Stenopus sulphurus</i>	0	0	0	.025	.001
All ELATERIDAE	.024	.040	0	.075	.036
BYRRHIDAE					
Indet. Byrrhidae	.022	0	0	0	.001
TENEBRIONIDAE					
<i>Cylindronotus laevioctostriatus</i>	0	0	0	.050	.021
SCARABAEIDAE					
Indet. Scarabaeidae	.143	.200	.065	0	.094
<i>Aphodius</i> sp.	.024	0	.033	0	.014
All SCARABAEIDAE	.167	.200	.097	0	.116
Indet. beetles	0	.042	0	0	.001
All COLEOPTERA	.310	.280	.097	.150	.210
CEREAL GRAIN					
	.048	0	.129	.150	.087
Total no. samples	42	25	31	40	138

Table 5.4 (continued)

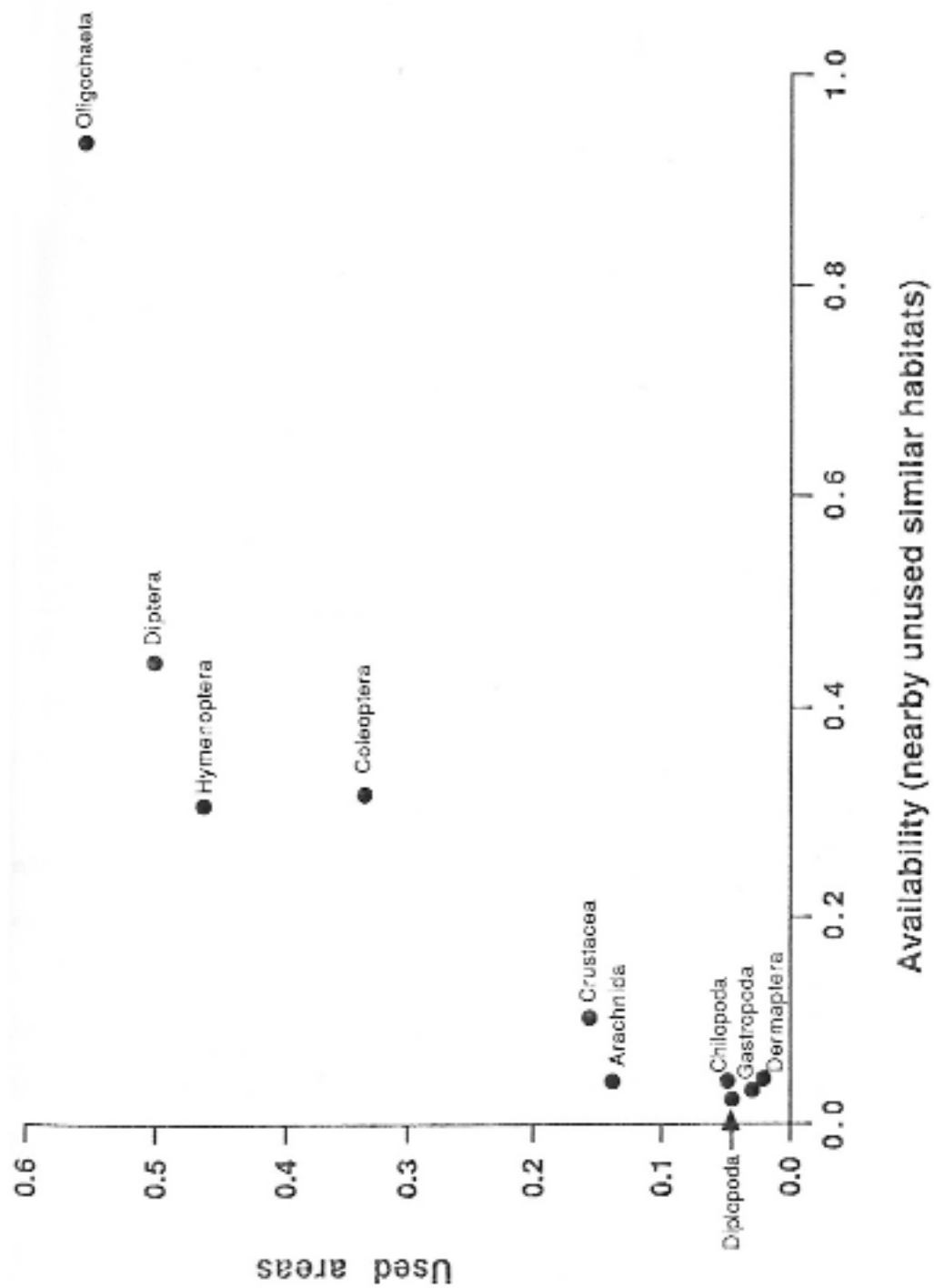


Figure 5.1

The relationship between the abundance of principal invertebrate prey taxa in feeding areas and their availability in surrounding areas. Data from Tables 5.2 and 5.3.

Spearman rank correlation coefficient:

$$r_s = 0.900, P = 0.01, n = 10$$

Recorded taxa from Wales are given in Table 5.2 together with an indication of those also recorded from specific feeding points (which reappear in Table 5.4), the study areas from which recorded, and the *AI* or frequency index. The *AI*s of taxa recorded in similar unused 'control' areas adjacent to feeding sites are given in Table 5.3.

The most frequent potential prey recorded from feeding areas (with an *AI* > .1), which were also present at actual feeding points (Table 5.4), are ranked in Table 5.5. Also given is the respective *AI* from nearby control sites, and the differences. There is a highly significant positive correlation (r_s 0.900, $P=0.01$) showing that Choughs are selecting generally rich invertebrate areas (Figure 5.1). Of these more numerous taxa, only the lumbricids were recorded as more plentiful away from feeding areas. Of the minor taxa, earwigs (Dermaptera) were slightly more numerous in the unused areas (*cf.* Tables 5.2 and 5.3) (see Section 5.4). Earthworms present by far the greatest discrepancy between feeding and control areas; the remaining 5 major invertebrate classes all show increased abundance in feeding areas.

Table 5.5 Summary of Tables 5.2 and 5.3. Principal prey taxa (with regional *AI* > .1) recovered from feeding areas and nearby unused areas (regional r_s 0.946, $P<0.01$, $n=6$); '+' value signifies greater abundance in feeding areas

Taxon	Availability (<i>AI</i>) in						Regional difference
	Feeding sites in Study areas					Unused areas	
	W1	W2	W3	W4	Region	Region	
OLIGOCHAETA	.670	.415	.438	.515	.553	.937	-.384
DIPTERA	.576	.396	.438	.485	.499	.443	+.056
HYMENOPTERA	.162	.491	.938	.564	.463	.304	+.159
COLEOPTERA	.518	.547	.125	.050	.336	.316	+.020
CRUSTACEA	.173	.264	.063	.199	.159	.101	+.058
ARACHNIDA	.047	.094	.417	.089	.138	.038	+.100

Figures 5.2a-b show the abundancies of prey in the feeding areas in the Welsh region and each of the 4 study areas therein. If all invertebrate classes are included in the analysis (*i.e.* including those with *AI* < .1), the highly significant association between feeding and control areas remains (r_s 0.877, $n=14$, $P<0.01$).

The main prey taxa (*AI* > .1) are Oligochaeta (lumbricid earthworms), Diptera (cranefly and dungfly larvae), Hymenoptera (ants), Coleoptera (Carabidae, Scarabaeidae, Elateridae, Tenebrionidae and Staphylinidae beetles), Crustacea (woodlice) and Arachnida (spiders and harvestmen). The indices of availability respond only to numbers of organisms and not to varying body sizes or calorific values (see Table 5.6, and Appendix X). The extra cost of feeding on small-bodied hymenopterans will be offset to some degree by their occurrence in large aggregations, for example ants of the *Lasius* genus (*AI* = .317), similarly with the smaller dipterous larvae (*AI* = .499). *Lasius* ants were present in all 4 study feeding areas (*AI* = .153 (Mwnt-Cemaes) to .510 (Newgale-Solva)). *Myrmica* ants were recorded from feeding areas in all but Mwnt-Cemaes but at far lower densities than *Lasius* spp. *L. alienus* (.209) and *L. flavus* (.093) were by far the commonest two prey species. Sawfly (Symphyta) larvae were recorded in 3/4 of the study feeding areas, and form a substantially sized prey item compared to other recorded hymenoptera (Table 5.2).

Key:

Ol Oligochaeta
Ar Arachnida
Cr Crustacea
Dp Diplopoda
Ch Chilopoda
Dm Dermaptera
Or Orthoptera
Dt Diptera
Hy Hymenoptera
Co Coleoptera

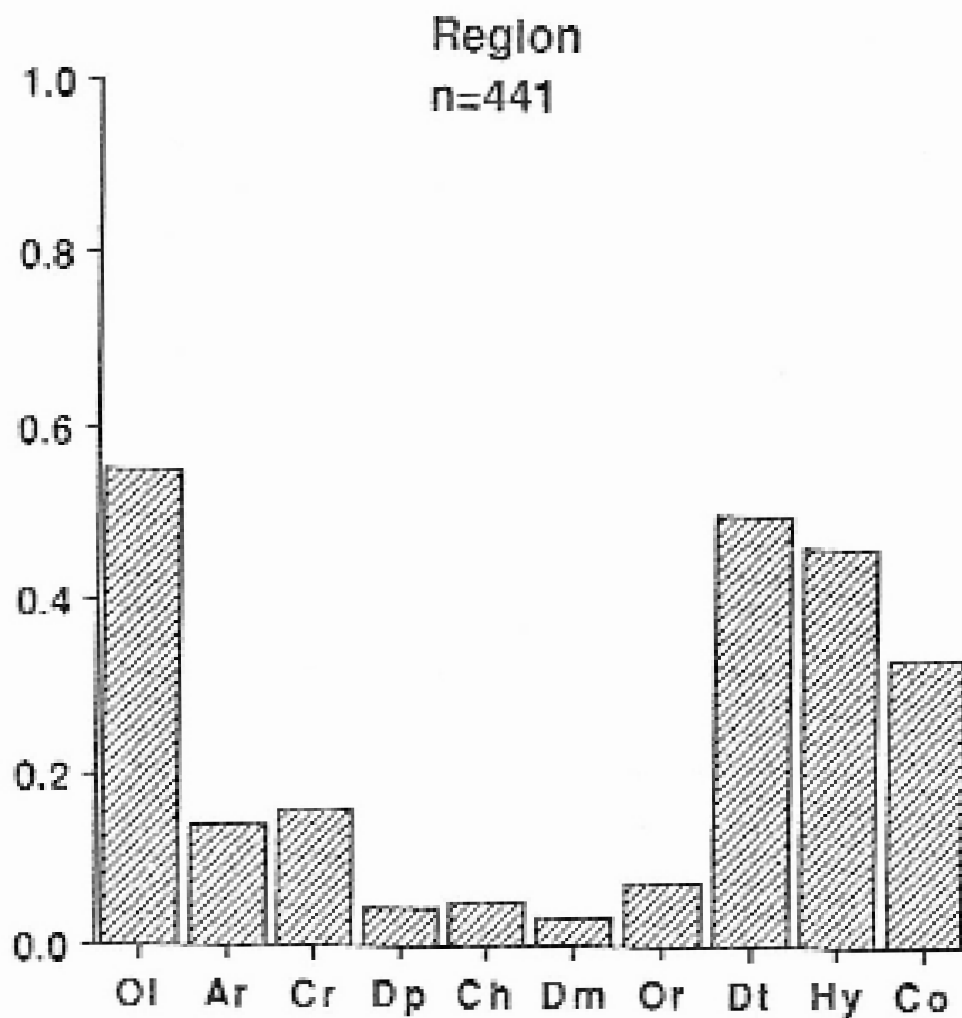


Figure 5.2a

Availability of principal invertebrate prey taxa (data from Table 5.2) in feeding areas within Welsh region (5.2a) and individual study areas (5.2b)

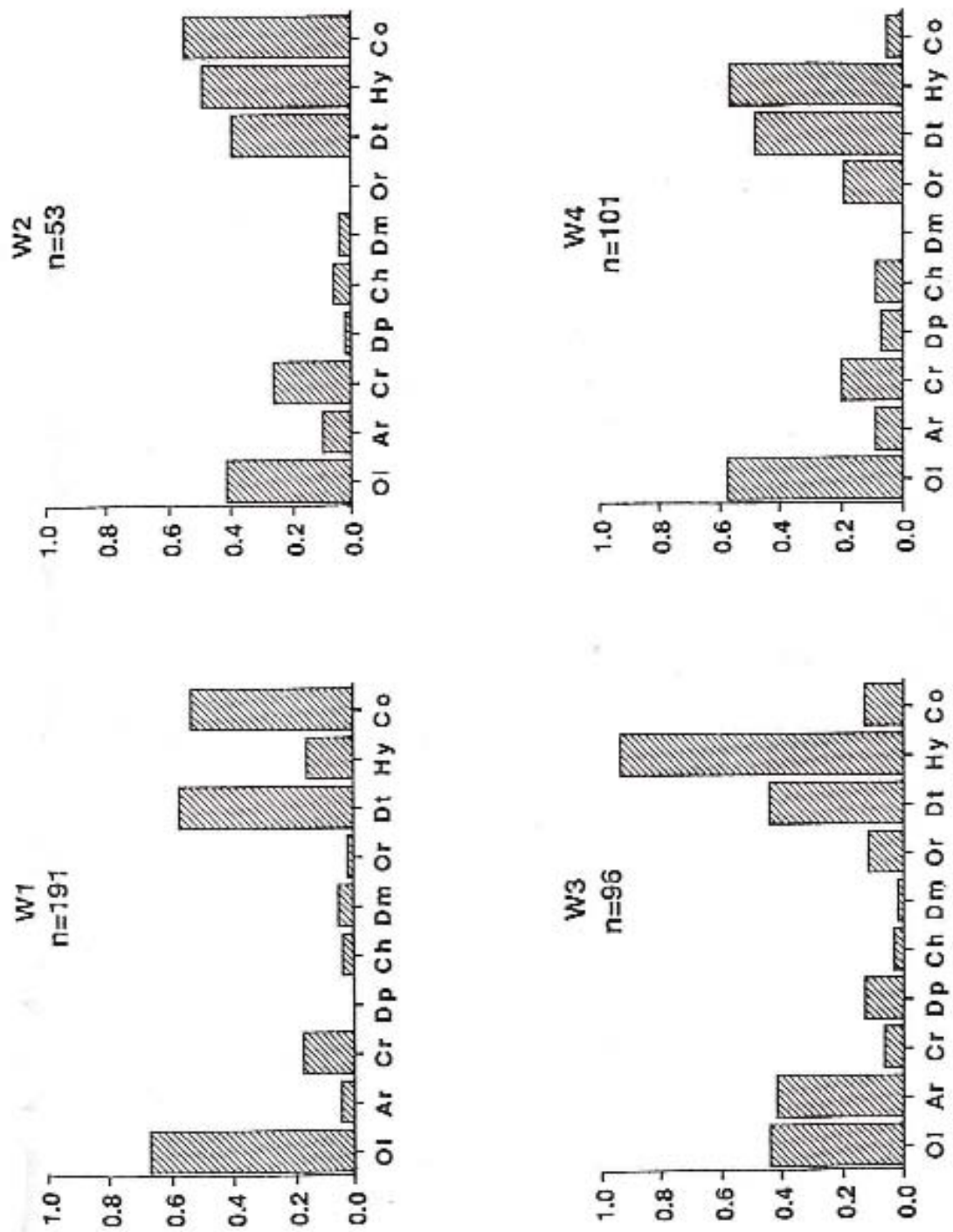


Figure 5.2b

Key:

Ol Oligochaeta
Ar Arachnida
Cr Crustacea
Dp Diplopoda
Ch Chilopoda
Or Orthoptera
Dt Diptera
Hy Hymenoptera
Co Coleoptera
Cg Cereal grain

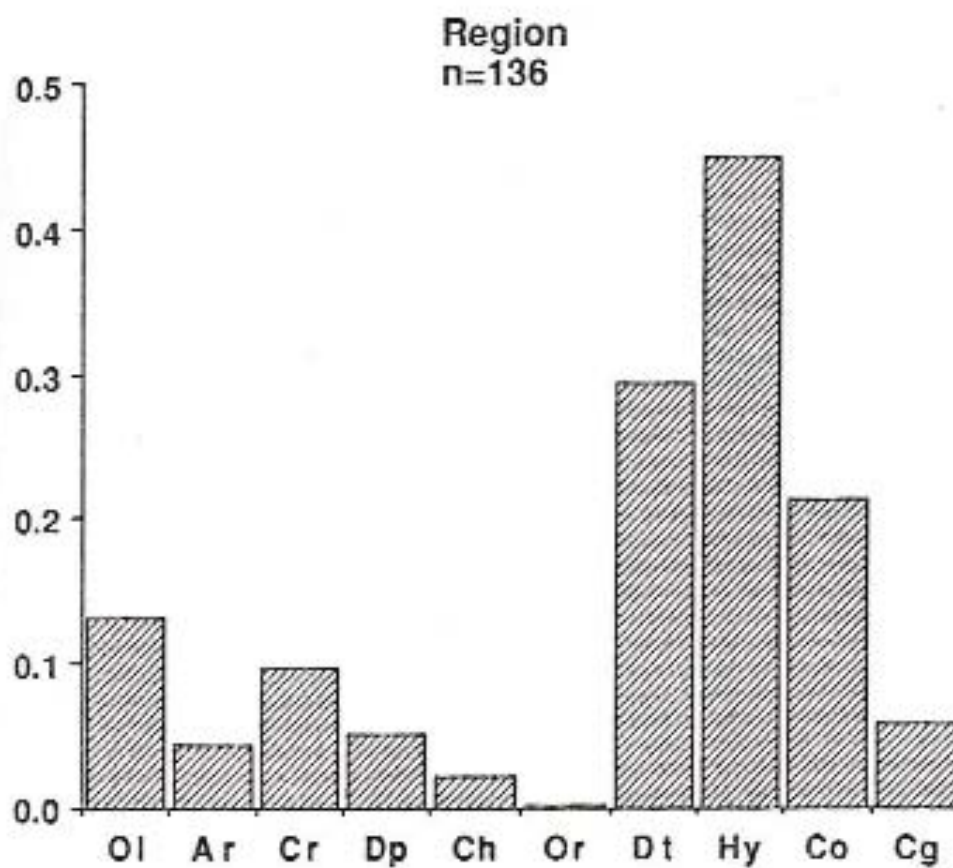


Figure 5.3a
Frequency of prey recovered from specific feeding sites (data from Table 5.4) within Welsh region (5.3a) and individual study areas (5.3b)

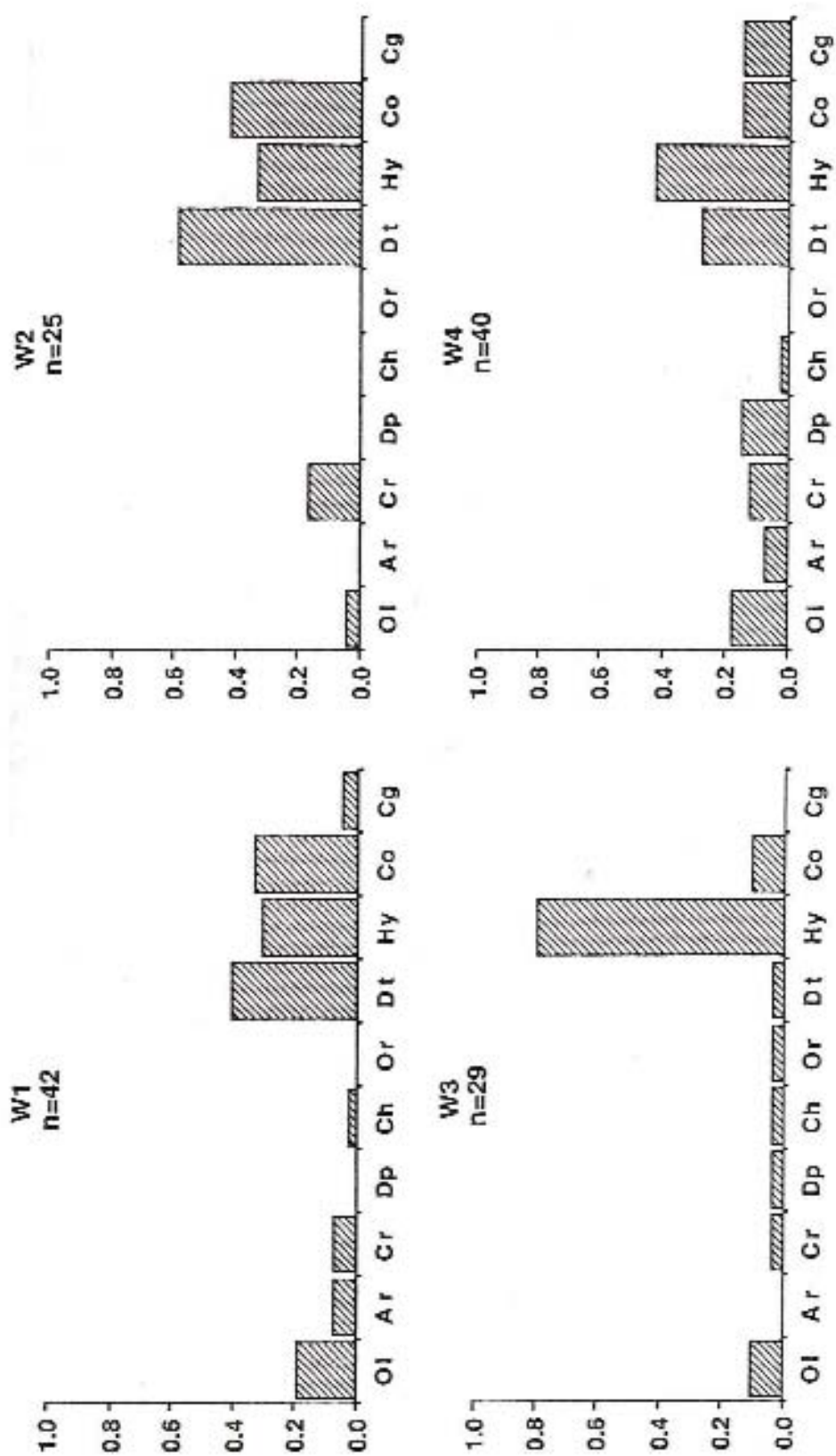


Figure 5.3b

Cereal grain, as already stated, being inanimate and lying as stubble on the surface of the ground, cannot and should not be sampled or assessed in the same way as live invertebrates, which actively conceal themselves. It has already been shown (Chapter 4) that arable land is used more where it replaces pastoral agriculture, and where a bird breeds influences where it forages (Richford 1978). In Newgale-Solva and Marloes, the most improved, agriculturally, of the study areas (4.3.4), cereal grain was found as frequently at feeding sites as coleoptera, if not more so (Table 5.4); this was not the case at Mwnt-Cemaes and Strumble.

Table 5.6 Approximate energy values of main prey items; A=adult, L=larva
(after Torvik & Ludvig 1988, except '*' after McDonald *et al.* 1988)

Taxon	kJ/g ⁻¹
Lumbricidae	20.0
Arachnida	25.1
Crustacea	15.9
Diplopoda	14.3
Chilopoda	20.9
Dermaptera	26.8
Hemiptera (A/L)	26.8
Lepidoptera (L)	22.5
Diptera (L)	24.2
Hymenoptera (A)	21.3
Coleoptera (A/L)	23.4
Cereal grain	13.0*

From the data presented in Table 5.4 and summarised in Figures 5.3a-b, based on investigations of probable prey at precise feeding points immediately following the birds' departure, Hymenoptera, Diptera (more specifically Nematocera), Coleoptera and Oligochaeta were the most frequent recoveries. Within the region as a whole, ants were recovered from nearly half of all samples (.442), and diptera larvae from just under a third (.290). The highest frequencies per study area were diptera larvae at Strumble and Mwnt-Cemaes (.440 and .405 respectively), and ants from Newgale-Solva and Marloes (.774 and .425 respectively). These data may be related to seasonal influences by comparing the left-most 3 columns in Table 5.7 (see Section 5.3.3).

From the availability indices given in Tables 5.2 and 5.5, earthworms are the most prolific large-bodied prey, and, therefore, per organism, offer the best reward for the predator. However, the dipterous content given in Table 5.2, shows that tipulid (crane-fly) larvae (=leatherjackets), with a body size comparable to smaller sized earthworms, have a high regional AI (.338) across the study range: from .309 at Mwnt-Cemaes to .386 at Marloes. Both these are subterranean prey giving no visual clues of presence and therefore will cost more energy to locate than the clumped and more visible dipterous and hymenopterous taxa, although these have smaller body sizes. Direct evidence with a telescope confirmed that dipterous larvae, especially tipulids, were taken throughout the year (*cf.* Table 5.7). No other family approaches the values for Lumbricidae and Tipulidae; even totalled indeterminate dipterous larvae have a mean value of only .073. The Bibionidae (in the same Nematocera suborder as the Tipulidae) is the only other family with a value >.03. It is interesting to note that in Mwnt-Cemaes, where land management emphasis is on pastoralism (4.3.4), Cyclorrhapha larvae (=maggots'), which include the dungflies, have an AI of .068 but are not represented in any of the remaining 3 study areas, nor were they found in the control sites at Mwnt-Cemaes. Evidence, however, was found in one faecal sample from Newgale-Solva (*cf.* Table 5.15). [Diptera larvae do not present well in faecal residue.]

Taxon	Frequency in			Availability in					
	Feeding sites			Used areas			Unused areas		
	W	B	PB	W	B	PB	W	B	PB
OLIGOCHAETA	.344	.097	0	.598	.540	.612	.450	.894	1.571
ARACHNIDA	0	.125	.063	.001	.166	.273	.120	0	0
CRUSTACEA	.125	.097	.063	.274	.035	.347	.200	.064	0
DIPLOPODA	.125	.042	0	.137	.025	0	.080	0	0
CHILOPODA	.063	.014	0	.085	.064	.001	.120	0	0
DIPLURA	0	0	0	0	.001	0	0	0	0
CERMATERA	0	0	0	.077	.030	0	0	.064	0
ORTHOPTERA	0	.031	0	0	.173	.025	0	0	0
HEMIPTERA	0	0	0	0	0	0	0	0	0
LEPIDOPTERA	0	0	0	0	0	.025	0	0	0

Table 5.7

Seasonal indices of frequency (feeding sites) and availability (Chough-used and unused areas) of invertebrate prey recovered in Welsh region (see Tables 5.2 - 5.4). Biological seasons: W = winter (November - February), B = Breeding (March - June), PB = Post-breeding (July - October)

Within the order Coleoptera, no single genus dominated, and certainly no species: only one carabid (*Amara aenea*) was positively identified from 3 study areas; carabids of the genus *Harpalus* and tenebrionids of the genus *Cylindronotus* were identified from 2 areas each; *Athous* spp. (Elateridae) were also located from 2. Indeterminate scarabaeids, possibly *Aphodius*, were found in all 4 study areas; these are expected wherever ungulate dung is present, as are the Geotrupidae (adults of both families will also use carrion and fungi; and their larvae, apart from dung, will feed on humus and decomposing plant material (Ritcher 1958)). Coleopteran species diversity was greatest in Mwnt-Cemaes feeding areas, where ≥ 12 genera were identified; ≥ 10 were recorded at Newgale-Solva but abundances were greatly reduced, ≥ 8 from Strumble, but only 6 from Marloes (Tables 5.2 & 5.4), the only area with a Coleoptera $AI < .10$ (Table 5.2).

Among the other prey items recorded, woodlice were present in all feeding areas throughout the year, and were recovered from specific feeding points similarly. Faecal evidence suggests that they are taken outside the breeding season (5.3.5). With a very similar AI , spiders were probably preyed upon in the summer months when Wolf spiders (Lycosidae), crab spiders (Thomisidae) and harvestmen (Opiliones) were common surface invertebrates. Additionally, millipedes (Diplopoda) and centipedes (Chilopoda) (=Myriapoda) were frequent and taken, especially at Newgale-Solva (cf. Table 5.15).

5.3.2 SIMILARITY COEFFICIENTS OF STUDY AREAS

Diversity is a crucial facet of ecological systems (Putman & Wratten 1984). In Section 4.3.4, it was stated that variation in habitat range justified the decision to choose more than one study area. Broadly speaking, of the 4 study areas selected, two, W1 and W2 (Mwnt-Cemaes and Strumble to the north) had an upland/pastoral/scrubby cliff physiography, whereas the two southern areas W3 and W4 (Newgale-Solva and Marloes) were more representative of lowland improved agriculture, though with better quality cliffs. It is possible to see from the data given in Tables 5.2 and 5.4, even though they under-represent the role of cereal grain, how this might affect Chough diet especially with regard to increased dependence on cereal and ants in the south, and earthworms, beetles and flies in the 'upland' areas. Mwnt-Cemaes showed the greatest diversity (Table 5.2) using Margalef's (1951) index:

$$D = \frac{S - 1}{\log_e N}$$

where D = index of diversity, S = number of groups or species, N = number of individuals. However, by applying Sorensen's (1948) quotient of similarity (QS):

$$QS = \frac{2j}{a + b}$$

where a = number of groups found in habitat A, b = number of groups found in habitat B, j = number of groups found in both habitats, the QS between the study areas were as follows (indeterminate taxa were excluded from equations):

$$\begin{aligned} W3/W4 &= .560 \\ W2/W4 &= .558 \\ W2/W3 &= .471 \\ W1/W4 &= .444* \\ W1/W2 &= .438 \\ W1/W3 &= .423 \end{aligned}$$

The study areas, grouped in all possible paired combinations have the following similarity quotients:

$$\begin{aligned}(W1+W4)/(W2/W3) &= .506 \\(W1+W2)/(W3/W4) &= \mathbf{.471^*} \\(W1+W3)/(W2+W4) &= .465\end{aligned}$$

The study areas and values in bold type* represent pairs at the extremes (both geographically and agriculturally) of the study range, where least similarity was expected. Therefore, whatever the differences in the physiography of general areas of Chough usage, there is no apparent geographical pattern to the invertebrate similarity of the feeding areas sampled.

5.3.3 SEASONAL EFFECTS ON PREY AVAILABILITY

Seasonal effects on prey availability are shown in Table 5.7. The frequency at specific feeding points shows that in the winter, earthworms and fly larvae (mainly tipulids), both with a frequency index of .344, and beetles (.188) are the main invertebrate prey taxa (the exact role of cereal grain could not be accurately assessed within the same methodology, see Section 5.3.5). These are all relatively large-bodied organisms; the much smaller-bodied hymenopterans also have a surprisingly high value (.156), and the *AI* does not fall below .2 within used areas. The earthworm quotient falls off dramatically with the onset of the breeding season although availability within used areas remains high throughout the year. The dipterous quotient also remains high at feeding points before tailing off sharply in the post-breeding phase; however, availability does remain fairly high throughout the year, peaking in the summer at .876 due to a high Nematocera value: =.718 (see Section 5.4).

The hymenopterous quotient increases with the year, rising progressively from the winter low to a post-breeding high of .844, replacing, to some extent, the diptera. At feeding points, presence of fly larvae doubles in the post-breeding phase even though availability (as measured in used areas), does not increase significantly: remaining at the .600 mark. As already stated (4.3.3), ant activity can be found in most months of the year, and Choughs were observed to feed on them in November, December (in Cornwall) and February, although it is suggested later (5.4) that they are used primarily as a food for nestlings. Annually, presence of hymenopterans was highest at Newgale-Solva (.918: the highest value for any taxonomic group in any study area), it was lowest at Mwnt-Cemaes (.142) where increased availability of Diptera and Coleoptera is evident (.576 & .518 respectively). It is quite clear from Table 5.7 that Choughs are specifically selecting ant-rich areas during the breeding season: within used areas, ant availability rises throughout the year (.214-.599-.612) agreeing with the frequency trend in specific feeding sites (.156-.403-.844), whilst in nearby 'control' areas the availability trend is reversed (.840-.106-.000) (see Figure 5.4).

Similarly with the coleoptera resource, a large dip in availability occurs in control areas during the breeding season, although the difference is negligible during the post-breeding season. The Coleoptera quotient rises to a peak at feeding sites of .278 during the breeding season (Table 5.7); exactly half being accounted for by dung-beetles (Scarabaeidae). This tails off to a low level in the post-breeding phase when it is somewhat compensated for by increased usage of ground-beetles (Carabidae). From the coleopterous and dipterous evidence, both with a fairly low post-breeding frequency of .094, Choughs appear to move away from the typical prey of pasture to that associated with the natural clifflands, and this is in line with the evidence presented in Section 4.3.3 which shows that usage of the cliffs increases through the year (see also Section 6.4).

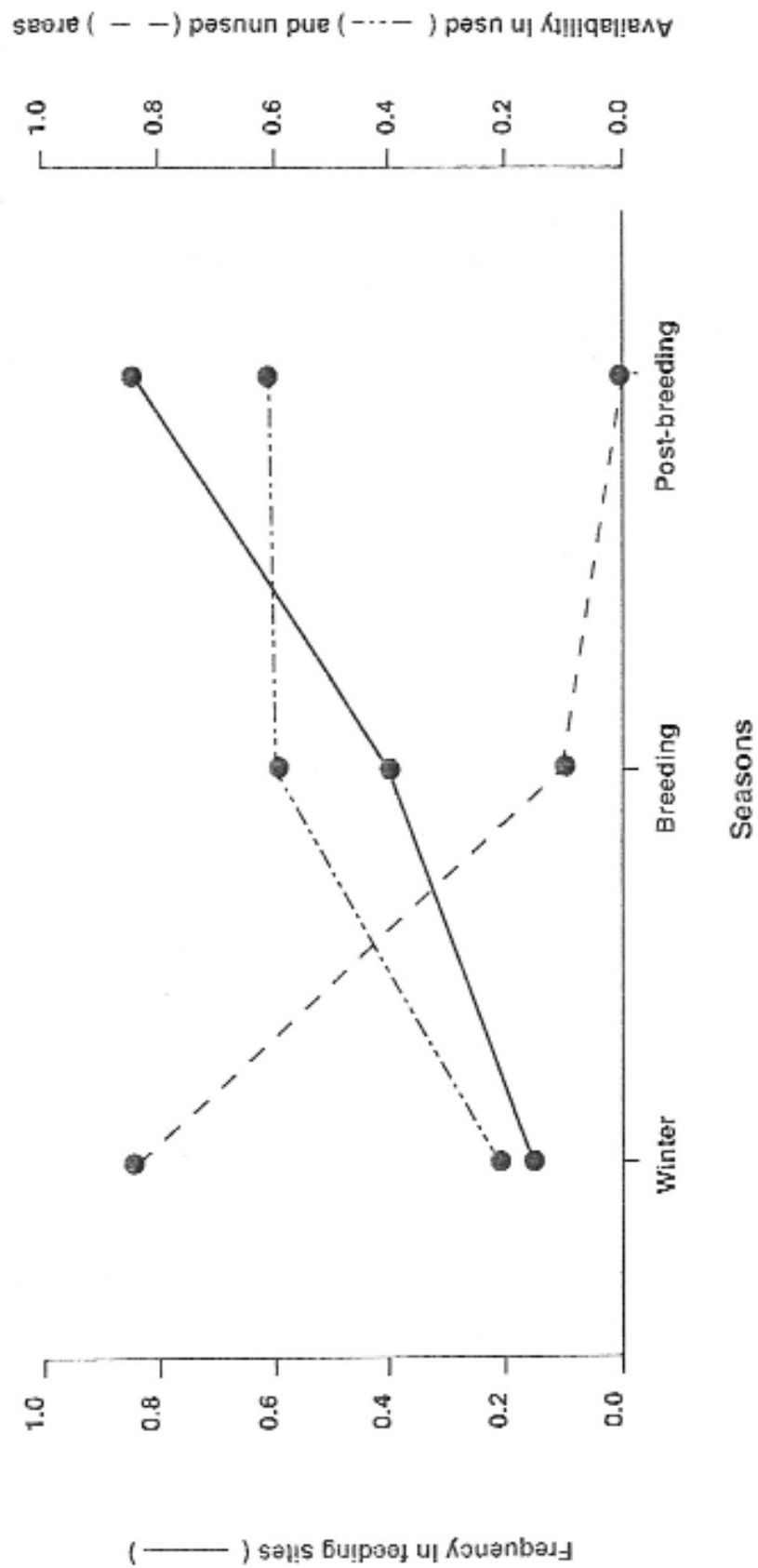


Figure 5.4
Seasonal change in the availability of ants in used and non-used areas, and the frequency of occurrence in feeding sites

Taxon	Availability in study areas											
	C1			C2			C3			Region		
	I	S	AI	I	S	AI	I	S	AI	I	AI	
OLIGOCHAETA												
'Small' lumbricidae	85	42	.857	51+	29	.711	35	21	.437		.677	
'Medium' lumbricidae	54	40	.633	51+	19	.622	56+	29	.657		.641	
Enchytraeids	93+	35	.864	34+	19	.468		5	.167		.521	
'Large' lumbricidae	6	5	.068	11	8	.162	14+	9	.175		.130	
All OLIGOCHAETA	238+	79	2.129	147+	47	1.712	119+	44	1.262		1.724	
ARACHNIDA												
Lycosidae	18	8	.170	4	3	.054	1	1	.006		.083	
Indet. spiders	6	6	.075	7	7	.117	0	0	0		.062	
Opiliones (harvestmen)	3+	1	.020	3+	1	.027	0	0	0		.016	
Thomisidae	0	0	0	1	1	.009	1	1	.006		.004	
All ARACHNIDA	27	15	.265	15	12	.207	2	2	.016		.167	
CRUSTACEA												
Indet. woodlice	0	0	0	22+	10	.279	10+	6	.119		.120	
Philoscia muscorum	0	0	0	5	3	.063	6	3	.063		.039	
Armadillidium vulgare	0	0	0	0	0	0	5	4	.063		.021	
Metoponorchus cingendus	1	1	.007	2	1	.018	0	0	0		.008	
Amphipoda sp.	0	0	0	6+	2	.063	0	0	0		.015	
All CRUSTACEA	1	1	.007	35+	14	.405	21+	12	.238		.198	

Table 5.8

Taxa, source and index of availability of prey taxa recovered from potential Chough feeding sites in Cornish study areas*: 'I' = no. of individuals recovered (+ = minimum count) from 'S' (no. +ve samples); 'AI' = availability index; *see Section 2.3.3

Table 5.8 (continued)

DIPLOPODA									
Indet. millipedes	3	3	.034	7	4	.090	1	1	.008
Chordeumatida	0	0	0	1	1	.009	0	0	0
Polydesmida	0	0	0	1	1	.009	0	0	0
All DIPLOPODA	3	3	.034	9	6	.108	1	1	.008
CHILOPODA									
Indet. centipedes	10	9	.122	6	5	.090	5	8	.119
Geophilomorpha	1	1	.007	0	0	0	0	0	0
All CHILOPODA	11	10	.129	6	5	.090	5	8	.119
DIPLURA/COLEMBOLA									
	0	0	0	2	2	.027	1	1	.008
DERMAPTERA									
<i>Forficula</i> sp.	5+	3	.045	6	5	.090	0	0	0
ORTHOPTERA									
Indet. grasshoppers	0	0	0	6+	2	.063	3+	1	.024
HEMIPTERA									
Indet. hemiptera	2	2	.020	2	2	.027	2	2	.024
LEPIDOPTERA									
Pyrallidae	1	1	.007	0	0	0	0	0	0
Indet. Noctuidae	1	1	.007	0	0	0	0	0	0
All Lepidoptera	2	2	.020	0	0	0	0	0	0
DIPTERA									
CYCLORRHAPHA									
Scatophagidae	3+	1	.020	0	0	0	3+	1	.024
Muscidae	0	0	0	4+	2	.045	0	0	0
Calliphoridae	1	1	.007	3+	1	.027	0	0	0
Rhagionidae	2	1	.014	0	0	0	0	0	0
Drosophilidae	0	0	0	1	1	.009	0	0	0
All CYCLORRHAPHA	5	5	.041	5-	3	.072	3-	1	.024

Table 5.8(continued)

Table 5.8 DIPTERA (continued)

NEMATOCERA									
Tipulidae	24+	15	.259	14	9	.198	0	0	.156
Mycetophilidae	4+	2	.034	3+	1	.027	0	0	.021
Bibionidae	0	0	0	3+	1	.027	0	0	.008
Sciaridae	0	0	0	2	1	.016	0	0	.005
Trichoceridae	1	1	.007	0	0	0	0	0	.002
Anisoplia	0	0	0	0	0	0	1	1	.003
All NEMATOCERA	29+	18	.299	22+	11	.261	1	1	.193
BRACHYCERA									
Dolichopodidae	3	2	.027	0	0	0	0	0	.010
Threvidae	2	1	.014	0	0	0	0	0	.005
Empididae	1	1	.007	0	0	0	1	1	.008
Asilidae	0	0	0	1	1	.009	1	1	.008
Stratiomyidae	0	0	0	2	1	.018	0	0	.005
All BRACHYCERA	6	4	.061	3	2	.036	2	2	.024
Indet. Diptera	6	6	.075	8+	3	.072	3	2	.032
All DIPTERA	47+	29	.463	41+	19	.450	9+	6	.079
HYMENOPTERA									
<i>Lasius flavus</i>	42+	15	.361	22+	8	.261	0	0	.221
Indet. <i>Myrmica</i>	6+	3	.054	3+	1	.027	15+	5	.151
<i>Lasius alienus</i>	8+	3	.068	10+	4	.117	4+	2	.040
<i>Myrmica rubra</i>	0	0	0	0	0	0	8+	3	.079
Indet. ants	2	2	.014	3	2	.036	1	1	.008
<i>Myrmica sulcinodis</i>	0	0	0	0	0	0	5+	2	.048
<i>Myrmica scabrinodis</i>	3+	1	.020	0	0	0	2	1	.016
<i>Formicularia fusca</i>	0	0	0	3+	1	.027	0	0	.008
Indet. Symphyta/sawflies	1	1	.007	0	0	0	1	1	.008
<i>Lasius fuliginosus</i>	1	1	.007	0	0	0	0	0	.005
(<i>Lasius</i> spp.)	51	19	.456	32+	12	.378	4+	2	.040
(<i>Myrmica</i> spp.)	9	4	.075	3+	1	.027	30+	11	.294
All HYMENOPTERA	63	26	.558	41+	16	.468	36+	15	.464

Table 5.8(continued)

Table 5.8 (continued)

COLEOPTERA										
CARABIDAE										
Indet. carabid	4	4	.048	3	2	.036	1	1	.008	.031
<i>Leistus</i> sp.	0	0	0	0	0	0	2	2	.024	.008
<i>Pterostichus</i> sp.	1	1	.007	1	1	.009	0	0	0	.005
<i>Amara aenea</i>	0	0	0	0	0	0	1	1	.008	.003
<i>Amara familiaris</i>	1	1	.007	0	0	0	0	0	0	.003
<i>Notiophylus hypocrita</i>	1	1	.007	0	0	0	0	0	0	.003
<i>Calathus</i> sp.	1	1	.007	0	0	0	0	0	0	.003
<i>Calathus melanocephalus</i>	1	1	.007	0	0	0	0	0	0	.003
<i>Nebria brevicollis</i>	0	0	0	0	0	0	1	1	.008	.003
All CARABIDAE	9	9	.082	4	3	.045	5	4	.040	.057
HYDROPHILIDAE										
<i>Cercyon haemorrhoidale</i>	1	1	.007	0	0	0	0	0	0	.003
<i>Sphaeridium scarabaeoides</i>	0	0	0	0	0	0	1	1	.008	.003
All HYDROPHILIDAE	1	1	.007	0	0	0	1	1	.008	.005
SILPHIDAE										
<i>Silpha obscura</i> sp.	1	1	.007	0	0	0	0	0	0	.003
STAPHYLINIDAE										
Indet. staphylinid	4	4	.048	2	2	.027	4-	2	.040	.039
<i>Aleochara</i> sp.	3	3	.034	0	0	0	0	0	0	.013
<i>Philonthus laminatus</i>	1	1	.007	3+	1	.027	0	0	0	.010
<i>Philonthus varius</i>	1	1	.007	1	1	.009	1	1	.008	.008
<i>Philonthus</i> sp.	2	2	.020	0	0	0	0	0	0	.008
<i>Oxytelus laqueatus</i>	0	0	0	3+	1	.027	0	0	0	.008
<i>Philonthus fuscipennis</i>	1	1	.007	1	1	.009	0	0	0	.005
<i>Tachyporus hypnorum</i>	1	1	.007	1	1	.009	0	0	0	.005
<i>Tachyporus chrysomelinus</i>	0	0	0	0	0	0	1	1	.008	.003
<i>Creophilus</i> sp.	1	1	.007	0	0	0	0	0	0	.003
<i>Ocypus</i> sp.	1	1	.007	0	0	0	0	0	0	.003
<i>Quedius</i> sp.	0	0	0	0	0	0	1	1	.005	.003
<i>Staphylinus aeneocephalus</i>	0	0	0	0	0	0	1	1	.008	.003
All STAPHYLINIDAE	15	13	.129	11+	7	.108	8+	5	.063	.102

Table 5.8(continued)

Table 5.8 COLEOPTERA (continued)

ELATERIDAE												
<i>Agriotes</i> sp.	12	11	.156	8+	5	.108	10	9	.143			.138
<i>Athous haemorrhoidalis</i>	3	3	0	5	4	.072	1	1	.008			.036
Indet. elaterid	2	2	.020	3	3	.045	1	1	.008			.023
<i>Selatosomus senus</i>	5	4	.054	0	0	0	0	0	0			.021
<i>Agriotes lineatus</i>	4+	2	.034	0	0	0	1	1	.008			.016
<i>Agriotes obscurus</i>	2	2	.020	0	0	0	0	0	0			.008
<i>Agrypus/Lacon murinus</i>	1	1	.007	1	1	.009	1	1	.008			.008
<i>Agriotes sputator</i>	0	0	0	0	0	0	1	1	.008			.003
All ELATERIDAE	30	25	.327	17+	12	.225	15	12	.167			.245
BYRRHIDAE sp.												
	0	0	0	1	1	.009	0	0	0			.003
TENEBRIONIDAE												
<i>Cylindronotus laevioctostriatus</i>	7	6	.062	4	2	.045	6	5	.095			.076
<i>Opatrum sabulosum</i>	0	0	0	2	1	.018	0	0	0			.005
<i>Cylindronotus striatus</i>	0	0	0	1	1	.009	0	0	0			.003
All TENEBRIONIDAE	7	6	.082	7	4	.072	6	5	.095			.083
SCARABAEIDAE												
Indet. scarabid	21	15	.238	11+	7	.153	4+	2	.040			.148
<i>Aphodius prodromus</i>	1	1	.007	7+	3	.081	0	0	0			.026
<i>Aphodius plagiatus</i>	6+	2	.048	0	0	0	0	0	0			.018
<i>A. punctato sulcatus</i>	3+	1	.020	3+	1	.027	0	0	0			.016
<i>Aphodius</i> sp.	0	0	0	0	0	0	3+	1	.024			.008
<i>Aphodius sphacelatus</i>	3+	1	.020	0	0	0	0	0	0			.008
<i>Aphodius cirratina</i>	0	0	0	0	0	0	3+	1	.024			.008
<i>Serica brunnea</i>	0	0	0	1	1	.009	0	0	0			.003
All SCARABAEIDAE	34+	18	.320	22+	10	.252	10+	3	.075			.221
CHRYSOMELIDAE												
Indet. chrysomelid	0	0	0	1	1	.009	0	0	0			.003
<i>Semylessa hiansis</i>	1	1	.007	0	0	0	0	0	0			.003
All CHRYSOMELIDAE	1	1	.007	1	1	.009	0	0	0			.005

Table 5.8(continued)

Table 5.8 COLEOPTERA (continued)

CURCULIONIDAE										
<i>Hypera</i> sp.	2	2	.020	0	0	0	0	0	0	.005
<i>Sitona waterhousei</i>	0	0	0	1	1	.009	0	0	0	.003
Indet. weevil	2	2	.020	1	1	.009	1	1	.008	.013
All CURCULIONIDAE										
Indet. beetles	4	4	.041	2	2	.018	1	1	.008	.023
	1	1	.007	1	1	.009	2	2	.024	.013
All COLEOPTERA	103-	63	1.007	66+	30	.748	50	28	.484	.760
GASTROPODA										
Indet. slug	3	3	.034	9	8	.144	0	0	0	.055
Indet. snail	0	0	0	1	1	.009	0	0	0	.003
<i>Nemoritis</i> sp.	0	0	0	0	0	0	1	1	.008	.003
All GASTROPODA	3	3	.034	10	9	.153	1	1	.008	.060
INDETERMINATE TAXA	1	1	.007	0	0	0	0	0	0	.003
Diversity index <i>D</i>		24.8			23.2			20.4		34.3
Total no. samples		147			111			126		384

Diversity index after Margalef (1951), see text p. 128

5.3.4 COMPARISON OF PREY AVAILABILITY IN WALES AND CORNWALL

The results of 384 soil samples collected from potential Chough-feeding areas in Cornwall over all seasons in 1988 are given in Table 5.8. The rankings of the most important vertebrate taxa ($AI > .10$) are almost the same as in the Welsh feeding areas shown in Table 5.2 (Table 5.9); with only Coleoptera and Diptera reversing positions. Some of the values (availability) differ considerably, notably Oligochaeta and Coleoptera but most of the taxonomic groups are remarkably similar. A Mann-Whitney U -test revealed no significant difference in ranks between the 2 regions ($U=54.5$, d.f. 10) over the wider prey spectrum but, as shown in Table 5.9, all except one of the most important 7 groups had a greater availability in Cornwall, although one other (Hymenoptera) was effectively tied with a difference of only .001. The respective availability of all groups is shown in Figure 5.5. The diversity in Cornwall at $D=34.3$ was nearly 8 points greater than the Welsh value

Table 5.9 Summary of ranks of main prey taxa in Cornwall ($AI > .1$) and respective positions in Wales with difference in Availability index (- = greater in Wales)

Rank	Taxon	Rank in Wales	Regional difference
1	OLIGOCHAETA	1	1.171
2	COLEOPTERA	4	0.424
3	HYMENOPTERA	3	0.001
4	DIPTERA	2	-0.168
5	CRUSTACEA	5	0.039
6	ARACHNIDA	6	0.029
7	CHILOPODA	7	0.067

In Cornwall it was necessary to select areas which were, based on Welsh observations, apparently suitable for Choughs. This could, of course, have caused bias. In an effort to reduce this factor, contiguous areas were also chosen, as in Wales, which were apparently slightly less suitable (*e.g.* with longer vegetation). The results are given in Table 5.10, and summarised in Table 5.11 with the respective positions and differences in Wales (comparative data from Table 5.3). Again Cornwall

Table 5.11 Summary of ranks of potential prey taxa in Cornwall and respective rankings in Wales with difference in AI ('-' = greater in Wales)

Rank	Taxon	Rank in Wales	Regional difference
1	OLIGOCHAETA	1	1.886
2	CRUSTACEA	5	0.278
3	COLEOPTERA	3	0.015
4	CHILOPODA	6=	0.075
5	DIPTERA	2	0.338
6	DIPLOPODA	10	0.080
7	ARACHNIDA	6=	0.027
8	ORTHOPTERA	11	0.024
9	HYMENOPTERA	4	0.296
10	GASTROPODA	6=	-0.030
11	DERMAPTERA	6=	-0.036

Taxon	Availability in study areas											
	C1			C2			C3			Region		
	I	S	AI	I	S	AI	I	S	AI	I	S	AI
OLIGOCHAETA												
'Small' lumbricidae	58	20	1.925	4	3	.500	25	21	.681	25	21	.681
'Medium' lumbricidae	44	20	1.575	16+	7	1.535	58	33	1.250	58	33	1.411
Enchytraeids	22	9	.750	6	4	.750	3	2	.056	3	2	.347
'Large' lumbricidae	5	3	.225	0	0	0	11	7	.236	11	7	.210
All OLIGOCHAETA	129	54	4.475	26+	10	2.750	101	41	1.917	101	41	2.823
ARACHNIDA												
Indet. spiders	2	2	.075	0	0	0	1	1	.014	1	1	.032
Lycosidae	1	1	.025	0	0	0	1	1	.014	1	1	.016
Thomisidae	0	0	0	1	1	.053	0	0	0	0	0	.008
Tetragnathidae	0	0	0	0	0	0	1	1	.014	1	1	.008
All ARACHNIDA	3	3	.125	1	1	.063	3	3	.042	3	3	.065
CRUSTACEA												
Indet. woodlice	0	0	0	3	2	.500	13	7	.264	13	7	.202
<i>Armadillidium vulgare</i>	0	0	0	0	0	0	8	7	.194	8	7	.113
<i>Philoscia muscorum</i>	0	0	0	0	0	0	9	4	.167	9	4	.097
All CRUSTACEA	0	0	0	3	2	.500	30	14	.569	30	14	.379
DIPLOPODA												
Indet. millipedes	1	1	.025	2	1	.167	7	3	.125	7	3	.097
Chordeumatida	0	0	0	0	0	0	1	1	.014	1	1	.008
All DIPLOPODA	1	1	.025	2	1	.167	8	4	.139	8	4	.105

Table 5.10 Taxa, source and index of availability of prey taxa recovered from control sites adjacent to potential feeding sites in Cornish study areas: 'I' = no. of individuals (+ = minimum count) recovered from 'S' (no. of +ve samples); 'AI' = availability index

Table 5.10 (continued).

CHILOPODA									
Indet. centipedes	4	4	.175	0	0	0	3	3	.069
Geophilomorphae	2	1	.050	0	0	0	0	0	.016
All CHILOPODA	6	5	.225	0	0	0	0	0	.113
DIPLEURA/COLLEMBOLA									
	0	0	0	1	1	.083	2	2	.032
ORTHOPTERA									
Indet. grasshoppers	0	0	0	0	0	0	3+	1	.042
HEMIPTERA									
Indet. hemiptera	0	0	0	0	0	0	5+	2	.048
LEPIDOPTERA									
Indet. moth	1	1	.025	0	0	0	0	0	.008
DIPTERA									
CYCLORRHAPHA									
Calliphoridae	0	0	0	1	1	.063	0	0	.008
Chloropidae	0	0	0	0	0	0	1	1	.014
All CYCLORRHAPHA	0	0	0	1	1	.063	1	1	.014
NEMATOCERA									
Tipulidae	3	3	.125	1	1	.083	0	0	.048
Mycetophilidae	0	0	0	0	0	0	1	1	.014
Bibionidae	1	1	.025	0	0	0	0	0	.008
All NEMATOCERA	4	4	.150	1	1	.083	1	1	.014
BRACHYCERA									
Empididae	1	1	.025	0	0	0	0	0	.008
Indet. Diptera	0	0	0	1	1	.083	1	1	.014
All DIPTERA	5	5	.175	3	2	.250	3	3	.105
HYMENOPTERA									
Indet. Myrmica	0	0	0	0	0	0	1	1	.014
									.008

Table 5.10 (continued)

COLEOPTERA										
CARABIDAE										
<i>Harpalus senus</i>	0	0	0	0	0	0	0	0	1	.014
<i>Radister bipustulatus</i>	0	0	0	0	0	0	0	0	1	.014
<i>Amsa tibialis</i>	0	0	0	0	0	4	2	.417	0	0
<i>Agonum muelleri</i>	1	1	.025	0	0	0	0	0	0	0
<i>Bembidion lunulatum</i>	1	1	.025	0	0	0	0	0	0	0
All CARABIDAE	2	2	.050	4	2	.417	2	.028	2	.073
STAPHYLINIDAE										
<i>Quedius</i> sp.	1	1	.025	0	0	0	0	0	0	0
<i>Philonthus</i> sp.	1	1	.025	0	0	0	0	0	0	0
Indet. staphylinid	0	0	0	1	1	.083	1	.014	1	.014
All STAPHYLINIDAE	2	2	.050	0	0	0	0	0	0	0
ELATERIDAE										
<i>Agriotes</i> sp.	2	2	.075	0	0	0	0	0	3	.069
Indet. elaterid	3	2	.100	0	0	0	0	0	1	.014
<i>Athous haemorrhoidalis</i>	1	1	.025	0	0	0	0	0	1	.014
<i>Agriotes scuminatus</i>	1	1	.025	0	0	0	0	0	0	0
All ELATERIDAE	7	6	.225	0	0	0	0	0	5	.083
DASCILLIDAE										
<i>Dascillus corvinus</i>	0	0	0	0	0	0	0	0	1	.014
SCARABAEIDAE										
<i>Aphodius</i> sp.	3+	1	.107	0	0	0	0	0	0	0
Indet. scarab.	1	1	.025	0	0	0	0	0	0	0
All SCARABAEIDAE	4+	2	.100	0	0	0	0	0	0	0
CURCULIONIDAE										
Indet. weevil	0	0	0	0	0	0	0	0	2	.042
CANTHARIDAE										
<i>Cantharus</i> sp.	1	1	.025	0	0	0	0	0	0	0
Indet. beetles	0	0	0	0	0	0	0	0	3-	.042
All COLEOPTERA	16	13	.450	5	3	.500	14-	.1	.222	.331
GASTROPODA										
Indet. snail	0	0	0	0	0	0	0	0	1	.014
Diversity index <i>D</i>	10.4		5.7		12.9		17.4			
Total no. samples	40		12		72		124			

Diversity index after Margalef (1951), see text p. 128

Table 5.10 (continued)

is shown to be more diverse with a greater abundance of most prey groups, with earthworms being very much more abundant. Only with Hymenoptera did Wales show an appreciably greater abundance. Perhaps no undue significance should be read into these results because of the subjective nature of the habitat selection. Table 5.12 gives the seasonal breakdown for those Cornish sites which were selected as being equivalent of the used areas in Wales (*cf.* Table 5.7). Interestingly, the hymenoptera, possibly crucial while rearing young (see Section 5.4), have very similar *AI*'s in the two regions during the breeding season (a difference of only .008). On the other hand, the Lizard region, which scores poorest of the 3 Cornish study areas (although still richer than any Welsh site) in areas rated as prime potential Chough feeding areas, is richest in the adjacent believed less suitable areas. It is possible to conclude that a slight shift in choice criteria of Cornish habitats (*or in management*) would affect the diversity indices given in Table 5.8. Nevertheless, the indices of the Cornish sites are all, bar one, greater than the Welsh counterparts: the exception is Mwnt-Cemaes, which reaches a higher value than West Penwith only. The index for the Cornish region (17.4) is more than 4 points greater than Wales (13.3). However, as mentioned already (5.2.2), diversity might be less important than abundance/availability of a few key species, such as ants, at critical times of the year (see Section 5.4).

5.3.5 FAECAL SAMPLING

A total of 449 faecal samples, including 15 cast pellets from Cornwall, were collected. Of these 335 (75%) were of Welsh origin (Table 5.13). In overview, most of the groups noted by Goodwin (1986) as food items were recovered (Table 5.14) and a number of additional finds were made (Table 5.15). Earwigs, the ubiquitous *Forficula auricularia*, formed a varying proportion of the prey items, up to 15%, at all main study areas despite a low recovery rate from feeding area soil cores (*cf.* Table 5.2). In contrast, the Orthoptera, noted by Goodwin (*ibid*) as prey, were represented only by a single ootheca of the Cockroach *Ectobius* sp.

Table 5.13 Numbers and sources of faecal and pellet samples

Area	Region	No.
W1 Mwnt-Cemaes	Dyfed	108
W2 Strumble	"	39
W3 Newgale-Solva	"	66
W4 Marloes	"	64
Rame peninsula	Cornwall	114*
Ramsey Island	Dyfed	49
Stackpole	"	9
Total		449

* includes 15 pellets

The overall impression is that the birds take relatively poorly mobile, even sessile, prey. Only one adult dipteran was recovered, the Yellow dung-fly *Scatophaga stercoraria*, which may have been consumed within its puparium whilst the bird was turning over dung, from which much of the fauna comes. Dipterous larvae, however, are much more frequent, occurring in >1/3 of the samples

Taxon	Availability in Potential feeding sites		
	W	B	PB
OLIGOCHAETA	2.217	1.679	1.271
ARACHNIDA	.031	.126	.365
CRUSTACEA	.054	.365	.083
OTHOLOPODA	.023	.057	.031
CHITLOPODA	.178	.063	.073
DIPLURA	.008	0	.021
DERMAPTERA	.031	.069	0
ORTHOPTERA	0	.044	.031
HEMIMPTERA	0	.044	.010
LEPIDOPTERA	0	.006	.010
DIPTERA			
Cyclorrhapha	.078	.044	0
Nematocera	.147	.314	.010
Brachycera	.039	.031	.021
Indet. diptera	.047	.088	.031
All DIPTERA	.310	.478	.062
HYMENOPTERA	.256	.591	.417
COLEOPTERA			
Carabidae	.054	.038	.073
Hydrophilidae	0	.006	.010
Silphidae	0	.006	0
Staphylinidae	.062	.138	.083
Elateridae	.248	.245	.146
Byrrhidae	.008	0	0
Tenebrionidae	.109	.057	.042
Scarabaeidae	.178	.358	.063
Chrysomelidae	0	.006	.010
Curculionidae	.008	.031	.010
Indet. beetles	0	.038	0
All COLEOPTERA	.667	.868	.448
MOLLUSCA	.016	.075	.063
OTHER	0	0	.010
Total no. samples	129	159	96

Table 5.12

Seasonal indices of availability in potential Chough areas of prey recovered in Cornish region (see Table 5.8). Biological seasons; W = Winter (November - February), B = Breeding (March - June), PB = Post-breeding (July - October)

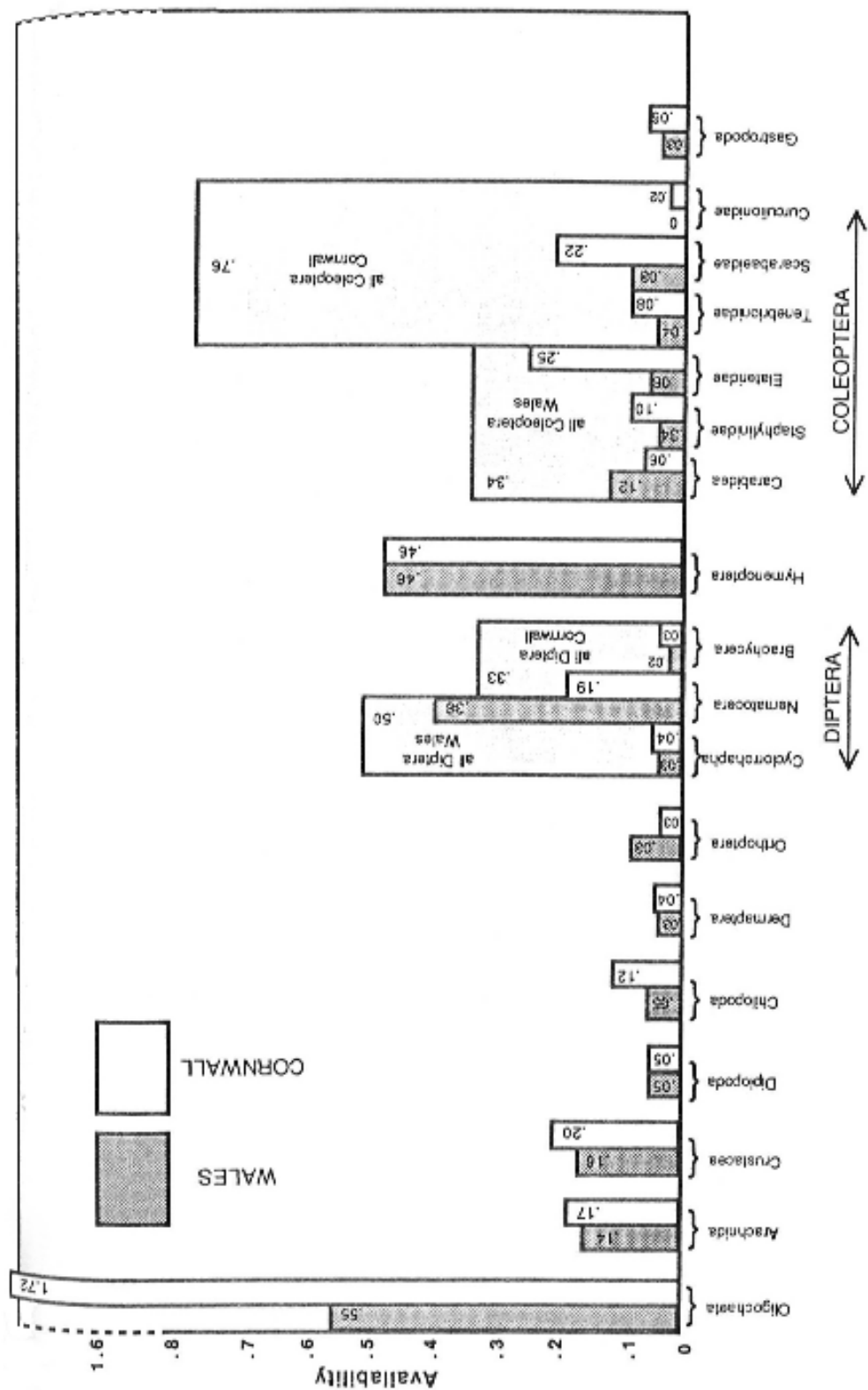


Figure 5.5

Comparative availability of invertebrate prey in Wales and Cornwall in feeding areas (Wales N = 441) and potential feeding areas (Cornwall N = 384). Left hand (shaded) section of bars represents Welsh values. Aggregated values for Diptera and Coleoptera families are also shown in same format

from the two northern, more pastoral study areas (Table 5.15). These included many tipulid head capsules. Other Diptera are represented by unidentifiable puparial fragments and parts of the puparium of the muscid *Morellia cf. hortorum*, which breeds in dung (Skidmore 1985). It is very probable that the value for dipterous larvae is an underestimate in that this is one element in the Chough's diet of which no identifiable part survives digestion well. The presence of wing fragments, sometimes identifiable to species level, implies that imagines of Diptera would have been recognisable had they been regularly taken.

Coleopterous evidence, as both larvae and adults (Table 5.16), is remarkably frequent, occurring in 84% of all Welsh samples: in >3/4 of those from each main study area, and in all but one of 66 from Newgale-Solva. Many of the taxa would have been obtained from beneath dung or by turning stones (as might the earwigs), in particular, carabid ground beetles and their larvae, whilst many others, including elaterid click beetles would have been taken by searching in pasture, where they can occur at densities of 2-3 million/acre (Wallwork 1976). Numerically, in the evidence, the dung beetles (Geotrupidae/Scarabaeidae), as imagines and larvae, are exceeded only by the ground beetles. Since *Aphodius rufipes* largely hibernates as a third instar larva, and *A. spicelatus* as an imago, it is not surprising that they appear thus in faeces during the winter (Tables 5.15 & 5.18). Some carabids, including *Carabus problematicus*, *C. violaceus* and *Nebria brevicollis* mate in late summer and autumn; the winter populations of these too is composed mainly of developing larvae and pupae (Wallwork 1970). Other carabids have an early activity peak in spring/early summer, and a late one in late summer/autumn; species which mate and oviposit early, overwinter as adults (*ibid.*). Table 5.15 gives the seasonal variations for all taxa in the Welsh assemblage; these data are summarised in Table 5.14 and Figure 5.6.

Table 5.16 Proportions of adult and larval Coleoptera present within the faecal evidence (n=no. of samples with beetle evidence) in Wales (all seasons) and Cornwall (winter only)

Taxon	Wales (n=233)		Cornwall (n=67)	
	Adults	Larvae	Adults	Larvae
Carabidae	.36	.13	.43	.06
Staphylinidae	.10	.02	0	0
Elateridae	.06	.01	0	0
Tenebrionidae	.09	0	.30	0
Scarabaeidae/Geotrupidae	.25	.06	.48	0
Curculionidae	.15	0	.06	0
Other	.22	.05	.04	0
All	.88	.24	.97	.06

Whilst the majority of the fauna appears to have been taken from well-grazed rough pasture, there is also a significant element from other habitats. The number of *Opatrum sabulosum* (from Newgale-Solva (W3) throughout the year and from Rame in Cornwall in the winter) was unexpected. Brendell (1975) does not record the species from Cornwall, although in faecal samples collected there, it occurred in 17% of 99 samples (Table 5.18; it is found in sandy or 'waste' areas, principally on the coast (*ibid*, Harde 1984), at the roots of plants (Brendell 1975), and will burrow in dry, sandy grassland (R. Crowson pers. comm.)) The absence of common sand-dune species is due to the rocky nature of the study coastline. The large ground beetle *Cychrus caraboides* is

Taxon	% Frequency in region			Year
	Season			
	W	B	PB	
OLIGOCHAETA	29	10	20	20
ARACHNIDA	3	3	0	2
CRUSTACEA	3	0	4	2
MYRIAPODA	4	1	2	3
DERMAPTERA	9	10	4	8
ORTHOPTERA	0	0	2	-
HEMIPTERA	1	2	0	1
LEPIDOPTERA	1	4	2	2
DIPTERA	15	49	18	29
HYMENOPTERA	4	0	36	9
COLEOPTERA (all)	81	89	95	84
Carabidae	37	30	62	39
Staphylinidae	11	4	22	10
Elateridae	1	16	0	6
Tenebrionidae	4	9	13	8
Scarabaeidae/Geotrupidae	12	37	24	24
Curculionidae	13	15	9	13
Other families	5	7	5	3
Indet. beetles	36	15	5	22
CEREAL GRAIN	49	2	9	23
OTHER	3	2	0	2
Total no. samples	117	105	55	277

Table 5.14
Seasonal frequency of prey (all ages) in West Wales as represented by percentage occurrence of remains in faecal samples; summary of Table 5.15

regarded by Lindroth (1973) as primarily a woodland species, only occurring in open country in mountain areas, although it has been found feeding upon snails on the machair of the Outer Hebrides (P. Buckland pers comm.). It is the only predominantly woodland element noted in the Chough's diet, although too much emphasis should not be placed upon a single individual, which may reflect a chance capture of a migrating animal. There is sufficient in the assemblage to infer some hunting along the edge of wetlands, possibly scavenged while drinking; Choughs were once recorded from such a habitat at Strumble, and this is the habitat where the curculionid (weevil) *Notaris bimaculatus* will occur on aquatic sedges (Cyperaceae). The hydrophilid *Hydrobius fuscipes* might similarly have been taken from adjacent to Marloes Mere (W4). Weevils, though featuring prominently in faecal samples and also in some collected in the Stackpole area (Haycock & Meyer 1988), were not encountered during routine live sampling (see Tables 5.2 - 5.4).

One anomaly in the assemblage is the apparent underestimation of ants, which were commonly observed to have been taken in season. Indeed, during the breeding season, ants appear to be a major influence on habitat selection (4.3.3), and yet their remains do not occur in a single faecal sample during that season (Table 5.14). This discrepancy is possibly explained if ants are selected only for feeding to nestlings (5.4, but see 5.3.7). Ant remains appear most frequently during the post-breeding season (36%), and all identified specimens were alates suggesting that predation occurred during swarming on ant mounds before flight. The catching of flying insects by a flock of Choughs has been witnessed in the Isle of Man in September (Batten *et al.* 1973).

It is possible that evidence of earthworms (chaetae and gizzard rings) in faecal residue has been overlooked in the past due to the need for differential examination (5.2.2). The frequency of earthworm evidence across the study region varies considerably, ranging from 6% in the Ramsey Island samples (Table 5.17) collected during the summer to 74% in the winter Cornish material (Table 5.18). The lowest Welsh (\bar{x} 20%) value of 12% at Mwnt-Cemaes contrasts with a high of 31% at Strumble (Table 5.15) - one of the few times that faecal data from these two otherwise similar study areas diverge (*cf.* Diptera, Coleoptera and cereal component variances of only 0-2%). The main variance was found within the winter season, when Cemaes birds took more tipulids.

Figure 5.6 shows the annual diet as represented by the percentage seasonal occurrence of detectable evidence from faecal analysis in Wales. There is close agreement between the Welsh and Cornish winter beetle evidence but the Cornish quotient of earthworms is greatly increased, balanced by less evidence of cereal grain. Choughs are also known to consume plant food: oats being a very important component in the Hebrides, occurring in nearly all winter faecal samples of Judy Warnes' 1982 study. This seems to decline southwards for grain, largely barley and wheat (+ occasional other seeds), appeared in 64 Welsh samples (23%), 77% of these being in the winter (Table 5.15): almost 50% of all winter samples contained evidence of cereal feeding. In Cornwall, cereal grain appeared in <10% of the winter Cornish samples (Table 5.18). In addition, one sample from Cornwall included the kernel from a wild or ornamental cherry *Prunus* sp. There is evidence to suggest that cereal and earthworm components are interchangeable as a source of bulk winter protein: in 120 samples with grain/earthworm evidence only 11 contained both, and there was a very strong separation of the two components ($P < 0.001$; Table 5.19). Given the general but hidden ubiquity of earthworms, cereal grain, where present, might simply present a 'cheaper' bulk food. Mollusc evidence was infrequent: only a single terrestrial Gastropod (*Discus rotundatus*) and fragments of the common marine mussel *Mytilus edulis*; the latter was possibly a result of Choughs scavenging along cliffs frequented by gulls.

Taxon	% Frequency in study area															
	W1				W2				W3				W4			
	W	B	PB	Y	W	B	PB	Y	W	B	PB	Y	W	B	PB	Y
OLIGOCHAETA	7	8	33	12	56	10	50	31	64	9	9	27	18	25	50	20
ARACHNIDA indet. spiders	3	0	0	1	0	5	0	3	5	18	0	5	0	0	0	0
Indet. Opiliones	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
CRUSTACEA indet. woodlice	0	0	11	2	0	0	0	0	0	0	0	0	8	0	0	6
MYRIAPODA	0	0	0	0	0	5	0	3	23	0	3	9	0	0	0	0
DERMAPTERA <i>Porficula</i> sp.	3	10	0	8	19	10	50	15	9	18	3	8	6	0	0	5
CETHOPTERA Blattidae																
<i>Ectobius</i> sp.	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0
HEMIPTERA (A)																
Coreidae <i>Erotopus scapha</i>	0	0	0	0	0	5	0	3	0	0	0	0	0	0	0	0
Pentatomidae <i>Dolycoris baccorum</i>	0	0	0	0	0	0	0	0	0	9	0	2	0	0	0	0
LEPIDOPTERA (L)	0	5	0	3	0	5	0	3	0	0	3	2	2	0	0	2
DIPTERA (L, all)	21	48	28	37	6	62	0	36	9	27	15	15	18	50	0	23
NEMATOCERA																
Tipulidae	14	41	17	30	0	62	0	33	9	27	12	14	16	42	0	20
Bibionidae	5	5	0	4	0	0	0	0	0	0	0	0	0	0	0	0
BRACHYCERA Tabanidae	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
CYCLOPHAPHA Phoridae	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0
Indet. diptera	3	2	11	4	6	0	0	2	0	0	0	0	0	8	0	2

Table 5.15

Prey as represented by remains in faecal samples. Percentage seasonal frequency of occurrence (positive samples/total samples) in Welsh study areas. Age: indeterminate full-grown except where stated: A =adults, L=larvae; seasons: W =winter (November - February), B =breeding (March - June), PB =post-breeding (July - October), Y =all year

5.3.6 PREY SIZE

In a small captive trial (see Appendix X), the Chough did not respond to prey of <5mm but care must be taken before attributing captive behaviour to wild counterparts since their exposure to varied stimuli is greatly reduced. Proven prey, as revealed by direct observation and especially by faecal evidence, include a number of taxa which are somewhat smaller. With aggregated prey (e.g. ants) this size character need not apply, and both *Myrmica* spp. and *Lasius* spp. form an important resource. The Collembola, almost uniformly <5mm in size, are represented by one record, but these soft-bodied animals are unlikely to survive passage through the gut in recognisable form. A number of small insects may be the result of casual ingestion whilst working over a range of habitats. The small hydrophilids of the genus *Cercon* occur both in dung and wet mud, and the related *Helophorus* could also be taken in the latter habitat. Other species, however, seem more likely to be the result of deliberate ingestion. The small ground beetles, *Bembidion lampros* and *Trechus obtusus*, do not exceed 4.5mm, and, whilst the former is both very shiny and fairly active, running about on dry open soils (Lindroth 1973), the latter is dull and less evident in its activity. Similarly, the weevils of the genus *Sitona* are only 3-5mm long but have brightly coloured scales, whilst the smaller *Brachysomus echinatus* (2.2-3.3mm) is both dull and sluggish, and is often found in association with moss on hillsides with short grass (Harde 1984). It seems probable that the bird is capable of responding to prey down to at least 3mm in its natural habitat; Warnes (1982) reached the same conclusion.

5.3.7 PELLET AND FAECES COMPARISON

The absence of cast pellets from Welsh sites (see 5.2.2) raises the possibility that faecal assemblages are not wholly representative of invertebrates ingested. Although the majority of taxa found in pellets in Cornwall are recorded from faeces in Wales, there are some discrepancies (Table 5.18), e.g. Lepidoptera (unrecorded in faeces); Diptera (unrecorded in pellets); and Hymenoptera, Scarabaeidae/Geotrupidae and Curculionidae (all under-recorded in faeces). These could at least be partly explained by seasonability in prey selection; it is suggested elsewhere (5.4) that ants are primarily taken as a food for nestlings, and that this accounts for various observational behaviours and the fact that during the breeding season they were not recorded from any of 105 faecal samples. If they are consumed by adults during the breeding season the expected frequency would be as in Cornwall (=2%), where they appeared in 2 of 99 faecal samples but also in 2 of only 15 pellets. The possibility therefore must remain that had pellets been available from Wales, ants might have been found to have featured in the adult diet at that time. On the other hand, ant remains in Cornwall represented winter diet, and the equivalent seasonal value for Wales was greater (=4%, n=117). (see Figure 5.6)

The remaining exceptions relate either to sporadic incidental prey items, such as *Sitona waterhousei*, a weevil which largely feeds on crucifers, or to the increased precision of identification which is possible with the less fragmented material from pellets, and this should be borne in mind with regard to the hymenopterous component. Some of the differences are also possibly size-related, in that the larger species of ground beetle (*Pterostichus melanarius* and *P. niger*) and the large Dumbledor beetle *Geotrupes spiniger* are more evident in the pellets, although smaller taxa, including lepidopterous larval head capsules also occur. Further experiments with captive birds would help to clarify whether larger prey are significantly under-represented in faecal samples.

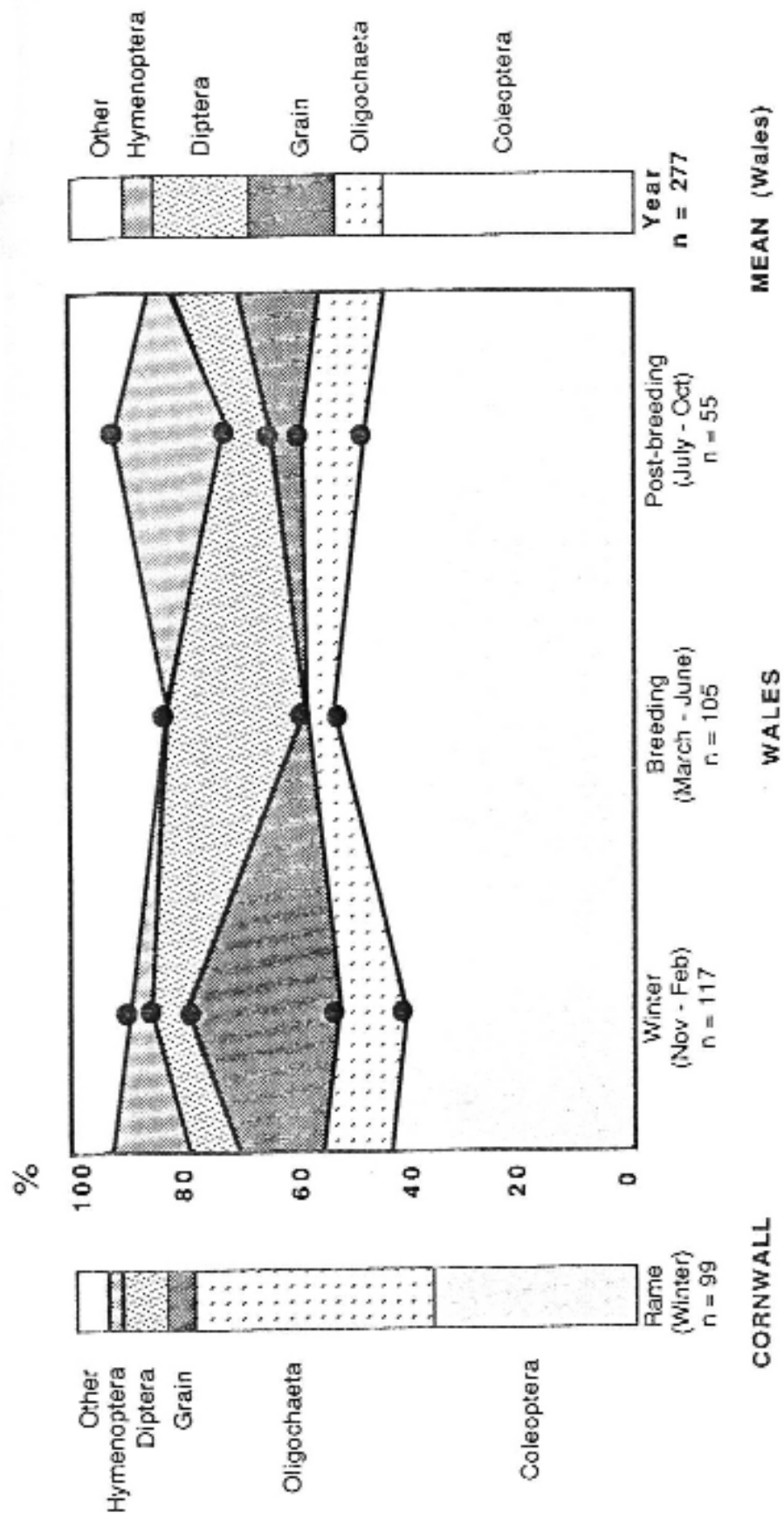


Figure 5.6
Adult Chough diet in Wales and Rame, Cornwall (winter) as indicated by the percentage seasonal occurrence of detectable faecal evidence

5.3.8 A COMPARISON OF CORNISH AND WELSH FAECAL SAMPLES

There appear to be no significant differences in terms of species diversity between the prey items of the Cornish and Welsh Choughs: dividing the number of taxonomic groups represented by the total number of samples in each region gives: Wales .332, and Cornwall .307.

There were differences within taxonomic groups: earthworms were clearly a more important element in the (winter) diet of the two immigrant Cornish birds (74% occurrence in 99 samples), than recorded for Welsh birds (winter = 29%, $n = 117$), exceeding the frequency occurrence for beetles (*cf.* Tables 5.14 & 5.18). The increased emphasis on earthworms in Cornwall could be explained by the birds' relative inexperience (Meyer 1990, see Appendix IV). It is possible that local edaphic, as well as seasonal factors, also caused some of the differences, although the birds clearly utilise both herbivore dung and sandy grassland in both regions. Indeed, because of the paucity of earthworms in the upper layers of the soil during summer, it is probable that the turning over of dried dungpats provided the Choughs with most of the summer earthworm component; tipulid larvae have also been noted to be similarly aggregated beneath dung (P. Skidmore pers. comm. to P. Buckland). There are, unfortunately, no summer Cornish samples. The dung beetle *Aphodius rufipes* present as larvae, identified by the mandibles, occurs in only two of the Welsh localities, Strumble and Newgale-Solva, and the absence of this apparently eurytopic animal (Landin 1961) from the Cornish material is probably not significant.

Taxon	% Frequency
OLIGOCHAETA	6
LEPIDOPTERA (L)	2
DIPTERA (L) (all)	29
NEMATOCERA Tipulidae	20
CYCLORRHAPHA Syrphidae	2
Indet.	6
HYMENOPTERA (all)	8
<i>Lasius</i> sp.	2
<i>L. alienus</i>	6
<i>L. flavus</i>	2
<i>Myrmica</i> sp.	4
COLEOPTERA (A, all)	98
CARABIDAE (all)	35
<i>Ahax parallelepipedus</i>	4
<i>Amara</i> sp.	10
<i>A. aenea</i>	2
<i>Calathus fuscipes</i>	6
<i>Harpalus</i> sp.	2
<i>Pterostichus</i> sp.	18
<i>P. nigrita</i>	2
indet.	8
STAPHYLINIDAE <i>Staphlinus ?acnocephalus</i>	6
ELATERIDAE indet.	2
BYRRHIDAE <i>Byrrhus</i> sp.	14
COCCINELLIDAE <i>Scymnus</i> sp.	2
SCARABAEIDAE (all)	76
<i>Amphimallon ?solstitialis</i>	76
<i>Cetonia ?aurata</i>	2
CURCULIONIDAE (all)	12
<i>Otiorhynchus ligneus</i>	10
indet.	2
GASTROPODA Helicidae <i>Trichia striolata</i>	2
CEREAL GRAIN	4
Total no. samples	49

Table 5.17
Frequency of prey taken by Choughs on Ramsey Island in July 1989 as represented by percentage occurrence of remains in faecal samples; age: A =adult, L =larva

Taxon	% Frequency	
	Faeces	Pellets
OLIGOCHAETA indet.	74	40
ARACHNIDA indet.	1	0
MYRIAPODA indet.	2	0
DERMAPTERA <i>Forficula</i> sp.	6	7
HEMIPTERA	0	7
LEPIDOPTERA (all)	0	20
Indet.	0	13
? <i>Lasiocampa</i> sp.	0	7
DIPTERA (all)	14	0
Indet.	2	0
NEMATOCERA (all)	10	0
Tipulidae	8	0
Bibionidae	2	0
CYCLORRHAPHA (all)	2	0
Muscidae <i>Morellia</i> ? <i>hortorum</i>	1	0
Scatophagidae <i>Scatophaga stercoraria</i>	1	0
HYMENOPTERA (A, all)	2	13
Indet. ants	2	7
Indet. wasps	0	7
COLEOPTERA (all)	55	80
Indet. (A)	6	0
Indet. (L)	0	7
CARABIDAE (all)	24	53
<i>Amara</i> sp. (A)	5	0
<i>Amara aenea</i> (A)	1	0
<i>Amara sulica</i> (A)	2	0
<i>Pterostichus madidus</i> (A)	2	0
<i>Pterostichus niger</i> (A)	0	13
<i>Pterostichus melanarius</i> (A)	0	7
<i>Trichocellus</i> sp.	0	7
Indet. (A)	16	20
Indet. (L)	1	7
TENEBRIONIDAE (A) <i>Opatrum sabulosum</i>	17	20
SCARABAEIDAE/GEOTRUPIDAE (A, all)	25	67
<i>Aphodius</i> sp.	18	7
<i>Aphodius sphacelatus</i>	1	0
<i>Geotrupes</i> sp.	7	7
<i>Geotrupes spiniger</i>	0	60
<i>Oxyomus silvestris</i>	1	0
CURCULIONIDAE (A, all)	1	20
<i>Brachysomus echinatus</i>	1	7
<i>Sitona</i> ? <i>waterhousei</i>	0	13
CEREAL GRAIN/SEEDS	8	7
INDET. FRAGMENTS	1	0
Total no. samples	99	15

Table 5.18
Frequency of winter prey at Rame, Cornwall as represented by percentage occurrence of remains in faecal samples and cast pellets; age: indeterminate full-grown except A=adult, L=larva

5.4 DISCUSSION

The abundance of the commoner invertebrate prey orders was, with the exception of the Oligochaeta, greater in feeding areas than in adjacent unused areas (Figure 5.1); Less usually taken prey was also more abundant in feeding areas, by a ratio of 7:1. Since faecal evidence does not support the hypothesis that ranges are selected for prey diversity (see below), it is likely that Choughs select foraging areas within ranges for prey richness.

Throughout this study, the role of the earthworm has been ambiguous. Barbash (1988) showed that Starling and Rook predation of leatherjackets caused appreciable and significant mortality. It was proposed in Section 5.2.2 that diversity is less important than the availability of key species at certain critical times of the year, and the possibility should be considered that Chough predation of preferential taxa causes localised depletion and affects the results of sampling in the wake of a feeding bout. Direct observation and the pattern of faecal evidence (Table 5.15) give the impression that earthworms are a regular and important prey of Choughs in West Wales. To avoid the problem of sampling locally depleted populations "the usual protocol is to disturb the birds whilst they are feeding and to sample along the search path immediately" (D.B.A.Thompson pers. comm.). However, in this study, an implicit requirement existed not to disturb Choughs, and no such licence, to enable legal disturbance, was therefore sought.

Taken in isolation, earthworm chaetae in faeces will overestimate the importance of earthworms to a greater extent than is likely with evidence from any other prey taxa. In Appendix X it is shown that the chaetae from just one earthworm can appear in at least 12 subsequent faeces. The sampling protocol ensured faecal sampling occurred on separate days in each study area during each visit, thus helping to counteract the problem of overestimation. The additional benefit of occasional direct observations during behavioural observations (Chapter 6), enable it to be stated with reasonable assurance that earthworms were at least a *regular* prey. The possibility also exists that the selection of feeding sites depends on arthropod availability, and that earthworms are taken adventitiously. If earthworms and cereal grain are interchangeable as a source of winter protein (Table 5.19), availability of cereal stubble, given its lower collection costs, will reduce earthworm intake. It is also possible that Choughs are preferentially seeking tipulids, which, as subterranean larvae, more closely resemble earthworms than arthropods. The exact role of the earthworm in Chough regional ecology requires further and specific research. Such questions are greatly influenced by the proportions of different habitats available, these are generally determined by farming practices (see Chapter 4).

Apart from earthworms, only earwigs (Dermaptera) were recorded as more numerous away from foraging sites. Faecal evidence (Table 5.14) suggests that earwigs are quite an important Chough food, as they certainly are on Islay, where they were recovered from >66% of 56 Chough pellets (Warnes 1982), and on Bardsey Island (Roberts 1982). Earwigs live on the surface or under stones and old cow-pats, therefore soil-sampling *per se* might under-record their presence. There seems little doubt, judging from faecal evidence (*cf.* Table 5.14), that other taxa, for example weevils (Curculionidae), were also under-represented by choosing soil-sampling in preference to pitfall- or suction-trapping as the primary method of prey investigation. On Islay, no earwig was found in 274 soil samples but 44 were taken from 313 pitfall-traps during the course of a year (Warnes 1982). However, at South Stack, although earwigs were taken by Choughs "consistently at all times of the year", they were not recovered from any of 400 soil samples nor from 240 pitfall-traps (Bullock 1980); a few were found in samples taken at actual feeding sites, as in the present study. This suggests that neither pitfall-traps nor soil-sampling adequately assesses earwig populations, which are surface active in the summer but hibernate below ground in the winter. During this study, randomised sampling within Chough feeding areas helped to overcome the problem insofar

as surface elements, such as loose stones etc., would be sampled *pro rata* as frequently as the substrate (see Section 5.2.1).

Table 5.19

The occurrence of grain and/or earthworms in the Chough's diet. Evidence from all 120 faecal samples collected which contained cereal grain and/or earthworm evidence

	Grain	Earthworms	Grain + earthworms	N
Distribution	59 (49%)	50 (42%)	11 (9%)	120
	$\chi^2 = 32.55$ d.f.1 P <0.001			

Previous studies have demonstrated the importance of Coleoptera as a major prey taxon (*e.g.* Bullock 1980, Roberts 1982, Warnes 1982), the present study confirms this. Although surface-active ground beetles, such as the Carabidae and Staphylinidae, were under-represented in soil-samples, the use of pitfall-traps would not have wholly redressed the balance (Greenslade 1964, Southwood 1978), since their efficiency is prone to error (Luff 1975), and they catch nocturnal-active taxa. A small experiment was carried out at the end of the study to help clarify the role of pitfall-trapping in Chough food resource studies, and it was found that many of the suitable carabids in Chough feeding areas were nocturnal (Appendix V). From the sampling evidence (Figures 5.2b & 5.3b), beetles were very much more numerous in the two northern study areas: W1/Mwnt-Cemaes and W2/Strumble. Mwnt-Cemaes also had a more diverse invertebrate fauna (Table 5.2) in those feeding sites which were accessible to sampling. Farther south with increasingly intensive agriculture, reduced diversity of Coleoptera is possibly offset by recourse to habitats where prey such as ants, grasshoppers (Orthoptera) and spiders are more abundant, although judged by faecal evidence alone, beetles are as important as in the more agricultural areas (Table 5.15).

Species selection alters: at Newgale-Solva more ground and rove beetles (Staphylinidae) are taken, at Marloes more dung beetles (mainly of the *Aphodius* genus). This latter fact is surprising given the pastoralism at Mwnt-Cemaes and Strumble. It could in part be explained by the reduced sample size at Marloes and a larger proportion of unidentified beetles, including possibly chafers of various species, which were known to occur frequently on the cliffs. The increased emphasis on diptera by Choughs at Mwnt-Cemaes might also have affected the dung beetle intake.

The life-cycles of beetles affect their availability to Choughs. Their frequency in Chough feeding areas/habitats reaches a peak during the months March through June (Table 5.7) but this is not reflected by the frequency of their remains in faecal samples (Table 5.14) - in which the percentage occurrence rises steadily throughout the year from 81% to 95% in the post-breeding period. The frequency of the Carabidae (the most important family) in faeces falls quite sharply during the Chough breeding season; with dung beetles, however, the frequency in feeding areas matches the faecal evidence more closely. The third ranking taxon in faecal sampling was Curculionidae, and yet weevils were never found in live sampling in Wales, although they did occur in the background

Cornish sampling (Table 5.8). The faecal evidence of rove beetles, which drops in the breeding season (Table 5.14), also differs from the frequency pattern of abundance (Table 5.7). This might be explained if certain kinds of food (*e.g.* ants) are selected preferentially for nestlings (see below). The bulk of adult diet during the breeding season is dipterous (occurrence 49%), and other coleopterans (scarabaeids (37%) and carabids (30%). Many of the species which compose these taxa are obtainable from cow dung, and this might well represent the 'cheapest' food, appropriate to adults, that is available at this time of year.

Dipterous larvae are a major prey category, as are, to a lesser extent, Crustacea, notably woodlice (Isopoda). These components are fairly evenly distributed within feeding areas across the study range (Table 5.2), a fact confirmed by faecal analysis (Table 5.15). Woodlice are characteristic of maritime crevice communities with a rich loam derived from drift and plant litter (Harding & Sutton 1985). The increased emphasis in northern feeding-sites on diptera larvae (note the high dung-fly (*Cyclorrhapha*) value at Mwnt-Cemaes and its absence elsewhere), does reflect increased pastoralism. The Nematocera, especially the tipulid, quotient holds up well in soil samples from all areas with the exception of Newgale-Solva, but they are taken more frequently in the northern pastoral areas. It was observed (5.3.3) that the emphasis on Diptera declined markedly after the breeding season despite a continuing availability, and again the dual possibility arises: that Choughs either exploit this resource little after breeding or do so so thoroughly that localised supplies are greatly depleted. The importance of employing a multi-factorial approach and not relying on any one investigation is emphasized since, unfortunately, dipterous evidence does not survive digestion well (5.3.1).

Cereal grain, far less nutritious (see below and Table 5.6), taken from the substrate surface, is an important winter dietary supplement in areas where improved agriculture reduces the availability of pastoral elements (5.3.5 & Table 5.18). Choughs thus adapt their feeding behaviour to both habitat and season, and are able to exploit a wide range of habitat types, usually avoiding intensively improved fields (Warnes 1982), especially in the winter if a shorter day length and reduced invertebrate activity enforces a migration into inland pasture and arable land.

Where soil-sampling under-represents particular taxa, such as earwigs, carabid beetles and some cliff fauna, faecal evidence helps to clarify the position. By having regard to all 'feeding exhibits' (the multifactorial approach mentioned above), a better understanding of the requirements of a species emerges even though comparative analysis is not possible due to differing methodology. For example, the consistency with which weevils and carabids are taken across the Welsh region is better shown by reference to Tables 5.14 & 5.15 than to Table 5.4. A more detailed analysis of seasonality in resource use by Choughs is required, this could involve DNA sequencing to assess elements in the diet not identifiable on faecal fragments (P. Buckland pers. comm.).

Anomalies remain however: the apparent decreased importance of tipulids in the diet during the post-breeding phase (possibly due to harder, drier soils), and the relative scarcity of spider and ant remains in faecal samples despite high seasonal abundance, and, in the case of ants, observed predation (but see Section 5.3.7). Warnes (1982) noted the non-selection of spiders (again with high field abundance) and ants on Islay, and contrasted this with increased usage in Anglesey: a largely heathland area quite different in its physiography (Bullock 1980). Evidence from faecal analysis in West Wales shows a far higher dependence on ants at Newgale-Solva, confirming that the Chough's diet varies with locality (*cf.* Tables 5.2 and 5.10).

Ants highlight this better than any other prey. Cowdy (1973), working on Skomer Island, was the first author to draw attention to their importance in Chough diet, although in 1926, Coombs watched Choughs feeding on ants in Cornwall, and subsequently agreed with Cowdy as to their

significance (1978); Holyoak (1967) noted the relationship on the Isle of Man in 1966. Warnes (1982) found ants to be unimportant on Islay, and cites only one observation of ant-feeding; she thought that ants might be uncommon in habitats frequented by Choughs. Bullock (1980) showed that the heathland ant *Leptothorax acervorum* was an important winter food from October right through to the beginning of June. In the precursor to the present study, ants, from both direct observation and faecal evidence, were taken in Cornwall in November and December (Meyer 1990, see Appendix IV); in Wales, ant-feeding was confirmed in November and February (5.4.1). Bullock proposed that different genera of ants were important prey in all 3 of the biotopes within his study: maritime (*Formica*), heathland (*Myrmica* and *Leptothorax*) and farmland (*Lasius*), and that from June to September they were "the most likely prey." Despite this, Owen (1985) concluded that Cowdy was "in error", and that ants were merely "taken seasonally in some areas when the ground is too hard for probing". The evidence from my study does not support Owen's view.

In this study, Choughs were frequently found to be feeding in ant-rich patches which appeared to be fairly localised in that ants were absent from, or much reduced in, nearby areas at the times of highest usage (Figure 5.4). Although based on a small sample, the data (Table 5.7) suggest that Choughs were selecting ant-rich habitats in the breeding and post-breeding seasons while largely ignoring the resource in the winter even though it was present. Various explanations are possible: (i) ant activity is very much reduced in the winter, and there are consequently fewer visual cues to promote hunting, whilst, in the summer, a super-abundance of highly active and visible organisms will trigger feeding; (ii) ants are positively discriminated for as a food for nestlings; and (iii) the cost, in terms of time and effort, of feeding on small-bodied prey at reduced densities is not economical during short winter days (see also Section 5.3.5). Ants are less energy-rich, calories per gramme, than beetles and fly larvae (Table 5.6), although, of course, hymenopteran food can sustain an animal as large as a male Giant anteater, which weighs up to 39kg; such an animal requires 7000 - 14000 large ants per day (Macdonald 1985).

It is possible that ants contain trace elements of value to young Choughs. At Newgale-Solva and Marloes, they dug so vigorously after ants that at times the feeding Choughs disappeared from sight. Birds feeding young must maximize the amount of food obtained within the constraints of maintaining their own condition (Richford 1978) and forage so as to maximize return per unit time (Royama 1970). The highest net energy gain (energy gained less the energy required to find and capture it) is achieved by choosing prey with a high nutritive value, large size and/or low handling time (*ibid.*, Zach 1979). If a small prey is locally abundant, the gular pouch may be filled as quickly as when larger, thinly distributed prey are available (Richford 1978).

In general, Choughs were foraging in areas which were generally rich in invertebrates (Figure 5.1), and not on very restricted foci of prey, but obviously this did not always apply. In the case of mound-building ants (eg. *Lasius* spp.), foci are very easily located, whereupon there is a virtually inexhaustible supply of prey organisms albeit of small body size. Diptera are also frequently to be found in discrete well-defined patches, and these too are often easily located, such as when in cowpats. Larval tipulids are sometimes found congregated beneath cowdung but distribution is generally related to the distribution of host plant communities (Freeman 1967, 1968) and also to vegetation height (den Hollander 1975), in which case they are presumably less easy to find than clumped epigeal taxa.

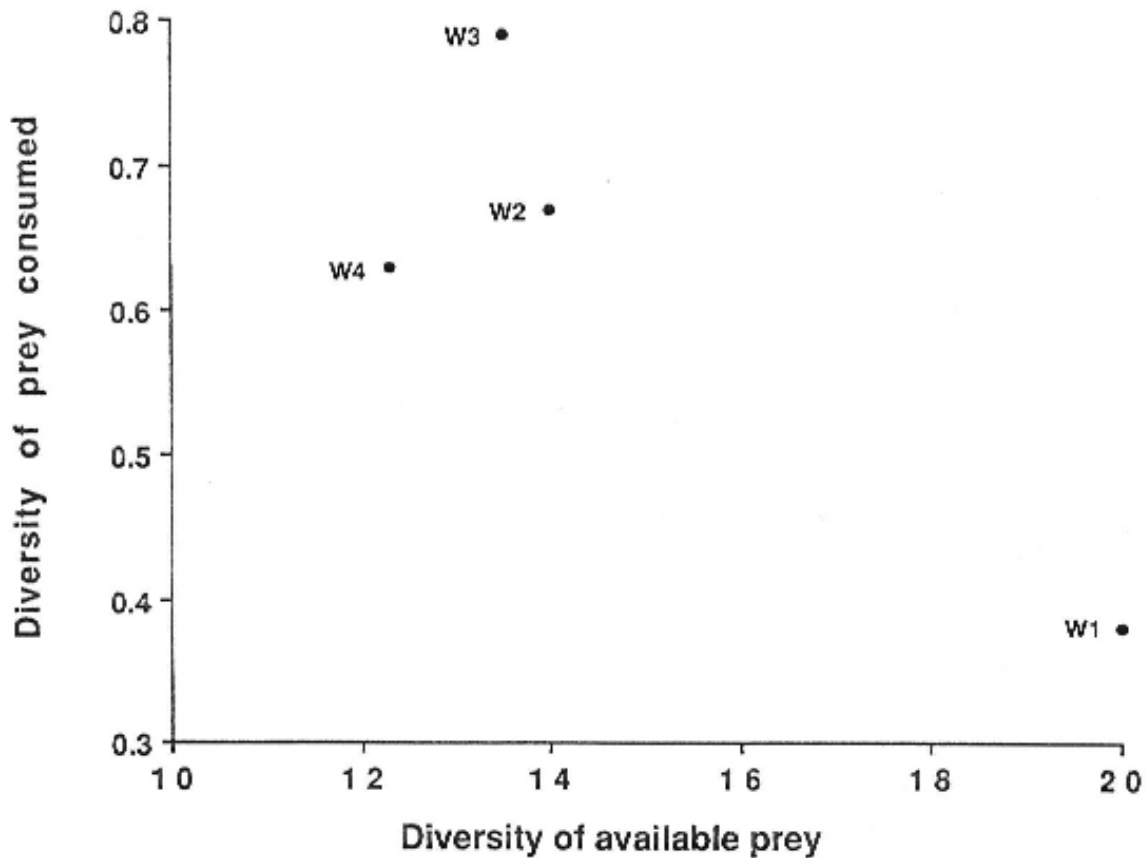
The larger-sized earthworms were never found in the soil cores extracted at feeding points (*cf.* Table 5.4), neither were they seen to be taken by the birds. Ruling out the theory that the resource was eaten out, it is suggested that habitats supporting the larger earthworms were not selected, or that the worms were passed over owing to the disproportionate costs involved in extracting and handling them from their deeper burrows (Thompson & Barnard 1984); soil samples, in this study,

were 6cm deep. Observations and the results of sampling also suggest that Choughs take the smaller-sized earthworms. No evidence existed to indicate whether Choughs took enchytraeid whiteworms (=potworms), it is thought unlikely due to their small body size relative to length but the possibility cannot be ruled out. In passing, it should perhaps be noted that earthworms have never been recorded as being taken by captive Choughs, except once in the present study (Appendix X).

It has already been mentioned that Choughs are able to switch between earthworms and cereal grain as a source of winter protein (Table 5.19). Grain, though, however cheap to obtain, is a poor food for young birds (Morse 1974); this is evinced by the fact that many granivorous birds switch to a protein-rich diet of insects when rearing their young (O'Connor 1984; see also Appendix X). Most invertebrates contain *ca.* 50% protein by dry weight (*cf.* only *ca.*15% in grain) (Linton 1927). Richford, who studied Jackdaws on Skomer Island (contiguous with Marloes), argued that when a bird is foraging for its young, time and energy expenditure are best repaid by selecting the most profitable food, therefore the nestling diet is probably the 'best' food available; he found that Jackdaws collected many spiders, principally *Xysticus cristatus* (the commonest thomisid), Hemiptera and Hymenopterous larvae, with perhaps as many as 60+ per sample. House martins select insects with the highest calorific value (Bryant 1973). Carrion crows, rearing newly-hatched young in north-east Scotland, offered a varied diet of small invertebrates, including bees, flies and spiders, but replaced these with tipulid and lepidopterous larvae when the nestlings were older (Yom-Tov 1975). Royama (1966) found that tits regularly punctuated loadings of caterpillars to their young with spiders, despite a higher collection cost and plentiful supplies of caterpillars. Feare (1984) notes the importance of spiders for Starling chicks, and O'Connor (1985) stresses their importance in many nestling diets, suggesting that they might contain trace nutrients lacking in caterpillars and leatherjackets.

The assumption is often made in Britain that the Chough is naturally a coastal species (for example, I suggested above (p.72) that inland migration in winter is "forced"), but elsewhere across its very wide range this is clearly not the case (*cf.* Figure 1.1). Goodwin (1986) proposes that the Chough originated as a montane species and subsequently spread to the cliffs in the west of its range. In north-west Europe, the coast might provide the only satisfactory combination of rocky terrain with caves, fissures etc which is neither covered by vegetation nor snow in the winter; it also remains frost-free, leaving accessible earthbound invertebrates in harsh conditions. Rare sub-zero temperatures in Cornwall (Meyer 1990, see Appendix IV) caused the surviving Chough of a pair to feed exclusively beneath the cover provided by the large rounded and lobed leaves of the Tree mallow, which grew in only one or two discrete zones. Had these not been available, it is possible that the Chough would either have not survived or moved away; Schifferli & Lang (1941) recorded Choughs, with young in the nest, feeding under the cover of woods after an unseasonable snowfall. In mild winters, pasture is apparently preferentially selected (Chapter 4). Why then is this abandoned when the return migration occurs in the early spring? Since invertebrate biomass increases rather than falls off at this time of the year (Wallwork 1976) and since Choughs were not known to travel more than a few hundred metres inland (usually pasture was available near the clifftop) it is possible that Choughs require: (i) cliff-based prey for their young, (ii) the security afforded by cliffs, and (iii) the opportunity for young birds to develop appropriate behaviours within this, their primary ecological niche. Such development, in an area as complex as habitat recognition, depends on the interaction of genetically controlled behaviour and morphology with learning and experiential feedback (O'Connor 1985). Further evidence of foraging economics suggests also that cliffs are the most profitable habitat *when of high quality* (Chapter 6); thus the migration into pastoral agriculture in the winter might indeed be *forced* if the cliffscape is of sub-optimum quality. It should also be remembered that cliffs could not be sampled as completely as pastoral habitats, and this might have depressed diversity indices.

Figure 5.7
Relationship between the diversity of available potential prey and diversity of prey consumed as shown by faecal analysis



It follows to ask from this: is the apparent greater diversity of potential prey at the northern pastoral study areas (Table 5.2) 'better' for Choughs than an increased dependence on fewer taxa, if such is indeed the case elsewhere? Despite the absence of detailed information on the abundances of all potential prey, the diversity of actual prey in the diet, as represented by faecal evidence (Table 5.15), does not support the hypothesis that availability of a wider prey spectrum is reflected in the Chough diet: the Mwnt-Cemaes area which shows the greatest potential prey spectrum ($D=19.6$) has by far the lowest frequency of prey taxa in the faecal collection (0.38), as is summarised in Figure 5.7. The key, in fact, might not be diversity but the availability of certain key taxa at certain different times of the year (Feare 1984). In the case of Choughs in West Wales, this might be summarised thus: cereals/earthworms in the autumn/winter; tipulids in the spring; other diptera in the summer; ants in the breeding season/summer; with coleoptera forming a year round resource, its great taxonomic variety ensuring there is usually something 'in season'. As has been shown in Ireland (Bullock 1983b) and Bardsey (Roberts 1982) there is recourse to seashores in the winter in some regions, possibly linked to where there is also an emphasis on machair or sand(dune) feeding (see Roberts 1983). This does not seem to apply in West Wales to any marked extent, there being only two possible sightings during the current study (both at Marloes), and it is possible that seashore feeding is replaced farther south by a movement a little away from the actual shore to the splash and maritime therophyte zones during hard weather periods, as indicated by observations in Cornwall (Appendix IV) and during the current study (Chapter 4).

Finally, I will discuss the background Cornish situation in the light of Chough-derived data from Wales. Figure 5.5 shows the relationship with regard to prey abundance in Welsh feeding areas with that at equivalent Cornish sites. Of the 18 invertebrate taxa most frequently found in Chough feeding areas in Wales, 13 (72%) were found to be more abundant in Cornwall; of the remainder, two were equal. Two of the 3 taxa for which Wales scored more highly than Cornwall are, however, very important: the Nematocera (including the tipulids) and the carabid ground beetles. The Hymenoptera (which includes the ants of course) was one for which no difference was found between the two regions.

It would not be very meaningful to correlate the ranks without correcting for the varying importance of different taxa. Looking at the 10 most frequently found taxa in faecal analysis (from data in Table 5.15), only the Carabidae, Curculionidae and Dermaptera are below tenth rank in invertebrate sampling undertaken at likely feeding sites in Cornwall (Table 5.8). These are 3 taxa that have already been identified as under-recorded in equivalent Welsh sampling; only the Carabidae scored less in Cornwall than Wales. As an order, the Coleoptera in Cornwall gave a value more than double that for Wales, but Diptera was about 40% greater in Wales than Cornwall (Figure 5.5). The distribution of larval tipulids responds to phytogeography (Freeman 1967), and this highlights an inherent difficulty in speculating the likely feeding sites for birds in areas uninhabited by them at the time; in other words, Choughs will be better at finding food than human imitators. Given this belief and the comparatively invertebrate-rich picture emerging from Cornwall, it is safe to conclude that sufficient food resources probably exist for Choughs provided the habitats which support the invertebrates also exist in sufficient quantities (Chapter 4).